Ekologie vybraných ptačích predátorů v závislosti na potravní nabídce

Habilitační práce

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Poděkování

Na tomto místě bych chtěl poděkovat zejména všem kolegům, spoluautorům a studentům, bez jejichž spolupráce by jednotlivé projekty nemohly být úspěšně realizovány. Na výzkumu poštolky obecné, kalouse ušatého a puštíka obecného se v rámci svých studentských prací na PřF JU podíleli především Aleš Dufek, Drahomíra Fainová, Václav Mikeš, Matěj Lövy a Václav Luka. Rád bych zde ocenil jejich pracovní nasazení v terénu i během sepisování následných výstupů, jejichž počet není zdaleka vyčerpán. Zvláštní poděkování patří Markétě Zárybnické (ČZU) a jejím kolegům za sdílení dat na paralelním projektu o sýci rousném. Díky společným zájmům vznikla plodná spolupráce, která v současné době výrazně přesahuje rámec této studie. Markétě děkuji především za vynikající spolupráci během sepisování manuskriptů a jejich revizi. Děkuji také grantovým agenturám za finanční podporu jednotlivých projektů. V neposlední řadě bych rád poděkoval své partnerce a ostatním členům rodiny za skvělé zázemí a pochopení zejména během sepisování této práce i pobytu v terénu. Zvláštní dík patří nejmenším členům mé rodiny. Můj dík patří také samotným studovaným druhům, které mne nepřestávají fascinovat svým chováním a variabilitou životních strategií. Nepochybuji, že řada dalších překvapivých zjištění mne čeká i v budoucnu.

Obsah

1. Úvod

Vztah predátor kořist přitahuje odedávna pozornost nejen odborné veřejnosti. Zvýšená pozornost byla věnována například vlivu ptačích predátorů na vývoj populací drobných savců (Korpimäki & Norrdahl 1991, Ylönen et al. 1991, Norrdahl & Korpimäki 1995). Jednotlivé druhy ptačích predátorů jsou v různé míře adaptované k lovu různých typů kořisti (kap. 1.1.), což vede k výrazným mezidruhovým rozdílům v loveckým strategiích. V obecné rovině však lze nalézt některé společné rysy. Teoretický základ představují především modely a hypotézy, které se týkají optimalizace příjmu potravy (Optimal diet theory; Schoener 1971, Pulliam 1974). Predátor nutně čelí rozhodnutí (1) v jakém potravním ostrůvku bude lovit, (2) jak dlouho zůstane v potravním ostrůvku, (3) jaký typ kořisti bude lovit a (4) v jakém biotopu (Pyke et al. 1977). Pro jednotlivá rozhodnutí predátora byla dále vytvořena celá řada detailních modelů, které predikují jeho chování (např. Pyke et al. 1977). Některé předpoklady byly u ptačích predátorů experimentálně ověřeny, především vztah mezi nabídkou hlavní kořisti v daném biotopu, početností predátorů (Galushin 1972, Millon & Bretagnolle 2008) a využitím potravní nabídky (Korpimäki 1986, Steenhof & Kochert 1988). Variabilita loveckých strategií je však u ptačích predátorů mnohem větší a může být na individuální úrovni ovlivněna i řadou dalších faktorů, které zahrnují především změny vnějších podmínek, kompetici nebo kvalitu jedince (Quinn & Cresswell 2004, Rutz & Bijlsma 2006). Důsledkem toho může být značná individuální variabilita v efektivitě lovu i složení potravy za různých podmínek (Navarro-López & Fargallo 2015). Výběr kořisti, způsob jejího získání a následná lovecká efektivita dále zásadním způsobem ovlivňuje také fitness jedince (Redpath 1995, Sergio et al. 2003, Lourenço et al. 2015).

Hlavním cílem této práce je rozšíření znalostí o potravních a reprodukčních strategiích vybraných druhů ptačích predátorů. Důraz je kladen především na porovnání strategií jednotlivých druhů v rámci areálu výskytu a v různých biotopech.

1.1. Morfologické adaptace ptačích predátorů

Mezi ptačími predátory, dravci (Accipitriformes a Falconiformes) a sovy (Strigiformes) patří mezi nejlépe adaptované formy k lovu živé kořisti. Pro většinu z nich je charakteristické, že mají výborný zrak a/nebo sluch, ostré drápy, zahnutý zobák s ostrými hranami ramfotéky a produkují vývržky.

Zrak je hlavním smyslem, který denní dravci využívají k lovu kořisti. Oči denních dravců jsou umístěny po stranách hlavy, což umožňuje v přední části zorného pole (278-300°) binokulární vidění (33-36°) a ve zbytku zorného pole vidění monokulární (122-130°). Slepý úhel za hlavou představuje 60-82° (O'Rourke et al. 2010a; porovnání tří druhů dravců: káně rudoocasá *Buteo jamaicensis*, jestřáb Cooperův *Accipiter cooperii*, poštolka pestrá *Falco sparverius*). Pomocí rotace oční bulvy mohou tito dravci navíc zúžit nebo rozšířit zorné pole (O'Rourke et al. 2010a). Velikost zorného pole u jednotlivých druhů odpovídá biotopu, který daný druh obývá nebo využívá k lovu. Druhy, které loví v otevřených biotopech, mají malý úhel binokulárního vidění, velký slepý úhel, střední pohyblivost oční bulvy a pomalé pohyby hlavy, zatímco druhy lovící v uzavřených biotopech mají široký úhel binokulárního vidění, malý slepý úhel, vysokou pohyblivost oční bulvy a rychlé pohyby hlavy (O'Rourke et al. 2010a, b).

Na rozdíl od denních dravců mají sovy díky speciálnímu umístění očí (v jedné rovině) zúžené zorné pole, ale velký úhel binokulárního vidění (např. puštík obecný *Strix aluco*, binokulární vidění 48°, zorné pole celkem 124°; Martin 1984) a značnou rotaci hlavy (až 270°; Walls 1942). Během rotace hlavy se krční obratle sov otáčejí nejen kolem svislé, ale částečně také okolo horizontální osy. Tím je zajištěno, že nedochází ke kolizi výběžků obratlů během rotace (sova pálená *Tyto alba*; Krings et al. 2017). Pohyblivost oční bulvy je u sov minimální a je kompenzována značnou pohyblivostí hlavy.

Oko dravců je kulovité, u sov je oko tubulární, opatřené sklerotikálním prstencem (Jones et al. 2007). U denních dravců se vyvinul výběžek kosti *os praefrontalia*, který funguje jako ochrana očí před oslněním. U některých specialistů může být tento výběžek redukován (např. včelojed lesní *Pernis apivorus* - lov blanokřídlých, převážně vos; orlovec říční *Pandion haliaetus* – lov ryb, jeho funkci přebírá opeření v okolí oka). Podobnou funkci pravděpodobně plní tmavý „vous“ po stranách hlavy u některých dravců (např. sokol stěhovavý *Falco peregrinus* nebo raroh prériový *Falco mexicanus*), který absorbuje sluneční záření (Jones et al. 2007).

Rozlišovací schopnosti oka (~ ostrost vidění) u denních dravců patří k nejlepším v rámci ptačí říše. Ostrost vidění se obvykle udává v počtech bílo-černých standardizovaných pruhů, které jedinec dokáže rozeznat v rámci jednoho úhlového stupně. Nejvyšší ostrost vidění byla zaznamenána u poštolky pestré (160 cyklů na jeden stupeň) a orla klínoocasého *Aquila audax* (132-142 cyklů na jeden stupeň; shrnuto v Potier et al. 2016). Opakované měření u poštolky pestré však ukázalo, že průměrná ostrost vidění je podstatně nižší (39,7-71,4 cyklů na stupeň; Gaffney & Hodos 2003). Pro porovnání, ostrost vidění u různých druhů pěvců se pohybuje mezi 28 a 46 cykly na jeden stupeň (Donner 1951). Zvýšená ostrost vidění je u dravců dána přítomností dvou žlutých skvrn s nejvyšší koncentrací světločivných buněk, hluboké centrální pro vnímání laterálního zorného pole a mělké temporální pro vnímání frontálního zorného pole (Oehme 1964, Tucker 2000). V sítnici oka se vyskytuje celkem 6 typů světločivných buněk - tyčinky pro vnímání světla a tmy, zdvojené čípky, 4 druhy čípků pro vnímání různých vlnových délek. Funkce zdvojených čípků je dosud nejasná, pravděpodobně slouží k vnímání polarizace a svítivosti nebo pohybu. Detailní analýza sítnice oka čtyř vybraných druhů dravců (káně lesní *Buteo buteo*, včelojed lesní *Pernis apivorus*, krahujec obecný *Accipiter nisus* a sokol stěhovavý *Falco peregrinus*) ukázala, že zdvojené čípky se ve žlutých skvrnách u většiny druhů nevyskytují (s výjimkou krahujce obecného) a ostrost vidění je tedy dána především vysokou hustotou čípků pro vnímání různých vlnových délek (Mitkus et al. 2017).

Díky přítomnosti čípků pro vnímání krátkých vlnových délek (320-400 nm) mohou přinejmenším některé druhy dravců vnímat optické signály v ultrafialovém spektru. U poštolky obecné (*Falco tinnunculus*) a káně rousné (*Buteo lagopus*) bylo experimentálně zjištěno, že dokáží detekovat stopy moči a trusu drobných savců, které jsou viditelné v ultrafialovém spektru (Viitala et al. 1995, Koivula & Viitala 1999). Dravci díky vnímání těchto pobytových stop mohou v rámci větší oblasti snadno vybrat loviště s vysokou denzitou drobných savců (Honkavaara et al. 2002). U sov nebyla schopnost vnímání krátkých vln v UV spektru zaznamenána (sýc rousný *Aegolius funereus*, Koivula et al. 1997) pravděpodobně díky absenci specifických čípků pro vnímání krátkých vln v ultrafialovém spektru (Bowmaker & Martin 1978). Zrak sov je přizpůsoben pro scotopické podmínky. Sovy postrádají žlutou skvrnu, v sítnici převažují tyčinky pro vnímání světla a tmy a nejvyšší ostrosti vnímání dosahují za šera (např. sova pálená, Orlowski et al. 2012). Nicméně, zrak sov není monochromatický a může hrát významnou roli i během dne. U sýčka obecného (*Athene noctua*) bylo experimentálně zjištěno, že sytost žlutého zbarvení zobáku mláďat může rodičům sloužit jako měřítko kvality mláděte. U velkých snůšek rodiče během krmení preferovali mláďata s více žlutým zobákem (Avilés & Parejo 2013).

Hlavním smyslem, který sovy využívají během lovu je sluch. Vývody zvukovodů jsou umístěny na okraji faciálního disku, který funguje podobně jako parabola (König & Weick 2008). Samotný vývod je opatřen záklopkou. Vývody zvukovodů jsou většinou umístěny asymetricky, což výrazně zvyšuje schopnost přesné lokalizace zvuku, zejména pro zvuky nad 5 kHz (Coles & Guppy 1988). Asymetrie vývodů zvukovodů umožňuje sovám, díky časovému posunu dolehnutí zvuku k oběma vývodům, poměrně přesně lokalizovat zvuk v horizontální rovině (azimut). Rozdíl mezi akustickým tlakem v obou zvukovodech slouží k upřesnění pozice na vertikální ose (elevace; Keller et al. 1998). Obecně platí, že u druhů se striktní noční aktivitou jsou vývody zvukovodů umístěny více asymetricky (např. sova pálená, sýc rousný). Velikost, tvar a opeření faciálního disku se také mezidruhově výrazně liší (König & Weick 2008). Adaptivní význam faciálního disku byl experimentálně ověřen u sovy pálené. Pokud byla pera faciálního disku odstraněna, došlo ke snížené schopnosti lokalizovat zvuk (Hausmann et al. 2009). Díky dobře vyvinutému sluchu mohou sovy v mozku vytvářet tzv. sluchové mapy (Takahashi et al. 2003), které mohou být kombinovány s vizuální mapou (Maczko et al. 2006). Sovy dokáží reagovat na sluchové vjemy velmi rychle, během experimentu byla sova pálená schopna měnit směr útoku s maximálním zpožděním 200 ms (Hausmann et al. 2008). Sovy pálené jsou schopné vnímat již zvuky o hlasitosti -12,6 dB o frekvenci 8 kHz a během života se jejich sluchové schopnosti příliš nezhoršují (Krumm et al. 2017). Naopak, starší sovy pálené posunují hranici vnímání i do vyšších frekvencí, zatímco mláďata vnímají pouze nízké frekvence (1-4 kHz, Kraemer et al. 2017). Ke zhoršení sluchu u mláďat sovy pálené došlo, pokud byla experimentálně vychována v hlučném prostředí (Efrati & Gutfreund 2011).

Také struktura opeření sov je výsledkem adaptace na noční lov. Na neslyšném letu se podílí absence háčků (hamuli) na konci vnějšího praporu, hřebínek na vnějším praporu a jemné volné struktury v poli praporů zajišťující jejich hebký povrch (Wagner et al. 2017). Experimentálně bylo ověřeno, že hřebínek vnějšího praporu optimalizuje laminarizaci proudění přes plochu křídla (Rao et al. 2017). Hřebínek vykazuje též variabilitu v rámci jednotlivých druhů sov, u druhů které mají obligátně noční aktivitu je hřebínek výraznější (Weger & Wagner 2016).

U krahujcovitých dravců (Accipitridae) se často vyskytuje značný polymorfismus ve zbarvení v rámci druhu. Roulin & Wink (2004) porovnali složení potravy polymorfních a monomorfních druhů rodů krahujec (*Accipiter*) a káně (*Buteo*). U krahujců nebyl rozdíl v potravě zjištěn, ale polymorfní druhy káňat měly v potravě vyšší zastoupení savců než monomorfní druhy. Autoři se domnívají, že zvýšený polymorfismus může komplikovat učení predátora kořistí. U polymorfního druhu jestřába černohřbetého (*Accipiter melanoleucus*) bylo zjištěno, že u tmavé formy existuje negativní korelace mezi loveckou aktivitou a intenzitou světla. Tmavé formy navíc vyhledávaly k lovu více uzavřené biotopy než světle vybarvení jedinci (Tate & Amar 2017). K podobným výsledkům překvapivě dospěl také Roulin (2004) u nočního predátora - sovy pálené. Světlé formy byly úspěšnější při lovu myšic (*Apodemus* sp.) a tmavé formy lovily častěji hraboše polního (*Microtus arvalis*). Autor nepředkládá detailní vysvětlení tohoto jevu, pouze uvažuje o možných rozdílech mezi hrabošem a myšicí v útěkovém chování za různých světelných podmínek.

Způsob, jakým se ptačí predátoři zmocní kořisti, se může výrazně lišit mezi jednotlivými druhy. Porovnání čtyř druhů sov při lovu laboratorních myší ukázalo, že sova pálená preferuje uchopení kořisti za hlavu, sýček obecný uchopuje kořist za tělo a žádná preference nebyla zjištěna u puštíka obecného ani kalouse ušatého (Csemerly et al. 2002). Také způsob usmrcení kořisti se mezidruhově lišil. Puštík obecný a kalous ušatý (*Asio otus*) po uchopení kořisti směřovali útoky zobákem na hlavu, za účelem ochrnutí nervové soustavy a znemožnění útěku kořisti. Sova pálená uchopí kořist za krk a třesením ze strany na stranu docílí dislokace obratlů. Sýček obecný svou kořist víceméně ubije zobákem. Tyto rozdíly pravděpodobně souvisí s mírou specializace k lovu drobných savců, přičemž sýček je spíše přizpůsoben k lovu hmyzu. Všechny druhy sov pevně svíraly svou kořist, čímž u některých myší způsobily smrt zadušením (Csemerly et al. 2002, 2009). K podobným výsledkům autoři dospěli také u poštolky obecné. Podobně jako sovy, poštolky obvykle drží po nějakou dobu kořist v pařátu za účelem jejího zadušení. Zobák je využíván k dobití kořisti údery do hlavy (Csemerly et al. 1998).

Síla stisku prstů nohy podléhá značné variabilitě, která může být z velké části vysvětlena pozitivní korelací s tělesnou hmotností (Sustaita & Hertel 2010). U sokolovitých dravců je síla stisku menší než u krahujcovitých, proto sokolovití dravci drží kořist v pařátech déle než krahujcovití dravci (Csemerly & Gaibani 1998). Opačně je tomu u síly stisku zobáku, kdy byly u sokolovitých dravců naměřeny vyšší hodnoty (Sustaita & Hertel 2010). U sokolovitých dravců je navíc přítomen zejk, který společně s řadou úprav muskulatury zobáku výrazně napomáhá při zabíjení a porcování kořisti (Sustaita 2008).

Podrobná analýza morfologie prstů a drápů dravců a sov v porovnání s ostatními ptáky ukázala, že zakřivení drápů, jejich délka v poměru k délce prstu a tvar zadního prstu zřetelně oddělili dravce od sov. U sov je zakřivení drápů zejména na prvním prstu méně výrazné, což souvisí se schopností sov více ohnout poslední článek prstu. Dráp na třetím prstu je u sov v poměru k délce prstu delší než u dravců a ostatních ptáků, neboť slouží k ovinutí kořisti a je umístěn naproti prvnímu prstu (tzv. zygodaktylní noha). Měřené charakteristiky se částečně překrývaly u dravců a ostatních druhů ptáků (Csemerly & Rossi 2006). Další analýzy morfologie prstů a drápů naznačují, že z dravců se obzvláště sokolovití příliš neliší od ostatních ptáků (Csemerly et al. 2012), což je v souladu s moderním pohledem na fylogenezi ptáků. Sokolovití dravci představují v současné době samostatnou linii blízce příbuznou pěvcům Passeriformes (např. Prum et al. 2015).

Trávicí trakt ptačích predátorů se v mnoha ohledech liší od trávicího traktu ostatních ptáků. Vole je u dravců vyvinuto, ale v porovnání s ostatními skupinami (např. hrabaví Galliformes) je poměrně malé. U sov vole zcela chybí a jeho funkci přejímá zvětšený *oesophagus* (Houston & Duke 2007). Vole je výrazně vyvinuté jen u některých mrchožravých forem dravců, např. u kondorů (Cathartidae). Většinu trávení u dravců zajišťují enzymatické procesy, svalovina žaludku je tedy podstatně méně vyvinuta například v porovnání se zrnožravými ptáky (Houston & Duke 2007). Délka tenkého střeva se výrazně liší mezi jednotlivými skupinami ptačích predátorů s různou strategií lovu. Druhy dravců, které loví aktivním způsobem (např. rod *Falco*, *Accipiter*) a sovy mají (po korekci s tělesnou hmotností) tenké střevo výrazně zkrácené oproti druhům, které loví vyhledáváním (např. rod *Buteo*, *Milvus*; Barton & Houston 1994).

V porovnání s ostatními ptáky jsou žaludeční šťávy predátorů výrazně kyselejší. Sovy mají oproti denním dravcům více zásadité pH v žaludku (2,4 vs. 1,7) a proto tráví méně kostí než denní dravci (Duke et al. 1975). Nejnižší pH (0,8) bylo zjištěno v žaludku orlosupa bradatého (*Gypaetus barbatus*), specialisty na trávení kostí (Houston & Copsey 1994). Dravci i sovy, podobně jako celá řada dalších ptačích taxonů, pravidelně vyvrhují nestrávenou potravu v podobě vývržků. Vývržky se formují v žaludku ze zbytků kostí, chlupů a opeření kořisti (Rhoades & Duke 1977). Zbytky potravy se v žaludku hromadí díky velmi malému otvoru mezi žaludkem a střevem (*pyloris*). Například u výra virginského (*Bubo virginianus*) má pylorický otvor v průměru 1,5 mm (Grimm & Whitehouse 1963). Vývržky jsou vyvrhovány 9 až 15 hodin po pozření kořisti, v závislosti na její hmotnosti (shrnuto v Houston & Duke 2007).

1.2. Studované druhy

Do této práce byly zahrnuty čtyři druhy ptačích predátorů specializovaných zejména k lovu drobných savců, z nichž tři druhy mají noční aktivitu a jeden druh je denním predátorem. U všech druhů existuje v různé míře obrácený dimorfismus ve velikosti, samice jsou větší a těžší než samci (např. Hudec & Šťastný 2005, Hudec & Šťastný 2005a). Převažujícím reprodukčním svazkem je sociální monogamie s biparentální péčí o mláďata. Výjimky jsou poměrně vzácné. Například sýci rousní mohou využívat sekvenční polyandrii (Korpimäki et al. 2011), zejména v troficky nepříznivých letech (Šindelář et al. 2015). Žádný ze studovaných druhů nestaví vlastní hnízdo a všechny druhy využívají buď hnízda jiných ptáků, nebo hnízdní dutiny. Sovy typicky obhajují své teritorium houkáním, denní dravci využívají fyzickou obranu hnízda. Většinu potravy pro mláďata zajišťuje samec, zejména v časné fázi vývoje mláďat (Hudec & Šťastný 2005, Hudec & Šťastný 2005a, König & Weick 2008). Jednotlivé druhy se liší hnízdním biotopem, strategií lovu i detailním složením potravního spektra.

1.2.1. Poštolka obecná (*Falco tinnunculus*)

Rozšíření poštolky obecné zahrnuje celou palearktidu a Afriku, kde se vyskytuje také v subsaharských oblastech (Village 1990). Jedná se o běžného sokolovitého dravce otevřené krajiny i urbánního prostředí (Šťastný et al. 2006). Podobně jako většina ostatních sokolovitých dravců poštolka nestaví vlastní hnízdo a k hnízdění využívá buď hnízda jiných ptáků, zejména krkavcovitých (Corvidae), hnízdní budky nebo dutiny ve skalách a v budovách (Hudec & Šťastný 2005). Hnízdní denzita v urbánním prostředí je mnohem vyšší než v otevřené krajině, pravděpodobně díky dostatečné nabídce kvalitních hnízdních příležitostí (shrnuto v Riegert 2005). V severních oblastech je denzita hnízdících párů pozitivně korelována s abundancí drobných savců (numerická odpověď), zejména z podčeledi Microtinae (Korpimäki 1984, 1994). V otevřené krajině střední a západní Evropy dochází také ke kolísání hnízdní denzity, ale hnízdní abundance je spíše ovlivněna klimatickými podmínkami, zejména teplotou v předchozím zimním období (Village 1990, Kostrzewa & Kostrzewa 1991). U městských populací byly zjištěny malé meziroční výkyvy v hnízdní denzitě, které jsou způsobeny buď dostatkem kvalitních hnízdních příležitostí nebo obecně menší potravní závislostí na drobných savcích (Plesník 1992, **Riegert et al. 2007 - příloha I**).

Vzhledem k tomu, že urbánní a mimoměstské populace vykazují řadu ekologických rozdílů (např. Plesník 1992), lze očekávat i rozdíly v genetické struktuře populací (Gehlbach 1996). Mezi sousedícími populacemi v městském a mimoměstském prostředí v Polsku nebyla zjištěna výrazná míra diferenciace (nízké Fst hodnoty), nicméně rozdíly byly signifikantní. Největší rozdíly byly nalezeny mezi dvěma urbánními populacemi ve městech Łódź a Waršava (Rutkowski et al. 2010). U poštolek v České republice také nebyl zjištěn výrazný rozdíl mezi urbánní a sousedící mimoměstskou populací (**Riegert et al. 2010 - příloha II**). Zároveň byla na studované lokalitě zjištěna vyšší míra genetické příbuznosti mezi jedinci v centru města v porovnání s periferií, která může být dána značnou věrností hnízdišti (např. Salvati et al. 1999, Kübler et al. 2005). Samci městských poštolek navíc často využívají stejná nocoviště v průběhu celého roku (**Riegert & Fuchs 2011 - příloha III**). V rámci celé populace v České republice byla také zjištěna poměrně vysoká návratnost jedinců, celkem 44% zpětných hlášení pocházelo ze vzdálenosti 10 km od místa kroužkování (Cepák et al. 2008).

1.2.2. Kalous ušatý (*Asio otus*)

Kalous ušatý má holarktické rozšíření, v České republice patří mezi nejhojnější druhy sov (Šťastný et al. 2006). Obývá lesy všech typů a v posledních desetiletích se stále častěji vyskytuje i ve městech (**Riegert et al. 2009 - příloha IV**). K hnízdění využívá hnízda jiných ptáků, zejména z čeledi krkavcovitých (Hudec & Šťastný 2005a). Také u kalouse ušatého byl v severních oblastech zjištěn pozitivní korelační vztah mezi hnízdní denzitou a abundancí drobných savců z nadčeledi Microtinae (Korpimäki & Norrdahl 1991a). U skotských kalousů byla vzdálenost mezi jednotlivými hnízdy negativně ovlivněna nabídkou hraboše mokřadního *Microtus agrestis*. Zároveň byl zjištěn pozitivní vztah mezi podílem párů, které zahnízdili a abundancí hraboše (Village 1981). V České republice nebyla hnízdní denzita kalouse nabídkou hraboše ovlivněna, pravděpodobně díky menším výkyvům v kolísání početnosti hraboše v porovnání se severními populacemi a větší nabídkou alternativních kořistí (Lövy 2007).

Kalous ušatý je ve většině areálu stálým druhem (Cepák et al. 2008), u severních populací může být nomadickým druhem v závislosti na nabídce drobných savců (Korpimäki & Norrdahl 1991a). Data z České republiky poukazují na vysokou návratnost, 73% zpětných hlášení bylo zjištěno do 10 km od místa kroužkování (Cepák et al. 2008). V průběhu zimního období se kalousi často shlukují na hromadných stávaništích, která mou být využívána po řadu let. Početnost kalousů na stávaništích v Moskvě byla ovlivněna abundancí drobných savců a výškou sněhové pokrývky (Sharikov et al. 2014).

1.2.3. Sýc rousný (*Aegolius funereus*)

Hnízdní areál sýce rousného zahrnuje mírný pás Eurasie a Severní Ameriky (Korpimäki & Hakkarainen 2012). V rámci areálu tento druh vyhledává jehličnaté a smíšené lesy (Hudec 1983), kde hnízdí v přirozených dutinách (zejména po datlu černém *Dryocopus martius*) nebo hnízdních budkách (Korpimäki & Hakkarainen 2012). Zatímco v severní Evropě stavy sýce rousného dlouhodobě klesají díky nevhodnému managementu lesa (Hakkarainen et al. 1997, Korpimäki & Hakkarainen 2012), ve střední Evropě je populace stabilní nebo rostoucí. V České republice byl v letech 1973-2003 zaznamenán nárůst v podílu obsazených kvadrátů (31-49%, Šťastný et al. 2006). V současné době se vyskytuje v České republice ve vhodných biotopech poměrně hojně. Hnízdní denzita sýce se v severních oblastech mění s nabídkou hraboše a norníka (Korpimäki & Norrdahl 1989), ve střední Evropě tento vztah nebyl zaznamenán. Důvodem absence numerické odpovědi byla stabilnější potravní nabídka a více typů kořisti (**Zárybnická et al. 2013 - příloha V**).

Sýc rousný je v porovnání s ostatními druhy sov striktně nočním druhem. Jeho aktivita začíná po soumraku a v našich podmínkách dosahuje maxima mezi 22-23 hodinou. Během krmení mláďat je aktivita prodloužena až do ranních hodin (Zárybnická 2009). Z hlediska migrace je sýc rousný stálým nebo přelétavým druhem. Samci jsou dlouhodobě věrni svým hnízdištím, v jejichž okolí se vyskytují po celý rok. Samice mohou vykazovat přelety, nejčastěji do vzdálenosti 20 km (Cepák et al. 2008).

1.2.4. Puštík obecný (*Strix aluco*)

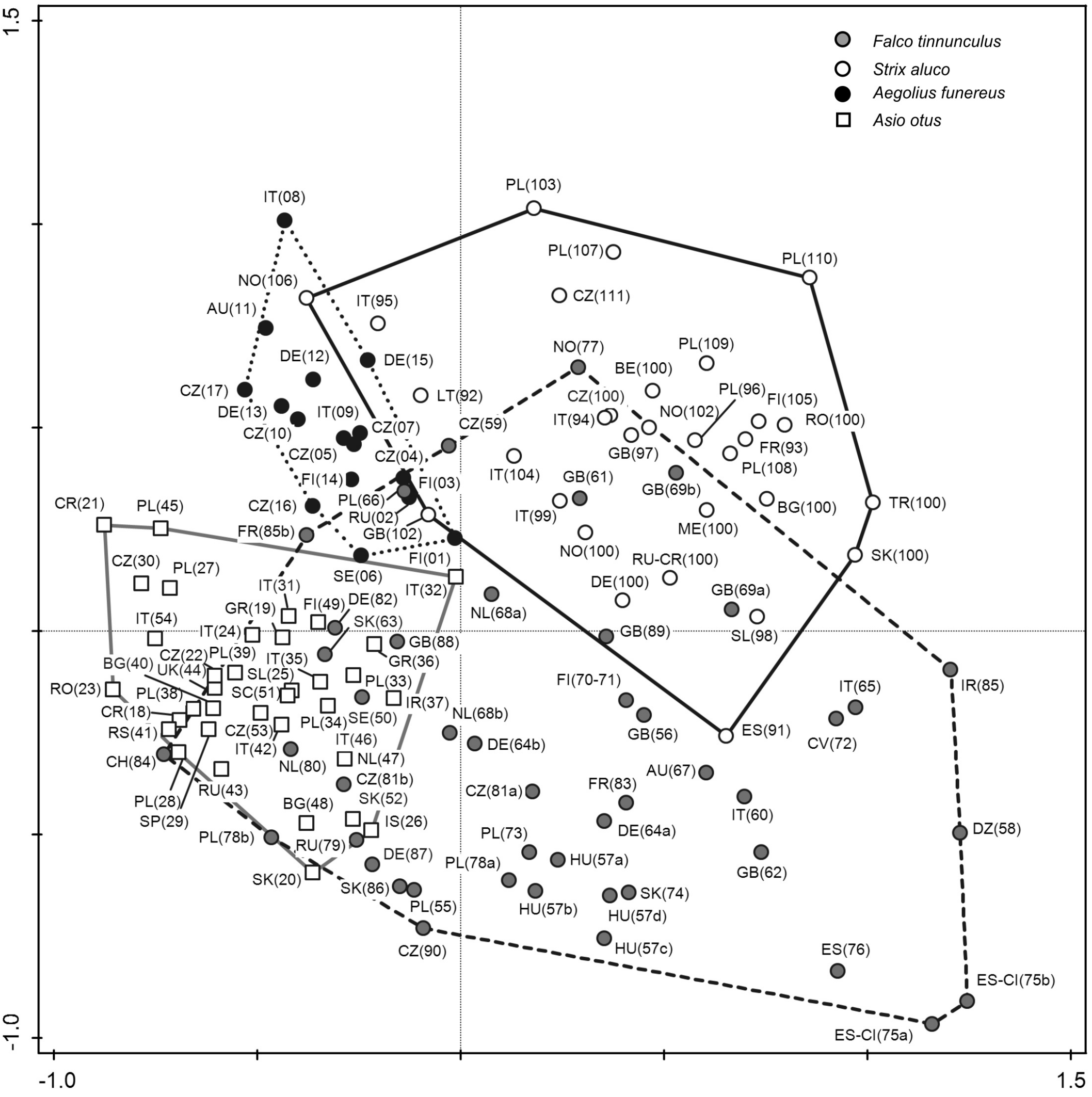
Areál puštíka obecného je rozdělen do dvou částí – evropské a východasijské (Hudec 1983). Ve střední Evropě se jedná o nejhojnější druh sovy, vyskytuje se prakticky ve všech typech lesních biotopů a běžně hnízdí také v městských parcích (Hudec & Šťastný 2005a, Šťastný et al. 2006). K hnízdění využívá přirozené dutiny nebo hnízdní budky (např. Petty 1999). Hnízdní denzita zejména mladých párů byla v severních oblastech pozitivně korelována s nabídkou drobných savců. U starších párů tento vztah nebyl signifikantní (Karell et al. 2009). Ve střední Evropě nejsou výsledky studií konzistentní, vztah mezi abundancí hlavní kořisti zejména myšic rodu *Apodemus* byl zjištěn u Švýcarské populace (Roulin et al. 2009), ale v České republice nebyl tento vztah potvrzen (**Luka & Riegert in press - příloha VI**). Rozdílné výsledky mohou být dány různými potravními zvyklostmi jednotlivých populací v souvislosti s potravní nabídkou na dané lokalitě.

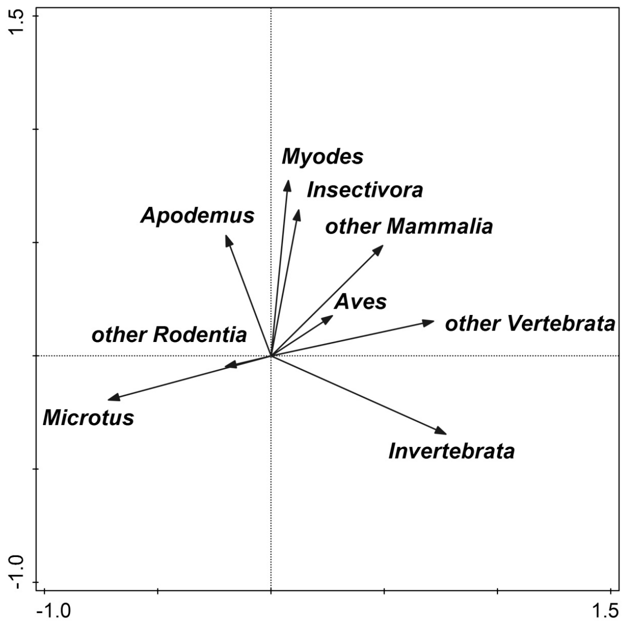
Puštík obecný je stálým druhem, v České republice bylo 78% jedinců kroužkovaných převážně jako mláďata na hnízdě zpětně nalezeno do 10 km od místa okroužkování (Cepák et al. 2008).

1.3. Složení potravy

V rámci dravců i sov s rozšířením na severní polokouli se řada druhů specializovala k lovu drobných savců. Ze studovaných druhů se jedná především o poštolku obecnou, kalouse ušatého a sýce rousného. V potravě puštíka obecného se obvykle vyskytuje také výrazný podíl drobných savců, ale také celá řada jiných obratlovců (např. Obuch 2011). Složení potravy specialistů i generalistů do značné míry odráží nabídku drobných savců na lovištích, ale je zároveň ovlivněna řadou dalších faktorů. Celková diverzita v potravě ptačích predátorů specializovaných k lovu drobných savců obvykle roste jižním směrem, zároveň se však tímto směrem snižuje průměrná velikost kořisti (Korpimäki & Marti 1995).

Porovnání 110 studií zabývajících se složením potravy u studovaných druhů ptačích predátorů přináší rozdíly v celkovém složení jejich potravy v rámci západní Palearktidy (obr. 1). Poštolka obecná vykazuje největší variabilitu v zastoupení hlavních složek potravy a její potravní nika se částečně překrývá s potravním spektrem všech studovaných druhů sov. Ve srovnání se sovami je potrava poštolky obecné charakterizována vysokým zastoupením rodu *Microtus* a pravidelnou přítomností bezobratlých (tab. 1), což je pravděpodobně způsobeno denní aktivitou tohoto predátora. Studované sovy vykazují menší variabilitu v zastoupení hlavních složek potravy a jejich spektra se prakticky nepřekrývají (obr. 1). Potrava kalouse ušatého je charakterizována celkově vysokým zastoupením rodu *Microtus* a ostatních hlodavců, zejména rodu *Apodemus* (tab. 1). Potrava sýce rousného je charakterizována vysokým podílem drobných savců, zejména rodů *Microtus*, *Myodes* a *Apodemus* a hmyzožravců (tab. 1). Potrava puštíka obecného vykazuje poměrně vyrovnané zastoupení více složek. Dominantním rodem jsou myšice rodu *Apodemus*, následují rody *Microtus* a *Myodes*. U puštíka obecného se na rozdíl od ostatních sov v potravě často vyskytují bezobratlí (tab. 1). Celkové zastoupení ptáků v potravě je podobné u všech studovaných druhů, ale mezi jednotlivými populacemi existuje značná variabilita (tab. 1).


● Falco tinnunculus
○ Strix aluco
● Aegolius funereus
□ Asio otus
1.5
-1.0
-1.0
1.5
IT(08)
PL(103)
PL(107)
PL(110)
NO(106)
AU(11)
IT(95)
CZ(111)
DE(12)
DE(15)
NO(77)
PL(109)
BE(100)
CZ(17)
DE(13)
CZ(10)
IT(09)
LT(92)
CZ(100)
PL(96)
FI(105)
NO(102)
RO(100)
IT(94)
CZ(07)
CZ(59)
FR(93)
GB(97)
PL(108)
CZ(05)
CZ(04)
IT(104)
FI(14)
FI(03)
GB(61)
GB(69b)
CR(21)
PL(45)
CZ(16)
PL(66)
RU(02)
IT(99)
BG(100)
TR(100)
ME(100)
FR(85b)
GB(102)
FI(01)
NO(100)
SK(100)
CZ(30)
PL(27)
SE(06)
RU-CR(100)
IT(31)
IT(32)
DE(100)
GB(69a)
GR(19)
FI(49)
DE(82)
NL(68a)
IT(54)
IT(24)
SK(63)
GB(89)
SL(98)
GB(88)
CZ(22)
PL(39)
IT(35)
GR(36)
BG(40)
UK(44)
SL(25)
PL(33)
FI(70-71)
IR(85)
IT(65)
RO(23)
PL(38)
SC(51)
IR(37)
CR(18)
PL(34)
SE(50)
NL(68b)
GB(56)
ES(91)
CV(72)
RS(41)
CZ(53)
IT(46)
DE(64b)
IT(42)
NL(47)
CH(84)
NL(80)
CZ(81b)
AU(67)
RU(43)
CZ(81a)
FR(83)
PL(28)
SK(52)
IT(60)
SP(29)
BG(48)
IS(26)
DE(64a)
DZ(58)
PL(78b)
RU(79)
DE(87)
PL(73)
HU(57a)
GB(62)
SK(20)
PL(78a)
SK(86)
SK(74)
HU(57b)
PL(55)
HU(57d)
CZ(90)
HU(57c)
ES(76)
ES-CI(75b)
ES-CI(75a)


1.5
-1.0
-1.0
1.5
Myodes
Insectivora
Apodemus
other Mammalia
Aves
other Vertebrata
other Rodentia
Microtus
Invertebrata

Obrázek 1. - Složení potravy vybraných druhů ptačích predátorů v západní Palearktidě s důrazem na zastoupení rodů *Microtus*, *Apodemus* a *Myodes* založené na procentuálním zastoupením počtu jedinců. Zahrnuty byly studie z hnízdního i mimohnízdního období napříč různými biotopy (n = 110 publikovaných studií; poštolka obecná 34, kalous ušatý 38, sýc rousný 17, puštík obecný 21). Do analýzy byly zahrnuty studie s minimálním počtem 50 položek v potravě, ale průměrný počet položek byl podstatně vyšší (průměr ± s.d., 3772 ± 9070). Mnohorozměrná data byla zhodnocena pomocí PCA analýzy (ter Braak & Šmilauer 2012), vstupní jednotku představovala lokalita. Některé studie z více lokalit v grafu mají více bodů, lokality jsou odlišené malými písmeny. Do analýzy vstupovalo procentuální zastoupení jednotlivých složek potravy, data byla před analýzou logaritmována. Celkový počet determinovaných položek byl použit jako kovariát. Ordinační diagramy zobrazují zvlášť vzájemnou polohu lokalit a hlavních složek potravy. Jednotlivé druhy predátorů jsou odlišeny různými symboly. Rozsah variability v rámci jednoho druhu je ohraničen polygony.

První a druhá ordinační osa společně vysvětlují 47,9% variability. První ordinační osa představuje gradient v zastoupení rodu *Microtus* (korelační koeficient -0,75), ostatních obratlovců (0,66) a bezobratlých (0,99). S druhou ordinační osou pozitivně koreluje zastoupení rodů *Myodes* (0,78), *Apodemus* (0,58) a hmyzožravců (0,62). Zastoupení ostatních hlodavců (zejména rody *Mus*, *Rattus* a *Micromys*) je slabě negativně korelováno s první ordinační osou (-0,18). Zastoupení ostatních savců pozitivně koreluje s první i druhou ordinační osou (0,40 a 0,39), zastoupení ptáků vykazuje s oběma osami také pozitivní vztah, ale s výrazně slabším korelačním koeficientem (0,23 a 0,15).

Jednotlivé studie jsou v grafu označeny dvoupísmennou zkratkou země a v závorce je uvedeno identifikační číslo publikace. Studie, které jsou součástí této práce, jsou vyznačeny tučným fontem. Zkratky zemí: AU – Rakousko, BE – Belgie, BG – Bulharsko, CR – Chorvatsko, CV – Kapverdy, CZ – Česká republika, DE – Německo, DZ – Alžírsko, ES-CI – Kanárské ostrovy, ES – Španělsko, FI – Finsko, FR – Francie, GB – Velká Británie, SE – Švédsko, GR – Řecko, HU – Maďarsko, CH – Švýcarsko, IR – Irán, IS - Izrael, IT – Itálie, LT – Litva, ME – Černá Hora, NL – Nizozemí, NO – Norsko, PL – Polsko, RO – Rumunsko, RS – Srbsko, RU-CR – Krym a Kavkaz, RU – Rusko, SC – Skotsko, SE – Švédsko, SK – Slovensko, SL – Slovinsko, TR – Turecko, UK – Ukrajina.

Identifikační čísla publikací: FI(01) Korpimäki (1988); RU(02) Boiko & Shutova (2005); FI(03) Jäderholm (1987); CZ(04) Pokorny et al. (2003); CZ(05) Pokorny (2000); SE(06) Hörnfeldt et al. (1990); CZ(07) Kloubec & Obuch (2003); IT(08) Mezzavilla et al. (1994); CZ(09) Vacik (1991); CZ(10) Pykal & Kloubec (1994); AU(11) Busch et al. (1991); DE(12) Schelper (1989); DE(13) Schwerdtfeger (1988); FI(14) Korpimäki (1987); DE(15) Plucinski (1981); **CZ(16) Zárybnická et al. (2013) – příloha V**; CZ(17) Rymešová (2006); CR(18) Mikuška et al. (2015); GR(19) Alizivatos & Gouner (1999); SK(20) Tulis et al. (2015); CR(21) Bencerić & Pavlovič (2010); CZ(22) Bencová et al. (2006); RO(23) Benedek & Sîrbu (2010); IT(24) Cecere et al. (2013); SL(25) Tome (2009); IS(26) Charter et al. (2012); PL(27) Cichocki et al. (2008); PL(28) Dziemian et al. (2012); SP(29) Escala et al. (2009); CZ(30) Gaďůrková (2013); IT(31) Galeotti & Canova (1994); IT(32) Galli et al. (2015); PL(33) Gryz & Krauze-Gryz (2015); PL(34) Hetmański et al. (2008); IT(35) Cecere & Vicini (2000); GR(36) Kafkaletou-Diez et al. (2008); IR(37) Khaleghizadech et al. (2006); PL(38) Kitowski (2013); PL(39) Lesiński et al. (2016); BG(40) Milchev & Ivanov (2016); RS(41) Purger & Krsmanovic (1989); IT(42) Sergio et al. (2008); RU(43) Sharikov & Makarova (2014); UK(44) Stasiak et al. (2012); PL(45) Stolarz et al. (2017); IT(46) Trotta (2010); NL(47) Wijnandts (1984); BG(48) Milchev et al. (2003); FI(49) Korpimäki (1992); SE(50)

Nilsson (1981); SC(51) Village (1981); SK(52) Krištín (1987); **CZ(53) Riegert et al. (2009) – příloha IV**; IT(54) Capizzi & Luiselli (1998); PL(55) Romanowski (1996); GB(56) Yalden (1980); HU(57) Katalin & Mária (2015); DZ(58) Souttou et al. (2007); CZ(59) Tomešek & Čermák (2009); IT(60) Simmi et al. (1997); GB(61) Simms (1961); GB(62) Yalden & Warburton (1979); SK(63) Darolová (1989); DE(64) Kübler et al. (2005); IT(65) Lovari (1974); PL(66) Skierczyński (2006); AU(67) Sumasgutner et al. (2013); NL(68) Bijlsma (2012); GB(69) Hirons (1984); FI(70-71) Korpimäki (1985), Itämies & Korpimäki (1987); CV(72) Ontiveros (2005); PL(73) Żmihorski & Rejt (2007); SK(74) Kečkéšová & Noga (2008); ES-CI(75) Carrillo et al. (1994); ES(76) Navarro et al. (2014); NO(77) Nodeland (2013); PL(78) Boratynski & Kasprzyk (2005); RU(79) Gavrilov & Zalesky (1961); NL(80) Cavé (1968); CZ(81) Plesník (1992); DE(82) Beichle (1980); FR(83) Boileau (2005); CH(84) Roulin (1996); IR(85) Khaleghizadech & Javidkar (2006); SK(86) Balát & Bauer (1955); DE(87) Piechocki (1975); GB(88) Fairley & McLean (1965); GB(89) Davis (1960); **CZ(90) Riegert et al. (2009) – příloha IV**; ES(91) Adánez (2000); LT(92) Balčiauskiene et al. (2006); FR(93) Baudvin & Jouaire (2006); IT(94) Capizzi (2000); IT(95) Capizzi & Luiselli (1998); PL(96) Grzedzicka et al. (2013); GB(97) Kirk (1992); SL(98) Kuhar et al. (2006); IT(99) Marchesi et al. (2006); BE-TR (100) Obuch (2011); NO(101) Overskaug et al. (1995); GB(102) Petty 1999; PL(103) Romanowski & Żmihorski (2009); IT(104) Sergio et al. (2007); FI(105) Solonen & Karhunen (2002); NO(106) Sunde et al. (2001); PL(107) Wiacek et al. (2009); PL(108) Zalewski (1994); PL(109) Zawadzka & Zawadzki (2007); PL(110) Żmihorski & Osojca (2007); **CZ(111) Luka & Riegert in press – příloha VI**.

Tabulka 1. Průměrné procentuální zastoupení z počtů položek (± s.d. a rozsah) vybraných složek potravy studovaných druhů ptačích predátorů. Data pochází ze 110 publikovaných studií v západní Palearktidě. Číslo v závorce v prvním řádku udává počet lokalit. Data pocházejí z hnízdního i mimohnízdního období.

	Falco tinnunculus (n = 55)	*Asio otus* (n = 39)	*Aegolius funereus* (n = 17)	*Strix aluco* (n = 30)
Microtus	43,1 ± 28,5 (0,0 - 95,5)	61,2 ± 25,6 (0,0 - 87,4)	34,6 ± 13,8 (1,9 - 52,6)	16,7 ± 16,3 (2,3 - 62,1)
Myodes	1,2 ± 2,4 (0,0 - 10,2)	1,1 ± 2,0 (0,0 - 10,2)	18,8 ± 13,1 (3,1 - 51,1)	9,8 ± 8,2 (0,0 - 33,1)
Apodemus	2,1 ± 2,9 (0,0 - 16,1)	14,0 ± 11,6 (0,0 - 59,3)	11,7 ± 10,8 (0,0 - 39,0)	20,9 ± 13,0 (0,4 - 51,1)
ostatní Rodentia	4,1 ± 4,3 (0,0 - 16,5)	13,5 ± 21,2 (0,0 - 93,4)	5,7 ± 4,8 (1,4 - 21,1)	4,8 ± 7,2 (0,0 - 26,3)
Insectivora	3,9 ± 7,0 (0,0 - 38,2)	1,9 ± 3,9 (0,0 - 18,7)	19,5 ± 10,4 (3,8 - 37,5)	7,8 ± 8,7 (0,0 - 38,1)
ostatní Mammalia	1,6 ± 5,4 (0,0 - 32,9)	0,1 ± 0,4 (0,0 - 2,2)	0,1 ± 0,5 (0,0 - 2,1)	7,8 ± 6,6 (0,6 - 30,0)
Aves	12,5 ± 14,5 (0,0 - 63,3)	7,3 ± 11,7 (0,0 - 63,4)	9,0 ± 15,1 (0,0 - 65,1)	12,3 ± 10,1 (1,2 - 44,4)
ostatní Vertebrata	5,2 ± 12,2 (0,0 - 76,4)	0,0 ± 0,1 (0,0 - 0,4)	0,0 ± 0,0 (0,0 - 0,0)	7,3 ± 8,4 (0,0 - 33,8)
Invertebrata	26,3 ± 25,7 (0,0 - 95,3)	0,9 ± 2,4 (0,0 - 10,3)	0,6 ± 1,8 (0,0 - 7,3)	12,6 ± 16,7 (0,0 - 76,5)

1.3.1. Poštolka obecná

V potravě poštolky obecné pravidelně dominují drobní savci, především zástupci rodu *Microtus* (Village 1990, tab. 1). Vysoké zastoupení hraboše (> 80%) je charakteristické především pro mimoměstské populace ve střední a severní Evropě (např. Plesník 1992, Roulin 1996). Nízké nebo prakticky žádné zastoupení hraboše v potravě vykazují populace z jižních oblastí, například z Itálie (Lovari 1974), Kapverdských ostrovů (Ontiveros 2005), Kanárských ostrovů (Carrillo et al. 1994), Alžírska (Souttou et al. 2007) nebo Iránu (Khaleghizadech & Javidkar 2006). V těchto oblastech se v potravě nápadně zvyšuje zastoupení bezobratlých, zejména rovnokřídlých - Orthoptera (Lovari 1974, Gil-Delgado et al. 1995), brouků - Coleoptera (Khaleghizadech & Javidkar 2006, Souttou et al. 2007), ale také plazů z čeledí Lacertidae a Gekkonidae (Carrillo et al. 1994).

Z ostatních hlodavců se v potravě poštolky obecné nejčastěji vyskytují zástupci rodů *Micromys*, *Mus* a *Rattus* (Plesník 1992, **Riegert et al. 2007 – příloha I**). Myšice rodu *Apodemus* se v potravě poštolek vyskytují jen vzácně (např. Kečkéšová & Noga 2008), ale jejich podíl může být vyšší u jižních populací (např. 16,1% - Francie, Boileau 2005). Častý výskyt myšic v potravě uvádí také Village (1990) ze Skotska. Nicméně, údaj nelze jednoduše porovnat s ostatními, neboť autor uvádí pouze podíl vývržků, ve kterých byly myšice zjištěny. Norníci rodu *Myodes* se v potravě poštolky vyskytují vzácně (< 3%). Hmyzožravci (Insectivora) tvoří pravidelnou složku potravy, nejčastěji se jedná o rody *Sorex*, vzácněji *Crocidura* a *Talpa*. Nejvyšší zastoupení hmyzožravců bylo zjištěno u poštolek ve Velké Británii (25%, Simms 1961) a v Norsku (18%, Nodeland 2013).

Bezobratlí tvoří pravidelnou složku potravy populací nejen v jižních oblastech, ale ve většině areálu výskytu (průměr 26%, tab. 1). Podobně jako v jižní Evropě jsou v potravě nejčastěji nalezeni zástupci brouků a rovnokřídlých (Itämies & Korpimäki 1987, **Riegert & Fuchs 2004 – příloha VII**, Sumasgutner et al. 2013).

1.3.2. Kalous ušatý

V potravě kalouse ušatého se ve srovnání s ostatními druhy vyskytuje průměrně nejvyšší podíl hraboše rodu *Microtus* (tab. 1). Jeho dominantní zastoupení (> 80%) vykazují populace ze střední a západní Evropy (Village 1981, Hetmański et al. 2008, **Riegert et al. 2009 – příloha IV**, Dziemian et al. 2012, Stasiak et al. 2012, Kitowski 2013, Gryz et al. 2015, Tulis et al. 2015, Lesiński et al. 2016, Stolarz et al. 2017), v severní Evropě bylo zastoupení hraboše o něco nižší (70%, Korpimäki 1992). Naopak nejnižší zastoupení (0-12%) hraboše bylo zjištěno v jižních oblastech, například v Řecku (Alivizatos & Goutner 1999), Itálii (Galli et al. 2015) nebo Iránu (Khaleghizadeh et al. 2009). U jižních populací byl zjištěn současný nárůst zastoupení ostatních druhů hlodavců, především rodů *Tatera*, *Gerbillus* (Khaleghizadeh et al. 2009), *Mus* (Alivizatos & Goutner 1999, Escala et al. 2009) nebo ptáků (Galli et al. 2015).

Myšice rodu *Apodemus* se v potravě kalouse ušatého vyskytují pravidelně, nejvyšší zastoupení (20-60%) bylo dokumentováno v jižní a střední Evropě, konkrétně například v Řecku (Alivizatos & Goutner 1999), Chorvatsku (Bencerić & Pavlovič 2010), Itálii (Galeotti & Canova 1994, Capizzi & Luiselli 1998, Cecere & Vicini 2000), Rumunsku (Benedek & Sîrbu 2010), Bulharsku (Milchev & Ivanov 2016) a České republice (Bencová et al. 2006, Gaďůrková 2013). Severním směrem jejich zastoupení v potravě klesá na hodnoty 10-15% (např. Polsko - Cichocki et al. 2008, Dziemian et al. 2012, Kitowski 2013, Rusko - Sharikov & Makarova 2014) a v potravě prakticky chybí na severní hranici jejich areálu (Korpimäki

1992). Celkové zastoupení myšic v potravě kalouse v Českých Budějovicích odpovídá spíše nižšímu průměru (14%, **Riegert et al. 2009 – příloha IV**). Norníci rodu *Myodes* se v potravě kalouse vyskytují vzácně (0-3%), nejvyšší hodnota pochází z Finska (10%, Korpimäki 1992). Hmyzožravci (nejčastěji rodu *Sorex*) tvoří podstatnou část potravy pouze v severních oblastech a ve Skotsku (10-20%, Korpimäki 1992, Village 1981). Výjimkou je také jejich vysoké zastoupení na Ukrajině (14%, Stasiak et al. 2012). V ostatních studiích nepřesahuje jejich celkové zastoupení 2%.

Ptáci mohou představovat u různých populací značnou část potravy, zřejmě v závislosti na lokálních podmínkách. Například nejvyšší údaj 63% pochází z hromadného nocoviště v urbánním prostředí severní Itálie (Galli et al. 2015). Průměrně však tvoří 7-12% potravy (tab. 1). Bezobratlí většinou tvoří zanedbatelnou složku potravy, jejich zastoupení většinou nepřesahuje 1%. Výjimkou jsou studie z jižního Slovenska (Krištín 1987), Itálie (Trotta 2010, Hetmanski et al. 2008) a Polska (Gryz & Krauze-Gryz 2015), kde zastoupení bezobratlých přesahuje 5% z celkového počtu determinovaných položek.

1.3.3. Sýc rousný

Rod *Microtus* v potravě sýce rousného zpravidla tvoří jednu z dominantních složek (tab. 1). Hraboš běžně dosahuje celkového zastoupení přibližně 40%, a to jak ve střední (Schwerdtfeger 1988, Bush et al. 1991, Vacik 1991, Pokorny 2000, **Zárybnická et al. 2013 – příloha V**) tak i v severní Evropě (Korpimäki 1987, Hörnfeldt et al. 1990). Výjimkou je studie ze Švýcarska, kde bylo v potravě zjištěno méně než 8% hrabošů rodu *Microtus* (Ravussin et al. 2016). Myšice rodu *Apodemus* tvoří také podstatnou část potravy a jejich průměrné zastoupení je srovnatelné se zastoupením u kalouse ušatého (tab. 1). V severních oblastech (Finsko, Švédsko) nebyly myšice v potravě zaznamenány, především z důvodu umístění populací sýce na hranici rozšíření rodu *Apodemus*. Rod *Myodes* představuje stálou složku potravy (tab. 1), nejvyšší zastoupení (> 40%) bylo zaznamenáno v severní Evropě (Jäderholm 1987, Hörnfeldt et al. 1990). Nejnižší hodnoty (< 5%) pocházejí ze střední Evropy (Plucinski 1981, **Zárybnická et al. 2013 – příloha V**). Nicméně, v rámci střední Evropy se objevují i studie s vyšším zastoupením (10-20%, Pokorny 2000, Pokorny et al. 2003, **Zárybnická et al. 2015 – příloha VIII**). Hmyzožravci se v potravě sýce vyskytují také pravidelně (tab. 1), nejčastěji se jedná o rody *Sorex* a *Neomys* (např. Jäderholm 1987, Schelper 1989, Rymešová 2006).

Ptáci obvykle tvoří minoritní část potravního spektra sýce rousného (< 10%), výrazně vyšší zastoupení bylo zjištěno v Rusku (19%, Boiko & Shutova 2005) a v Německu (65%, Plucinski 1981). Bezobratlí se v potravě sýce rousného vyskytují velmi vzácně (< 1%). Výjimkou je studie z Moskvy, kde autoři zaznamenali celkové zastoupení 7% (Boiko & Shutova 2005).

1.3.4. Puštík obecný

Díky značnému oportunismu tvoří rod *Microtus* v potravě puštíka obecného průměrně nejnižší podíl v rámci studovaných druhů ptačích predátorů (tab. 1). Nejvyšší zastoupení (> 40%) bylo zaznamenáno převážně v severních oblastech, konkrétně v Norsku (Sunde et al. 2001, Obuch 2011), Velké Británii (Petty 1999) a Litvě (Balčiauskiene et al. 2006). Naopak nejnižší zastoupení (< 5%) bylo zjištěno v jižních oblastech, konkrétně ve Španělsku (Adánez 2000), Francii (Baudvin & Jouaire 2006), Černé Hoře a Turecku (Obuch 2011).

V rámci střední Evropy je celkové zastoupení hraboše v potravě spíše nízké (5%, Żmihorski & Osojca 2006, **Luka & Riegert in press – příloha VI**) nebo střední (10-20%, Zalewski 1994, Grzedzicka et al. 2013).

Norníci rodu *Myodes* tvoří pravidelnou součást potravy puštíka obecného a jejich zastoupení se výrazně liší mezi studovanými populacemi (tab. 1). Nejvyšší podíl byl zjištěn v Norsku (27%, Sunde et al. 2001). Jižním směrem jejich zastoupení v potravě klesá, například Polsko 10-15% (Żmihorski & Osojca 2006, Wiacek et al. 2009), Česká Republika 10-11% (Obuch 2011, **Luka & Riegert in press – příloha VI**), Slovinsko 2 % (Kuhar et al. 2006), Turecko < 1% (Obuch 2011). Myšice rodu *Apodemus* mají v potravě puštíka průměrně poměrně nízké zastoupení (tab. 1), ale rozdíly mezi jednotlivými populacemi mohou být značné. Nejvyšší zastoupení (> 30%) je dokumentováno z České Republiky (Obuch 2011, **Luka & Riegert in press – příloha VI**), Polska (Wiacek et al. 2009, Grzedzicka et al. 2013), Itálie (Sergio et al. 2007) a oblasti Krymu a Kavkazu (Obuch 2011). Celkově je jejich podíl v potravě puštíka ve střední Evropě značně variabilní (4-38%), jejich zastoupení může vykazovat značnou variabilitu i na menší geografické škále, např. v rámci Slovenska (0-30%, Obuch 2011). Nejnižší zastoupení (< 1%) bylo popsáno ze severní hranice areálu myšic v Norsku (Sunde et al. 2001, Obuch 2011) a ve Velké Británii (Petty 1999). Ostatní hlodavci se v potravě puštíka vyskytují méně často. Jedná se zejména o druhy z čeledi Muridae a Gliridae (Obuch 2011).

Hmyzožravci jsou v potravě puštíka nejčastěji zastoupeni rody *Sorex*, *Neomys* a *Talpa* (např. Obuch 2011) a jejich podíl může u některých populací přesahovat 30% (Belgie - Obuch 2011, Polsko - Romanowski & Żmihorski 2009). Průměrně však dosahují mnohem nižších zastoupení (tab. 1). Z ostatních savců se v potravě puštíka obecného vyskytují zejména zástupci letounů (Chiroptera, např. Kuhar et al. 2006, Obuch 2011). Ptáci tvoří významnou složku potravy (tab. 1), jejich nejvyšší zastoupení bylo zjištěno v polské Toruni (42%, Zalewski 1994). Podobný podíl ptáků v potravě (45%) byl zjištěn u lesní populace v Itálii (Marchesi et al. 2006). Nejnižší zastoupení bylo zároveň zaznamenáno u lesní populace v Polsku (3%, Wiacek et al. 2009). Zastoupení ptáků v potravě puštíka tedy pravděpodobně nevykazuje žádný nápadný trend.

Na rozdíl od předchozích dvou druhů sov se v potravě puštíka vyskytuje vyšší podíl ostatních obratlovců (tab. 1). Puštíci často loví obojživelníky a vzácně také ryby (Obuch 2011). Od ostatních studovaných sov se složení potravy puštíka obecného liší také pravidelným výskytem bezobratlých (tab. 1). Nejčastěji se jedná o zástupce brouků a rovnokřídlých (Obuch 2011) nebo motýlů (Overskaug et al. 1995). Některé populace mají v potravě nemalý podíl slimáků čeledi Limacidae (až 10%), kteří jsou pravděpodobně konzumováni v období nedostatku hlavních složek potravy (Obuch 2011).

1.4. Faktory ovlivňující složení potravy

Kromě geografické pozice se na variabilitě složení potravního spektra podílí další biotické i abiotické faktory. Mezi nejvýznamnější faktory patří dostupnost potravy, sezónní změny a vliv klimatických podmínek, ale také například vliv individuálních loveckých strategií nebo kvalita a stáří jedince.

1.4.1. Vliv abundance hlavní kořisti

Kolísání abundance drobných savců během let je známým fenoménem a pravidelnost nebo amplituda cyklů byla studována v různých částech Evropy (např. Jędrzejewski &

Jędrzejewska 1996). V severních oblastech jsou obvykle cykly drobných savců (*Microtus agrestis* a *Myodes glareolus*) pravidelné (3-4 leté) s velkým rozdílem abundance mezi fází pesima a optima. Jižním směrem se však amplituda i cyklicita snižuje v závislosti na sněhové pokrývce (Hansson & Henttonen 1985). K podobným výsledkům dospěli také Mackin-Rogalska & Nabagło (1990) u hraboše polního (*Microtus arvalis*). Dalším gradientem, který byl na území Evropy zjištěn, je postupné zvyšování amplitudy a pravidelnosti cyklů hraboše polního od Baltského moře směrem do střední Evropy (Tkadlec & Stenseth 2001). V současné době se spekuluje o obecném slábnutí cyklů drobných savců rodu *Microtus* a *Myodes* na území severní i střední Evropy, které je způsobené klimatickými změnami (Hörnfeldt et al. 2005, Cornulier et al. 2013, Gouveia et al. 2015). Tyto trendy nebyly v některých oblastech potvrzeny, například ve Finsku na základě dlouhodobých dat o reprodukční úspěšnosti vybraných ptačích predátorů (Sundell et al. 2004). Případné slábnutí cyklů může být způsobeno i jinými faktory. V případě studijní plochy v Krušných Horách nelze zanedbat vliv postupného stárnutí porostů vysazeného smrku pichlavého *Picea pungens* (Zárybnická et al. 2017a). Díky tomu je biotop v současné době vhodnější k výskytu zejména myšic rodu *Apodemus*, jejichž populace na lokalitě nyní vykazují pravidelné tříleté cykly. Také u norníka rudého *Myodes glareolus* byl v posledních letech zaznamenán na studijní ploše nárůst početnosti a 3-5 leté cykly. Na studované lokalitě navíc nebyl zjištěn celkový pokles početnosti hraboše mokřadního, pouze nebyly prokázány pravidelné cykly (Zárybnická et al. 2017a).

Vliv abundance na zastoupení hlavní kořisti v potravě ptačích predátorů dokládá celá řada víceletých studií. Pozitivní vztah mezi zastoupením hlavní kořisti a její abundancí na lovišti (funkční odpověď predátora, Abrams 1982) byl dokumentován nejen u studovaných druhů, ale také u řady dalších druhů dravců a sov (např. *Buteo buteo* - Reif et al. 2001, *Buteo lagopus* - Pasanen & Sulkava 1971, Francksen et al. 2017, *Circus cyaneus* - Redpath & Thirgood 1999, *Circus pygargus* - Salamolard et al. 2000, *Tyto alba* - Bernard et al. 2010, *Asio flammeus* - Korpimäki and Norrdahl 1991).

U poštolky obecné je preferovanou kořistí hraboš rodu *Microtus* (např. Casagrande et al. 2008). Funkční odpověď byla u poštolky obecné dokumentována například u finské populace (Korpimäki 1986, Korpimäki and Norrdahl 1991). V hnízdních sezónách, kdy byly abundance hraboše na lovišti vysoké, byl hraboš preferovanou kořistí. Během jeho nedostatku na lovištích vzrůstal v potravě podíl ptáků, hryzce vodního *Arvicola terrestris* a rejsků rodu *Sorex*. Abundance norníků, hryzců ani rejsků neměla na složení potravy signifikantní vliv. K podobným závěrům dospěl také Village (1982) ve Skotsku v mimohnízdním období. Podíl vývržků, které byly tvořeny výhradně hrabošem mokřadním (*Microtus agrestis*), byl pozitivně korelován s abundancí hraboše na lovišti. V hnízdní sezóně tento trend nebyl průkazný. V roce s nízkou abundancí hraboše se v potravě zvýšilo zastoupení ptáků, rejsků a žížal (Lumbricidae), ale jejich podíl nevykazoval signifikantní vztah s abundancí hraboše (Village 1982, 1990). V České republice byla částečná funkční odpověď zjištěna u urbánní populace v hnízdním období, neboť vliv abundance hraboše na složení potravy byl pouze indikativní. V letech s nízkou abundancí hraboše byl v potravě zjištěn vyšší podíl hmyzu, zejména brouků z čeledi Carabidae a rovnokřídlých z čeledi Tettigonidae. Nicméně, nárůst podílu hmyzu v potravě hrál zanedbatelnou roli, pokud bylo počítáno s biomasou kořisti (**Riegert et al. 2007 – příloha I**). Rozdíly mezi finskými, skotskými a českými populacemi mohou být dány především méně výraznou fluktuací početnosti hraboše ve střední Evropě.

Také u kalouse ušatého byl zjištěn pozitivní vztah mezi zastoupením rodu *Microtus* v potravě a jeho abundancí na lovišti. Zastoupení hraboše bylo navíc negativně korelováno s celkovou diverzitou v potravě. Během let s nízkou abundancí hraboše vzrůstal v potravě slovinských kalousů podíl zejména myšic rodu *Apodemus* a ptáků (Tome 2003). K podobným závěrům dospěli také v Nizozemí (Wijnandts 1984) a Itálii (Sergio et al. 2008), kde se v období nedostatku hraboše zvyšoval podíl myšic rodu *Apodemus* a ptáků v potravě. U skotské populace kalouse byl zjištěn pozitivní vztah mezi zastoupením hraboše mokřadního v potravě a jeho abundancí na lovišti, zastoupení ptáků však bylo celkově velmi nízké a alternativní kořistí byli rejsci rodu *Sorex* (Village 1981). U finských kalousů byla v hnízdním období také zjištěna pozitivní korelace mezi zastoupením hrabošů rodu *Microtus* v potravě a jeho abundancí na lovišti, zastoupení ostatních významných složek potravy s abundancí hraboše nebylo korelováno (Korpimäki 1992). Negativní korelaci s abundancí hraboše vykazovalo zastoupení drobných savců z čeledi Muridae (rody *Rattus*, *Micromys*, *Mus*) a ptáků. Významný vliv abundance hraboše na celkové složení potravy byl zjištěn také u zimujících kalousů na Slovensku (Tulis et al. 2015). Výsledky z České republiky také dokládají vysoké zastoupení hraboše v potravě kalousů ve všech čtyřech hnízdních sezónách (60-90%), v letech s jeho nižší abundancí na lovišti se v potravě zvýšil především podíl myšic rodu *Apodemus* (7-35%) a zastoupení ptáků bylo stabilně nízké (2-5%, **Riegert et al. 2009 – příloha IV**).

Podobné výsledky můžeme sledovat u sýce rousného. Například ve Finsku (Korpimäki 1988) byl v hnízdním období dokumentován pozitivní vztah mezi zastoupením hraboše v potravě a jeho abundancí na lovišti, indikativní pozitivní korelace byla zjištěna navíc u norníka rodu *Myodes*. Negativní korelaci s abundancí hraboše vykazovali rejsci a ptáci, kteří byli alternativní kořistí. Během hnízdní sezóny si sýci navíc vytvářeli zásoby kořisti, které jim pomáhaly překonat krátkodobé nedostatky hlavní potravy způsobené nevhodnými klimatickými podmínkami (např. sněhová pokrývka, Korpimäki 1987). Ve střední Evropě je situace odlišná. Přestože bylo v potravě sýce zjištěno vysoké zastoupení rodu *Microtus* (47%), jeho zastoupení v potravě nebylo korelováno s abundancí hraboše na lovišti. Funkční odpověď byla zjištěna pouze pro myšice rodu *Apodemus* (**Zárybnická et al. 2013 – příloha V**). Norníci rodu *Myodes* se v potravě sýce vyskytují v omezené míře (3%), ale nevykazují korelační vztah s jejich abundancí na lovišti. S nabídkou drobných savců pravděpodobně souvisí i klesající zastoupení norníků a myšic a rostoucí zastoupení ptáků v potravě sýce s nadmořskou výškou, ale abundance drobných savců nebyla v tomto případě stanovena (**Zárybnická et al. 2017 – příloha IX**). Výrazný pozitivní vztah byl zjištěn zejména mezi nadmořskou výškou a zastoupením ptáků z čeledi Fringillidae, kteří byli v potravě zastoupeni převážně pěnkavou obecnou (*Fringilla coelebs*). Na základě výsledků bodového sčítání představuje pěnkava obecná jeden z nejhojnějších druhů studované oblasti (Kloubec et al. 2015) a lze tedy předpokládat, že ve vyšších polohách pěnkava představuje vhodnou alternativní kořist (**Zárybnická et al. 2017 – příloha IX**).

Přestože je puštík obecný potravním oportunistou, můžeme u něj nalézt podobné trendy ve složení potravy. Ve Finsku tvořili drobní savci podčeledi Microtinae (*Microtus*, *Myodes*, *Arvicola*) 18-31% potravy (Solonen & Karhunen 2002). Vyšší zastoupení drobných savců bylo zjištěno v letech, kdy byla vyšší abundance hrabošů rodu *Microtus* na lovištích. V letech s nízkou abundancí hraboše byla potrava více různorodá a vzrůstal podíl prakticky všech ostatních složek, zejména obojživelníků a ptáků (Solonen & Karhunen 2002). Anglická populace vykazovala až 80% hraboše mokřadního v potravě a jeho zastoupení kolísalo podle abundancí na lovištích (Petty 1999). V letech s nízkou abundancí se v potravě zvyšovalo zastoupení obojživelníků (zejména skokanů *Rana temporaria*) a ptáků. Obě tyto složky potravy zároveň vykazovaly negativní korelační vztah s abundancí hraboše (Petty 1999). Populace ve střední Evropě mohou být z velké části závislé na abundanci myšic rodu *Apodemus* (39%, **Luka & Riegert in press – příloha VI**). Nabídka myšic do značné míry determinuje složení potravy. V období nedostatku myšic vzrůstá v potravě podíl hrabošů, norníků a ptáků. Zastoupení myšic v potravě klesá v průběhu hnízdního období a pozitivně koreluje s reprodukčními parametry (**Luka & Riegert in press – příloha VI**).

1.4.2. Sezónní změny složení potravy a vliv klimatických faktorů

Změny ve složení potravy v průběhu roku jsou do značné míry spojeny se změnou klimatických podmínek. V hnízdním období se diverzita potravy obvykle zvyšuje, což je dáno dostupností více typů kořistí. U studovaných druhů se jedná zejména o zvýšení podílu hmyzu a ptáků (zejména mláďat) a ostatních složek potravy v hnízdním období (např. poštolka obecná: Darolová 1989, Plesník 1992; kalous ušatý: Nilsson 1981, Rubolini et al. 2003, **Riegert & Fuchs 2004 – příloha VII**, Bencová et al. 2006; sýc rousný: Korpimäki 1986; puštík obecný: Petty 1999, Zawadzka & Zawadzki 2007, Romanowski & Żmihorski 2009). Ve většině studií je v hnízdním období dokumentován pokles zastoupení hraboše v potravě. Výjimkou je studie na sýci rousném ve Finsku, kde byl díky vysoké sněhové pokrývce zjištěn nižší podíl hraboše v potravě v mimohnízdním období (Korpimäki 1986). K podobným závěrům dospěl také Tome (2009) u kalouse ušatého ve Slovinsku. Během mimohnízdního období bylo zastoupení hraboše nižší než v hnízdním období, ale pouze v letech, kdy byla abundance hraboše na lovištích vysoká.

Během mimohnízdního období se složení potravy může výrazně měnit v závislosti na klimatických faktorech. V průběhu zimního období byla například u poštolky obecné ve Varšavě prokázána negativní korelace mezi teplotou a zastoupením ptáků v potravě (Żmihorski & Rejt 2007). Podobné výsledky uvádí také **Riegert & Fuchs (2011) – příloha III**, kdy bylo zimování urbánních poštolek ovlivněno sněhovou pokrývkou. U samců, kteří během tuhé zimy neopustili svá nocoviště, byl zjištěn pozitivní korelační vztah mezi zastoupením ptáků a negativní vztah pro zastoupení hraboše v potravě a počtem dnů se sněhovou pokrývkou. Také u kalouse ušatého v Sofii byl v průběhu zimního období zjištěn postupný nárůst zastoupení hraboše a ostatních drobných savců s maximem v lednu a postupným poklesem jejich zastoupení v jarních měsících. Zastoupení ptáků vykazovalo opačný trend (Milchev et al. 2003). U populací kalouse ve střední Evropě může být situace odlišná, v potravě zimující populace byl v prosinci (oproti březnu) zaznamenán snížený podíl hrabošů a zvýšený podíl myšic, ale podíl ptáků byl stabilně nízký (Dziemian et al. 2012).

1.4.3. Vliv loveckého biotopu

Potravní nabídka se může výrazně lišit mezi různými biotopy, což se odráží ve složení potravy ptačích predátorů (např. Casagrande et al. 2008). Skotské poštolky obecné, které lovily na pastvině, měly vyšší diverzitu v potravě v porovnání s jedinci, kteří lovili ve školkách pro mladé jehličnany. Poštolky, které lovily na pastvině, měly v potravě zvýšený podíl ptáků a nižší podíl hraboše (Village 1982). V potravě lesní populace puštíka obecného v Polsku byl ve srovnání s populací ze zemědělské krajiny zjištěn zvýšený podíl hmyzožravců, norníků a obojživelníků (Romanowski & Żmihorski 2009). Nejvýraznější rozdíly můžeme sledovat ve složení potravy populací z urbánního prostředí a okolní krajiny. Poštolky obecné ve velkých městech mohou mít v potravě zvýšený podíl ptáků, díky velké vzdálenosti z centra města na periferní loviště (Fairley & McLean 1965, Bozsko 1967, Beichle 1980, Yalden 1980, Darolová 1989, Plesník 1992, Romanowski 1996, Piatella et al. 1999, Kübler et al.

2005, Sumasgutner et al. 2013). Podobný trend byl zjištěn také u urbánní populace kalouse ušatého (Kiat et al. 2008) a puštíka obecného (Grzedzicka et al. 2013). V menších městech může být zastoupení ptáků v potravě poštolek a kalousů srovnatelné s mimoměstskými populacemi, díky malé vzdálenosti na periferní loviště (**Riegert et al. 2009 – příloha IV**). Nicméně, i v menších městech dochází ke zvýšení celkové diverzity v potravě (Boratynski & Kasprzyk 2005).

1.4.4. Vliv použité metody

Reálné složení potravy se může lišit od zjištěných údajů díky použití různých metod. V historii popisu potravního spektra ptačích predátorů byla využita celá řada metodických přístupů. Mezi základní patří (1) přímé sledování, (2) použití automatizované videotechniky, (3) rozbor zbytků potravy (4) rozbor obsahu trávicího traktu a (5) rozbor vývržků (Mlíkovský 1998, Marti et al. 2007). Každá z uvedených metod má své výhody i nevýhody, a proto se obecně doporučuje kombinovat více metod současně (např. Rutz 2003, **Zárybnická et al. 2011 – příloha X**).

Rozbor vývržků ze stávanišť, nocovišť nebo přímo z hnízd je tradiční metoda, kterou autoři využívali k popisu potravního spektra již v první polovině minulého století (např. Errington 1930). Tato metoda je obecně vhodnější pro studium potravního spektra sov. Oproti denním dravcům sovy stráví menší podíl kostí, což je dáno nižším pH v obsahu žaludečních šťáv dravců (Duke et al. 1975, Cummings et al. 1976). Zároveň mají sovy tendenci méně často dekapitovat kořist, což umožňuje uchování znaků na lebce (Errington 1932, ale např. **Zárybnická et al. 2011 – příloha X**), které jsou klíčové k determinaci u všech skupin obratlovců. Další nevýhodou je, že u velkých kořistí je navíc stanovení počtu ulovených jedinců problematické. Není například zřejmé, zda predátor nevyužíval kořist opakovaně nebo zda nepozřel pouze část kořisti a zbytek ponechal na místě (Marti et al. 2007). V neposlední řadě lze uvést fakt, že zdaleka ne všechny vývržky jsou většinou nalezeny, obzvláště pokud se jedná o materiál sbíraný mimo hnízdo. Správné přiřazení vývržku ke studovanému druhu může být také problematické, pokud jsou vývržky sbírány bez předchozích pozorování na lokalitě a jsou určovány pouze na základě rozměrů, tvaru a dalších charakteristik. Klíče k určování vývržků jsou sice dostupné (např. Mlíkovský 1998, Burton 1984), sami autoři však nedoporučují determinaci bez ověření druhové příslušnosti na základě pozorování (Marti et al. 2007). Vývržky jsou nejčastěji zpracovány pomocí roztoku NaOH (Schueler 1972). Mezi nesporné výhody rozboru vývržků patří poměrně snadný a rychlý sběr velkých vzorků bez následného rušení predátorů (Marti et al. 2007). Vývržky lze navíc sbírat v jakémkoliv ročním období, a pokud je sběr vývržků spojen s individuálním značením a následným pozorováním, lze analyzovat také individuální variabilitu ve složení potravy (**Riegert & Fuchs 2011 – příloha III**).

Rozbor zbytků potravy na trhaništích nebo i na hnízdišti často vhodně doplňuje rozbory vývržků (např. **Riegert et al. 2007 – příloha I**, **Riegert et al. 2009 – příloha IV**). Nevýhodou je, že větší a nápadnější položky déle vydrží odolávat klimatickým vlivům a jsou lépe zjistitelné. Díky tomu může dojít k nadhodnocení velkých položek. Řešením tohoto problému jsou pravidelné odběry v kratších intervalech (Marti et al. 2007). Metoda je vhodná především u druhů, které se z velké části živí ptačí kořistí, neboť opeření je ve vývržcích často degradováno nebo zcela chybí díky tomu, že kořist může být před pozřením z velké části zbavena opeření (např. Rutz 2003). Během kombinování materiálu z rozboru vývržků je třeba vzít v úvahu maximální možný počet položek z jednotlivých částí těla kořisti, aby nedocházelo k duplikacím položek (Marti et al. 2007).

Rozbor obsahu žaludku člověkem usmrcených jedinců byl používán především ve starších studiích (např. Lovari 1974). Dnes se tato metoda využívá pouze v případě, že existuje jiný zdroj uhynulých jedinců (Overskaug et al. 1995, Adánez 2000). Alternativou může být získání potravy z trávicího traktu bez usmrcení zvířete, například masáží volete u dravců (Errington 1932). Nicméně, tyto metody jsou na znatelném ústupu (Marti et al. 2007).

Přímé sledování jedinců je časově nejnáročnější metodou, kterou lze využít během lovu (Rijnsdorp et al. 1981) nebo při donášení kořisti na hnízdo (Dykstra et al. 2003, Nodeland 2013). Pomocí této metody lze v potravě detekovat i položky, které jsou obtížně zjistitelné jinými metodami. V potravě puštíka obecného bylo například možné přímým sledováním stanovit podíl žížal, které nebyly zjištěny rozborem vývržků (Southern 1969). Metoda je nevhodná pro studium potravního spektra druhů s noční aktivitou a druhů, které hnízdí v uzavřených dutinách. Metodu lze také obtížně aplikovat v průběhu mimohnízdního období, kdy se predátoři v krajině pohybují nepředvídatelně (Marti et al. 2007). Někteří autoři metodu kombinovali se zajištěním mláďat na hnízdě (Petersen & Keir 1976) nebo zabráněním dospělým ptákům předat potravu mláďatům, například umístěním mláďat do klece (Sulkava 1964).

V dnešní době se často používají automatizované metody, které nevyžadují přítomnost pozorovatele. Jedná se o fotopasti nebo kamery umístěné v blízkosti hnízda (např. Lewis et al. 2004, López-López & Urios 2010, **Zárybnická et al. 2011 – příloha X**, Navarro-López et al. 2014, García-Saldago et al. 2015). Výhodou automatizovaných systémů je možnost kontinuálního záznamu z prakticky celého hnízdního období a to včetně nočního snímání (např. Huckschlag 2008) za minimálního rušení hnízdícího páru. Nevýhodou jsou především vysoké požadavky na technické vybavení a finanční pokrytí projektu (např. Zárybnická et al. 2016).

Zajímavým doplňkem tradičně používaných metod může být použití analýzy stabilních izotopů (Hobson 2011). Studie potravy orla jestřábího (*Aquila fasciata*) však prokázala, že pomocí této metody nedošlo k výraznému rozšíření potravního spektra, které bylo zjištěno pomocí vývržků. Autoři navíc uvádějí některé nevýhody této metody, zejména nutnost předchozí znalosti potravního spektra studovaného druhu (Resano-Mayor et al. 2014).

V literatuře existuje hojná dokumentace k porovnání některých z uvedených metod u různých druhů ptačích predátorů. Obecně lze říci, že (1) rozbor vývržků obvykle umožní determinovat více položek do nižších taxonů než ostatní metody, zejména v porovnání s přímým sledováním (*Circus cyaneus*: Redpath et al. 2001) nebo záznamem z kamerových systémů (rod *Accipiter*: Huang et al. 2006, García-Salgado et al. 2015; rody *Accipiter* a *Buteo*: Tornberg & Reif 2007). Totéž platí pro porovnání rozboru zbytků potravy se záznamem z kamerového systému. U jestřábů lesních (*Accipiter gentilis*) byl za použití kamerového systému podhodnocen podíl velkých ptáků a nadhodnocen podíl malých ptáků (Sveen 2006). Uspokojivé výsledky v tomto ohledu přinesla u stejného druhu kombinace rozboru zbytků potravy s dohledáváním telemetricky označených jedinců (Rutz 2003). U nočních druhů predátorů nejsou metody přímého sledování aplikovatelné. Pomocí kamerového systému bylo u sýce rousného zjištěno, že (2) analýza vývržků výrazně podhodnotila celkový počet položek v potravě, pravděpodobně díky časté dekapitaci drobných savců před donesením na hnízdo (**Zárybnická et al. 2011 – příloha X**). Porovnání rozboru vývržků a zbytků potravy ukázalo, že (3) ve zbytcích potravy jsou podhodnoceny malé typy kořisti (*Falco peregrinus*: Oro & Tella 1995). Zároveň bývá (4) zastoupení ptáků stanovené rozborem zbytků potravy vyšší v porovnání s rozborem vývržků a opačný trend platí pro zastoupení savců (např. orel skalní *Aquila chrysaetos*: Seguin et al. 1998, orel iberský *Aquila adalberti*: Sánchez et al. 2008).

1.4.5. Vliv kompetice a výběru loveckých biotopů

V rámci syntopického výskytu různých ptačích predátorů specializovaných k lovu stejné kořisti nutně dochází k překryvu potravních nik. Existence přímé či nepřímé (exploatační) kompetice často vede k rozšíření potravní niky (např. Steenhof & Kochert 1988, Garcia & Arroyo 2005, Skierczyński 2006, Tornberg & Haapala 2013). Například u syntopických kalousů ušatých a sov pálených v Polsku v potravě převládali hraboši (kalous ušatý 91%, sova pálená 67%), nicméně potrava sovy pálené vykazovala vyšší diverzitu především díky vysokému zastoupení hmyzožravců (31%, Hetmański et al. 2008). Skierczyński (2006) z Polska uvádí výrazný překryv potravních nik tří studovaných druhů ptačích predátorů. K největším překryvům docházelo mezi kání lesní a poštolkou obecnou (Pianka B index 0,87), poštolkou obecnou a kalousem ušatým (0,85) a nejmenší překryv byl zjištěn mezi kání lesní a kalousem ušatým (0,74). Ze všech tří druhů měl kalous ušatý nejužší potravní niku (kalous ušatý B = 2,41; poštolka obecná B = 5,35; káně lesní B = 7,45). V severních oblastech jsou potravní niky všech predátorů poměrně úzké díky omezenému výběru typu kořisti (B index, poštolka obecná 1,95; kalous ušatý 1,21; sýc rousný 1,95) a dochází ke značným překryvům ve složení potravy (Korpimäki 1985a). Nejvýraznější překryv byl zjištěn mezi kalousem ušatým a kalousem pustovkou (Pianka index 0,90) a sýcem rousným (0,68), překryvy ve složení potravy poštolky obecné a různých druhů sov nebyly tak výrazné (kalous ušatý 0,49; kalous pustovka 0,40; sýc rousný 0,57).

K méně výrazným překryvům ve složení potravy dochází mezi spíše oportunistickým puštíkem obecným a potravními specialisty. V Itálii byla například v potravě puštíka obecného zjištěna celkově širší potravní nika než u kalouse ušatého a překryv potravních nik byl minimální zejména u lesních populací (Pianka index 0,16). Populace z více otevřené krajiny vykazovaly výraznější překryv nik (0,64), což bylo pravděpodobně způsobeno výběrem podobných loveckých biotopů (Capizzi & Luiselli 1998). Zajímavé výsledky uvádí Hirons (1984) z intenzivně spásaných lokalit v Anglii. Během studia potravního spektra poštolky obecné a puštíka obecného zjistil celkově nízké zastoupení hraboše a norníka ve vývržcích. Podíl jednotlivých složek bohužel nebyl stanoven z celkového počtu determinovaných položek, ale byl vyjádřen podílem vývržků, ve kterých se daná složka vyskytovala. Nicméně, porovnáním potravních spekter obou druhů se syntopickým výskytem je zřejmé, že v potravě poštolky obecné se často vyskytovali drobní savci různých rodů (zejména *Microtus*, *Micromys*, *Sorex*), ještěrky (*Lacerta*) a ptáci. V potravě puštíka se z drobných savců vyskytovali nejčastěji myšice, vzácněji také hraboši a norníci. Významnou složku u obou druhů představoval hmyz, především brouci a u poštolek také motýli. Zvýšený podíl hmyzu v potravě byl pravděpodobně způsoben nízkou abundancí hraboše i norníka na lovištích díky intenzivnímu managementu (Hirons 1984).

Během let s různou potravní nabídkou lze navíc sledovat výrazné změny v překryvu nik a šíři potravní niky ptačích predátorů. U finských kalousů ušatých a poštolek obecných je dokumentován velký překryv nik (80-95%), který byl ještě výraznější v letech s vysokou abundancí hraboše na lovištích (Korpimäki 1987a). V letech s nízkou abundancí hraboše došlo k rozšíření potravních nik u obou druhů, a to zejména u sousedících párů poštolek a kalousů. Alternativní kořistí byli u poštolky v letech pesima hraboše zejména hmyz a ptáci, u kalouse se jednalo především o rejsky a norníky (Korpimäki 1987a). K podobným výsledkům dospěl také **Riegert et al. (2009 – příloha IV**) v České republice, kde u městské populace poštolek a kalousů dominoval v potravě obou druhů hraboš polní. V letech s nízkou abundancí hraboše na lovištích došlo ke zvýšení zastoupení ostatních složek potravy. Zatímco u kalousů ušatých se v potravě zvýšilo zastoupení myšic rodu *Apodemus*, u poštolek došlo ke zvýšení zastoupení hmyzu. Přítomnost hmyzu v potravě poštolky lze vysvětlit denní aktivitou a zrakovou orientací při výběru kořisti (Village 1990). Hmyz se v potravě poštolek navíc objevuje po neúspěšném útoku na drobné savce (**Riegert & Fuchs 2004 – příloha VII**). U kalouse s noční aktivitou a sluchovou orientací během lovu lze absenci hmyzu v potravě očekávat. Vhodnou alternativní kořistí je tedy v tomto případě myšice, která svou aktivitu omezuje do nočních hodin (Halle & Stenseth 2000). V rámci města se složení potravy mezidruhově lišilo. U poštolek lovících na periferii (**Riegert et al. 2007a – příloha XI**) nebyl zjištěn signifikantní vztah mezi zastoupením hraboše v potravě a vzdáleností hnízda od centra města. Naproti tomu, u kalouse lovícího běžně v zástavbě (**Lövy & Riegert 2013 – příloha XII**) vzrůstal podíl hraboše v potravě s rostoucí vzdáleností hnízda od centra (**Riegert et al. 2009 – příloha IV**).

1.4.6. Vliv věku a individuální variability

Lovecké schopnosti jedince se vyvíjí v průběhu života (např. Csermely & Sponza 1995) a díky tomu se může výrazně měnit i složení potravy. Zlepšení loveckých schopností má adaptivní význam, například u maďarských puštíků obecných docházelo v průběhu života ke zlepšení schopnosti ulovit alternativní kořist, což umožnilo starším jedincům úspěšně vyvést vyšší počet mláďat (Sasvári et al. 2000). Costantini et al. (2005) naopak uvádí meziročně konzistentní rozdíly ve složení potravy mezi sousedícími páry hnízdících poštolek, které sdílejí stejná loviště. Podobné výsledky uvádí Manganaro et al. (1990) u puštíků obecných hnízdících ve stejném parku v Římě.

Individuální rozdíly byly zjištěny také u zimujících samců poštolek v urbánním prostředí. Samci, kteří měli v potravě vyšší zastoupení ptáků, neopouštěli svá nocoviště ani během tuhé zimy. U těchto samců bylo navíc prokázáno, že podíl ptáků v potravě byl pozitivně korelován s počtem dnů se sněhovou pokrývkou (**Riegert & Fuchs 2011 – příloha III**). Schopnost udržet si nocoviště v průběhu zimy může přinášet adaptivní výhodu pro následující reprodukční období. Samci, kteří jsou na hnízdišti přítomni brzy na jaře, snáze získají partnera (Village 1985) a časně hnízdící páry mají zároveň vyšší reprodukční potenciál (Beukeboom et al. 1988, Dijkstra et al. 1982, Meijer et al. 1990, Korpimäki & Wiehn 1998). Na stejné studované lokalitě bylo zároveň v průběhu hnízdního období zjištěno, že hmotnost samice negativně koreluje se vzdáleností hnízda od centra města. U samců nebyl zjištěn žádný trend (**Riegert et al. 2010 – příloha II**). Samice poštolky obecné si přednostně vybírají menší samce pro jejich vyšší lovecké kvality (Hakkarainen et al. 1996). Lepší manévrovací schopnosti menších samců (s kratšími křídly) pravděpodobně zvyšují schopnost ulovit kořist i v troficky nepříznivém období (Hakkarainen & Korpimäki 1995). Jelikož se nepotvrdilo, že by reprodukční úspěšnost a hmotnost samců vykazovala trend se vzdáleností hnízda od centra města, je obtížné tyto výsledky jednoduše interpretovat na studovaném gradientu urbanizace (**Riegert et al. 2010 – příloha II**). Nesporně by bylo zajímavé tyto výsledky ověřit v rámci většího města.

1.5. Prostorová aktivita predátorů a výběr loveckých biotopů

Rozloha domovského či loveckého okrsku vykazuje značnou variabilitu na vnitrodruhové i mezidruhové úrovni a je pozitivně korelována s tělesnou hmotností. Predátoři mají navíc okrsky obecně větší než omnivorní a herbivorní druhy (Schoener 1968). U ptačích predátorů rozlohu okrsku z velké míry určuje složení potravy, druhy s vyšším podílem ptáků v potravě mají větší okrsky (Peery 2000). V rámci domovských okrsků nebývá využití jednotlivých biotopů rovnoměrné, neboť ne všechny biotopy v rámci okrsku jsou lovecky vhodné (např. Sodhi & Oliphant 1992, Marzluff et al. 1997, Selås & Rafoss 1999, Rutz 2006, Vlachos et al. 2014). Prostorové využití okrsku samcem a samicí vykazuje většinou značné překryvy, nicméně může docházet k částečné separaci lovišť v rámci hnízdícího páru (Craig et al. 1988, Village 1990).

Rozloha domovských a loveckých okrsků se mění v závislosti na distribuci potravních zdrojů (např. Kouba et al. 2017) a rozmístění jedinců v přírodě. U poštolky obecné ve Skotsku byla rozloha domovského okrsku negativně korelována s abundancí hraboše mokřadního (Village 1982). Nicméně, rozlohu okrsku (1-5 km^2) zároveň výrazně ovlivnila kompetice mezi sledovanými jedinci. V průběhu zimního období byly okrsky hájeny jedinci, v průběhu hnízdního období bylo celým párem hájeno pouze nejbližší okolí hnízda. Díky tomu docházelo v hnízdním období k největším překryvům domovských okrsků (Village 1982), což souvisí také ze zvýšenou vnitrodruhovou agresivitou v mimohnízdním období (Wicklund & Village 1992).

V urbánním prostředí je situace v některých ohledech odlišná. Páry hnízdící v centru měst prakticky nemají možnost hájit loviště, která se nacházejí na periferii města. V souladu s předchozím zjištěním pak páry hájí v hnízdním období jen nejbližší okolí hnízda, ale rozloha loveckých okrsků (zejména samců, kteří zajišťují většinu přinášené potravy) se nápadně zvětšuje (až 25 km^2), díky ještě výraznějším překryvům než u populace ve volné krajině. Zároveň pro urbánní prostředí platí, že lovecké okrsky jedinců z centra jsou několikanásobně větší než okrsky jedinců z periferie města díky kompetici s rezidentními páry na periferních lovištích, která vede k častému střídání lovišť (**Riegert et al. 2007a – příloha XI**). Také u kalouse ušatého mohou být lovecké okrsky urbánních párů větší než okrsky párů z volné krajiny (Henrioux 2000). V případě urbánních kalousů však nejsou rozdíly tak výrazné jako u poštolek, neboť kalousi běžně loví v zástavbě města (např. Getz 1961, **Lövy & Riegert 2013 – příloha XII**). Poštolky i kalousi využívají k lovu převážně otevřené biotopy (např. Village 1990, Henrioux 2000), ale existují mezi nimi rozdíly ve výběru konkrétních stanovišť. U městských poštolek byla zjištěna výrazná preference ruderálních biotopů, které se hojně vyskytují na periferii města (**Riegert et al. 2007 – příloha I**). Kalousi na téže lokalitě preferovali porosty stromů a především jejich okraje, které zde představují významná refugia drobných savců (**Lövy & Riegert 2013 – příloha XII**). K podobným výsledkům dospěli Galeotti et al. (1997), kteří u kalousů v otevřené krajině zaznamenali preferenci biotopů spojených se systémem dopravy (stromořadí, náspy a okraje silnic).

Také u lesních populací ptačích predátorů lze nalézt výrazné rozdíly ve využití různých biotopů. Rozloha domovských okrsků samců sýce rousného ve Finsku se měnila v závislosti na složení biotopů. S vyšším zastoupením smrkových porostů klesala rozloha domovských okrsků. Autoři tento jev vysvětlují celkově vyšší potravní nabídkou a lepším úkrytem před predátory ve smrčinách v porovnání s borovými lesy a mýtinami (Santageli et al. 2012). Mladé rozvolněné smrčiny, byť nepůvodního druhu smrku pichlavého *Picea pungens*, byly vhodným biotopem k lovu také u české populace sýce rousného (**Zárybnická et al. 2015a – příloha XIII**). V blízkém okolí obsazených budek (< 25 m) byl zaznamenán vyšší podíl smrku pichlavého a smrku ztepilého než u budek, které nebyly sýcem obsazeny. Porosty smrku pichavého na studované lokalitě představují významný lovecký biotop pro adultní sýce rousné, což bylo dokumentováno pozitivním korelačním vztahem mezi zastoupením myšic rodu *Apodemus* v potravě a podílem smrku pichlavého v širším okolí budek (< 750 m). Porosty smrku ztepilého jsou kompaktnější a pravděpodobně slouží spíše vyvedeným mláďatům jako úkryt před predátory než jako lovecký biotop adultních jedinců (**Zárybnická et al. 2015a – příloha XIII**).

1.6. Lovecké chování a úspěšnost lovu

Prakticky všichni ptačí predátoři využívají více loveckých taktik. Lovecké chování může být značně flexibilní v závislosti na nabídce potravy, typu loveckého biotopu, věku a pohlaví jedince (např. Schipper et al. 1975, Collopy & Bildstein 1987). U nočních druhů je studium loveckého chování obtížně uchopitelné. Díky tomu bylo v rámci studovaných druhů nejvíce studií věnováno loveckému chování poštolky obecné.

1.6.1. Lovecké úsilí

Celkové lovecké úsilí ovlivňuje kombinace různých faktorů, zejména nabídky potravy, počtu mláďat na hnízdě a rozdělení úloh v rámci páru. Energetická náročnost letu je obecně pozitivně korelována s hmotností jedince (Masman & Klaasen 1987). U samic poštolky obecné, které jsou v průměru o 20% těžší než samci, byla zjištěna signikantní negativní korelace mezi denním výdajem energie a podílem času, po který byly pozorovány na lovištích. Samice byly zároveň na lovištích pozorovány méně často než samci (Jönsson et al. 1996). Autoři se domnívají, že samice pravděpodobně nebyly často pozorovány z důvodu loveckých aktivit pro vlastní potřebu nebo neochotou lovit za nepříznivých trofických podmínek. U samců tento vztah nebyl signifikantní, neboť samci poštolek zajišťují většinu potravy donesené na hnízdo (Jönsson et al. 1996). Výsledky jsou v souladu se studií z urbánního prostředí ve střední Evropě (**Riegert et al. 2007 – příloha I**), kdy samice byly na lovištích pozorovány s mnohem nižší frekvencí než samci. Frekvence výskytu samic na lovištích se zvýšila pouze v letech s vyšší abundancí hraboše. Na rozdíl od severských populací ve Finsku (např. Wiehn & Korpimäki 1997), samci poštolek ve střední Evropě reagovali na sníženou nabídku hlavní kořisti zvýšením loveckého úsilí (**Riegert et al. 2007 – příloha I**). Významnou roli loveckého úsilí samce pro úspěšné vyvedení mláďat dokládají také experimentální studie. U hnízd poštolek ve Finsku, kde byla mláďata experimentálně přikrmována, došlo ke snížení loveckého úsilí samic, ale u samců nebyl tento rozdíl signifikantní (Wiehn & Korpimäki 1997).

Rozdíly v loveckém úsilí mezi hnízdy s různým počtem mláďat jsou dokumentovány pomocí experimentů, kdy byla do některých hnízd přidána mláďata a z jiných hnízd byla naopak mláďata odebrána (shrnuto v Dijkstra et al. 1990). U hnízd, kde bylo mládě přidáno, byl zaznamenán signifikantně vyšší podíl třepotání u obou rodičů v porovnání s hnízdy, kde byl počet mláďat redukován (samice a samci) nebo i s kontrolní skupinou (pouze samci). Zároveň došlo ke zvýšené frekvenci příletu na hnízdo s kořistí (Dijkstra et al. 1990). V přirozených podmínkách nejsou rozdíly tak nápadné. U finských poštolek nebyl zjištěn výrazný rozdíl v loveckém úsilí (podílu třepotání) rodičů u hnízd s různým počtem mláďat, ale s rostoucím počtem mláďat se zvyšovala frekvence příletů s kořistí na hnízdo (Tolonen & Korpimäki 1994). Míru loveckého úsilí může v rámci areálu rozšíření výrazně ovlivnit také poměr mezi délkou dne a noci. U finských sýců rousných byla délka doby strávená lovem během jedné noci výrazně kratší v porovnání s populací ve střední Evropě (Zárybnická et al. 2012).

1.6.2. Lovecké techniky a úspěšnost lovu

Sovy většinou využívají lov z posedu (puštík obecný - Overskaug et al. 1995, sýc rousný - Korpimäki & Hakkarainen 2012), u kalouse ušatého je častým způsobem lovu nízký let nad vegetací, ale může využívat různé lovecké techniky včetně lovu z posedu (např. Wijnandts 1984). Poštolky obecné využívají více loveckých technik, které se liší energetickou náročností a průměrnou úspěšností lovu (Rijnsdorp et al. 1981). Lze je rozdělit do dvou základních kategorií - lov z posedu a lov za letu. Energeticky nejnáročnějším způsobem lovu je u poštolek třepotání na místě (Pettifor 1983), které dravci umožňuje sledovat větší plochu loviště najednou (Rijnsdorp et al. 1981). Zároveň byla u třepotání zjištěna vyšší lovecká úspěšnost za jednotku času v porovnání s ostatními loveckými technikami (kroužení, lov z vyvýšeného posedu a ze země), zejména při lovu drobných savců (Rijnsdorp et al. 1981, Masman et al. 1988). Použití jednotlivých loveckých technik se může výrazně lišit za různých trofických podmínek (**Riegert et al. 2007 – příloha I**), v průběhu roku i dne a za různých klimatických podmínek (Rijnsdorp et al. 1981, Shrubb 1982, Village 1983).

Poštolky v Nizozemí pravidelně využívaly třepotání během nejvyšší aktivity hraboše, což vedlo ke zvýšené lovecké úspěšnosti (Rijnsdorp et al. 1981). Také u populace ve střední Evropě docházelo ke zvýšenému využití třepotání během let, kdy byla abundance hraboše na lovištích vysoká (**Riegert et al. 2007 – příloha I**). Poštolky využívají třepotavý let především v hnízdní sezóně, kdy se zvyšují energetické nároky díky krmení mláďat. Existují však výrazné rozdíly mezi oběma pohlavími. Samice využívají třepotavý let obecně v menší míře a častěji loví z posedu, zejména v hnízdním období (Village 1983).

U poštolek je navíc běžné, že ulovenou potravu uschovají pro pozdější konzumaci (Rejt et al. 2000), což vede k optimalizaci příjmu potravy během troficky nepříznivých období. Obvykle je menší potrava pozřena, středně velká potrava donesena na hnízdo a větší položky jsou uschovány (Masman et al. 1986, Korpimäki et al. 1994). K podobným výsledkům dospěl také Korpimäki (1987) u sýce rousného, kde uschovaná potrava sloužila k překlenutí krátkodobě troficky nevýhodných podmínek, např. při vysoké sněhové pokrývce. U párů, v jejichž blízkosti hnízdil kompetitor, byly zásoby potravy navíc menší v porovnání s páry, které hnízdily bez přítomnosti kompetiora což bylo zřejmě způsobeno podobnou potravní nabídkou na lokální úrovni (Korpimäki 1987). Uschovávání potravy je typické především pro ptačí predátory v hnízdní sezóně. V mimohnízdním období bylo pozorováno pouze u menších druhů, které se často vyskytují v chladných oblastech. Z dalších druhů sov je to především kulíšek nejmenší *Glaucidium passerinum* (Korpimäki & Hakkarainen 2012).

Klimatické podmínky mají značný vliv na výběr lovecké techniky. Poštolka obecná využívá třepotavý let především za větrného počasí (Rijnsdorp et al. 1981, Village 1983, Riegert et al. 2007b). Energetické výdaje na třepotavý let jsou výrazně nižší za čerstvého větru (4-12 m/s, Rijnsdorp et al. 1981), kdy poštolka doslova visí nad terénem bez pohnutí křídel (Village 1983). Za vyšší nebo nižší rychlosti větru než je optimum poštolky méně ochotně třepotají (Rijnsdorp et al. 1981). Také teplota ovlivňuje způsob lovu, poštolky v chladnějším období využívají spíše lov z posedu, což ale pravděpodobně souvisí s výše uvedenými rozdíly v hnízdním a mimohnízdním období (Village 1983). Efektivitu třepotavého letu negativně ovlivňují i další klimatické faktory, například déšť a mlha (Rijnsdorp et al. 1981). Samotná míra použití třepotavého letu výrazně ovlivňuje jeho opětovné použití. Poštolky po neúspěšném útoku z třepotavého letu obvykle pouze změní místo kde často opět třepotají (Rijnsdorp et al. 1981, **Riegert et al. 2007 – příloha I**).

Klimatické faktory výrazně ovlivňují také loveckou aktivitu sov. U telemetricky sledovaných kalousů ušatých byla zjištěna nejvyšší lovecká aktivita za nocí, kdy nebyly žádné srážky, mlha nebo krupobití. Aktivita kalousů za sněžení byla srovnatelná s optimálními podmínkami, což bylo pravděpodobně způsobeno tím, že kalousi během lovu využívají nejčastěji sluch (Wijnandts 1984). Hluk, který je vedlejším produktem některých klimatických jevů, je tedy společně s nabídkou potravy hlavním faktorem determinujícím loveckou aktivitu a úspěšnost lovu sov. U kalouse ušatého a kalouse pustovky (*Asio flammeus*) klesala schopnost lokalizovat kořist s experimentálně zvýšeným hlukem v prostředí (Senzaki et al. 2016). U sýce amerického (*Aegolius acadicus*) bylo zjištěno, že s každým zvýšením hluku o jeden decibel došlo ke snížení lovecké úspěšnosti o 8% (Mason et al. 2016). V potravě polských kalousů ušatých klesalo za deštivých podmínek zastoupení myšic a vzrůstal podíl hraboše. Autoři tyto výsledky však vysvětlují především vlivem klimatických podmínek na aktivitu kořisti (Romanowski & Żmihorski 2008).

V neposlední řadě lze uvést vliv individuálních charakteristik na úspěšnost lovu. U samců poštolky obecné a sýce rousného byl zjištěn negativní vztah mezi loveckou úspěšností a tělesnými rozměry, především délkou křídla v poměru k hmotnosti (Hakkarainen & Korpimäki 1995, Hakkarainen et al. 1996). U sýce rousného bylo navíc zjištěno, že tento vztah byl signifikantní pouze v letech nízké abundance hlavní kořisti (Hakkarainen & Korpimäki 1995).

1.7. Reprodukční parametry

1.7.1. Velikost snůšky a hnízdní úspěšnost

Reprodukční parametry studovaných ptačích predátorů vykazují značnou variabilitu na geografické škále. Dále jsou ovlivněny řadou proximátních (Meijer et al. 1990) i ultimátních (Daan et al. 1990) faktorů, například potravní nabídkou, kvalitou a stářím jedince, načasováním hnízdění, klimatickými faktory, typem a umístěním hnízda (Plesník 1992) nebo hnízdní denzitou (Salvati 2001).

1.7.1.1. Geografická variabilita

Velikost snůšky obvykle vzrůstá se zeměpisnou šířkou (např. poštolka obecná - Carrillo & González-Dávila 2009, sýc rousný - Korpimäki & Hakkarainen 2012). U denních predátorů, jakým je poštolka obecná, je tento trend pravděpodobně způsoben prodlužující se délkou dne a tedy prodlužující se dobou, kdy je možné lovit kořist (Carrillo & González-Dávila 2009). Samotná délka dne však nevysvětluje celou variabilitu a vliv ostatních faktorů není zanedbatelný, zejména poměr mezi evapotranspirací v hnízdní sezóně a předcházející zimě (Carrillo & González-Dávila 2010). U sov naopak dochází ke zkracování noci se vrůstající zeměpisnou šířkou. Větší snůšky u sýce rousného v severních oblastech jsou tedy spíše vysvětlovány celkově vyšší potravní nabídkou v hnízdním období (Korpimäki & Hakkarainen 2012).

Datum snesení prvního vejce u poštolky obecné roste o 6 dnů s každou zvýšenou zeměpisnou šířkou o 10° (Carrillo & González-Dávila 2009). Délka fotoperiody v hnízdním období, která je pozitivně korelována se zeměpisnou šířkou, však nevysvětluje tuto variabilitu jako jediný faktor. Poštolky hnízdí dříve v oblastech s vyššími zimními a jarními teplotami a nižším jarním úhrnem srážek (Carrillo & González-Dávila 2010). Nicméně i zde lze očekávat korelační vztahy se zeměpisnou šířkou. Počet vyvedených mláďat u sýce rousného je pozitivně korelován se zeměpisnou šířkou (Korpimäki & Hakkarainen 2012). U poštolky obecné tento vztah nebyl prokázán, pravděpodobně díky kombinaci vlivu dalších faktorů (Carrillo & González-Dávila 2009).

1.7.1.2. Vliv potravní nabídky

Potravní nabídka je jedním z hlavních faktorů, které ovlivňují reprodukční parametry na lokální úrovni (např. Korpimäki 1989, Dijkstra et al. 1990, Wiehn & Korpimäki 1997). S rostoucí potravní nabídkou na lovištích je obvykle pozitivně korelována velikost snůšky a počet mláďat na hnízdě (více druhů - Lehikonen et al. 2011; sýc rousný - Korpimäki 1987b; kalous ušatý - Korpimäki 1992, Village 1981; poštolka obecná - Korpimäki & Wiehn 1998, **Riegert et al. 2007 – příloha I**, puštík obecný - **Luka & Riegert in press – příloha VI**). Vzhledem k tomu, že je potravní nabídka obvykle korelována se složením potravy (kap. 1.4.1.), byl u studovaných druhů často zjištěn pozitivní vztah mezi zastoupením hlavní kořisti v potravě a reprodukčními parametry (např. sýc rousný - **Zárybnická et al. 2013 – příloha V**; kalous ušatý - Sergio et al. 2008; puštík obecný - Roulin et al. 2009, **Luka & Riegert in press – příloha VI**). Nicméně, hlavní kořisti se mohou lišit s geografickou pozicí populace. Zatímco u sýce rousného v severních oblastech se jedná o hraboše rodu *Microtus* a norníky rodu *Myodes* (Korpimäki 1987b), u populace ve střední Evropě to jsou především myšice rodu *Apodemus* (**Zárybnická et al. 2013 – příloha V**, **Zárybnická et al. 2015 - VIII**). Různými způsoby tak mohou obě populace docílit podobné míry reprodukce (Zárybnická et al. 2009).

U ptačích predátorů se vyvinuly některé mechanismy, které mohou zmírnit negativní vliv nedostatku potravy na míru reprodukce. Jedním z nich je zvýšení asynchronity líhnutí mláďat za současného snížení velikosti snůšky (brood reduction hypothesis, Lack 1954). U finské populace sýce rousného byla v období nedostatku hraboše zjištěna nižší míra mortality u více asynchronních snůšek. Díky tomu bylo zajištěno, že dojde k úhynu jen některých mláďat a zbytek mláďat bude úspěšně vyveden (Valkama et al. 2002). Zároveň byl v období nedostatku hraboše na hnízdo přinášen překvapivě větší počet těžších kořistí než v letech s vyšší abundancí hraboše (Hakkarainen & Korpimäki 1994). U finských poštolek obecných nebyl podobný mechanismus prokázán, poštolky v letech nedostatku hraboše sice snášely menší snůšky, ale míra asynchronity byla vyšší v letech s vysokou abundancí hraboše (Wiebe et al. 1998).

Dalším mechanismem může být zvýšení loveckého úsilí rodičů. Vzhledem k tomu, že v severních oblastech jsou meziroční rozdíly v abundanci hlavní kořisti až 100 násobné (Wiehn & Korpimäki 1997), je pro ptačí predátory v těchto oblastech prakticky nemožné vyrovnat nedostatek kořisti samotným zvýšeným loveckého úsilí. Ve střední Evropě je situace poněkud odlišná, neboť meziroční kolísání abundance drobných savců nejsou tak výrazná (např. Zárybnická et al. 2015b, Zárybnická et al. 2017a). Díky tomu nejsou například poštolky obecné nuceny v letech s nižší abundancí kořisti výrazně snížit velikost snůšky a zvýšené lovecké úsilí je dostatečným mechanismem k udržení poměrně stabilní míry reprodukce (**Riegert et al. 2007 – příloha I**).

1.7.1.3. Vliv načasování hnízdění

S postupem hnízdní sezóny obvykle klesá velikost snůšky (např. Dijsktra et al. 1982, Village 1986, Beukeboom et al. 1988, Daan et al. 1990, Meijer et al. 1990, Korpimäki & Wiehn 1998, Korpimäki & Hakkarainen 2012, **Luka & Riegert in press – příloha VI**, Zárybnická et al. 2015b). Díky tomu je automaticky celková reprodukční úspěšnost později hnízdících párů výrazně nižší v porovnání s páry, které zahnízdí dříve v sezóně. Mechanismy, které ovlivňují tento trend, zahrnují především fyziologická omezení v hormonální produkci (melatonin, luteinizační hormon, prolaktin) s prodlužující se délkou dne (Meijer et al. 1990), vliv změny potravní nabídky (Village 1986) a kvalitu hnízdících jedinců, která úzce souvisí s kvalitou teritoria (Sergio et al. 2007a).

Vliv potravní nabídky může být komplikovaný, obzvláště v severních oblastech. U sýce rousného ve Finsku se míra korelace mezi velikostí snůšky s načasováním hnízdění výrazně měnila v průběhu pravidelných cyklů hraboše (Korpimäki & Hakkarainen 1991). Během nízké a rostoucí fáze cyklu hraboše tento vztah nebyl signifikantní. V letech s maximální abundancí byl tento vztah silně negativní, ale vykazoval meziroční variabilitu. Pokud byla hnízdícím párům experimentálně přidána potrava, vliv abundance hraboše na lovištích se zcela vytratil (Korpimäki & Hakkarainen 1991). Vliv potravní nabídky na velikost snůšky v kombinaci s načasováním hnízdění byl zjištěn také u finských poštolek, ale míra vztahu se nelišila mezi jednotlivými fázemi populačního cyklu hraboše (Korpimäki & Wiehn 1998). U populace sýce rousného ve střední Evropě byla velikost snůšky a celková míra reprodukce (počet vyvedených mláďat) méně závislá na datu zahnízdění než u finské populace, což bylo způsobeno relativně stabilní nabídkou drobných savců ve střední Evropě, především myšic rodu *Apodemus* (Zárybnická et al. 2015b). Také u populace puštíka obecného ve střední Evropě byl zjištěn pozitivní vztah mezi zastoupením myšic v potravě a mírou reprodukce, ale vztah mezi zastoupením hraboše v potravě a mírou reprodukce nebyl prokázán. Zastoupení myšic v potravě bylo navíc negativně korelováno s načasováním hnízdění (**Luka & Riegert in press – příloha VI**).

Vliv kvality jedince na míru reprodukce je úzce spojen s kvalitou teritoria a oběma výše zmíněnými faktory – potravní nabídka a načasování hnízdění (např. Sergio & Newton 2003, Sergio et al. 2017). Kvalita jedince se navíc mění v průběhu života, starší jedinci mají vyšší reprodukční úspěšnost (Karell et al. 2009) díky jejich rozsáhlejším loveckým zkušenostem (Sasvári et al. 2000), zvyšujícímu se reprodukčnímu potenciálu samic v průběhu života (Newton 1986) nebo časnějšímu zahnízdění starších jedinců (Village 1985). Na základě četných empirických důkazů o kauzálním propojení kvality jedince a teritoria s načasováním hnízdění je možné považovat datum zahnízdění za proměnnou vyjadřující kvalitu jedince (site-dependent model, shrnuto v Sergio et al. 2007a).

1.7.1.4. Vliv ostatních faktorů

Z ostatních faktorů může reprodukční úspěšnost ptačích predátorů ovlivňovat zejména predační tlak, který se liší v rámci větších geografických celků, ale i na lokální úrovni mezi jednotlivými biotopy. Významným predátorem hnízd sýce rousného v Evropě je kuna lesní (*Martes martes*). Predační tlak na hnízda sýce se však výrazně liší v rámci Evropy. Zatímco u finské populace je predace kunou minimální (< 5% hnízd bylo predováno), u české populace představuje významný negativní vliv na počet vyvedených mláďat (cca 25% hnízd bylo predováno). I přes vysoký predační tlak byla celková reprodukční úspěšnost všech párů populace v České republice vyšší než ve Finsku, což bylo způsobeno vyšší hnízdní denzitou sýce v České republice a stabilními potravními podmínkami (Zárybnická et al. 2015b). Míra predace se také může lišit v rámci lokality mezi jednotlivými biotopy. U sýce rousného v Norsku byla predace kunou lesní nejvyšší v uzavřených biotopech (smrkové porosty), kde kuna budky využívala také k odpočinku. Důsledkem toho sýci méně ochotně hnízdili ve smrkových porostech (Sonerud 1985).

Hnízdní preference u sýce rousného se mohou měnit v závislosti na míře potenciálního predačního tlaku v průběhu hnízdní sezóny (**Zárybnická et al. 2017b – příloha XIV**). V okolí budek, které byly predovány, bylo zjištěno vyšší zastoupení listnatých porostů. Zároveň byl u hnízd, která nebyla predována, zjištěn pozitivní vztah mezi zastoupením listnatých porostů v okolí hnízdní budky a načasováním hnízdění. Sýci si tedy na začátku hnízdní sezóny vybírali spíše budky v jehličnatých porostech. Budky v listnatých porostech se stávaly více bezpečnými až po olistění stromů v pozdější fázi hnízdního období (**Zárybnická et al. 2017b – příloha XIV**). Ke zvýšené predaci může docházet v nepřímé závislosti na abundanci drobných savců (např. Bêty et al. 2001, Wilson & Bromley 2001, Ims et al. 2013). Drobní savci tvoří podstatnou část potravního spektra kuny lesní (Jędrzejewski et al. 1993). V období jejich nedostatku dochází k přeorientování zejména na mláďata ptáků, sýce rousného nevyjímaje. V souladu s tím byla míra predace hnízd sýce rousného kunou lesní negativně korelována s abundancí myšic rodu *Apodemus* (**Zárybnická et al. 2015c – příloha XV**).

Výrazné rozdíly v reprodukční úspěšnosti byly zjištěny porovnáním urbánních populací s populacemi ve volné krajině. U městských populací poštolky obecné v České republice byla reprodukční úspěšnost stabilně vyšší než u populací v otevřené krajině (např. Praha: 4,3 vs. 2,8 mláďat/hnízdo, Plesník 1992). Srovnatelné údaje pochází i z menších měst (České Budějovice: 4,6 mláďat/hnízdo, **Riegert et al. 2007 – příloha I**), rozloha města tedy nemusí být rozhodující. Hlavním faktorem je pravděpodobně kvalita hnízdních příležitostí, neboť hnízdní úspěšnost poštolek v uzavřených dutinách je vyšší než na otevřených hnízdech (Fargallo et al. 2001). Možný vliv na zvýšenou míru reprodukce může mít také absence velkých predátorů (např. výr velký *Bubo bubo*) ve městech. Zanedbatelné rozdíly mezi subpopulacemi v centru města a na jeho periferii byly zaznamenány v Německu (Berlín: 4,8 vs. 4,6 mláďat/hnízdo, Kübler et al. 2005). Ke zcela opačným výsledkům dospěla Sumasgutner et al. (2013, 2014) ve Vídni, kde reprodukční úspěšnost poštolek vzrůstala směrem z centra k periferii města (1,0 vs. 4,0 mláďat/hnízdo) díky špatným trofickým podmínkách v centru města. U kalouse ušatého byla v Českých Budějovicích zjištěna podobná reprodukční úspěšnost (2,8 mláďat/hnízdo, Riegert 2011) v porovnání s průměrem z otevřené krajiny (2,7 mláďat/hnízdo, Hudec & Šťastný 2005a).

1.7.2. Kondice a růst mláďat

Růst mláďat může ovlivňovat celá řada faktorů, zejména potravní nabídka (Wiehn & Korpimäki 1997, Karell et al. 2009a), složení potravy (Navarro-López et al. 2014), pohlaví (Laaksonen et al. 2004), pořadí líhnutí (Massemin et al. 2002), velikost snůšky (Costantini et al. 2009), objem vejce (Anderson et al. 1997) nebo počasí (Costantini et al. 2009). Růst mláďat je definován třemi základními parametry: růstová rychlost, inflexní bod a asymptota (např. Starck & Ricklefs 1998).

Vliv více vybraných faktorů na parametry růstu byl studován například u mláďat finských poštolek obecných. Během experimentu byla vybraná mláďata přikrmována, vliv tohoto zásahu však překvapivě nebyl potvrzen u žádného z růstových parametrů. Rozdíly byly zjištěny mezi mláďaty různého pořadí líhnutí, zejména v 19. dni po vylíhnutí. Růst byl pomalejší u posledních mláďat, během dalšího vývoje se však hodnoty parametrů mláďat vyrovnávaly a před opuštěním hnízda (26. den) byly u všech mláďat srovnatelné. Zároveň byl zjištěn různý vývoj hmotnosti a tělesných rozměrů. Zatímco nárůst hmotnosti ustal v 19. dni, růst tělesných rozměrů pokračoval až do období vzletnosti (Massemin et al. 2002). Vzhledem k tomu, že u ptačích predátorů jsou samice větší než samci (reversed size dimorphism, např. Village 1990, Korpimäki & Hakkarainen 2012), lze očekávat výrazné rozdíly v růstu obou pohlaví a liší se tedy také energetické výdaje pro vyvedení samců a samic. Mláďata z hnízd poštolek, ve kterých byly důsledkem experimentálního zásahu přítomny pouze samice, vykazovala horší kondici než mláďata z hnízd, kde byly přítomní i samci. Rozdíly byly nápadné především v roce, kdy byla abundance hlavní kořisti nízká. Autoři tento výsledek vysvětlují vyšší kompeticí v hnízdech, kde byly pouze samice (Laaksonen et al. 2004). Rozdíly v růstu jednotlivých pohlaví byly zjištěny také u sýce rousného (**Zárybnická et al. 2015d – příloha XVI**). Na rozdíl od výše zmíněné studie u poštolky obecné (Massemin et al. 2002) byl zjištěn vliv potravní nabídky na růst mláďat. Během zvýšené abundance myšic a hraboše na lovištích se zvýšila zejména rychlost růstu a hodnota inflexního bodu. Vliv potravní nabídky na asymptotu (maximální hmotnost) nebyl prokázán. Podobně jako u předchozích studií byl zjištěn rozdíl mezi mláďaty různého pořadí líhnutí, maximální hmotnost byla nejvyšší u dříve vylíhlých sourozenců (**Zárybnická et al. 2015d – příloha XVI**).

2. Souhrn

V souladu s předchozími studiemi byl zjištěn vliv abundance drobných savců na potravní chování studovaných ptačích predátorů a u některých druhů (sýc rousný, puštík obecný) i reprodukční parametry studovaných druhů ve střední Evropě. Strategie jednotlivých studovaných druhů se mohou výrazně lišit, zejména při porovnání populací ze střední a severní Evropy. Výrazné rozdíly v ekologii některých studovaných druhů lze sledovat také na gradientu urbanizace. Hlavní výsledky lze shrnout do následujících bodů:

1) Žádný ze studovaných druhů nevykazoval oproti populacím v severní Evropě numerickou odpověď na nabídku drobných savců. Důvodem je pravděpodobně méně výrazné kolísání abundance hlavní kořisti na lovištích, širší nabídka alternativních kořistí ve střední Evropě a/nebo dostatek kvalitních hnízdních příležitostí v urbánním prostředí.

2) Urbánní populace se v některých ekologických aspektech liší od populací ve volné krajině (např. stabilně vysoká reprodukční úspěšnost). Genetická struktura urbánní a navazující mimoměstské populace poštolky obecné se však výrazně nelišila. U samic byl zjištěn negativní vztah mezi tělesnou hmotností a vzdáleností hnízda od centra města. U samců tento vztah nebyl potvrzen. V rámci urbánní populace byli jedinci v centru příbuznější, což může být důsledkem značné věrnosti hnízdišti a vysokou návratností mladých jedinců do rodného hnízdiště.

3) Ke stanovení potravního spektra je vhodné kombinovat tradiční metody s použitím kamerových systémů. Díky tomu je možné s větší přesností stanovit počty jednotlivých kořistí, neboť zejména drobní savci byli u sýce rousného před donesením na hnízdo často dekapitováni. Proto byly jejich počty za použití metody rozboru vývržků podhodnoceny.

4) Složení potravy studovaných druhů do značné míry odráželo abundanci drobných savců na lovištích. Hlavní kořist se však lišila mezi jednotlivými druhy. V potravním spektru denního predátora (poštolky obecné) a jednoho z nočních predátorů (kalous ušatý) dominovali hraboši rodu *Microtus*. U puštíka obecného a sýce rousného lze v potravě nalézt také různé zastoupení hraboše, nicméně celkové složení potravy ovlivňuje abundance myšic rodu *Apodemus*, které jsou díky noční aktivitě vhodnějším typem kořisti. Podíl myšic v potravě puštíka obecného klesal v průběhu sezóny.

5) U všech studovaných druhů během nedostatku hlavní kořisti vzrůstal podíl alternativních složek potravy. Alternativní kořistí byl u poštolky obecné především hmyz (Carabidae, Orthoptera). V mimohnízdním období bylo složení potravy poštolky obecné ovlivněno sněhovou pokrývkou, alternativní kořistí byli především ptáci. U syntopických kalousů ušatých se v potravě v období nedostatku hraboše zvyšoval podíl myšic. Sýc rousný využíval jako alternativní kořist zejména hraboše, rejsky rodu *Sorex* a ptáky. Zastoupení ptáků (zejména pěnkavy obecné) se v potravě sýce zvyšuje s rostoucí nadmořskou výškou. U puštíka obecného lze v období nedostatku myšic sledovat zvýšené zastoupení ptáků a hmyzožravců.

6) Zvýšené lovecké úsilí může zmírnit negativní vliv nedostatku hraboše na lovištích. Poštolky obecné v letech s nízkou abundancí hraboše trávily na lovištích více času. Zároveň lovící jedinci využívali energeticky méně náročné techniky lovu, podíl třepotání se zvýšil

v letech s vyšší abundancí hraboše. Díky zvýšené kompetici o hlavní kořist na lovištích také docházelo k jejich častému střídání. Zvýšené lovecké úsilí tedy představuje na rozdíl od severních populací dostačující mechanismus, který přispívá k optimalizaci složení potravy i během troficky méně výhodných podmínek.

7) Mechanismus, který umožňuje koexistenci predátorů se stejnou potravní specializací, byl studován u syntopických poštolek obecných a kalousů ušatých v urbánním prostředí. Urbánní poštolky obecné k lovu využívaly zejména loviště na periferii města. Díky tomu byly jejich lovecké okrsky výrazně větší v porovnání se studiemi z otevřené krajiny. Rozloha okrsku nebyla ovlivněna nabídkou hraboše, ale umístěním hnízda v rámci města. Ke zvětšování okrsků výrazně přispěla i kompetice s páry hnízdícími na okraji města (viz. předchozí bod). Kalous ušatý naopak v urbánním prostředí často loví přímo v zástavbě, kde využívá především okrajové biotopy. Separace lovišť tedy výrazně přispěla ke zmírnění vlivu nepřímé kompetice mezi denním a nočním predátorem.

8) Reprodukční parametry se u poštolky obecné v urbánním prostředí během let příliš neměnily a nebyly korelovány s nabídkou hraboše. Ke stabilní reprodukci přispělo zvýšené lovecké úsilí v letech s nízkou abundancí hraboše a dostatek kvalitních hnízdních příležitostí. Reprodukční parametry sýce rousného a puštíka obecného byly pozitivně korelovány s abundancí myšic na lovištích. U puštíka obecného byl ověřen negativní vztah mezi mírou reprodukčních parametrů a načasováním hnízdění.

9) Růstové parametry byly ovlivněny abundancí drobných savců. Konkrétně, rychlost růstu a inflexní bod byly u sýce rousného pozitivně korelované s abundancí hrabošů a myšic. Z dalších faktorů, které ovlivňují růstové parametry, lze uvést pohlaví a pořadí mláděte během líhnutí.

10) Predační tlak může výrazně ovlivnit výběr hnízdiště a to i v průběhu hnízdní sezóny. Sýci rousní si na začátku hnízdní sezóny vybírali spíše budky, které byly umístěny v jehličnatých porostech. Budky v listnatých porostech byly bezpečné až po olistění stromů v pozdější fázi hnízdního období. Optimálním biotopem pro lov i zahnízdění sýce rousného je v našich podmínkách mozaika hustých a rozvolněných lesních porostů, kdy rozvolněné porosty jsou využívány k lovu a husté porosty poskytují ochranu před predátory.

11) Nepřímý vliv abundance drobných savců na populace různých druhů je pravděpodobně v mírném pásu běžnější, než se původně předpokládalo. Myšice jsou dominantní kořistí kuny lesní, která je zároveň predátorem hnízd sýce rousného. Míra predace hnízd sýce rousného kunou lesní byla negativně korelována s abundancí myšic.

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Příloha I

Riegert J, Dufek A, Fainová D, Mikeš V, Fuchs R. 2007:

Increased hunting effort buffers against vole scarcity in an urban kestrel *Falco tinnunculus* population

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Increased hunting effort buffers against vole scarcity in an urban Kestrel *Falco tinnunculus* population

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Capsule In years with low vole abundance birds visited hunting grounds more frequently and for longer.

Aims To describe diet composition, hunting behaviour, habitat choice and reproductive success of urban Kestrels during changing vole abundance.

Methods For five years, we studied the hunting effort of Kestrels in a medium-sized city during the breeding season. Pitfall traps were used for determining vole abundance. Kestrel diet composition was determined from pellet analyses. The number of eggs and offspring was recorded during at least two consecutive visits for each nest and each breeding stage.

Results In contrast to larger European cities, the Common Vole *Microtus arvalis* was a key part of the Kestrels' diet and did not fluctuate significantly according to vole availability. Reproductive success was quite high and stable throughout years with different vole abundance. In years of low vole abundance, the arrival frequency at hunting grounds and time spent there increased. During years with a low vole population, Kestrels had less hunting success and the rate of successful visits decreased. Therefore, Kestrels probably had to change hunting grounds more frequently. During low vole years Kestrels used less demanding techniques, e.g. perching, despite the lower success of these hunting techniques, to avoid extremely high energetic costs.

Conclusions An increase in hunting helps to maintain a proper diet and consequently reproductive success. Vole abundance did not change dramatically during the study period, as reported by studies from western and northern Europe. The proportion of ruderal habitats on the city periphery is higher than in more monotonous farmland habitats. Ruderal habitats can be important when Kestrels look for mammals other than voles, especially during vole scarcity.

The reproductive output of small-mammal-eating raptors usually decreases during a food shortage. The greatest between-year differences were found for Long-eared Owl *Asio otus* (Korpimäki 1992) and Eurasian Kestrel *Falco tinnunculus* (Korpimäki & Rita 1996) in northern Europe, where the population of small mammals is cyclic (Hansson & Henttonen 1985). As there are no regular three-year prey cycles in temperate latitudes, large non-cyclic multi-annual changes of small-mammal abundance are observed (Tkadlec & Stenseth 2001) and the reproductive output of farmland mammal-eating raptors changes (Plesník 1992, Salamolard *et al.* 2000). The most obvious reactions of raptors to food shortages are (1) moving to areas with a higher abundance of prey, especially in northern latitudes (Korpimäki 1985a, 1985b), and (2) expanding diet to alternative prey (Korpimäki 1986, Reif *et al.* 2001).

The Eurasian Kestrel is a small raptor that feeds primarily on small mammals, particularly on voles *Microtus* spp. in central and northern Europe (Korpimäki 1986). Among the raptors, Kestrels have colonized European cities most successfully. Urban Kestrels have an excellent opportunity to feed on birds, as their availability does not usually change markedly between years. Studies of urban Kestrels in large European cities usually show a high proportion of birds in the diet (Beichle 1980, Darolová 1986, Plesník 1992, Romanowski 1996, Witkowski 1962, Yalden 1980).

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We studied the diet composition of Kestrels in the medium-sized city of České Budějovice from 1997 (Riegert & Fuchs 2004). In comparison with large European cities, the number of Kestrels was low and did not fluctuate according to vole availability. Voles were always the main prey. Reproductive success was quite high and stable in spite of years with different vole abundance. This observation leads to the question: how do Kestrels from České Budějovice buffer against vole scarcity? We propose that changes in hunting behaviour help to maintain the hunting yield, consequently keeping a high level of reproductive success. Our hypothesis is that during vole scarcity: (1) Kestrels spend more time on hunting grounds; (2) Kestrels employ less energetically demanding hunting techniques; and (3) females hunt more frequently.

METHODS

Study area and Kestrel population

We studied an urban population of Eurasian Kestrels in the city of České Budějovice (49°N, 14°E, area 30 km^2, human population 100 000), in the southern part of the Czech Republic. We estimated the numbers of breeding pairs during the study period to be 36 (1999), 37 (2000), 35 (2001), 36 (2002) and 34 (2003). Kestrels bred both in the city centre and its periphery, usually within loft-windows, holes or boxes on buildings.

The hunting grounds are situated outside the developed area of the city, 2–5 km from the city centre. The hunting grounds were mostly meadows (36%), cereal fields (35%) and ruderal habitats (19%). The remainder (10%) consisted of alfalfa, rape and cornfields. The proportion of each habitat was estimated each year from detailed mapping of the city surroundings within a radius of 6 km from the centre. The proportion of habitats did not change markedly between years (less than 3% of any habitat). Ruderal habitats were defined as long-term abandoned areas with mainly *Cirsium*, *Rumex* and *Calamagrostis* species growing and with tall vegetation cover (up to 1.5–2 m).

Trapping of small mammals

We assessed the availability of small mammals during the years 1999–2003. We used 100 pitfall traps (plastic bottles with a cut neck and 2-litre capacity) each year. These traps were installed on ten Kestrel hunting grounds (ten traps per hunting ground made up a trap line) in the second half of July. The timing of trapping was determined by the approximate end of the breeding season, when the last Kestrel chicks were fledged. The traps were filled with a 4% fusion of formaldehyde and exposed for 17 days. The trap lines were placed in two types of vegetation cover: meadow (six lines) and ruderal (four lines). The trapping effort was 1700 trap-nights each year.

Reproductive output

The numbers of eggs and offspring were recorded during at least two consecutive visits per nest and for each breeding stage (incubation, hatching and chick rearing).

Diet composition

After fledging, we collected food remains and pellets from the nests to determine the diet composition. We identified 1446 prey items from 46 nests. The material was dried and all feather remains were characterized. The remaining material was dissolved in a solution of NaOH (Schueler 1972). Small mammals were identified from skulls according to the method of Anděra & Horáček (1982); birds were identified from beaks and humeri using a reference collection. Remains of insects were sorted into categories of similar size, morphology and colour. Further information is available in Riegert & Fuchs (2004).

Hunting behaviour

In total, more than 35 hunting grounds were visited each breeding season, from the beginning of May to mid-July, with a total of 137 visits (mean ± sd per year, 28 ± 15 visits). A visit involved 30–90 minutes of observation on a hunting ground, totalling 186 hours of observations (mean ± sd per year, 37.0 ± 0.7 hours). Observations started at the beginning of chick rearing (according to the first date of hatching). The factor day in the season (consecutive day number after start of chick rearing in the population) was balanced to the first hatching date. Observations were conducted on rainless days.

We gathered data on 666 hunting Kestrels (pseudoreplications included), which performed a total of 7003 hunting events. According to the results of a parallel study on wing-tagged Kestrels (Riegert *et al.* 2007), we believe that the mean number of Kestrels observed was at least 35 individuals each year (35% of observations each year refer to wing-tagged Kestrels, *n*

= 57 tagged male Kestrel). Therefore, pseudoreplications did not represent the main source of variability.

A hunting event was defined as the continuous use of any hunting technique that concluded with an attack or movement to another place. We distinguished four categories of hunting techniques according to Village (1983): (1) *hovering*; (2) *perching*, typical after unsuccessful long-term hovering (unlike Village (1983) we included only perching that terminated with a ground attack to eliminate inactive perching); (3) *hunting from ground* was restricted to short-cut alfalfa fields, where entrances to rodent burrows are easily recognizable (Kestrels walked among burrows, often waiting by the entrance); (4) *hunting by low flight* resembles Sparrowhawk *Accipiter nisus* foraging behaviour, in which the Kestrel surprised the prey (usually birds in scrubs or on field).

Hunting success

Hunting success was measured as a proportion of successful strikes from all those made. We considered a strike to be a hunting action that was followed by immediate landing. A successful strike was defined as when the observer saw vertebrate prey being carried off. Insect prey is usually eaten immediately (Village 1983, Riegert & Fuchs 2004) and could be overlooked when carried. In total, we recorded 514 strikes (both from hovering and perching) or hunting on the ground.

Statistical analysis

Multivariate data on diet composition and hunting techniques were analysed using redundancy analysis (RDA, CANOCO for Windows software, Braak & Šmilauer 1998) and visualized in CANODRAW (Šmilauer 1992). The percentages were log-transformed, and statistical significance was computed using Monte-Carlo *P*-tests with unrestricted permutations. The annual changes of reproductive output were compared using Kruskal–Wallis median tests (STATISTICA 5.0, Statsoft, Inc. 1996), with Bonferroni correction. The preference of hunting habitats was analysed using Ivlev's preference index (Jacobs 1974). The availability and use of each habitat was expressed as the proportion of time spent by the observer and Kestrels in each habitat. We also computed Spearman rank correlations between vole abundance, diet composition, reproductive parameters and Ivlev's preference index, respectively. Other results were obtained using generalized linear models (GLM, MathSoft, Inc. 1997), with forward selection of factors according to Mallows' Cp-statistic (Mallows 1973). According to the data distribution of dependent variables, we used Poisson, binomial, gamma or quasi-likelihood models, with relevant link functions (McCullagh & Nelder 1989).

For all parameters of hunting behaviour, we tested the influence of these factors: year, hunting habitat (meadows, cereals, ruderals and others), day in the season (according to first observation date for each season separately) and sex of the individual. For hunting success, we also tested the type of hunting technique (see above). Factor year was used instead of direct pooled vole abundance, because of possible pseudoreplication within each year data (for each year we gathered single pooled vole abundance only). The relationship with vole abundance was probed by Spearman rank correlations between pooled vole abundance and mean dependent variable values (n = 5 years). We used pooled numbers of caught voles for each year, because the exact correlation of a hunting ground to a particular trap-line was not possible. This occurrence was caused by rapid changes of main habitat types during hunting, even within small areas. The factor day in the season was positively correlated with vegetation height ($r_s = 0.23$, $P < 0.05$). Therefore, we included the day in the season into GLM analyses only. Wind conditions (0 = calm, 1 = slight, 2 = medium, 3 = strong) were used as a co-variate.

For most analyses, a data unit was represented with one observed individual (pesudoreplications included, n = 666). For frequency of arrivals, we used one day of observation as a data unit (n = 149). In the case of hunting success, we used either separate strikes (n = 514) or visits (n = 666) as data units.

RESULTS

Vole abundance

In total, we trapped 221 Common Voles *Microtus arvalis* out of 307 mammals caught (72%). Other mammals were less abundant: Shrews *Sorex minutus* and *S. araneus* (23%), Harvest Mice *Micromys minutus*, Field Mice *Apodemus* sp. (4%) and White-toothed Shrews *Crocidura suaveolens* (1%). The highest number of voles caught was recorded in 2002 (Fig. 1a), a peak vole year. In 2000 and 2003, vole abundance reached minimum values. The change of vole abundance during the years was significant (GLM, Table 1, Fig. 1a). Vole abundance was significantly higher in

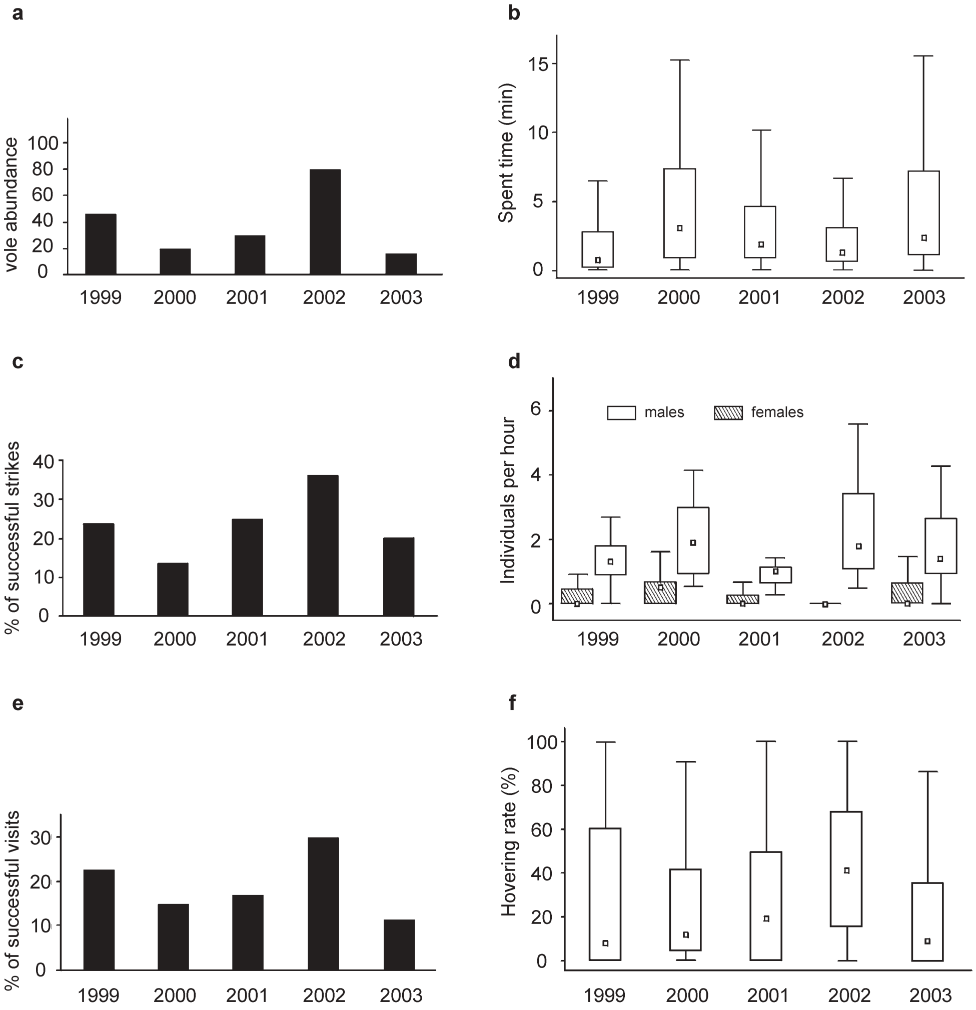

Figure 1. (a) Total number of voles caught per year; (b) time spent on hunting grounds; (c) success of strikes; (d) frequency of arrivals at hunting grounds; (e) success of visits; (f) hovering rate. For box-and-whisker plots: small square, median; box, 25–75% of data; whiskers, non-outlier range.

ruderals in comparison with meadows (Table 1). During the years with high vole abundance, values were markedly higher in ruderals. During low or medium vole years, vole abundance in both habitats was similar (Table 1, Fig. 2).

Diet composition

The Common Vole was frequently brought to the nest in all five years (Table 2). Its proportion by numbers changed between years, partly according to vole availability. The vole proportion within the biomass was stable, decreasing only in the year 2003 (low vole year), when the biomass proportion of other mammals (*Sorex* sp., *Micromys minutus*) increased. However, during the first low vole year (2000), the proportion of voles within biomass was comparable with other years. The proportion by numbers of ingested insects (mainly small Carabidae and Tettigoniidae) was negatively correlated with vole availability ($r_s = -0.75$, $P < 0.05$, $n = 5$). However, these changes were negligible relative to the biomass. The proportion of birds (Sparrows *Passer* sp., Blackbirds *Turdus merula* and tits *Parus* sp.) was the most stable diet component throughout the research period (Table 2). The impact of vole abundance to changes in diet composition by numbers was indicative (RDA, Monte Carlo permutation test, $F = 3.06$, $P = 0.07$), while not being significant relative to the biomass (RDA, I and II axes 93.1%, Monte Carlo permutation test, $F = 0.46$, $P = 0.13$).

Reproductive output

Reproductive parameters changed slightly during the

Table 1. Statistical analysis of changes of vole abundance, frequency of arrivals at hunting grounds, time spent on ground, hunting success and hovering rate of Kestrels.

Dependent variable	Model type	Independent variable	df	Explained variability (%)	β	P
Vole abundance	Poisson	year	45	33.21	–	0.0001
		habitat	44	5.20	[a]	0.0268
		year * habitat	40	3.81	–	0.0312
Females per hour	quasi-likelihood	year	144	1.03	–	0.0910
Males per hour	quasi-likelihood	year	144	2.15	–	0.0421
Spent time (min)	gamma	year	661	8.4	–	<0.0001
		day in season	660	1.15	–0.32	0.0123
Strike number	Poisson	year	661	1.47	–	0.1018
Strike success	binomial	technique	510	7.05	[b]	<0.0001
		year	506	1.22	–	0.0497
Visit success	binomial	year	661	5.55	–	<0.0001
Hovering rate (%)	gamma	year	661	7.60	–	<0.0001

GLM, forward selection. For hunting data we used wind condition (0–3) as a co-variate. [a]Vole abundance was higher on ruderals. [b]Hovering was the most successful technique.

study period (Table 3). A significant decrease of egg numbers was recorded in the second lowest vole year (2003), but not the first (2000). The lower mean parameters of reproduction in 2003 were caused by a low mean egg number laid, rather than chick loss. The mean number of eggs and hatchlings increased in response to vole abundance positively (r_s = 0.64, P < 0.05 and r_s = 0.61, P < 0.05 respectively, n = 5 years), but the mean number of fledglings and total reproductive output did not show any relationship to vole abundance (r_s = 0.26, P > 0.1 and r_s = 0.11, P > 0.2 respectively, n = 5 years).

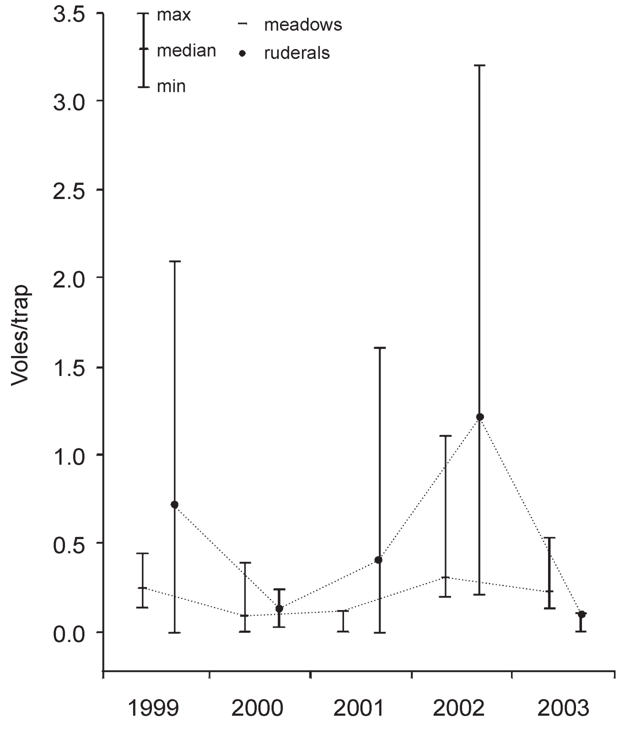

Figure 2. Index of vole abundance (voles/trap) in ruderals and meadows (1999–2003). A data unit is represented by a trap (n = 500).

Hunting habitats

The values of Ivlev's preference index randomly shifted throughout the years. The only trend was a decreasing avoidance of meadows. Ivlev's preference index did not significantly change for any habitat in relation to vole abundance (Table 4). The strongest positive correlation was found for ruderals.

Hunting effort

We analysed the frequency of male and female arrivals to hunting grounds and time spent there by an individual. The mean frequency of arrivals changed significantly among years for males, but was indicative for females only (GLM, Table 1, Fig. 1d). For both sexes, it was negatively correlated with vole abundance, but significant for males only (males, r_s = –0.71, P < 0.05; females, r_s = –0.18, P > 0.05). The highest number of hunting males and females was recorded in both low vole years (2000 and 2003), as well as the peak vole year 2002. The time spent by an individual on a hunting ground changed significantly among years (Table 1) and its mean was negatively correlated with vole abundance (r_s = –0.68, P < 0.05). In low vole years, the time spent on a hunting ground increased significantly (Fig. 1b). The number of strikes per visit changed among years indicatively (Table 1), increasing in low vole years (r_s = –0.12, P > 0.05).

Table 2. Diet composition of Kestrels (n = 46 nests).

Category	Year	Voles	Other mammals	Birds	Insects	Total
Number (n (%))	1999	355 (80.1)	5 (1.2)	18 (4.2)	64 (14.2)	443
	2000	99 (73.1)	0 (0.0)	7 (4.9)	30 (21.9)	136
	2001	234 (68.2)	8 (2.3)	8 (2.3)	93 (27.1)	343
	2002	267 (88.7)	11 (3.7)	7 (2.3)	16 (5.3)	301
	2003	164 (73.5)	15 (6.7)	13 (5.8)	31 (13.9)	223
	total	1119	39	53	234	1446
Biomass (g (%))	1999	7809 (95.4)	88(1.1)	276 (3.4)	13 (0.2)	8186
	2000	2187 (95.3)	2 (0.1)	100 (4.4)	6 (0.3)	2296
	2001	5148 (94.9)	136 (2.5)	120 (2.2)	19 (0.3)	5423
	2002	5874 (95.2)	187 (3.0)	105 (1.7)	3 (0.1)	6169
	2003	3608 (88.8)	255 (6.3)	195 (4.8)	6 (0.2)	4064
	total	24 626	668	796	47	26 138

Table 3. Mean parameters and statistical analysis of reproductive output of Kestrels.

Year	Eggs	Hatchlings	Fledglings	Losses	Number of nests
1999	5.77	5.31	5.00	0.77	13
2000	5.89	5.33	5.00	0.89	9
2001	5.56	5.32	4.22	1.33	9
2002	5.80	5.60	4.90	0.90	10
2003	4.67	4.36	3.82	0.78	11
H	14.31	12.30	9.12	1.62	
P	0.0064	0.0152	0.0583	0.8046	

Kruskal–Wallis median test, n = 52 nests, critical P-value after Bonferroni correction was set at 0.0125.

Table 4. Values of Ivlev's preference index for main habitat types and Spearman rank correlation values in relation to vole abundance.

	Meadows	Cereals	Ruderals	Others
1999	–0.66	0.25	0.29	–0.39
2000	–0.57	0.00	0.04	0.37
2001	–0.18	0.66	0.21	–0.43
2002	–0.06	–0.27	0.23	0.23
2003	–0.01	0.20	–0.18	–0.30
r_s	0.21	–0.56	0.62	0.24
P	>0.05	>0.05	>0.05	>0.05

Hunting success

Hunting success was analysed in two ways: success of each separate strike and success of individual visits (for both 0–1 distribution). In the first case, we added a strike-type factor: those made from hovering and perching, hunting on the ground and hunting by low flight. The success of separate strikes and visits both changed significantly among years (Table 1) and annual values were positively correlated with vole abundance (strike success, $r_s = 0.94$, $P < 0.05$; visit success, $r_s = 0.97$, $P < 0.05$), the highest success being recorded during the peak vole year (Fig. 1c,e). Individual strike success was dependent on strike type (Table 1): the highest success was recorded in hovering (42.4%), followed by perching (33.3%), hunting on the ground (14.4%) and hunting by low flight (9.9%).

Hunting techniques

Vole availability affected the use of hunting techniques (RDA, I and II axes explained 82.3% of variability). During the peak vole year, we recorded the highest proportion of hovering (RDA, Monte Carlo permutation test, $F = 0.15$, $P = 0.05$). In the rest of the years, the proportion of other techniques increased. The proportion of hovering was clearly negatively correlated with the proportion of perching, and also with hunting on the ground (Fig. 3). Hunting by low flight was not correlated with other hunting techniques (Fig. 3), but a partially negative correlation was found with vole abundance. The proportion of hovering, the most energetically demanding technique, changed significantly among years (Table 1). It was positively correlated with vole abundance (Fig. 3, see also Fig. 1f).

DISCUSSION

Vole fluctuation

During the five years we recorded both peak and low phases in the abundance of the Common Vole. In low vole years its summer abundance was 24.0% of that in the peak year. The differences are less pronounced in comparison with northern latitudes and western Europe: spring in Scotland 7.0% (Village 1986), Finland 0% (Korpimäki & Wiehn 1998); summer in Siberia (Potapov 1997) and France (Salamolard *et al.* 2000) 0%.

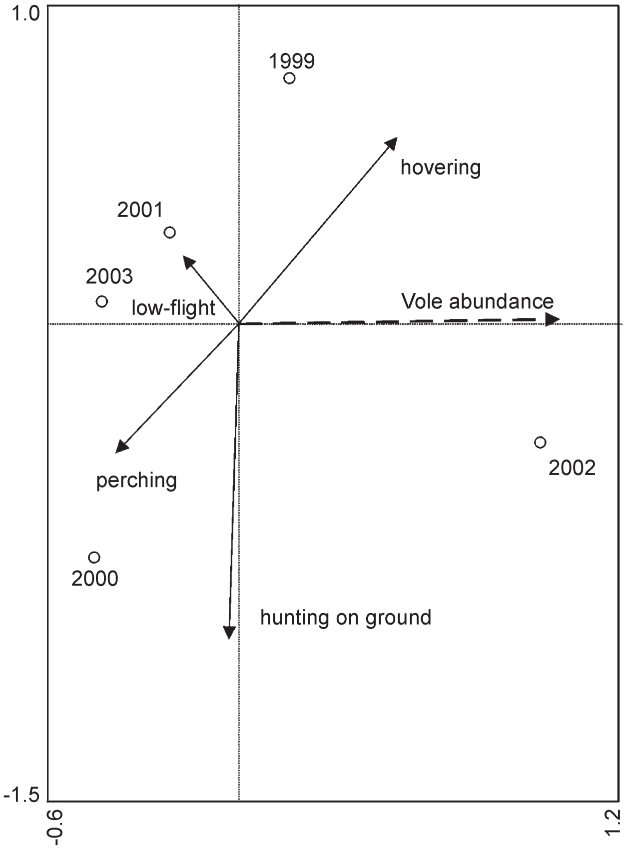

Figure 3. Projection scores of recorded hunting types (from percentages) of Kestrels (1999–2003) related to pooled vole abundance. RDA, I and II canonical axes explain 82.3%. Monte Carlo permutation test, $P = 0.05$.

Plesník (1992) also found a more pronounced decrease in spring (0.1%) and autumn (4.5%) of abundance in the agricultural regions of the eastern Czech Republic. According to our results, these slight changes in abundance may not simply be due to the existence of vole refuges (i.e. ruderals), because vole abundance in ruderals and meadows was similar during low vole years.

Diet composition

During low abundance of Microtinae rodents, the proportion of alternative prey in the diet increases in many vole-eating raptors (Korpimäki 1985a, 1986). Various birds, mammals or invertebrate species can be substituted for voles (Finland, 4% during peak vole years versus 22% during low vole years, Korpimäki 1985a), shrews (Scotland, 10% versus 55%, Village 1982) and insects (UK, 50% versus 90%, Yalden & Warburton 1979). Birds are taken as the common alternative prey in urban locations, the highest proportion being found in large cities (Korpimäki 1985a). Surprisingly, no study reports changes in the proportion of birds in the diet depending on vole abundance in urban areas. Plesník (1992) noted annual fluctuations (32–48%), but had no data on vole availability on the city periphery.

In České Budějovice, the proportion of voles in the diet by biomass was stable during the study period. We recorded a slight decrease only during one low vole year, when the proportion of other mammals increased. The proportion of voles by number changed according to their abundance indicatively. However, alternative prey was represented by insects that were negligible within the biomass (Riegert & Fuchs 2004). In spite of the high availability of birds in the city, their proportion as prey was not only very low, but also stable during the vole cycle (2.3–5.8% by number). It is quite a different situation in a large city. Vole availability in the city centre is permanently very low (Čiháková & Frynta 1996), therefore birds are a constant high proportion of the Kestrels' diet.

Reproductive output

It is generally accepted that the breeding success of vole-eating raptors depends on food availability (Korpimäki 1986). A significant decrease of reproductive output during poor vole years was found in Kestrel populations in Norway (3.7 versus 2.8 fledglings/nest, Hagen 1952) and Finland (5.0 versus 2.4 fledglings/ nest, Korpimäki & Rita 1996). A notable part of these differences is due to clutch size reduction; the rest of the nest loss is due to higher mortality of chicks during a period of vole scarcity. Plesník (1992) also found marked changes of reproductive output in agricultural land in the eastern Czech Republic (4.3 versus 2.8 fledglings/nest). The output of Kestrels in Prague (Plesník 1992) was more stable during the study period (4.1 versus 3.7 fledglings/nest), explained by a lower dependence of the Kestrels on vole prey. However, data on vole abundances were not included. In spite of the very low proportion of birds in the diet of our Kestrels, the overall reproductive success remained stable during the years, similar to the results of Plesník (1992). The decreased fledgling number in 2003 was caused by the small number of eggs laid and not by losses of chicks during rearing.

Kestrel behaviour and vole fluctuation

Changes in the hunting behaviour during the vole cycle were pronounced. Hunting effort increased during low vole years, particularly the arrival frequency at the hunting ground (significant for males and indicative for females) and time spent there. These results could be indirect evidence that a longer time spent on the hunting ground compensates for a lower number of hunting opportunities in low vole years. The prolonged time spent at the hunting grounds does not buffer against vole fluctuation by itself. During low vole years, visit success rates decreased. Therefore, Kestrels probably had to change hunting grounds more frequently, as shown by an increased arrival frequency in low vole years.

The indicative increase of strikes during years with lower vole abundance gives indirect evidence that Kestrels also hunt on less profitable (i.e. smaller) prey. These results agree with Laaksonen *et al.* (2004), who found that prey delivery during low vole years was higher than in peak years, but prey biomass was still higher during peak vole years. Indirect evidence of smaller prey caught during vole scarcity gives an increased proportion of other smaller mammals (shrews, Harvest Mice) in the diet of our Kestrels in the year 2003.

An increased hunting effort would increase the energy costs to an unprofitable level. Therefore, our Kestrels use less demanding techniques during low vole years, such as perching (Pettifor 1983), despite the lower success rate of these hunting techniques.

Changes of hunting behaviour of Kestrels in České Budějovice in low vole years buffered against vole scarcity to such a degree that greater losses of reproductive output were prevented. We do not consider an effect of numerical response, because of the similar number of breeding pairs despite different vole availability during the study period. Similarly, there was no significant preference for any habitat during low vole years; preference for ruderals was indicative only.

To date, increased hunting effort has been studied only sporadically as a potential mechanism for buffering against vole scarcity. Unlike our results, Wiehn & Korpimäki (1997) report the consistent hunting effort of Finnish farmland Kestrels in years with different vole abundance. The increase of foraging effort during scarcity of the main prey was documented in skuas *Catharacta* sp. (Klomp & Furness 1992, Hamer *et al.* 1991). However, in these cases, reproductive output decreased dramatically.

The ability to increase hunting effort on manipulated brood size has been recorded many times (reviewed by Dijkstra *et al.* 1990). Usually, with an increased number of chicks, hunting effort also increased. However, a study that included the availability of voles did not record a significant increase of hunting effort during low vole years (Wiehn *et al.* 2000).

The mechanism we found for buffering against vole fluctuations is not common in vole-eating raptors. The explanation as to why our results are contrary to other studies suggests the following questions.

1. How do the Kestrels in České Budějovice successfully buffer against vole fluctuation? The crash in vole abundance in our study area is less pronounced compared to other studies. Vole abundance even during low vole years still allowed our Kestrels to hunt effectively. Furthermore, during low vole years Kestrels indicatively increased their preference for ruderals. These habitats were probably the main source of other mammals (e.g. shrews, Harvest Mice), whose proportion increased indicatively in the diet of our Kestrels during the low vole year of 2003. The surroundings of cities differ from farmlands in the occurrence of more numerous and diverse hunting habitats, which also contain ruderals. We propose that our Kestrels have a better chance to locate such habitats than Kestrels from a more monotonous farmland landscape.
2. Why did the diet of our Kestrels not expand to birds in low vole years? The diet expansion described by other studies is not connected with a change in hunting habits (Korpimäki 1986). Raptors visit a fixed hunting ground, where they look for the main prey. If that prey type is not available, they attack an alternative one. Our Kestrels exhibited the same type of diet expansion. However, insects and not birds were the alternative prey. Furthermore, our Kestrels hunt in the surroundings of the city (J. Riegert *et al.* unpubl. data), and the available bird prey are mainly inside the city.

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Příloha II

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Genetic variability, body characteristics and reproductive parameters of neighbouring rural and urban common kestrel (*Falco tinnunculus*) populations

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ORIGINAL ARTICLE

Genetic variability, body characteristics and reproductive parameters of neighbouring rural and urban common kestrel (*Falco tinnuculus*) populations

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Abstract We tested the genetic and ecological differences between neighbouring urban and rural populations of common kestrels (*Falco tinnuculus*) in southern Bohemia. The aims were to (1) assess the genetic variability of the studied kestrel populations using microsatellite markers, (2) check the genetic relatedness of individuals within the urbanization gradient, and (3) compare possible gradients of body characteristics and reproductive parameters on the urbanization gradient. The mean expected allelic polymorphism did not differ among the studied populations, which were not genetically separated ($F_{ST} = 0.0003$, $P = 0.781$). Also, an individual assignment test did not show a separation of these populations. Urban kestrels that bred in the city centre were indicatively more related than others, and no relationship was found in the rural kestrel population. Kestrel females were heavier towards the city centre, but males did not show this relationship. Nest distance from the city centre had no significant effect on any of the tested reproductive parameters. Our results do not support the notion of genetic differentiation between rural and urban kestrels, but revealed trends in body characteristics and genetic relatedness along the urbanization gradient.

Keywords Assignment test · Genetic variability · Microsatellite · Population ecology · Raptor · Site fidelity

Introduction

Among raptors, the common kestrel (*Falco tinnunculus*) has most successfully colonized European cities (e.g., Kuźniak 1996; Luniak et al. 2001; Fuchs et al. 2002; Weissmair et al. 2002). Consequently, their ecology has changed in several aspects. The density of urban kestrels is higher than that of rural populations (e.g., Salvati et al. 1999; Plesník 1992). The reproductive success of kestrels in cities is more stable over time compared to rural populations, e.g., Prague versus Eastern Bohemia (Plesník 1992). The choice of nest site has changed as well, since rural kestrels usually use abandoned corvid nests (Prokop 2004), while urban birds prefer semi-closed holes on buildings, e.g., loft-windows (Darolová 1992; Wassmer 2001; Riegert 2005). The breeding success of kestrels that occupy semi-closed holes (or nest boxes) is usually higher compared to tree-nesters (Hasenclever et al. 1989; Plesník 1992; Fargallo et al. 2001). Kestrels that breed in city centres have to fly to distant hunting grounds inhabited by its main prey, *Microtus* voles (Cramp and Simmons 1987). As a consequence, kestrels from large cities enrich their diet with birds, especially small passerines and young feral pigeons (Yalden 1980; Korpimäki 1985; Darolová 1989; Plesník 1992; Romanowski 1996; Piattella et al. 1999; Salvati et al. 1999). The kestrels in the small- to medium-sized urban area of České Budějovice, Czech Republic, feed mainly on small mammals, especially on common

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voles (*Microtus arvalis*) (Riegert and Fuchs 2004). Some differences have already been found by comparing the hunting effort and success of urban and rural kestrels in České Budějovice. Urban kestrels had lower hunting success and hunted with higher effort than rural kestrels. The lower effectiveness of the urban population may be because they frequented unfamiliar hunting grounds, often changing them due to competition with the periphery kestrels (Riegert et al. 2007a).

Recently, particular differences between urban and rural population were described at the genetic level. Comparison of genetic data of kestrel chicks among urban, suburban and rural population in a Warsaw district showed significantly higher polymorphism of the rural population (Rutkowski et al. 2006).

In the light of these findings, we tested the differences between rural and urban kestrels in South Bohemia. The main objectives of this paper were to (1) assess the genetic variability of the studied kestrel populations, (2) check the genetic relatedness of individuals along the urbanization gradient, and (3) compare body characteristics and reproductive parameters of individuals along this gradient.

Materials and methods

Study area and kestrel population

The study was conducted during the breeding seasons 2002–2006 in the České Budějovice basin (Českobudějovická pánev), South Bohemia (49°N, 14°E; 30 km^2, 100,000 inhabitants, 250–300 m a.s.l.) and its rural surroundings of approximately 100 km^2 (370–400 m a.s.l.). The urban population included pairs from České Budějovice, where kestrels usually bred in loft-windows, holes or nest-boxes on buildings, with the highest breeding density in the city centre (Riegert 2005). The rural population was located in a farmland northwest of České Budějovice, where the kestrels mainly used the abandoned nests of magpies (*Pica pica*) on electric pylons. The population of kestrels in České Budějovice is annually composed of a mean of 35.6 breeding pairs, with a breeding density of 1.2 pairs/km^2 (Riegert et al. 2007b), while the size of the farmland population was approximately 20 pairs each year and a breeding density of 0.7 pairs/km^2 (Mikeš 2003).

Field data collecting

We assessed the summer availability of small mammals for both populations independently from 1997 to 2006 on kestrel hunting grounds (for details, see Mikeš 2003; Riegert et al. 2007b). The kestrels were trapped near their breeding places using an imitation eagle owl (*Bubo bubo*). The animals were caught with a mist-net with a 50 mm mesh, when they were incubating their eggs or when their chicks were hatching. Up to 0.2 ml of blood per individual was collected from *v. axillaris* and preserved in 96% ethanol.

We gathered blood samples from 20 rural (17 males and 3 females) and 49 urban kestrels (32 males and 17 females). In total, 49 adult males (2002: 1; 2003: 18; 2004: 13; 2005: 14; and 2006: 3) and 20 adult females (2002: 1; 2003: 8; 2004: 4; 2005: 5; and 2006: 2) were trapped. We caught both individuals of a pair in ten cases. The distribution of nests was deliberate in the urban population, as more individuals bred in the city centre, and it was concentrated on a high-voltage transmission line for rural kestrels (Fig. 1).

The examination of an array of body characteristics included data from kestrels that were trapped before the start of this study, thus not subjected to genetic analysis. The total of 96 individuals was studied (26 females and 70 males). Body weight was obtained using Pesola scales (max 300 g), and tarsus length using a slide calliper and wing length using a ruler. The crop of each individual was also palpated for the presence of prey in its crop. The equivalent mean spring vole weight for our study area (22 g; Kapoun 2007) was subtracted from the body weight of individuals that consumed prey.

Data on reproductive success was performed only for the urban population, because access to electricity pylons was restricted. We used data from years 1997–2005, from a total of 112 urban kestrel nests in České Budějovice and a minimum of five visits per nest (1997: 16; 1998: 10; 1999: 13; 2000: 9; 2001: 9; 2002: 10; 2003: 10; 2004: 16; and 2005: 19). We recorded the number of eggs and chicks during rearing as well as the number of fledged young.

Laboratory work

We used genetic markers developed for the peregrine falcon (*Falco peregrinus*) (Nesje et al. 2000), whose suitability for the common kestrel has been recently demonstrated by several studies (Hille et al. 2003; Rejt et al. 2004; Casagrande et al. 2006; Rutkowski et al. 2006). All samples were analyzed at 7 microsatellite loci: NVH fp86-2, fp82-2, fp79-4, fp46-1, fp31, fp13, and fp5. Total DNA was extracted from blood samples using the Jet Quick–Blood Cell Culture DNA Spin Kit (Genomed) according to the manufacturer's protocol and stored at −20°C. For polymerase chain reaction (PCR), we used the HotStarTaq DNA Polymerase kit (Qiagen) according to the recommended protocol. A 25-µl reaction mixture contained template DNA (mean concentration ± SD: 65 ± 37 µg/ml), 10 pmol of labelled (forward) primer, 10 pmol non-labelled (reverse) primer. The amplification reaction was carried out

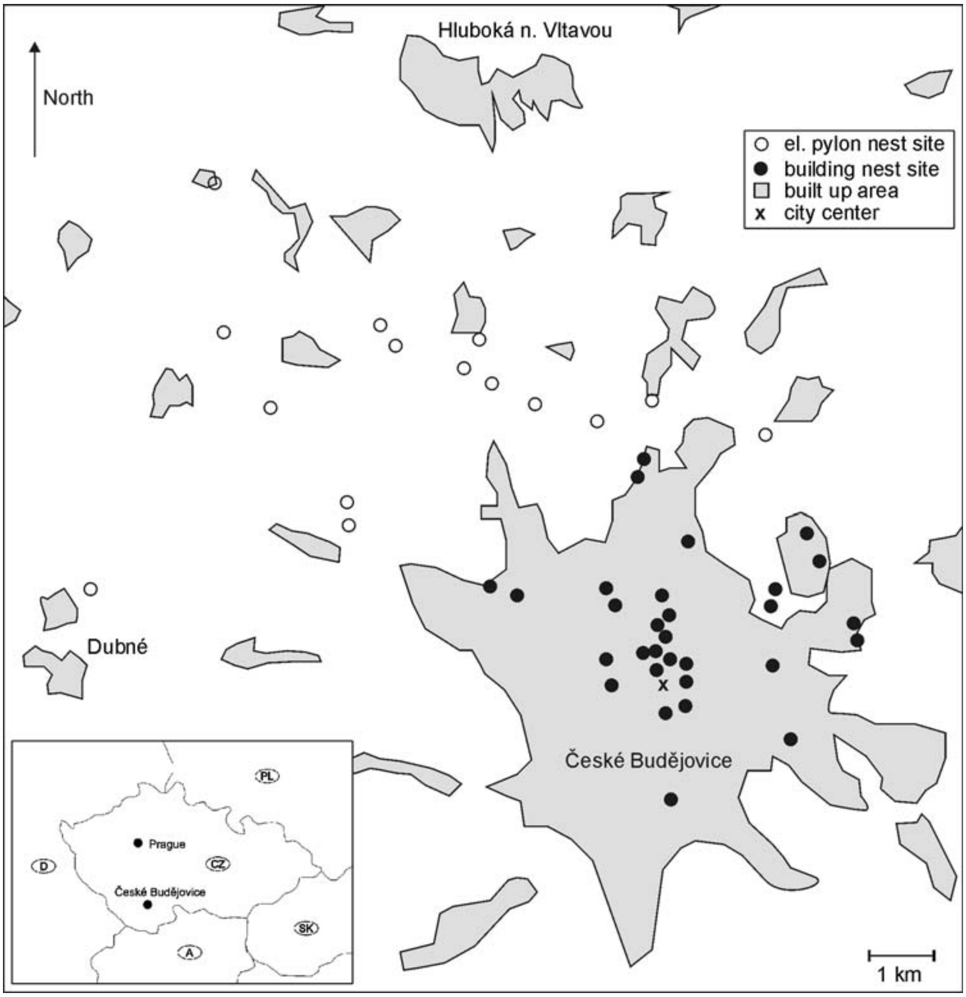

Fig. 1 Distribution of urban and rural common kestrel (*Falco tinnunculus*) nests

in the following manner: 94°C/15 min, 35 cycles of 94°C/1 min, 55°C/1 min and 72°C/1 min. Final extension was done at 72°C for 10 min. For fragment analysis, 0.5 µl PCR products were diluted and mixed with 10.25 µl formamide and 0.25 µl internal lane standards (500-LIZ; Applied Biosystems). The amplified fragments were subsequently analyzed on an ABI 3130 (Applied Biosystems). DNA fragment sizes were estimated using GeneMapper v. 3.7 software.

Statistical analyses

We analyzed three main datasets: genetic data (rural and urban populations), body characteristics (rural and urban populations), and reproductive parameters (urban population). These datasets did not overlap for all individuals. For example, the reproductive output of some nests was not possible to gather or the terrain was not suitable for trapping and vice versa. Additionally, we tested the distribution and quality of nesting holes along the gradient of urbanization for the city population, because the nest position and nest quality may influence the nesting site choice.

We performed the linkage disequilibrium tests in Arlequin (Schneider et al. 2000). The results showed that the loci were unlinked (Chi-square tests, *P* at least 0.41). Within-population H-W equilibrium tests were computed using 100 172 permutations, using Fstat v. 2.9.3.2 (Goudet 2001, http://www.unil.ch/izea/softwares/fstat.html). The loci were also checked for frequency of null alleles using the ENA correction in the FreeNA software (Chapuis and Estoup 2007). Genetic differentiation of the populations was assessed using F_{ST} (Weir and Cockerham 1984). Additionally, we used an individual assignment test (Rannala and Mountain 1997) to visualize our results. The test was completed using 20,000 bootstraps, implemented in Arlequin (Schneider et al. 2000). The significance of the differences between populations in observed and unbiased expected heterozygosity (Nei and Roychoudhury 1974) and allelic polymorphism (Petit et al. 1998) were analyzed using the Wilcoxon matched pairs test in STATISTICA 5.5 (Statsoft Inc. 2006).

Spatial distribution of genetic variability was tested in two ways. First, we compared genetic versus geographic distance for all couples of individuals (data pooled from both populations) using the Mantel test. Second, we tested the similarity of allelic occurrence (0–1) among individuals along the gradient of urbanization for urban and rural kestrels separately using RDA analysis facilitated by the Canoco program (Braak and Šmilauer 1998). We chose the distance of nest from city centre as the key parameter for establishing the urbanization gradient. České Budějovice is a more than 700-year-old settlement with historical "core", towards which the built-up area proportion increases. The effect of nest distance from the city centre to allelic occurrence was tested by the Monte Carlo permutation test using 1,000 permutations. Mantel tests to determine genetic and geographic distances were computed using the Passage software.

The correlations of body characteristics (body weight, wing length/body weight, tarsus length/body weight) and reproductive output (egg number, chick number, number of fledged young) with the distance of the nest from the city centre were performed by single regression using STATISTICA 5.5 (Statsoft 2006). We tested male and female body characteristics separately, because the males were (on average) 55 g lighter than females (mean ± SD, males: 192.2 ± 17.4 g, $n = 70$; females: 246.9 ± 23.2 g, $n = 26$). We used vole abundances (related to each population separately) as a covariate to eliminate its negative impact when voles were scarce.

For additional analysis of nest site characteristics, we used only urban nest sites on buildings (76.7% of all recorded nest sites), because nest boxes do not represent "natural" places suitable for nesting. In total, we examined 33 nests. We recorded the height of the nest above ground (m) and nesting-hole volume (cm^3). These parameters were tested along the urbanization gradient (distance of nest from city centre) using single regression in STATISTICA 5.5 (Statsoft 2006).

Results

Genetic variability

The test showed that the distribution of alleles in locus NVH fp79-4 significantly differed from H-W equilibrium in both kestrel populations (H-W equilibrium tests, $P_{(\mathrm{rural})} = 0.001$, $P_{(\mathrm{urban})} = 0.001$). Therefore, we excluded the locus from further analyses. We also found increased occurrence of null alleles in the locus NVH fp79-4 (by frequency 0.245), which was already excluded from further analyses. After exclusion, the F_{ST} values were similar in all loci (95% confidence interval for: F_{ST} using ENA, 0.0112–0.0057 and F_{ST} not using ENA, 0.0083–0.0071).

The mean heterozygosity of the examined loci did not differ significantly between the populations (Table 1; Wilcoxon matched pairs test, $Z = 0.17$, $P = 0.866$) and the studied populations exhibited a similar degree of allelic richness (Table 1; Wilcoxon matched pairs test, $Z = 1.26$, $P = 0.208$). The populations were not genetically differentiated from each other ($F_{ST} = 0.0003$, 95% bootstrap percentile values, 0.0113–0.0060, $P = 0.781$), which was supported by the individual assignment test (Fig. 2).

The positive relationship between genetic and geographic distances from the pooled data of both populations was indicative (Mantel test, $r = 0.04$, $P = 0.0581$). When we tested the direct effect of nest distance from city centre to allelic similarity for each population separately, we obtained different results. We found indicative effect of the factor for the urban population (Monte Carlo permutation test, $F = 1.28$, $P = 0.0893$, $n = 49$). Individuals that bred near the city centre were more related to each other than individuals from the periphery. For the rural population, this relationship was not significant (Monte Carlo permutation

Table 1 Main characteristics of common kestrel (*Falco tinnunculus*) genetic diversity

Locus	Range	No. of alleles		Allelic richness		Heterozygosity observed		Heterozygosity expected		F_{IS}		P	
		R	U	R	U	R	U	R	U	R	U	R	U
NVH fp86-2	136–142	4	4	3.93	3.82	0.75	0.74	0.54	0.59	−0.4	−0.25	0.164	0.001
NVH fp82-2	128–140	7	7	5.65	5.51	0.45	0.61	0.69	0.66	0.36	0.07	0.047	0.135
NVH fp46-1	118–128	5	6	4.87	5.11	0.6	0.43	0.71	0.63	0.16	0.33	0.297	0.013
NVH fp31	130–140	5	5	4.58	4.44	0.35	0.49	0.64	0.61	0.46	0.19	0.008	0.164
NVH fp13	92–100	5	5	4.73	4.74	0.65	0.63	0.64	0.65	−0.02	0.03	0.577	0.174
NVH fp5	102–122	9	11	7.36	8.05	0.85	0.74	0.82	0.81	−0.03	0.10	0.409	0.094
Mean		5.83	6.33	5.19	5.28	0.61	0.61	0.67	0.66	0.09	0.08		

The level of statistical significance after Bonferroni correction was set at 0.008

R Rural population, *U* urban population

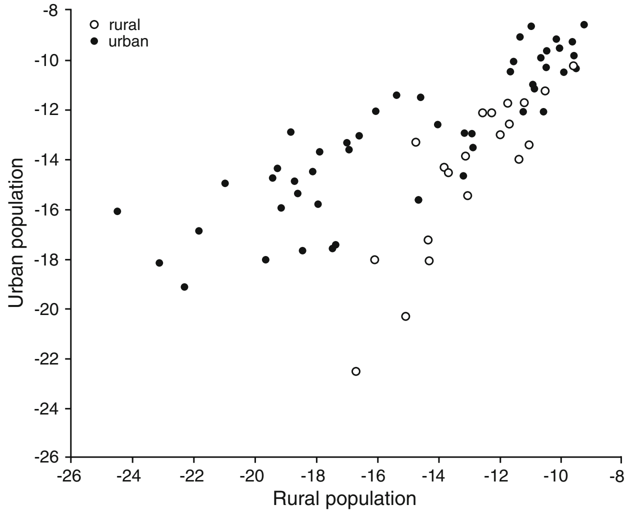

Fig. 2 Assignment of individual kestrels to urban and rural populations (log-likelihood values, individual assignment test)

Table 2 Statistical results for body characteristics of kestrels on the urbanization gradient

Sex (*n*)	Parameter	*r*	R^2	*P*
Males (70)	Body weight	−0.13	0.02	0.2826
	Wing length/body weight	0.12	0.01	0.3336
	Tarsus length/body weight	0.10	0.01	0.4123
Females (26)	Body weight	−0.41	0.17	0.0362
	Wing length/body weight	0.51	0.23	0.0106
	Tarsus length/body weight	0.55	0.30	0.0052

Pooled data from urban and rural population, single regressions (covariate: vole abundances)

test, $F = 1.014$, $P = 0.4420$, $n = 20$). A comparison of genetic variability within each sex was not significant (Monte Carlo permutation tests, males: $F = 0.876$, $P = 0.2621$, females: $F = 0.924$, $P = 0.5420$).

Body characteristics and reproductive output

Kestrel females (from both populations) showed a significant correlation between body characteristics and distance of nest from city centre, but males did not show this relationship (Table 2). Females breeding closer to city centre were heavier (Fig. 3) and showed lower proportion of both tested indices (wing length/body weight, tarsus length/body weight).

Nest distance from the city centre did not significantly affect any of the tested reproductive parameters in urban kestrel population: egg number (single regression, $r = 0.09$, $R^2 = 0.008$, $P = 0.3536$, $n = 112$), chick number (single regression, $r = 0.01$, $R^2 < 0.001$, $P = 0.9094$, $n = 112$) or number of fledged young (single regression, $r = -0.04$, $R^2 = 0.001$, $P = 0.7034$, $n = 112$).

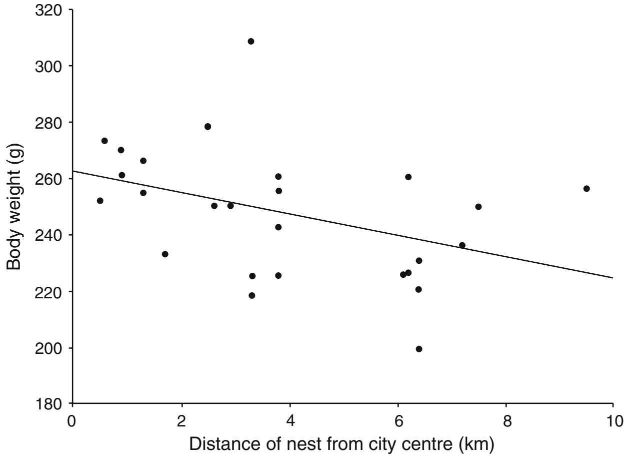

Fig. 3 The relationship between female body characteristics and distance of nest from city centre (regression, covariate: vole abundance, $P < 0.05$, $n = 26$)

Nest site characteristics

Active nest sites occurred mainly in the city centre (Fig. 4a). We did not find any relationship between the volume of nesting hole and nest distance from city centre (single regression, $r = 0.05$, $R^2 = 0.003$, $P = 0.7639$, $n = 33$), but the nest holes in the centre were situated higher above the ground than those in the periphery (single regression, $r = -0.59$, $R^2 = 0.342$, $P = 0.0002$, $n = 33$, Fig. 4b).

Discussion

Genetic variability between populations

It has been proposed that populations separated by different life styles or geography may lead to genetic differentiation (Andrzejewski et al. 1978; Gehlbach 1996). The urban population of kestrels described here ecologically differs in many ways from their rural counterparts. They occupy nesting sites on buildings, show high and stable reproductive output (Riegert et al. 2007b), and do not defend their hunting ranges (Riegert et al. 2007a, c). However, we did not find any marked genetic differences between the studied populations. Rural and urban kestrel populations showed a similar degree of genetic polymorphism, which is in concordance with a study on various kestrel populations in Warsaw and its surroundings (Rejt et al. 2004; Rutkowski et al. 2006). These authors also reported higher genetic variability for rural populations and supposed that

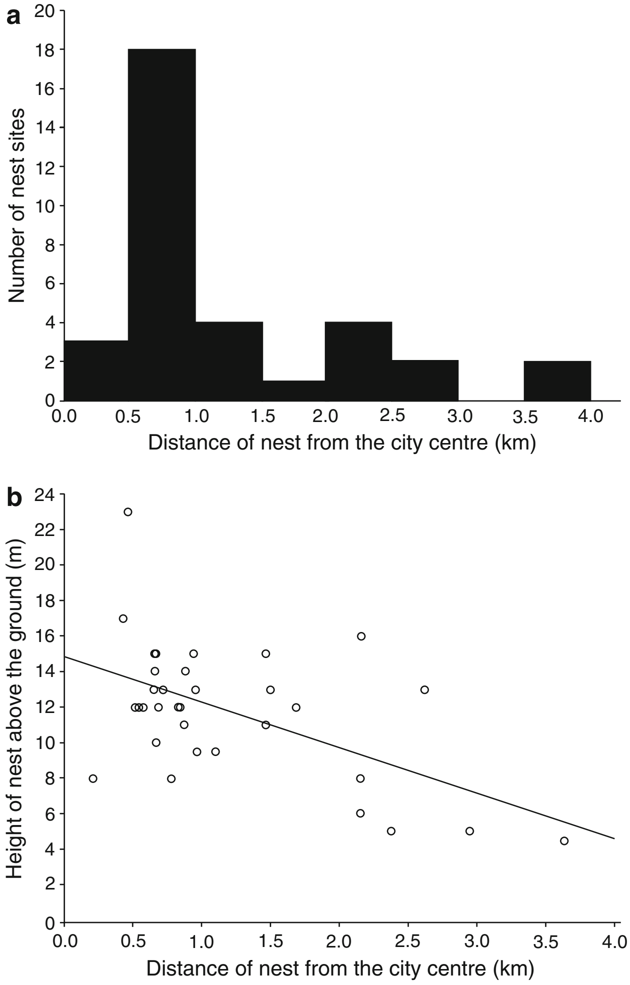

Fig. 4 Nest site characteristics of urban kestrels along the urbanization gradient: **a** distribution of nests, **b** height of nest above the ground

gene flow from the rural kestrel population to the city might be stronger than vice versa. Our results do not agree with these findings. The allelic richness of the kestrel populations studied in České Budějovice was similar and the F_{ST} value was very low. Furthermore, the result of the individual assignment test did not reveal a significant degree of genetic differentiation of the studied populations. The possible reasons for this discrepancy may be the potentially extensive gene flow between the neighboring populations and the relatively small area of the built-up part of the city.

Genetic variability within populations

Individuals breeding close to each other were more genetically related than others. However, the correlation coefficient was weak and thus we analyzed these relationships for both populations separately. Urban kestrels that bred in the city centre were more related to each other while such a relationship was not found in the rural kestrel population. We suppose that the gradient of relatedness found may be correlated with some ecological trait, such as a higher re-occupation rate (or high site fidelity) of kestrels in that location. A relatively high re-occupation rate was also found in other cities in Europe (Salvati et al. 1999; Kübler et al. 2005), and our previous ringing data supports this interpretation. For rural kestrels, we recorded only three males staying for at least 2 years at one nest site, while urban kestrels were more faithful to their nesting sites (three females and seven males for at least 2 years at one nest site) (J. Riegert, unpublished data).

Body characteristics, reproductive success and nest site choice

We found a correlation between the measured body characteristics and nest distance from the city centre for urban kestrel females. We suppose that the mate choice of the urban kestrel females may be connected with other factors than quality of males, especially nest site quality. The nest site is primarily chosen by a male and is the subject of competition during early phase of the breeding season (Village 1990). In addition, nest site quality directly affects the female mate choice, since breeding success of kestrels that occupy semi-closed holes in cities is higher compared to other nesters (Hasenclever et al. 1989; Plesník 1992; Fargallo et al. 2001). According to our results, suitable nesting opportunities were available especially on the old-buildings that occur in the city centre, which are situated higher above the ground than those on the periphery. This observation is in agreement with the "general rule" of kestrel nest site choice in high buildings (Darolová 1992). The fact that heavier (and probably higher quality and/or older) females often breed in the city centre underscores our notion that they compete for suitable nesting sites. This competition possibly leads to the non-random distribution of urban kestrel females occurring in České Budějovice.

We did not find any significant relationship between the reproductive output and nest distance from city centre of urban kestrels. Breeding in urban areas can be quite dangerous, especially due to human activities, but the interpretation of this is complicated by the lack relevant reports about this topic. Unfortunately, we have no exact data on potential causes of nesting failure for our kestrels. However, Plesník (1992) recorded a 60.9% loss of young caused by human activity in Prague, while this figure was only 13% for farmland kestrels. Therefore, the apparent advantage of suitable nesting sites in the city centre can be counterbalanced by new possible risks, such as threats from humans.

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Příloha III

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Fidelity to roost sites and diet composition of wintering male urban Common Kestrels (*Falco tinnunculus*)

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Fidelity to roost sites and diet composition of wintering male urban Common Kestrels *Falco tinnunculus*

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Abstract. During harsh winters, partially migratory raptors face to making a decision whether leave their breeding sites or not. However, decision to leave brings advantages for maintaining own body condition, but also disadvantages for further reproduction. We studied individual variability in fidelity to roost sites during two winters. The kestrel males in České Budějovice (Southern Bohemia) roost near their breeding sites for most of the winter. Individuals occupy the same roost site continuously, unless they temporarily leave the city. We collected pellets at the males' roost sites from November to April in 1996/1997 and 1997/1998. We analysed the factors that affect males' presence (proportion of days with snow cover — PSC, snow depth and mean temperature). There were fewer absences, overall, in 1997/1998 than in 1996/1997, probably due to milder weather conditions, and better prey availability. Individuals responded differently to periods of snow cover; some males left the city but others remained. Males that remained had a higher proportion of non-vole prey (birds, insectivors and insects) in their diet compared to those that left. Moreover, the proportion of birds in diet was positively correlated with PSC in males that stayed at roost sites during the period with snow cover. We suggest that males able to feed on birds during snow cover could remain in the city in harsh winters, and this would give them an advantage during competition for breeding sites in the following spring.

Key words: diet composition, *Falco tinnunculus*, Kestrel, winter roost fidelity, urbanization

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INTRODUCTION

Mortality of wintering raptors largely depends on weather conditions and prey availability (Kostrzewa 1988). When the main prey becomes less available, raptors obviously exploit alternative ones (Village 1981, Angelstam et al. 1984, Korpimäki 1988, Jędrzejewski et al. 1994, Reif et al. 2001, Sánchez et al. 2009). When a snow cover occurs, vole eating specialists like Common Buzzard *Buteo buteo*, Common Kestrel *Falco tinnunculus* and Harriers *Circus* sp. shift to more available prey, such as carrion or birds (Kostrzewa & Kostrzewa 1991) or change their hunting techniques (Schipper et al. 1975). In partial migrants, some individuals leave the area and seek for a more suitable environment. However, a decision to leave breeding area is connected with disadvantages during following spring. For example, resident Common Kestrels in Scotland gained their mates earlier than migratory individuals (Village 1985). Similar results were obtained in Merlins *Falco columbarius* from Saskatchewan. On the other hand, non-migratory Merlins trapped in following summer were lighter than migratory ones (Warkentin et al. 1990).

The Common Kestrel is almost entirely migratory in northeast Europe. The northern limit of its winter distribution follows the line of the permanent winter snow cover (Village 1990). Populations breeding in Central Europe are partially migratory (Cramp 1987). Long-term data from the Czech Ringing Centre show that juveniles are migratory and leave their natal territories during late summer (Riegert 2008). Adult kestrels may or may not be migratory, with no apparent pattern. In agreement with results from other European countries, they usually stay at their breeding territories for a longer period than juveniles (Village 1990).

Among raptors, the Common Kestrel has settled in urban areas most successfully. Winter population density has been estimated in farmland (i.e. Village 1982, Voříšek 1991, Plesník 1992), but not in urban areas. This is because standard counting methods can not be used (Plesník 1992). Observations from several cities in Central Europe show that urban kestrels are often resident during the non-breeding season (Warsaw — Romanowski 1996, Manchester — Yalden 1980, Bratislava — Darolová 1989, Prague — Plesník 1992), roosting in the vicinity of their breeding sites (Cramp 1987), but a systematic study of wintering urban kestrels in Central Europe has not been done.

During the non-breeding season, resident kestrels at southern latitudes feed mainly on insect groups such as Orthoptera or Coleoptera (Piatella et al. 1999), but northern populations depend on small mammals, especially Microtinae voles (Village 1990). Therefore, kestrels wintering in Central Europe are likely to be more influenced by weather conditions due to presence of snow cover that can affect their ability to gain sufficient food. This implies that weather conditions might affect wintering habits of urban kestrels. Because snow cover makes voles less available (Canova 1989), we expected a lower proportion in the diet. On the other hand, birds are the only component of the diet, whose availability does not depend on snow conditions and may play a significant role as alternative prey during harsh winters (Żmihorski & Rejt 2007).

We analyzed changes in overall diet composition between the two winters, among individual males and the effect of distance between the roost site and the city centre. We also studied the patterns of wing-tagged male kestrel wintering in a small to medium sized city České Budějovice (Czech Republic). In agreement with findings from other central and western European cities, some kestrels were present close to the breeding sites for almost the whole year and they used stable sites for roosting (e.g. Yalden & Warburton 1979). Based on six-year observations (Riegert 2005), we can assume that the presence of females is restricted to the period between early spring (late January–March) and autumn (early November). Juveniles moved from the city earlier than females, most often during September. Therefore we concentrated on the roosting behaviour and diet of male kestrels. We tested 1) the effect of mean snow depth and the duration of snow cover on the occurrence of kestrels at roost sites during the winter. Since we recorded great individual differences in the wintering of males, we tested 2) if the diet composition of males that stay during snow cover in the city differs from those leaving their roost sites. For these males, we tested 3) if the proportion of birds and mammals in their diet correlates with mean snow depth and duration of snow cover.

MATERIAL AND METHODS

Field work

The study was conducted in České Budějovice (Southern Bohemia, altitude 300 m, 49°58´N, 14°29´E; area 40 km^2; radius 4 km; 100 000 inhabitants). The kestrel population includes 40–50 nesting pairs each year (Riegert & Fuchs 2004). Individuals were caught near their breeding sites using an imitation of Eagle Owl *Bubo bubo*. Male kestrels were wing-tagged in the 1996 breeding season using the methodology of Village (1982) and those males were the same individuals studied in both winters.

During the winters (November–February) of 1996/97 and 1997/98 we monitored the roost sites of eight wing-tagged male kestrels males using 1) regular two-weekly night controls using a flashlight to confirm the identity of a male, and 2) pellet collections. Roost sites were situated both in the city-centre and on the periphery, usually on building downspouts under the roof, and close to the breeding site used during breeding season. The minimum distance between roost sites was 200 metres (mean ± s.d.: 2600 ± 1100 m). Pellets were collected every 2–4 weeks from November to April (11 pellet collections in 1996/97 and 10 in 1997/98, mean ± s.d.: 12.6 ± 1.2 pellets per roost site and collection). The males were considered absent when we did not detect any pellets under roost sites and flashlight night controls confirmed this suggestion. Data on weather conditions were obtained from the Czech Hydrometeorological Institute in České Budějovice. For each interval between the collections, we calculated mean snow depth, mean daily temperature and proportion of days with snow cover within the interval (PSC)(Table 1).

Pellet analysis

The pellets were dried and all feather-remains were identified. The remainder was dissolved in a solution of NaOH (Schueler 1972). Small mammal species were determined using skull features described by Anděra & Horáček (1982) and bird species by beak and humeri using a reference

Table 1. Weather conditions during the winter 1996/97 and 1997/98. Winter duration is related to different number of controls (see Methods). PSC — proportion of days with snow cover in given time interval.

Winter	Mean snow height ± SD (cm)	PSC (%)	Mean temperature ± SD (°C)	Winter duration
1996/97	1.64 ± 1.92	43.3	3.05 ± 3.53	203
1997/98	0.75 ± 1.53	13.7	3.37 ± 2.49	186

collection. Insect remains were sorted into categories of similar size, shape and colour. For all diet components, the total numbers of fragments in each pellet (mandibles, pelvics, humeri, tarsi, elytrae and coxae) were divided by their occurrence in a prey body. The most numerous fragments defined the final number of prey items in a pellet. We identified 1632 prey items from 2122 pellets during the winters 1996/97 (835 prey items, 1156 pellets) and 1997/98 (797 prey items, 966 pellets).

Statistical analyses

The presence of kestrels at roost sites and the proportion of birds and voles in the diet were analysed using Generalized Linear Models (GLM, forward selection, logit or log link function respectively), which allows multi-factor tests on binomial models (McCullagh & Nelder 1989). The year factor was used as a covariate. The selection and order of factors in a model was defined by Mallows Cp-statistics (Mallows 1973). These factors included: mean temperature, mean snow depth, PSC and roost site (1–8). Mean temperature was negatively correlated with PSC (Spearman rank correlation, $r_s = -0.57$, $p = 0.006$). Thus, we used only PSC in further calculations. Besides weather factors, we used roost site to control spatial autocorrelations. We performed the following analyses: (i) factors determining the overall presence of males at a roost site were tested using the GLM model with binomial error distribution, additionally, (ii) we tested the effect of PSC on the occurrence of each male separately; for males that stayed at roost sites during snow cover (n = 4), we tested (iii) the effect of PSC on the proportion of birds and voles in the diet using GLM models with gamma error distribution; (iv) differences in diet composition between males that stayed at roost sites and those that left were computed using ANOVAs in STATISTICA software (Statsoft, Inc. 1996). We used Bonferroni's correction for results from dependent tests. The effect of winter, individual and distance of the nest from city centre (for details see Riegert et al. 2007) were tested by multivariate analysis (RDA, Monte Carlo permutation tests) using Canoco software (Braak & Šmilauer 1998) and visualised in CANODRAW (Šmilauer 1992).

RESULTS

Fidelity to roost sites

During the more severe winter of 1996/97 only one male was present continually all winter. This contrasted with the winter of 1997/98, when only a single male was absent for half the winter. GLM analysis showed that roosting habits of individual males differed significantly. In addition, the presence at the roost sites was negatively affected by the proportion of days with snow cover (PSC)(Table 2). We tested the effect of mean snow depth and PSC on the presence of each male at its roost site separately. The effect of snow depth had no significant effect on any male ($p \geq 0.13$ in all cases), but the effect of PSC separated the males into two groups. PSC had a significant negative effect on the occurrence of four males that during a period of snow cover in the winter of 1996/97 left their roost sites (males #1, 2, 5 and 7). In the other

Table 2. Factors affecting the presence of males at roost sites (8 males, n = 288 pellet collections, GLM binomial model) and factors affecting the proportion of birds and voles in the diet of males that stayed in the city during periods of snow cover (4 males, n = 66 pellet collections, GLM gamma models). Data pooled for both winters studied, factor year was used as a covariate.

Dependent variable	Independent variable	% of explained variability	β	p
Male occurrence at roost sites (0–1)	Roost site	11.4		0.005
	PSC	4.7		0.026
% of birds in the diet	PSC	12.2	0.43	0.002
	Roost site	3.0		0.431
% of voles in the diet	PSC	9.5	-0.45	0.018
	Roost site	9.3		0.058

Table 3. Presence of males at roost sites and the effect of PSC on the presence of individual males at roost sites (GLM binomial models), n = 36 controls for each male. Factor year was used as a covariate. * — the male was present in all controls.

Male #	% of controls the male was present		% of explained variability	β	p
	in 1996/97	in 1997/98			
1.	45.5	100.0	18.1	-0.62	0.060
2.	54.5	50.0	25.4	-0.53	0.027
3.	63.6	100.0	7.2	+0.42	0.268
4.	63.6	100.0	27.9	+0.48	0.017
5.	18.2	100.0	17.3	-0.54	0.057
6.	100.0	100.0	0.0	*	1.000
7.	54.5	100.0	29.5	-0.75	0.027
8.	81.8	100.0	12.5	+0.49	0.184

four males (#3, 4, 6 and 8), we recorded no effect or a positive effect and the males were faithful to their roost sites even during longer periods of snow cover (Table 3).

Diet composition

The Common Vole *Microtus arvalis* was the dominant component in the winter diet of all males (41.7–96.0% by numbers), followed mainly by insects (1.0–34.5% by numbers) and birds (0.0–16.1% by numbers). Insects were represented mainly by large Tettigonidae grasshoppers and Carabidae beetles, which proportion increases during the late autumn (Riegert & Fuchs 2004). Multivariate analysis showed that overall diet composition changed significantly between the two winters (RDA, Monte Carlo permutation test, F = 5.03, p = 0.012). The winter 1997/98 was characterized by increased proportion of voles and subsequent decrease of proportion of other diet items (Fig. 1). Diet composition significantly differed among kestrel male individuals (RDA, Monte Carlo permutation test, F = 2.79, p = 0.047), but we did not find significant effect of distance of nest from city centre (RDA, Monte Carlo permutation test, F = 0.53, p = 0.625).

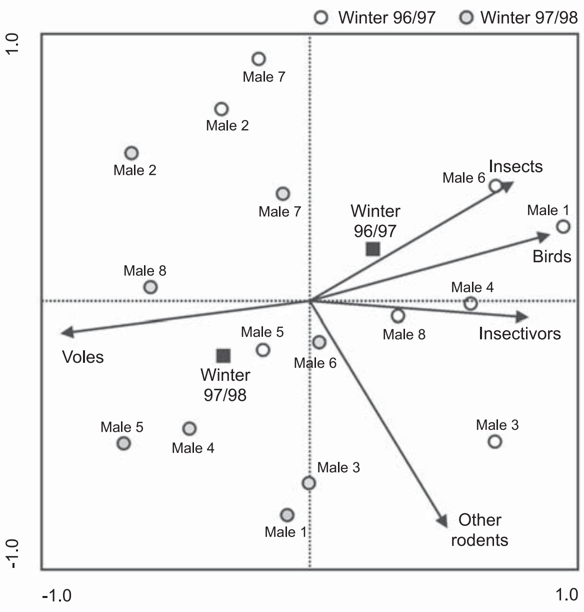

Fig. 1. Projection scores of main diet components for each kestrel male during the winter 1996/98 and 1997/98 with centroids for the years (RDA analysis).

The proportion of voles was significantly higher in the males that left their roost sites during snow cover (Table 4). In the males that stayed, voles were partially substituted by other rodents (genus *Mus*, *Apodemus* and *Micromys*), birds (genus *Passer*, *Parus* and *Turdus*) and shrews (genus *Sorex* and *Crocidura*), but the differences were indicative for only a proportion of other rodents. Further, we concentrated on the group of males that did not leave their roost sites. We found that the proportion of birds in their diet was positively correlated with PSC while the proportion of voles was negatively correlated (GLM, Table 2, Fig. 2). Other diet components were not affected. Individual differences in the proportion of birds and voles in the diet among these males were not significant (Table 2).

DISCUSSION

The duration of snow cover had a significant effect on the wintering habits of the studied male kestrels. However, the effect of PSC may be closely related to vole abundance. The second winter (1997/98) was milder compared to the first (1996/97). Simultaneously, between the summer of 1997 and 1998 the population density of the Common Vole increased dramatically (using pit-

Table 4. The overall percentages (mean ± SD) of diet components in the males that were present/absent during periods of snow cover (two tailed ANOVA, males #1, 2, 5, 7 vs. 3, 4, 6, 8). The limit of significance after Bonferroni's correction was set at 0.008. Significant results are marked with asterisk.

Diet component	Absent	Present	d.f.	F	p
Voles	79.8 ± 12.5	67.5 ± 20.9	1	6.22	0.005*
Other rodents	1.9 ± 3.2	8.3 ± 10.8	1	6.59	0.012
Insectivors	1.7 ± 2.1	0.0 ± 0.0	1	2.37	0.127
Birds	2.1 ± 11.3	6.5 ± 4.2	1	2.05	0.156
Other vertebrates	0.4 ± 1.4	0.4 ± 1.7	1	0.00	0.948
Insects	15.8 ± 17.6	15.6 ± 12.9	1	0.16	0.694

fall traps we caught 37 voles per 100 traps in July 1997 and 154 voles in 1998, Riegert 2005). Thus, we cannot separate clearly the effect of weather conditions and vole abundance in a sample of two winters. The weather conditions (the low number of days with snow cover) as well as good prey availability may have caused the continual winter presence of most of the males. The increased proportion of voles in the diet during the winter 1997/98 provides indirect evidence on the importance of vole availability to successful wintering. Also Village (1990) found a negative relationship between vole availability and winter mortality of kestrels.

The winter roosting of kestrels in urban areas has not been studied previously. Available data describe between-year changes in the density of wintering kestrels in farmland populations (e.g. Village 1990, Voříšek 1991, Plesník 1992). In these studies, the density of kestrels decreased with the increasing number of days with snow cover, whereas the temperature had not significant effect. Our data are partially in agreement with these results, the PSC had a significant effect on some males and the presence of males at roost sites differed significantly among individuals. In four males, presence was negatively affected by the PSC, but our data do not support a significant effect of snow cover depth.

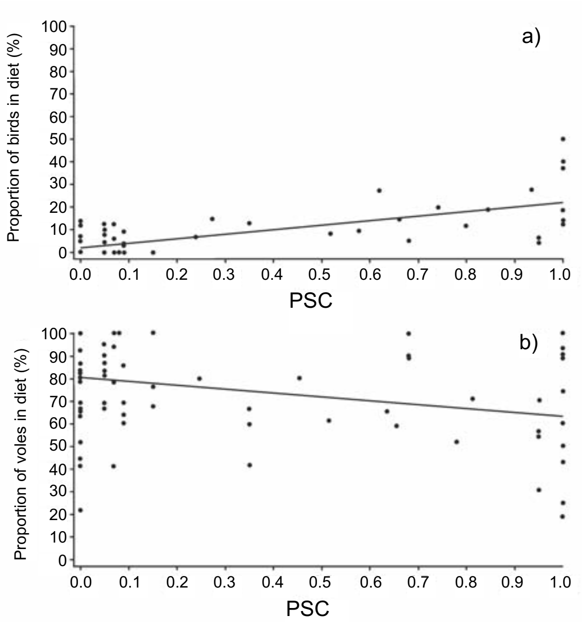

Fig. 2. The effect of the proportion of days with snow cover (PSC) to proportion of a) birds and b) voles in the diet of kestrel males that stayed in the city during the harsh winter 1996/97 (males # 3, 4, 6, and 8, n = 66 pellet collections).

The Common Vole is the most important prey in the winter diet of kestrels in České Budějovice (74% by numbers). Similar results were found by Żmihorski & Rejt (2007) in central Poland (62% by numbers). The proportion of voles in the diet was significantly higher in the males that left their roost sites during periods of longer snow cover in the winter of 1996/97. Other rodents, shrews and birds enriched the diet of males that remained during this period that is in concordance with alternative prey hypothesis (Angelstam et al. 1984). The overall proportion of birds in the kestrels' winter diet was lower in comparison to other urban populations at similar latitudes: this study 4.3%, Manchester 63.3% (Yalden 1980), Bratislava 17.5% (Darolová 1989), Prague 45.4% (Plesník 1992). This is probably caused by small area of the city when the kestrels mostly hunt on the city periphery (Riegert et al. 2007). In spite of the low proportion of birds in the diet, we suppose that they are essentially important for the wintering of kestrels, especially during periods with snow cover, when voles become less available (Canova 1989). In the males that remained, the proportion of birds in the diet increased with increased PSC. However, we cannot exclude a possibility that the differences in proportion of voles and birds in the diet of leaving and resident males is simply driven by the fact that we have no data on pellet composition for leaving males from middle of winter. So this lack of data can drive the differences. If this result is driven by the differences in wintering strategy, we suggest that feeding "opportunist" individuals may be better equipped for wintering than vole "specialists". Further, we suppose that only the males, which are able to supplement voles with birds, may outlast periods with snow cover in the city. This may bring them a competitive advantage for breeding sites in the following spring, increasing possibility to gather female early in the breeding season (Village 1985). As a consequence of physiological processes (Meijer et al. 1990), kestrel pairs breeding earlier in the spring have larger clutches (Dijsktra et al. 1982, Village 1986, Korpimäki & Wiehn 1998). Moreover, early breeding kestrel pairs obviously produce more chicks (Village 1990). Similar results have been documented for other raptor species — Bearded Vultures *Gypaetus barbatus* and Spanish Imperial Eagles *Aquila adalberti* (Margalida et al. 2003, 2007).

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STRESZCZENIE

[Przywiązanie do miejsc noclegowych i skład pokarmu samców pustułki zimujących na terenie miasta]

Ptaki drapieżne, których znaczną część bazy pokarmowej stanowią norniki, w czasie zimy mogą zmieniać swą dietę. Dodatkowo, gatunki należące do częściowo wędrownych mogą w okresie zimy przenosić się na bardziej odpowiednie tereny. Decyzja o porzuceniu lęgowiska może jednak negatywnie odbijać się na rozrodzie w kolejnym sezonie lęgowym z powodu m. in. zajęcia gorszego miejsca lęgowego.

W pracy badano czynniki wpływające na przywiązanie do miejsc noclegowych ośmiu osobników (wyłącznie samców) pustułki gniazdujących w Czeskich Budziejowicach. Analizowano zarówno czynniki pogodowe — wysokość i długość zalegania pokrywy śnieżnej i średnią temperaturę, jak i preferencje pokarmowe badanych ptaków. Badania prowadzono zimą 1996/7 i 1997/8 obserwując te same osobniki. Samce pustułek schwytano w sezonie lęgowym i wyznakowano indywidualnie znaczkami skrzydłowymi.

W okresie polęgowym samce pustułek nocują w pobliżu miejsc lęgowych. W okresie od listopada do lutego miejsca takie sprawdzane były co dwa tygodnie, w celu określenia obecności ptaków. W tych samych miejscach, co dwa-cztery tygodnie zbierano wypluwki. Nieobecność ptaka podczas nocnych kontroli oraz brak wypluwek wskazywały na czasową emigrację danego osobnika z miasta. Dla każdego okresu pomiędzy zbiorami wypluwek określano średnią wysokość pokrywy śnieżnej, średnią dzienną temperaturę oraz udział dni z zalegającą pokrywą śnieżną w całym badanym danym okresie (PSC). Jako, że średnia dzienna temperatura była skorelowana z udziałem dni z pokrywą śnieżną, tylko ta ostatnia zmienna została użyta w analizach.

Zimą 1996/7 obserwowano tylko jednego samca, który był obecny w mieście przez całą zimę, Natomiast zimą 1997/8, wszystkie badane ptaki były obserwowane zimą w mieście tylko jeden samiec opuścił teren badań na około połowę okresu zimowego. Wyniki te związane są z warunkami pogodowymi — zima 1996/7 była surowsza niż 1997/8 (Tab. 1), a zagęszczenie norników, a przez to ich udział w diecie pustułek — mniejszy (Fig. 1). Na obecność samców pustułki negatywnie wpływał udział dni z pokrywą śnieżną (Tab. 2, 3). Można wyróżnić dwie reakcje osobników związane z zaleganiem pokrywy śnieżnej. Część osobników odlatywała z miasta, pozostałe pozostawały w okolicy swoich lęgowisk. Te osobniki, które opuszczały lęgowiska, miały większy udział norników w diecie niż te, które zostawały blisko miejsc lęgowych (Tab. 4). Ponadto udział ptaków w diecie samców, które pozostawały w mieście, był pozytywnie skorelowany z udziałem dni z zalegającą pokrywą śnieżną, zaś udział w pokarmie norników — skorelowany negatywnie (Fig. 2). Autorzy sugerują, że samce, które potrafią żerować na pokarmie innym niż norniki podczas okresów z zalegającym śniegiem mogą pozostawać w mieście, co w konsekwencji może przynosić im korzyść w okresie lęgowym, gdy muszą współzawodniczyć o miejsca lęgowe.

Příloha IV

Riegert J, Lövy M, Fainová D. 2009:

Diet composition of Common Kestrels *Falco tinnunculus* and Long-eared Owls *Asio otus* coexisting in an urban environment

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Diet composition of Common Kestrels *Falco tinnunculus* and Long-eared Owls *Asio otus* coexisting in an urban environment

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We studied the dietary composition of urban populations of Common Kestrels (*Falco tinnunculus*) and Long-eared Owls (*Asio otus*) under fluctuating vole abundance in České Budějovice during 2002–2005. Common Voles were the dominant prey. In poor vole years, the dietary proportion of alternative prey increased in both species. Long-eared Owls fed more on mice and related rodents, whereas the Common Kestrels' diet shifted to insects. The different alternative diets may be due to species-specific daily activity, hunting techniques and/or hunting habitats. Furthermore, we examined the possible relationship between the distance from a nest to the city centre and the proportion of voles in the diet. The Kestrel diet was not markedly influenced by distance, but for Long-eared Owls an increasing distance was associated with an increasing dietary proportion of voles.

1. Introduction

The Common Kestrel (*Falco tinnunculus*) and Long-eared Owl (*Asio otus*) are two raptor species that have successfully moved into urban habitats. The Common Kestrel is the most frequent diurnal bird of prey in the cities of Central Europe (Riegert 2005). The first records of kestrels breeding in urbanized areas of the Czech Republic are from 1950s (Hudec 1986), and presently they inhabit all Czech cities in high densities (Šťastný *et al.* 2006). Similarly, in some Central-European cities, the breeding density of the nocturnal Long-eared Owl can be high (Prague: 0.29 pairs/km^2, Fuchs *et al.* 2002; Leszno: 0.16 pairs/km^2, Kuźniak 1996; České Budějovice: 0.31–0.50 pairs/km^2; Lövy 2007).

In farmland habitats both species primarily feed on small rodents, especially Microtinae voles (Village 1981, Village 1990, Korpimäki 1992). However, the urban environment differs from farmland, for example, in being free of large predators such as the Eagle Owl *Bubo bubo*, by increased threat from humans and by increased (or altered) nesting opportunities. Perhaps the most conspicuous difference between farmland and urban habitats is that vole abundance is higher in the former (Čiháková & Frynta 1996). Therefore, vole-eating predators are either forced to hunt voles outside the city and/or feed on alternative prey.

The coexistence of these vole-eating specialists has previously been studied in farmland areas (Korpimäki 1987), but data from urban areas have

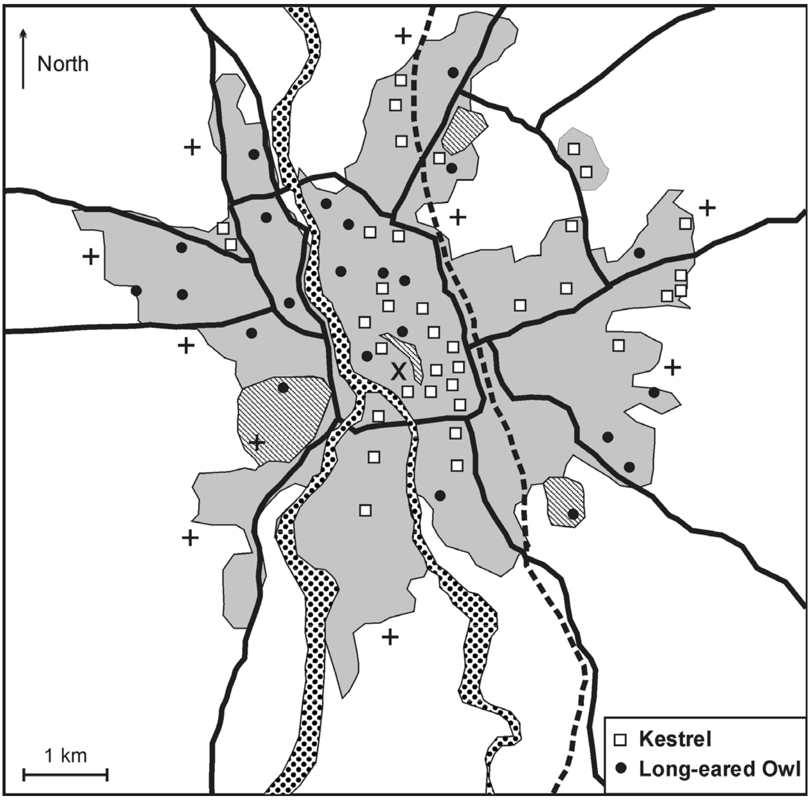

Fig. 1. Locations of Common Kestrel and Long-eared Owl nesting sites in České Budějovice. Grey area = built-up land; striped area = park or cemetery; dotted area = river; solid line = main road; dashed line = railway; x = the city centre; + = vole-trapping site.

been lacking. Neighbouring pairs of Kestrels and Long-eared Owls in Finland have shown less diet overlap than more distant nesters, and the extent of diet overlap has been shown to correlate with the availability of small mammals (Korpimäki 1987).

Our study is the first to investigate the diet of Kestrels and Long-eared Owls in urban conditions simultaneously. Our aim was to compare the dietary composition of these two species over a four-year period of fluctuating vole availability across an urban-rural gradient in České Budějovice, Southern Czech Republic. We made three predictions regarding vole availability, in concordance with the optimal diet theory (Pyke 1984). (1) With decreasing vole abundance the proportion of alternative prey should increase in the diet of both species. (2) Alternative prey should be different for Kestrels and Long-eared Owls due to different daily activities, hunting techniques and/or interspecific competition. (3) For both species, the proportion of main vole prey in the diet should be higher for pairs breeding far away from as compared to those breeding near to the city centre.

2. Material and methods

The study was conducted in the city of České Budějovice (Southern Bohemia, 49°N, 14°E; 40 km^2; 100,000 inhabitants; 250–300 m a.s.l.). Long-eared Owls breed in old Magpie (*Pica pica*) nests, often in parks (Fig. 1). Kestrels breed in old buildings, with the highest breeding density being in and adjacent to the city centre (Fig. 1). The population size of Long-eared Owl in the city area is up to 15 breeding pairs each year, while Kestrels have up to 40 breeding pairs each year. The land-cover composition (proportion of different habitat types) changed less than 3% at any Owl/Kestrel hunting area during the study period (for details, see Riegert *et al*. 2007).

The availability of the Common Vole (*Microtus arvalis*) was assessed each year. Voles have been studied from 1997 to 2005, with abundance peaks in 1998, 2002 and 2005. One hundred plastic two-litre pitfall traps, with 4% formaldehyde as killing and preserving agent, were installed at a total of ten Kestrel and Long-eared Owl hunting ar-

Table 1. Diet composition (percent of all prey items; mean ± SD) of Common Kestrels and Long-eared Owls during 2002–2005 in České Budějovice. # items = number of prey items in the data; # nesting = number of recorded nesting attempts.

Year	Microtinae	Muridae	Other mamm.	Birds	Other vertebr.	Insects	# items	# nesting
Kestrel								
2002	87.5 ± 5.2	2.1 ± 2.3	0.7 ± 0.5	2.7 ± 2.4	1.4 ± 1.9	5.6 ± 5.2	301	9
2003	74.3 ± 7.6	2.5 ± 2.0	0.9 ± 1.1	5.9 ± 3.0	1.5 ± 1.8	14.9 ± 9.9	223	7
2004	93.5 ± 6.9	0.5 ± 1.1	0.2 ± 0.4	0.3 ± 1.2	1.7 ± 5.7	3.8 ± 3.7	408	15
2005	90.6 ± 7.1	0.9 ± 1.6	0.7 ± 0.7	1.9 ± 2.2	1.4 ± 1.7	4.5 ± 4.8	692	19
Long-eared Owl								
2002	90.1 ± 5.9	7.3 ± 5.0	0.5 ± 0.8	2.1 ± 1.7	0	0	1,304	8
2003	68.9 ± 12.5	23.5 ± 9.5	2.9 ± 3.6	4.7 ± 4.2	0	0	1,351	10
2004	60.2 ± 5.2	35.3 ± 6.7	1.5 ± 2.4	3.0 ± 1.6	0	0	334	4
2005	87.7 ± 4.0	10.0 ± 0.3	0.2 ± 0.3	2.1 ± 2.1	0	0	1,060	11

eas (Fig. 1). Transects of ten traps at each of the ten areas in the second half of the July, active for 17 days, were used each year. Six transects were placed in meadows and four in urban wastegrounds (ruderal areas).

Nesting attempts and diet composition were assessed from April to July each year during 2002–2005. Nests were regularly visited to verify nesting attempts. Food composition was assessed from 33 nests of Long-eared Owl and 50 nests of Common Kestrel (Table 2). At the end of each breeding season, pellets and all remains of prey (feathers of birds, body parts of bats and lizards, etc.) were collected inside of and adjacent to the Kestrels' nesting cavities, and from the Long-eared Owl nests. Small mammals were determined by identifying skulls using Anděra and Horáček (1982), and birds by beak and humeri using a reference collection. Remains of insects were sorted into categories of similar size, morphology and colour. The numbers of voles, mice and shrews were determined by the number of jaws found, while the number of birds was estimated by detected feathers.

Multivariate Regression Trees (MRT) based on Euclidean distances (De'ath 2002) were used to test the first and second predictions. The analysis was computed using R 2.8.1 software (R Development Core Team 2008). Each nesting attempt represented a sample, and the proportion of each component (voles, mice, birds, other mammals, vertebrates and insects) in the diet represented 'species' for the purpose of analysis. Raptor species (Owl/Kestrel) and study year were used as explanatory variables.

Generalized Linear Models (GLMs) were used to test the third prediction, viz. the impact of distance from a nest to the city centre on the dietary proportion of voles (the main prey for both species). As the availability of voles was expected to decrease toward the city centre (Čiháková & Frynta 1996), the proportion of voles in diet was used as the dependent variable and the distance from a nest to the city centre was used as an explanatory variable. Each nesting attempt was used as an independent replicate (sample); for pseudoreplication possibility, see below.

A Gamma error distribution was assumed and an inverse link function used (McCullagh & Nelder 1989) and forward selection of factors using Mallow's Cp-statistics were used to select the final model (Mallows 1973). The GLM factors were the distance to the city centre (an approximation of urbanization), raptor species, and an interaction between these two. Vole abundance was used as a covariate. The same analysis was also run for the Owl diet only.

Using every breeding attempt as an independent data point might introduce pseudo-replication (Hurlbert 1984). However, for both raptor species the observed nesting patterns suggest this problem to be negligible. For Long-eared Owl, no repeated breeding at the same nest was documented for consecutive years, and for Kestrels, only three pairs stayed at the same nesting site for two consecutive years. These findings were supported by wing-tag-

Fig. 2. Multivariate regression tree based on Euclidean distances for the Common Kestrel and Long-eared Owl diets (variance explained = 0.56). Diet bars, from left to right: Microtinae, Muridae, other mammals, birds, other vertebrates and insects.

ging Kestrels and using radio telemetry for both species (Riegert *et al.* 2007a, Lövy 2007).

The annual diversity of diet composition was computed using the standardized Gibson Index (Colwell & Futuyma 1971), and diet overlap was assessed according to Pianka (1974). The data unit was represented by the sum of individuals for each species or genus, depending on the accuracy of identification.

3. Results

The Common Vole was the most frequent species, making up to 79.6% of all trapped small mammals, followed by shrews (17.9%) and harvest and field mice (2.6%). The highest numbers of voles were caught in 2002 and 2005 (79 and 98 individuals, respectively). The years 2003 and 2004 were characterised by low occurrences of voles (20 and 21 individuals, respectively). The number of voles per 100 traps varied significantly between years (Chi-square test; $\chi^2 = 87.4$, df = 3, $P < 0.0001$).

The diet composition of both species changed across the study period, but Common Voles remained the dominant prey, making up over 60% of all prey items in both species (Table 1). Both species took more alternative prey in the poor vole year of 2003, and Long-eared Owls did so also in 2004 (Table 1, Fig. 2). However, the alternative prey differed between the two species (Fig. 2; 56% of variance explained in the MRT). In the diet of Long-eared Owl, the most frequent secondary prey were mice (*Apodemus, Micromys, Mus* and *Rattus*). In years with poor vole availability, mice comprised a considerable part of the owl diet (Figs. 2–3).

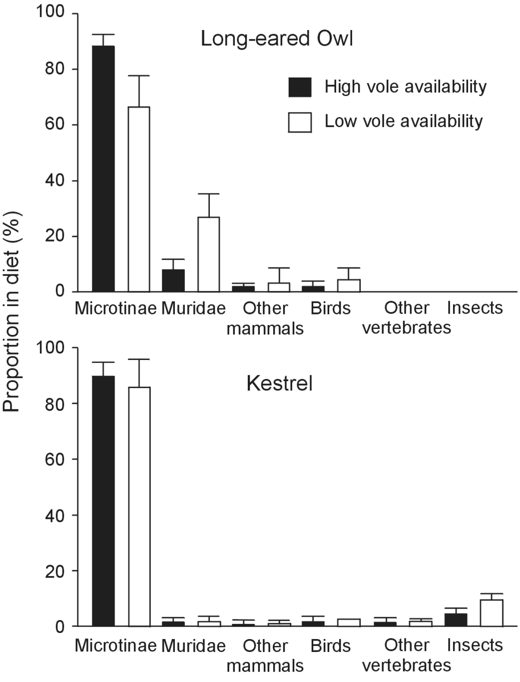

Fig. 3. Mean (± SD) proportions of diet items in the diets of Common Kestrel and Long-eared Owl during good (2002, 2005) and poor (2003, 2004) vole years.

Table 2. Diet composition (Gibson's index) of Long-eared Owls and Common Kestrels, and their diet overlap during 2002–2005 in České Budějovice. The right-hand column refers to the number of voles caught per 100 traps.

Year	Long-eared Owl	Kestrel	Overlap	Voles /100 traps
2002	1.27	1.27	0.78	79
2003	2.09	1.60	0.51	20
2004	2.43	1.46	0.43	21
2005	1.33	1.17	0.80	98
Mean	1.78	1.38	0.63	218

Kestrels had a more diverse diet than Long-eared Owls (Table 2). For example, Kestrels used a higher proportion of insects than did Short-eared Owls, particularly in 2003 (Fig. 2, Table 1). The insect prey mainly comprised ground beetles (Carabidae) and grasshoppers (Tettigonidae). The diet overlap between the two species was lower in the poor vole years of 2003 and 2004 (0.43–0.51) than in good vole years (0.78–0.80).

The dietary proportion of voles significantly differed between the two species (GLM, 12.2% of variation explained df = 81, F = 12.77, P = 0.0006). The distance between nest and city centre alone had no impact on the proportion of voles, when tested using pooled Kestrel and Long-eared Owl data (GLM; $P > 0.2$). However, the interaction between distance and raptor species was marginally significant, suggesting a species-specific distance response (GLM; 8.1% of variation explained, df = 79, F = 5.69, P = 0.0916). Kestrel diet was not influenced by the distance between nest and city centre, but Long-eared Owl individuals breeding further from the city centre had a higher proportion of voles in their diet than those breeding closer (Fig. 4). A separate analysis of Long-eared Owl diet along the urbanization gradient confirmed this distance response (GLM; 7.1% of variation explained, df = 31, F = 5.93, P = 0.0212).

4. Discussion

The diet of raptors may change when they inhabit urban areas. For example, Kestrels in large cities often enrich their diet with birds (Witkowski 1962, Beichle 1980, Darolová 1986, Romanowski 1996). However, we did not observe such a switch in České Budějovice. The proportion of birds was consistently low. The proportion of *Microtus* voles was very high, however, resembling the diet composition of rural Kestrels. The proportions of Muridae, other mammals, birds and other vertebrates were generally low.

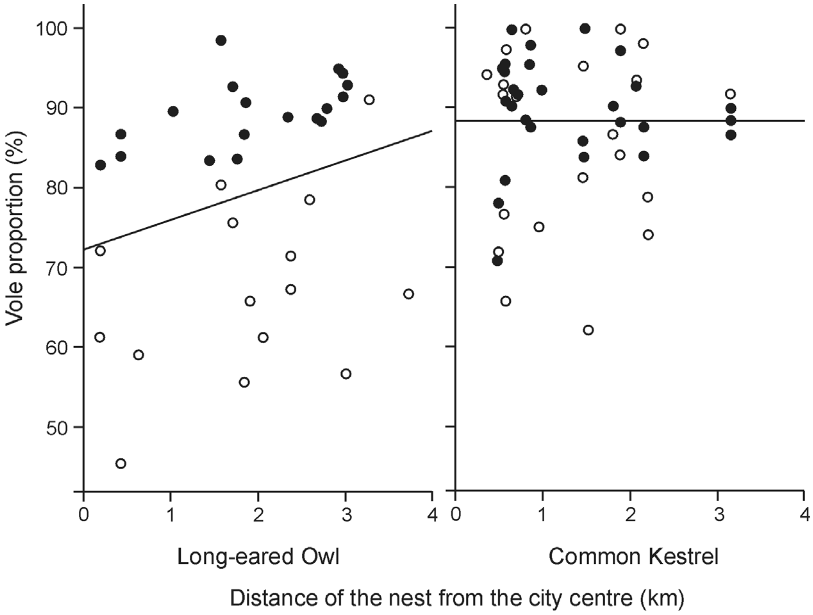

Fig. 4. The effect of distance between nest and city centre on the proportion of voles in the diets of Long-eared Owls and Common Kestrels. Filled circles = years of high vole abundance (2002, 2005); open circles = years of low vole abundance (2003, 2004).

The breeding-season foraging ecology of the Long-eared Owl in urban environments is poorly understood. In our study, *Microtus* voles were the most frequent prey. The observed food composition, with abundant voles, an increased proportion of Muridae and low proportion of other mammals and birds, is comparable with data collected from natural sites in Europe (Wijnandts 1984, Korpimäki 1992, Tome 2003). Moreover, we did not detect remains of insects in the diet of Long-eared Owl, which is in line with the above-mentioned studies.

Vole availability appeared to be the single most important factor determining diet composition for both Kestrel and Long-eared Owl, as voles formed the major portion of the diet for both species. Furthermore, the dietary proportion of voles generally decreases when this prey is scarce. However, Kestrel diet did not follow this trend, a result that is difficult to interpret. Nevertheless, the superior significance of voles (our first prediction) is in accordance with other studies dealing with this topic: for the Long-eared Owl, see Tome (1994, 2003) Korpimäki (1992) and Wijnandts (1984), and for the Kestrel, see Village (1982), Korpimäki (1985) and Korpimäki and Norrdahl (1991).

Insect abundance in Kestrel diet increased during vole scarcity, while Muridae represented an alternative prey for Long-eared Owls. Such dietary diversification was further supported by a smaller diet overlap during years of low as opposed to years of high vole abundance. Our results from a medium-sized city are consistent with those of Korpimäki (1987), who found a less pronounced diet composition overlap in sympatric Kestrels and Long-eared Owls during poor vole years in farmland. The different alternative prey between the two species may be partly explained by differences in daily activities (Korpimäki 1987) and different hunting techniques. Kestrels, as diurnal predators, hunt almost exclusively by sight, which is suitable also for catching ground beetles during daylight. Moreover, insect prey may often be taken after non-successful strikes, whose frequency increases during periods of vole scarcity (Riegert & Fuchs 2004). In contrast, the nocturnal Long-eared Owl hunts mainly by hearing (e.g., Henrioux 2000, Wijnandts 1984). Relatively quiet beetles do not represent a suitable alternative prey, and hence the mainly nocturnal Muridae species become the predominant alternative prey, supporting our second hypothesis.

Our third prediction was not fully supported by observations. Distance between nest and city centre had a marginally significant effect on the diet of Long-eared Owls, coinciding with the decreasing vole abundance (and consequently proportion in the owl diet) toward city centre. The difference between the two species is similar to our earlier results on hunting activities revealed by telemetry and wing-tagging. While kestrels almost exclusively hunt in rural areas (Riegert *et al.* 2007a), Long-eared Owls often hunt in edge habitats within the city area, such as waste-grounds along streams, power-line openings and railway-track verges (Fig.1; see also Lövy 2007). Such habitats host a high diversity of small mammals, especially Muridae mice (Briner *et al.* 2005, Suchomel & Heroldová 2006). Kestrels hunt mostly by hovering (Village 1990), which allows them to control a large area (Village 1983). This technique is thus well-suited for hunting on large waste-ground areas at the city periphery. Long-eared Owls, on the other hand, hunt using harrier-like flight near the ground, and hovering is rare (Cramp 1985). Galeotti *et al.* (1997) and Henrioux (2000) also mention a perch-and-wait hunting technique, which is common in raptors. These strategies do not allow large areas to be controlled, but represent suitable techniques to hunt along corridor-like habitats (Galeotti *et al.* 1997).

We suggest that the observed differences between Common Kestrel and Long-eared Owl diet in the urban environment of České Budějovice are caused by several factors. Apart from the obvious difference in diurnal activity, habitat types used for hunting and particularly hunting techniques also have significant impacts on diet composition.

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Tuulihaukan ja sarvipöllön ravinnon koostumus kaupunkiympäristössä

Tutkimme tuulihaukan (*Falco tinnunculus*) ja sarvipöllön (*Asio otus*) ravinnon koostumusta vaihtelevien myyräkantojen aikana České Budějovice'n kaupungissa 2002–2005. Peltomyyrä oli tavallisin saalis. Huonoina myyrävuosina muun ravinnon osuus kasvoi molemmilla lajeilla. Tällöin sarvipöllöt saalistivat enemmän hiiriä ja niiden lähisukulaisia, tuulihaukkojen alkaessa saalistaa enemmän hyönteisiä. Erilaiset vaihtoehtoiset saaliskohteet voivat selittyä petojen erilaisella vuorokausirytmillä, saalistustekniikalla tai saalistusympäristöillä. Tutkimme myös, vaikuttaako pesän ja kaupungin keskustan välinen etäisyys saaliin koostumukseen. Tuulihaukalla vaikutusta ei havaittavasti ollut, mutta sarvipöllöllä kasvava etäisyys kaupungin keskustaan näkyi myyrien kasvavana osuutena ravinnossa.

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The role of *Apodemus* mice and *Microtus* voles in the diet of the Tengmalm's owl in Central Europe

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Abstract Based on a long-term dataset (1999–2010), we investigated how the availability of main prey affects the breeding density and food ecology of the Tengmalm's owl (*Aegolius funereus*) in the Czech Republic. In particular, we assessed the role of *Microtus* voles and *Apodemus* mice in the diet, based on the main predictions of the optimal diet theory that the diet composition depends on the availability of the main prey. We found that (i) the Tengmalm's owl exhibited no numerical response to the availability of *Microtus* voles and *Apodemus* mice in the field; (ii) the availability of *Apodemus* mice in the field positively affected their proportion in the diet (26 %), and despite a high proportion of *Microtus* voles in the owls' diet (47 %), no relationship was found between their availability in the field and proportion in the diet; (iii) the proportion of *Apodemus* mice was negatively correlated to the proportion of *Microtus* voles, *Sorex* shrews and birds in the diet, but no similar relationship was detected for *Microtus* voles; (iv) the reproductive output of Tengmalm's owls was positively correlated to the proportion of *Apodemus* mice in the diet, as well as to *Apodemus* mice and *Microtus* vole availability in the field; and (v) diet diversity and diet overlap were not significantly affected by the abundance of *Apodemus* mice and *Microtus* voles. Therefore, the validity of these main optimal diet theory predictions was not confirmed, especially for *Microtus* vole prey, due to an opportunistic choice between *Apodemus* mice and *Microtus* voles. We suggest that the reproductive output of nocturnal raptors in Central Europe may be less dependent on *Microtus* vole supply than that of their northern counterparts.

Keywords *Aegolius funereus* · Boreal owl · Diet composition · Food availability · Reproductive output · Temperate zone

Introduction

Small-mammal-eating raptors face multiannual changes in the availability of their preferred prey. In general, they have three main options for reducing their reproductive costs during a food shortage. They can (i) move to another area to breed, (ii) remain, but not breed (i.e., a numerical response: Galushin 1974; Korpimäki 1984, 1994; Petty et al. 1995, 2000; Poulin et al. 2001; Brommer et al. 2002; Norrdahl and Korpimäki 2002; Millon and Bretagnolle 2008; Karell et al. 2009), or (iii) reduce their consumption of main prey (i.e., a functional response: Korpimäki 1985a; Steenhof and Kochert 1988; Korpimäki et al. 1994).

A numerical response was found in northern latitudes where most vole-eaters are nomadic (e.g., Korpimäki 1984; reviewed by Poulin et al. 2001). In Central Europe, these relationships are not pronounced and other factors may also influence spring raptor densities (e.g., winter climatic conditions or the availability of breeding sites, Kostrzewa and Kostrzewa 1991). A functional response is often followed by an increase in diversity in the diet, as predicted

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by the optimal diet theory (Schoener 1971; Pulliam 1974). As a consequence, food availability often has a positive effect on the reproductive output of raptors, especially in northern latitudes (Village 1981; Korpimäki 1986a, 1992; Jędrzejewski et al. 1994; Potapov 1997; Salamolard et al. 2000). However, the reproductive response of raptors to main prey availability may vary considerably with latitude which directly affects the regularity of small-mammal cycles (Jędrzejewski and Jędrzejewska 1996). In Northern Europe, populations of small mammals show regular cyclicality and great multiannual changes of abundance (Hansson and Henttonen 1985). In contrast, there are no regular prey cycles at temperate latitudes, although large multiannual changes in abundance have been reported (Tkadlec and Stenseth 2001).

In Northern Europe, Microtinae voles comprise the main prey of most birds of prey and owls, and the proportion of voles in the diet is usually closely related to their availability in the field (Korpimäki 1985b, 1986b, 1988, 1992). Abundances of small rodents at northern latitudes usually show regular 3–4 year cycles (Hansson and Henttonen 1985; Korpimäki and Hakkarainen 1991). When vole abundance is low, the proportion of alternative prey in the diet, usually Soricidae shrews and birds, increases (Korpimäki 1985b). In Central Europe, voles are important prey for birds of prey and owls, but their diet is regularly enriched with other prey species (e.g., Village 1990; Jędrzejewski and Jędrzejewska 1996; Salamolard et al. 2000).

The Tengmalm's owl (*Aegolius funereus*) is a nocturnal avian predator feeding mainly on small mammals (Korpimäki 1981). In general, voles constitute its main prey in Northern and Central Europe (Sulkava and Sulkava 1971; Korpimäki 1988; Schwerdtfeger 1988; Schelper 1989; Hörnfeldt et al. 1990; Kloubec and Vacík 1990; Pokorný et al. 2003). During vole scarcity, Tengmalm's owls in Northern Europe mainly take shrews (*Sorex* spp.), birds and, albeit with lower frequency, mice as well of the Muridae family (*Micromys minutus*, *Mus musculus* and rarely *A. flavicollis*; Sulkava and Sulkava 1971; Korpimäki 1988; Hörnfeldt et al. 1990). In contrast to northern populations, Tengmalm's owls from Central Europe regularly enrich their diet with mice (*Apodemus* spp.), shrews, birds and occasionally dormice of the Gliridae family (Schwerdtfeger 1988; Schelper 1989; Kloubec and Vacík 1990; Holý 2002; Pokorný et al. 2003; Sobotová 2008; Davidová 2009; Dvořáčková 2009; Komrsková 2009; Vopálka 2012). However, there has been no long-term study on the diet of the Tengmalm's owl in relation to food availability in Central Europe.

Based on a long-term dataset on the breeding ecology of Tengmalm's owls in the Ore Mountains (Czech Republic), we aim to characterize the effect of food availability on breeding density (i.e., the numerical response) and diet composition (i.e., the functional response) in Central European Tengmalm's owls. According to the optimal diet theory predictions, the diet composition should depend solely upon the availability of the main prey (Schoener 1971; Pulliam 1974). In particular, only the absolute abundance of preferred prey is important for the optimal diet and the relative abundance of non-preferred prey is unimportant (Pulliam 1974). Secondly, the diet diversity of predators should increase when the abundance of the preferred prey decreases (Schoener 1971). Thirdly, at fixed food densities, a prey type is either included or completely excluded from the diet. Since there is weak empirical evidence for the third prediction and animals regularly show partial preferences (reviewed by Pyke 1984), we used the first and second prediction to assess the role of *Microtus* voles and *Apodemus* mice in the diet of Tengmalm's owls. We also examined the relationship between the proportion of each prey type in the diet and reproductive output. In order to distinguish main and alternative prey, we tested the following predictions: (i) the main prey is the most frequently encountered prey in the diet and its proportion in the diet depends on its availability in the field; (ii) the amount of the main prey consumed is negatively associated with the amount of all other alternative preys consumed in the diet; (iii) reproductive output is positively associated with the amount of the main prey in the diet and the main prey availability, but negatively associated with diet diversity; and (iv) diet diversity decreases and diet overlap increases among breeding pairs with the increase of the main prey availability. Furthermore, we compared these results with those from northern Tengmalm's owl populations.

Materials and methods

The study area and Tengmalm's owl population

This study was conducted between 1999 and 2010 in the Czech Republic. The study area approximately 70 km^2 in size is situated in forests damaged by industrial air pollution on plateaus in the Ore Mountains (50°N, 13°E; 735–956 m a.s.l.), close to the border with Saxony. The habitat at this study site is covered by spruce (*Picea abies*) forest fragments, open areas, forest clearings (dominated by wood reed *Calamagrostis villosa*), solitary trees (mostly European beech *Fagus sylvatica*), and plantations of blue spruce (*Picea pungens*), birch (*Betula* spp.), European mountain ash (*Sorbus aucuparia*) and European larch (*Larix decidua*). During the study period, we installed 164 nest boxes (100 in the first year) due to a lack of natural nesting cavities. The yearly occupancy of the nest boxes varied between 8 and 26 % (mean ± SD; 14.0 ± 6.0 %).

Pellet analyses and reproductive parameters

Tengmalm's owl females usually keep their nests clean during incubation and brooding (Kuhk 1969; Korpimäki 1981), but they do not remove food remains and pellets during the feeding period. Hence, a layer of pellets and other prey remains accumulates at the bottom of the nest-hole during the nestling period (Sulkava and Sulkava 1971). From 1999 to 2010, we recorded 195 breeding attempts by Tengmalm's owls (mean ± SD; 16.3 ± 5.6 nests per year) of which 103 were successful (i.e., at least one fledgling produced during the breeding attempt). We recorded the exact numbers of young produced in 93 nest boxes, although we did not record the exact number of fledged chicks for the first year (1999). We analyzed the diet composition of 121 nesting attempts (103 successful nesting attempts and 18 failed nesting attempts or abandoned nests). Nest abandonment was mainly caused by pine marten (*Martes martes*) predation ($n = 12$). Prey remains were collected during the period when most young were present in the nest box (from late April to the end of July) during regular nest visits (every 7–14 days). The remaining material from nest boxes was collected after the chicks had fledged, as described in Korpimäki (1981). The material was moistened using water with a small amount of detergent added. The material was dissolved in a 5 % NaOH solution (Schueler 1972), and the bony remains blanched using a 2–5 % hydrogen peroxide solution. Small mammal species were identified based on skull morphology according to the method of Anděra and Horáček (2005), and feather remains, beaks and skulls were used with a reference collection for bird species.

In total, we determined 8,537 prey items (mean ± SD; 70.7 ± 31.5 items per nest box), of which 8,233 were small mammals and 304 were birds. The majority of small mammals were determined to species level (63.2 %) and the rest were determined to genus (*Apodemus* or *Microtus*). Of the birds, we determined 262 individuals (86.2 %) to their species and/or genus. For the purpose of further analyses, we divided prey items into four groups: *Microtus* voles (field vole *M. agrestis*, common vole *M. arvalis*, European pine vole *M. subterraneus*, and *Microtus* spp.), *Apodemus* mice (*Apodemus* spp.), *Sorex* shrews (common shrew *S. araneus* and pygmy shrew *S. minutus*) and birds. Scarce species, such as the bank vole (*Myodes glareolus*), water vole (*Arvicola terrestris*), house mouse (*Mus musculus*), southern water shrew (*Neomys anomalus*), Eurasian water shrew (*N. fodiens*), bicoloured shrew (*Crocidura leucodon*), hazel dormouse (*Muscardinus avellanarius*), brown long-eared bat (*Plecotus auritus*) and European mole (*Talpa europaea*) were not included in the analyses.

Small-mammal availability

The abundance of small mammals was assessed using the snap-trap capture method during the period from 1999 to 2010. The trapping was carried out at the start of June by setting up snap traps in three one-hectare areas each year (100 × 100 m squares with a 10-m spacing) (Pelikán 1971). The traps were left out for 3 days and checked daily in the morning (for details, see Zárybnická et al. 2011). We calculated the number of captured individuals per 100 trap nights in each trapping area. All captured mammals ($n = 368$) were identified to species level and were grouped into three small-mammal categories: *Microtus* voles (field vole, common vole and European pine vole), *Apodemus* mice, and *Sorex* shrews.

Statistical analyses

Using a linear regression analysis (STATISTICA software, StatSoft, Inc. 2008) we examined the relationships between (1) mean annual small-mammal abundances (independent variable) and annual breeding density (dependent variable) with a covariate number of nest boxes; (2) mean annual abundances of voles, mice and shrews (independent variables) and annual diet composition (proportion of voles, mice and shrews as dependent variables respectively); (3) pooled mean annual abundances of voles and mice (independent variables) and mean annual diet diversity (Shannon's index, Shannon and Weaver 1963) and mean annual diet overlap (Pianka 1973, dependent variables); and (4) the mean annual number of fledglings per nest (dependent variable) and mean annual abundance of mice and voles in the field and annual proportion of mice and voles in the diet (independent variables). Using Spearman rank correlations (STATISTICA software, StatSoft, Inc. 2008), we examined relationships between mean annual proportions of particular prey groups in the diet. The relationship between the proportion of small-mammal genera in the field and their proportion in the diet was expressed by Manly's standardized selection ratio B_i with 95 % confidence intervals (Manly et al. 2002). Statistical significance was obtained using the Chi square test (STATISTICA software, StatSoft, Inc. 2008).

Results

Abundance of small mammals

Apodemus mice were the small mammals captured most frequently (48.1 %, represented almost exclusively by the yellow-necked mouse), followed by *Microtus* voles (23.6 %, mainly the field vole) and *Myodes* voles (18.2 %, bank vole) and the least overall abundances were recorded for *Sorex* shrews (9.8 %, mainly common shrew; Table 1). The abundance of *Apodemus* mice changed considerably during the study period, with peaks in 2004, 2007 and 2010, while the abundance of *Microtus* and *Myodes* voles did not change markedly except for an increase in 2010 (Fig. 1).

Table 1 Spring small-mammal abundances in the field and diet composition of breeding Tengmalm's owls ($n = 121$ nests) in the Ore Mountains, Czech Republic during 1999–2010 (n indicates the number of individuals)

Prey species or group	Small-mammal abundance		Diet composition	
	n	%	*n*	%
Microtus arvalis	4	1.1	355	4.2
M. agrestis	81	22.0	2,724	31.8
M. subterraneus	2	0.5	6	0.1
Microtus spp.			913	10.7
Myodes glareolus	67	18.2	268	3.1
Arvicola terrestris	1	0.3	25	0.3
Apodemus spp.			2,229	26.1
Apodemus flavicollis	172	46.7		
Apodemus sylvaticus	5	1.4		
Mus musculus			1	<0.1
Sorex araneus	34	9.3	1,334	15.6
Sorex minutus	2	0.5	214	2.5
Neomys anomalus			4	<0.1
Neomys fodiens			15	0.2
Crocidura leucodon			1	<0.1
Muscardinus avellanarius			141	1.7
Plecotus auritus			1	<0.1
Talpa europaea			2	<0.1
Aves			304	3.6
Total	368	100.0	8,537	100.0

Breeding density

The yearly breeding density of the Tengmalm's owl varied between 0.15 and 0.44 breeding pairs per km^2 ($n = 195$ breeding attempts), representing (mean ± SD) 0.25 ± 0.09 breeding attempts per km^2. The relationship between the pooled abundance of *Apodemus* mice and *Microtus* voles and Tengmalm's owl breeding density was not significant (the regression coefficient $\beta = -0.25$, $t = 8.104$, $P = 0.3776$), and no significant relationship was recorded for *Microtus* voles ($\beta = -0.02$, $t = 6.310$, $P = 0.1325$) or *Apodemus* mice separately ($\beta = -0.04$, $t = 8.708$, $P = 0.2434$).

Diet composition

Microtus voles were the dominant prey animals (46.8 %, represented mainly by field voles), followed by mice (26.1 %, *Apodemus* spp.), *Sorex* shrews (18.1 %, mainly the common shrew), birds (3.6 %), bank voles (3.1 %, *Myodes glareolus*) and other rodents (2.3 %, Table 1). Birds were represented mainly by the chaffinch (*Fringilla coelebs*, 17.2 % of the individual birds determined), song thrush (*Turdus philomelos*, 10.3 %), European robin (*Erithacus rubecula*, 8.8 %), warblers (*Phylloscopus* spp., 7.3 %), other thrushes (*Turdus* spp., 6.9 %), blackbird (*Turdus merula*, 4.2 %), yellowhammer (*Emberiza citrinella*, 3.4 %) and tits (*Parus* spp., 8.0 %).

The proportion of *Apodemus* mice in the diet correlated negatively with the proportion of *Microtus* voles (Spearman rank correlations, $r_s = -0.78$, $P < 0.05$), *Sorex* shrews ($r_s = -0.59$, $P < 0.05$) and birds ($r_s = -0.76$, $P < 0.05$). The proportion of *Microtus* voles did not correlate with the proportion of *Sorex* shrews ($P = 0.3125$) and birds ($P = 0.4156$). We found significant differences between the total availability of small-mammal genera in the field and their total proportion in the diet (Chi square

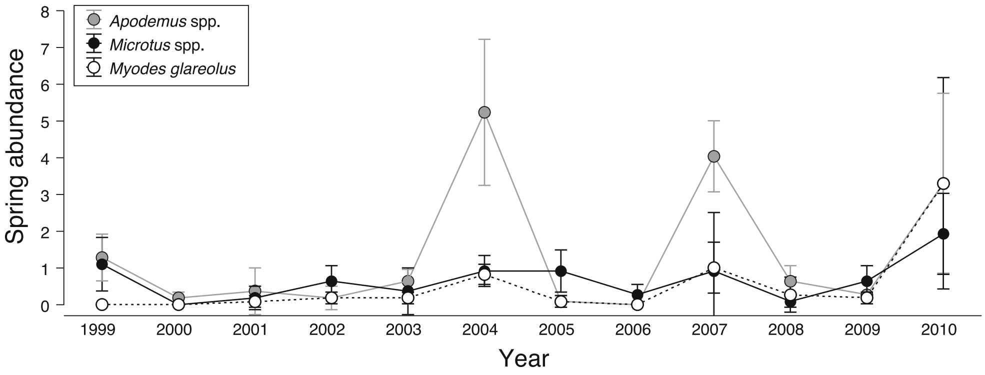

Fig. 1 Changes in spring abundance of *Microtus* voles, *Apodemus* mice and *Myodes glareolus* voles in the field in the Ore Mountains, Czech Republic from 1999 to 2010. Mean annual numbers of individuals per 100 trap nights and trapping area ± SD are given

test, $\chi^2 = 56.1$, $df = 3$, $P < 0.0001$). *Microtus* voles ($B_i = 0.435$, 95 % CI 0.194–0.676) and *Sorex* shrews ($B_i = 0.407$, 95 % CI 0.171–0.644) were hunted disproportionately more than would be indicated by the relative size of their populations, while preferences for *Myodes* voles ($B_i = 0.038$, 95 % CI 0.002–0.074) and *Apodemus* mice ($B_i = 0.119$, 95 % CI 0.016–0.222) were weak (Fig. 2). *Apodemus* mice availability in the field positively affected their proportion in the diet ($\beta = 0.84$, $t = 2.796$, $P = 0.0007$; Fig. 3a), but this relationship was not significant for *Microtus* voles ($\beta = 0.01$, $t = 5.485$, $P = 0.9875$; Fig. 3b) or *Sorex* shrews ($\beta = -0.05$, $t = 3.332$, $P = 0.8754$; Fig. 3c).

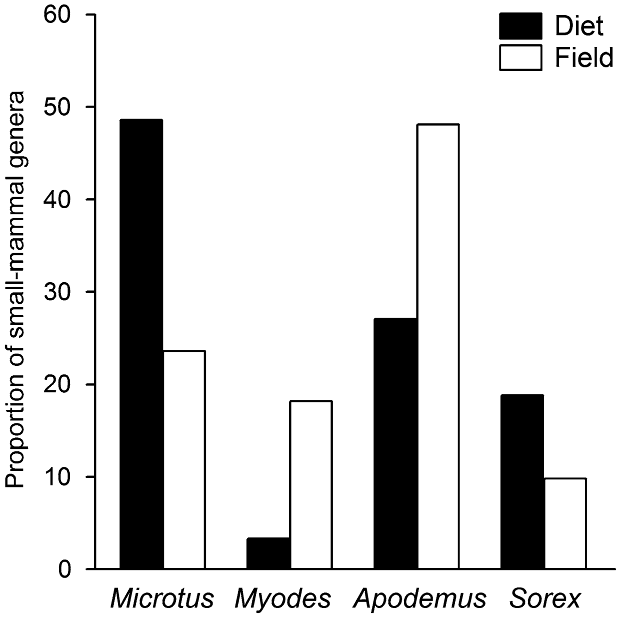

Fig. 2 Proportions of small-mammal genera in the diet of the Tengmalm's owl and in the field in the Ore Mountains, Czech Republic from 1999 to 2010

Diet diversity (Shannon's index, Table 2) was not significantly affected by the pooled abundance of *Apodemus* mice and *Microtus* voles in the field ($\beta = -0.09$, $t = 11.420$, $P = 0.7859$). Furthermore, this relationship was not significant when *Apodemus* mice ($\beta = 0.01$, $t = 12.268$, $P = 0.4156$) and *Microtus* vole ($\beta = -0.04$, $t = 11.452$, $P = 0.2894$) abundances were examined separately. The mean diet overlap between pairs of nests was high (mean ± SD; 0.876 ± 0.072, Table 2), but we did not find its relationship with pooled *Microtus* vole and *Apodemus* mice availability in the field ($\beta = 0.02$, $t = 27.493$, $P = 0.9581$), nor when mice ($\beta = 0.02$, $t = 30.301$, $P = 0.9464$) and voles ($\beta = 0.14$, $t = 23.548$, $P = 0.6644$) were examined separately.

Reproductive output

No relationship was found between the mean number of fledged young and diet diversity ($\beta = -0.10$, $t = 1.861$, $P = 0.7621$), but we found a positive relationship between the proportion of *Apodemus* mice in the diet and the mean number of fledglings ($\beta = 0.72$, $t = 4.708$, $P = 0.0130$; Fig. 4a). We also found significant positive relationships between the number of fledged young and the availability of *Apodemus* mice ($\beta = 0.78$, $t = 7.226$, $P = 0.0051$; Fig. 4b) and *Microtus* voles in the field ($\beta = 0.75$, $t = 4.668$, $P = 0.0077$; Fig. 4d). The relationship between the proportion of *Microtus* in the diet and number of fledglings was not significant ($\beta = -0.03$, $t = 3.937$, $P = 0.4365$; Fig. 4c).

Discussion

As with other raptors in Central Europe (Kostrzewa and Kostrzewa 1991), we did not find a significant correlation between small-mammal abundance and Tengmalm's owl

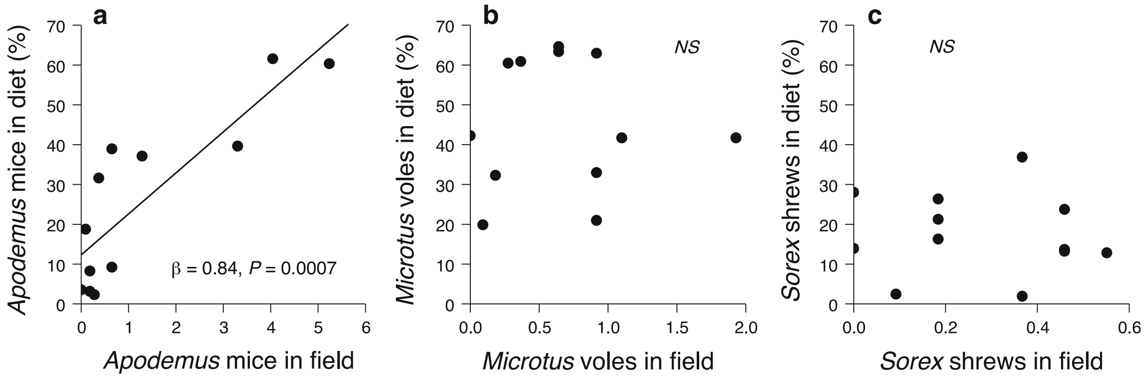

Fig. 3 Relationships between the proportion in the diet and spring abundance in the field for **a** *Apodemus* mice, **b** *Microtus* voles and **c** *Sorex* shrews. Proportions of prey in the diet are given as the annual proportion, and mean annual abundances in the field as the number of individuals per 100 trap nights and trapping area. Linear regressions were used. The scales of the *horizontal axes* differ between the *panels*

Table 2 Number of Tengmalm's owl nesting attempts, mean Shannon's diversity index (*H*′), diet overlap, and abundances of *Microtus* voles and *Apodemus* mice in the field (the number of individuals per 100 trap nights and trapping area) for each study year

Years	Number of nesting attempts	*H*′ (mean ± SD)	Diet overlap (mean ± SD)	Abundances of voles and mice
1999	9	0.781 ± 0.189	0.811 ± 0.173	2.39
2000	5	0.894 ± 0.325	0.723 ± 0.204	0.18
2001	12	0.979 ± 0.137	0.834 ± 0.155	0.55
2002	18	0.535 ± 0.214	0.946 ± 0.081	0.83
2003	7	0.860 ± 0.381	0.875 ± 0.138	1.01
2004	9	0.712 ± 0.094	0.864 ± 0.139	6.15
2005	8	0.791 ± 0.217	0.940 ± 0.051	1.01
2006	18	0.629 ± 0.193	0.946 ± 0.055	0.28
2007	9	0.912 ± 0.205	0.951 ± 0.043	4.96
2008	7	1.084 ± 0.151	0.825 ± 0.130	0.73
2009	8	0.574 ± 0.225	0.965 ± 0.044	0.92
2010	11	0.702 ± 0.097	0.827 ± 0.107	5.23
Mean ± SD	10.08 ± 3.95	0.788 ± 0.159	0.876 ± 0.072	2.04 ± 2.06

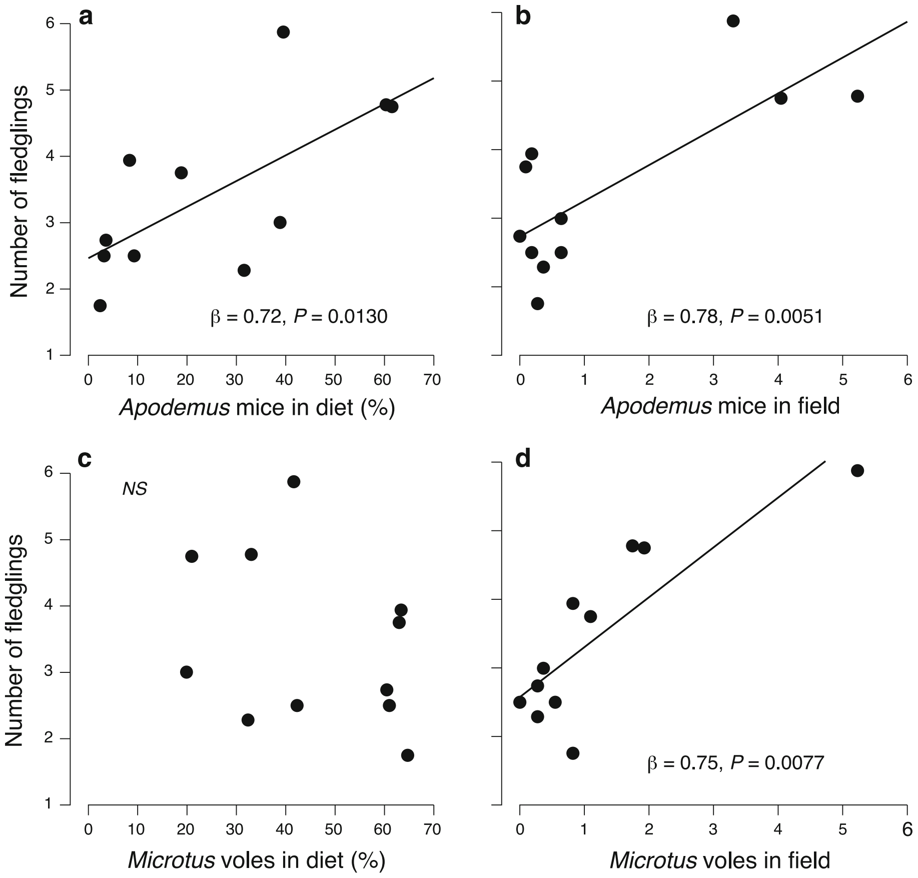

Fig. 4 Relationships between the number of fledglings and **a** the proportion of *Apodemus* mice in the diet of the Tengmalm's owl, **b** the abundance of *Apodemus* mice in the field, **c** the proportion of *Microtus* voles in the diet and **d** the abundance of *Microtus* voles in the field. Values are given as the mean number of fledglings per nest box, annual proportions of prey items in the diet or mean annual abundances in the field (the number of individuals per 100 trap nights and trapping area). Linear regressions were used

breeding density. We suggest that a combination of other factors, such as predation by pine martens and weather conditions, may offer a better explanation of changes in Tengmalm's owl breeding density in our study area (M. Zárybnická and K. Šťastný, unpublished data).

The diet of Tengmalm's owls in our study consisted predominantly of small mammals (96 %). This proportion is similar to Tengmalm's owl diet compositions reported from higher latitudes in Northern Europe (Sulkava and Sulkava 1971; Korpimäki 1981, 1986b, 1988; Hörnfeldt et al. 1990). In northern populations, voles (mainly *Microtus* spp. and bank voles) represent 60–90 % of the Tengmalm's owl's diet (Sulkava and Sulkava 1971; Korpimäki 1988; Hörnfeldt et al. 1990). In addition to voles (50 %, represented mainly by *Microtus* voles), we also recorded a high proportion of *Apodemus* mice (26 %)

in the diet of our Tengmalm's owls. This result is likely due to the geographical distribution of mice (namely the yellow-necked mouse) which makes them less available as prey in the north (Aulagnier et al. 2008). Similarly to these findings, voles (15–75 %) and *Apodemus* mice (10–40 %) were the most frequent prey of Tengmalm's owls during the breeding season in other areas of Central Europe (Schelper 1972, 1989; Beneš 1986; Schwerdtfeger 1988; Kloubec and Vacík 1990; Pokorný et al. 2003; Rymešová 2006).

Based on the high proportion of *Microtus* voles in the diet of Tengmalm's owl in our study area, it might be expected that its diet composition would be driven by *Microtus* vole availability in the field, as predicted by the optimal foraging theory (i.e., our first prediction). However, we found a positive relationship between *Apodemus* mice availability in the field and their proportion in the diet, while this relationship was not significant for *Microtus* voles. In comparison, Korpimäki (1988) showed a clear positive relationship in Northern Europe between the proportion of *Microtus* voles in the diet and their availability in the field. We suggest that this difference may be partially explained by the exclusively nocturnal activity of *Apodemus* mice compared to the cathemeral activity of *Microtus* voles (Halle and Stenseth 2000), together with the mice's preference for wooded habitats (Anděra and Horáček 2005). Therefore, mice in Central Europe are suitable prey, with similar activity and habitat preferences to Tengmalm's owls. Simultaneously, our owls exploited *Microtus* voles more than would be indicated by the relative size of their populations in the field. This can be explained by their lesser mobility and preference for open habitats (Anděra and Horáček 2005) making them more vulnerable to capture in general, especially during poor *Microtus* vole years (2000, 2003 and 2006). Alternatively, the absence of a functional response to the availability of *Microtus* voles can be partially explained by the frequent records of decapitated vole prey found in nest boxes, which may cause their underestimation in the diet (Zárybnická et al. 2011). This is because most of the species-specific features are concentrated in the head, and it is therefore difficult to identify decapitated samples. Unfortunately, we have no detailed data to compare decapitation rates in voles and mice.

The underrepresentation of mice in the diet may be explained by their greater mobility (Niethammer and Krapp 1978, 1986), and thus they are probably caught only when their abundance increases considerably. In agreement with this, the proportion of mice in the diet increased in 2004 and 2007 (60.3 and 61.6 %, respectively), when their availability in the field was extremely high. In 2010, we recorded a similar availability of *Microtus* voles and *Apodemus* mice in the field, and their proportion in the diet was almost the same (41.7 vs. 39.6 %, respectively).

The proportion of *Sorex* shrews (18 %) and birds (4 %) in our study was comparable to that of Central and Northern European populations (Sulkava and Sulkava 1971; Schelper 1972, 1989; Beneš 1986; Korpimäki 1988; Schwerdtfeger 1988; Hörnfeldt et al. 1990; Kloubec and Vacík 1990; Pokorný et al. 2003; Rymešová 2006). *Sorex* shrews were exploited disproportionately more than would be indicated by the relative size of their population. Birds were represented mainly by thrushes, finches and tits. The high abundance of these bird species as prey has also been documented by other authors (Sulkava and Sulkava 1971; Schelper 1972, 1989; Korpimäki 1981, 1988; Pokorný 2000; Pokorný et al. 2003). We suggest that these species are probably easy for Tengmalm's owls to hunt, due to their conspicuous behaviour (e.g., singing from elevated points).

According to our second prediction, the proportion of main prey should negatively affect the proportion of other prey items in the diet. We found that the proportion of *Apodemus* mice negatively correlated with the proportion of *Sorex* shrews, birds and *Microtus* voles in the diet. The proportion of *Microtus* voles did not correlate with the proportion of birds and shrews in the diet, probably due to its overall high proportion in the diet (see above). According to our second prediction, *Apodemus* mice may also be considered as main prey. Simultaneously, we can consider birds and shrews as alternative prey. The great importance of *Apodemus* mice in the diet of our Tengmalm's owls also highlights the positive relationship between the mean number of fledged young and the proportion of *Apodemus* mice in the diet, as well as their availability in the field (i.e., our third prediction). This relationship was also found for *Microtus* voles, but only the abundance of *Microtus* voles in the field was positively related to the number of fledged young. This is in line with the results from northern latitudes, where Korpimäki (1987) showed a positive correlation between spring *Microtus* vole availability and both the clutch size and number of fledglings.

We did not detect a negative relationship between diet diversity and main prey availability which contradicts our fourth prediction. This relationship was not significant for *Microtus* voles, *Apodemus* mice, or for pooled datasets. This is likely a consequence of there being two main prey types in the Tengmalm's owl's diet, a higher than expected proportion of *Microtus* voles in the diet (especially during poor vole years), together with the absence of regular cycles of vole and mice abundance in Central Europe (Korpimäki 1986c; Jędrzejewski and Jędrzejewska 1996). Furthermore, the mean diet overlap did not correlate either with abundances of *Microtus* voles or *Apodemus* mice in the field, nor with the pooled dataset.

The optimal diet theory assumes that predators should hunt the most valuable prey types when prey is abundant

(Schoener 1971; Pulliam 1974). *Apodemus* mice and *Microtus* voles are of similar weight (20–30 g per individual; Zárybnická et al. 2009), and thus represent a similar energy gain. Therefore, voles can be substituted by mice—and vice versa—according to their availability in the field, and thus both represent main prey for our Tengmalm's owls. It has been documented that Central European owls foraging on *Microtus* voles and *Apodemus* mice exhibit lower feeding rates to produce a similar number of fledglings, compared to northern owls foraging on voles and shrews (Zárybnická et al. 2009, 2012). Thus, based on previous tests, we believe that Tengmalm's owls breeding in Central Europe benefit from not being fully dependent on voles as prey and less pronounced cyclicity of vole abundance. In contrast, the reproductive output of Tengmalm's owls from northern populations depends entirely on vole abundance (Korpimäki 1988; Korpimäki and Hakkarainen 1991). As far as is known, this is the first study from Central Europe showing that the diet composition and reproductive output of a nocturnal raptor can be influenced by two main prey types. We were not able to find clear support for the predictions of the optimal diet theory for *Microtus* vole prey in Tengmalm's owls breeding in Central Europe.

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Příloha VI

Luka V, Riegert J.

Apodemus mice as the main prey that determines reproductive output of Tawny Owl (*Strix aluco*) in Central Europe

Population Ecology (In press)

Apodemus mice as the main prey that determines reproductive output of Tawny Owl (*Strix aluco*) in Central Europe

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Abstract

During the years 2008-2014, we studied diet composition, number of breeding pairs, and reproductive output of Tawny Owls in Central Europe (Czech Republic) in relation to availability of main prey in the field. We also performed a meta-analysis on diet composition of Tawny Owl in Europe that confirmed the important role of *Apodemus* mice in Tawny owl diet in Central Europe. In concordance, *Apodemus* mice were the main prey of Tawny Owl in our study area (38.7%), and *Microtus*/*Myodes* voles (15.4%), birds (12.1%) and others (33.8%) were alternative prey. We found a positive relationship between the proportion of *Apodemus* mice in the diet and their abundance in the field (beta = 0.23, P = 0.001). Availability of main prey (*Apodemus* mice, *Microtus*/*Myodes* voles or *Sorex* shrews) in the field was not correlated with number of breeding pairs. Proportion of birds in diet (expressed by scores from multivariate analysis), which was inversely related to proportion of *Apodemus* mice, was positively correlated with laying date (beta = 0.66, P = 0.012) and negatively correlated with clutch size (beta = -0.45, P = 0.004) and brood size (beta = -0.16, P = 0.076). We also found negative relationships between laying date and clutch size (beta = -0.13, P = 0.014) and brood size (beta = -0.07, P = 0.057). Our results support the idea that diet and breeding ecology of owls in Central Europe is mainly driven by the availability of *Apodemus* mice that are suitable prey due to their similar habitat requirements and nocturnal activity.

Key words Diet composition · Hunting · Laying date · Nocturnal predator · Prey choice · Reproduction

Introduction

The consumption of main prey by raptors is often positively correlated with prey density in the field (i.e., functional response). These relationships have been documented for various raptor species (e.g., Snowy Owl *Nyctea scandiaca* - Gilg et al. 2006; Tawny Owl *Strix aluco* - Roulin et al. 2009; Rough-legged Hawk *Buteo lagopus* - Therrien et al. 2014). However, variation in the proportion of main diet components can also be found within one year. For example, Boreal Owl (*Aegolius funereus*) males in Norway hunted mainly *Myodes* voles during snow cover and when the snow disappeared they switched to *Microtus* voles (Jacobsen and Sonerud 1993). Thus, availability of main prey can considerably change both between- and within-years which may cause changes in raptors' feeding tactics.

Changes in prey density may further trigger different responses that depend on the importance of main prey in the diet and availability of alternative prey. Predators that depend on a main prey whose abundance fluctuates widely on a cyclical basis and where alternative prey does not compensate for these changes often show a positive relationship between density of main prey and number of breeding pairs (i.e., numerical response). These responses have been found in some avian predators, especially at northern latitudes (e.g., six raptor species - Korpimäki 1994; Ural Owl *Strix uralensis* - Brommer et al. 2002; Snowy Owl *Nyctea scandiaca* - Gilg et al. 2006; Tawny Owl *Strix aluco* - Karell et al. 2009; Northern Saw-whet Owl *Aegolius acadicus* - Bowman et al. 2010), but also at temperate latitudes of the Northern Hemisphere (e.g., Montagu's Harrier *Circus pygargus* - Salamolard et al. 2000; Millon and Bretagnolle 2008). The mechanisms beyond these relationships are nomadism and changing proportion of breeding/non-breeding individuals according to food supply at a locality, however the factors that influence population size and growth may be more complex (Hone and Sibly 2002). Some studies from temperate latitudes show a lack of numerical response (e.g., Boreal Owl - Zárybnická et al. 2013, 2015a) that may be caused by exploiting more than one main prey type or no pronounced between year changes in prey abundances (i.e., small mammals), both leading to more stable numbers of breeding pairs between years. Similarly, owl populations in urban areas may not exhibit a numerical response to main prey because of the use of more than one alternative prey types or modified hunting behaviour (e.g., Long-eared Owl *Asio otus* - Lövy 2007).

Prey abundance may also affect demographic components. Most evidence in birds of prey abundance comes from variations in breeding performance. During good trophic years pairs produce more young compared to poor trophic years (e.g., Long-eared Owl - Korpimäki 1992; Sergio et al. 2008; Montagu's Harrier - Millon and Bretagnolle 2008; Barn *Owl Tyto alba* - Pavluvčík et al. 2015). Beyond these relationships various behavioural adaptations such as hatching asynchrony (e.g., Valkama et al. 2002) and siblicide or fratricide (e.g. Margalida et al. 2004) have been brought to light. However, within-year variability in reproductive performance has also been described (e.g., Verhulst and Nilsson 2008). Both observational and experimental studies have shown that under good trophic conditions raptors often lay earlier and produce larger clutches and broods (e.g., Dijkstra et al. 1980; Beukeboom et al. 1988; Dijkstra et al. 1990; Aparicio 1994; Korpimäki and Wiehn 1998; Lehikoinen et al. 2011; Catry et al. 2017).

The Tawny Owl is a medium-sized nocturnal opportunistic predator inhabiting almost the whole of Europe excluding northern areas (Cramp and Simmons 1988). It breeds in tree cavities that can be successfully substituted with nest boxes (e.g., Roulin et al. 2009). The diet composition of the Tawny Owl has been studied across the whole of Europe (e.g., Sunde et al. 2001; Zawadzka and Zawadzki 2007; Obuch 2011). Although, rodents are generally the most common Tawny Owl prey, some populations or individuals show high proportions of other components (especially birds and amphibians). Similarly, the representation of the two most available rodent groups in Tawny Owl diet (*Apodemus* mice and *Microtus*/*Myodes* voles) is variable and probably reflects their availability in the field (Obuch 2011). More recently, there is a growing body of evidence that *Apodemus* mice and not *Microtus*/*Myodes* voles are the main prey of several Central European owl species (Marchesi et al. 2002; Roulin et al. 2009; Zárybnická et al. 2013; Chausson et al. 2014).

The main aim of this study is to reveal the role of main prey in the ecology of the Tawny Owl population in Central Europe. To assess the importance of different prey across Europe, (1) we performed a meta-analysis of diet composition of Tawny Owl. Further, (2) we analyzed the diet composition of Tawny Owl in our study area (Central Bohemia) and tested the effect of prey availability on diet composition. We also assessed (3) the effect of prey availability on the number of breeding pairs. Finally, (4) we tested the effect of diet composition on breeding performance both between-years (i.e., clutch size, brood size and number of fledglings) and within a year (i.e., the relationship with laying date).

Methods

Study area

The study was conducted between the towns of Mělník and Mnichovo Hradiště (district Mladá Boleslav) in Central Bohemia (50°30'N, 14°47'E, 190 km^2, 220-400 m a. s. l.). The landscape within the study area changes from southwest to northeast. The southwestern part of the area is situated in CHKO Kokořínsko along the river Pšovka, in the vicinity of the town Mšeno. The landscape has a canyon like character with typical eroded sandstone rocks covered mainly by forest (forests 46.7%, arable land 40.1%, permanent crops, orchards and meadows 11.4%, urban areas 1.3%, water surfaces 0.5%). The northeastern part of the area is located in the vicinity of the town Mnichovo Hradiště and is more developed and more used for agriculture than the former (arable land 39.8%, forests 33.1%, permanent crops, orchards and meadows 21.9%, urban areas 3.5%, water surfaces 1.7%). The forests within the study area consist mainly of acidophilus beech and pine-oak forests dominated by Scots Pine *Pinus sylvestris* (60%) and Norway Spruce *Picea abies* (20%).

During the years 2008-2014, a total of 60 nest boxes were installed within the study area. The nest boxes were made of spruce wood, the bottom measured 30 × 30 cm and height was 55 cm (back) and 45 cm (front). The entrance hole was 17.5 cm in diameter. Nest boxes were checked each year at the end of March to detect nest box occupancy. Occupied nest boxes were further checked at least three times to assess reproductive parameters and collect material for diet composition analyses. During the autumn, we repaired damaged nest boxes and prepared them (i.e., cleaning the leaf litter) for the next breeding season. The annual occupancy of nest boxes varied between 12 and 20% per year (mean ± SD, 15.7 ± 4.0, Table 1). When we recorded predation by martens (*Martes* sp.), the nest box was relocated during the following winter.

Table 1. Nest box occupancy and reproductive parameters of Tawny Owl during the years 2008-2014

Year	Number of available nest boxes	Number of occupied nest boxes (%)	Clutch size per nest box ± SD	Brood size per nest box ± SD	Number of fledglings per nest box ± SD	Reproductive success (%)
2008	30	6 (20)	3.7 ± 1.0	2.2 ± 1.3	2.0 ± 1.3	55
2009	50	6 (12)	3.3 ± 0.8	2.0 ± 1.4	1.8 ± 1.2	55
2010	59	12 (20)	4.7 ± 0.7	3.2 ± 1.9	2.8 ± 1.9	61
2011	58	7 (12)	2.7 ± 1.1	1.4 ± 1.4	1.3 ± 1.1	47
2012	57	11 (19)	4.1 ± 1.3	1.9 ± 2.2	1.6 ± 2.2	40
2013	57	7 (12)	3.4 ± 1.3	2.9 ± 1.8	2.9 ± 1.8	83
2014	57	8 (14)	2.8 ± 1.2	1.6 ± 1.8	1.3 ± 1.8	45

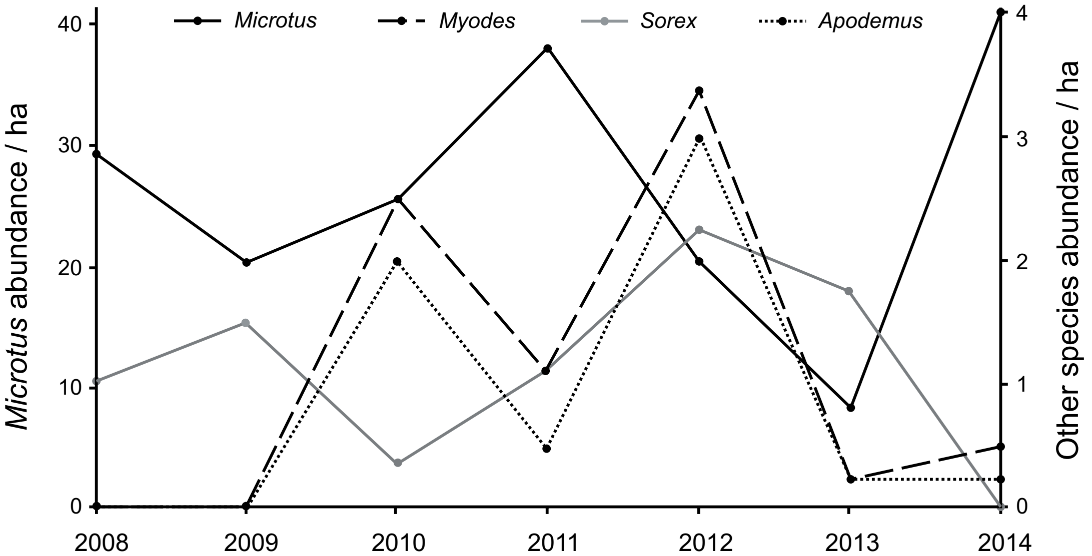
Food supply

The abundance of small mammals was assessed using the snap-trap capture method (Pelikán et al. 1972). The captures were carried out twice each year (2008-2014) during the turn of March and April and during the turn of September and October. The traps were laid out in four squares within the study area (two squares on meadows and two squares in forests). Each square covered an area of 100 × 100 m, a couple of traps were placed within a span of 10 m with a total of 242 traps at 121 points in each square. The traps were exposed for three nights and checked once a day in the morning to avoid data losses caused by scavengers. All caught mammals were determined to species (n = 1,267 individuals).

Diet composition

Pellets and prey remains from the nest box bottom (i.e., rubble) were collected in the breeding period during three visits to nest boxes occupied by Tawny Owl. The first visit was carried out in order to check for nest box occupancy, the second visit took place during the presence of the chicks in the nest box and the third visit immediately after the chicks had fledged. The material from the nest boxes was put into a 5% solution of NaOH for one day (Schueler 1972). Feather remains were carefully picked up before the dissolving process. After the hair debris were dissolved, the samples were rinsed using a dense sieve under running water. Washed samples were then dried and bones were sorted into various categories including mammalian jaw bones and bird beaks, tarometatarsi, humeri and metacarpal bones. Small mammals were determined by identifying skulls using Anděra and Horáček (2005), and birds by feathers and beaks using a reference collection. Thrush-sized and sparrow-sized birds were determined using humeri and/or femuri. Number of individuals was assessed according to the maximal number of a particular bone from the left and right side of a prey body or according to the

Fig. 1 Changes in abundances of small mammals in the field during the years 2008-2014



maximal number of parts that can be found on a prey body (e.g., humeri, femuri and number of upper and lower incisors). We determined 2,268 individuals to 38 taxa based on 24,134 bone and feather remains from fledglings' pellets found in 39 nest boxes (mean ± SD, 58.1 ± 38.0) of which 1,916 individuals were rodents. In 604 cases (31.5%), only upper or lower incisors were present, and individuals were considered as non-determined rodents. For the purpose of further analyses, diet components were classified into seven main groups: Birds, Muridae - mainly *Apodemus* sp. mice (less frequently also *Mus musculus*, *Rattus norvegicus*), Arvicolidae - mainly *Microtus*/*Myodes* sp. voles (less frequently also *Arvicola terrestris*), Soricidae - mainly *Sorex* sp. (*Sorex araneus*, *Sorex minutus*, rarely also *Neomys fodiens*), Gliridae (*Glis glis*, *Muscardinus avellanarius*), and non-determined rodents and amphibians (Table S1 in Electronic Supplementary Material).

Reproductive success

We estimated reproductive success based on visits to nest boxes during the breeding season. We recorded the number of eggs and chicks in the nest box and the number of fledged young. During the study period, we recorded a total of 57 nesting attempts of Tawny Owl (mean ± SD, 8.1 ± 2.4 per year). From these attempts, 39 were successful (at least one fledgling was produced) with a total of 114 fledglings produced (mean ± SD, 2.9 ± 1.4 per nest). During nest box visits we determined the age of chicks to assess approximate laying date (i.e., day from 1 January of particular year).

Statistical analyses

Meta-analysis of literature data was performed in Canoco 5 software, using redundancy analysis (RDA) that is suitable for calculating inter-correlated variables (Šmilauer and Lepš 2014). The data unit was each study (Table S2 in Electronic Supplementary Material). Log-transformed percentages of the numbers of the following prey were used as response variables: *Apodemus* mice, *Myodes* and *Microtus* voles, Gliridae dormice, insectivores, other mammals (mainly bats), birds, insects, amphibians and other groups (mainly lizards, fish and invertebrates apart from insects - e.g., crayfishes and slugs). The number of determined prey items in each study was used as a covariate. We tested the effect of latitude and longitude on diet composition, statistical significances were obtained using Monte-Carlo permutation tests.

Multivariate data on the effect of environmental factors on diet composition were calculated using variance partitioning by principal coordinate analysis of neighbour matrices (PCNM) in Canoco 5 software (ter Braak and Šmilauer 2012), the method recently recommended by Marrot et al. (2015). This multivariate analysis enabled us to separate the effect of space predictors (i.e., geographical position of nest box) from the effect of primary predictors (Legendre and Legendre 2012). Moreover, this analysis is suitable for calculating inter-correlated variables, such as proportions of diet items (i.e., when the proportion of one item increases, the proportion of other items decreases), since all these variables enter the analysis simultaneously. The analysis included nine steps: (1) primary predictor test (i.e., preliminary test of the overall effect of primary predictors on the dataset), (2) primary predictor selection by partial redundancy analysis (RDA) using forward selection based on partial Monte-Carlo permutation tests, (3) principal coordinate analysis (PCoA) based on Euclidean distances (i.e., finding the main space predictors based on coordinates), (4) PCNM for all predictors (i.e., preliminary test of the overall effect of space predictors on the dataset), (5) PCNM selection (i.e., the choice of space predictors based on coordinates using forward selection and partial Monte-Carlo permutation tests), (6) spatial effects analysis (i.e., assessing the amount of variability explained by space predictors), (7) primary predictor effects analysis (i.e., assessing the amount of variability explained by primary predictors), (8) joint effects analysis (i.e., assessing the amount of variability explained by both predictor types) and (9) removal of spatial effects (Šmilauer and Lepš 2014). The data unit was represented by each nesting attempt. Response variables were represented as percentages of the numbers of each main diet component (*Apodemus* mice, *Microtus*/*Myodes* voles, Gliridae, Rodentia unidetermined, insectivores, birds and amphibians) that were log-transformed prior to analysis as recommended by Šmilauer and Lepš (2014). As a covariate we used the total number of identified prey items in the nest box. Nest box ID and year were used as random factors to eliminate biases in occupancy rate among nest boxes during the study period. The following factors were used as explanatory variables: spring, autumn and total yearly abundance of main small mammal groups (*Microtus*/*Myodes* voles, *Apodemus* mice, *Sorex* shrews - individuals/ha) and also their abundances in the previous year. Statistical significance was obtained by Monte-Carlo permutation tests.

Partial regressions between number of breeding pairs and abundance of prey in the field were computed for each prey species separately using regressions in Statistica 12 software. We used proportion of occupied nest boxes as the dependent variable and abundance of a particular prey species in the field (individuals/ha) as the independent variable. Using the same method, we analyzed relationships between abundance of *Apodemus* mice in the field (independent variable) and its proportion in the diet and clutch size (dependent variables), and between laying date (dependent variable) and clutch size and brood size (independent variables).

The effect of diet composition on breeding parameters (laying date, clutch size, brood size and number of fledglings) was tested using scores from the first and second ordination axes (from the above mentioned PCNM analysis) that represented the main gradients in our dataset (i.e., gradient of unidentified rodents - *Microtus*/*Myodes* and Gliridae on first ordination axis, and gradient *Apodemus* mice - birds and insectivores on second axis). A diet item was considered to be associated with an ordination axis when the value of its regression coefficient reached at least 0.6. Further, we built a GLM model (dependent variable - laying date) and GLMM models (dependent variables - clutch size, brood size and number of fledglings) with scores from the first and second ordination axes, year and nest box ID as independent variables. In GLMM models, we used previous reproductive stage as covariates (i.e., laying date in the analysis of clutch size, clutch size in the analysis of brood size and brood size in the analysis of number of fledglings) to eliminate their influence on subsequent breeding stages. Since data on laying date did not significantly differ from Gaussian distribution (Kolmogorov-Smirnov test, $P = 0.226$), we used identity link function in the GLM analysis. In GLMMs, we used log link function for Poisson distributions. We used forward selection of independent variables using AIC criterion and showed only significant results.

Results

Food supply

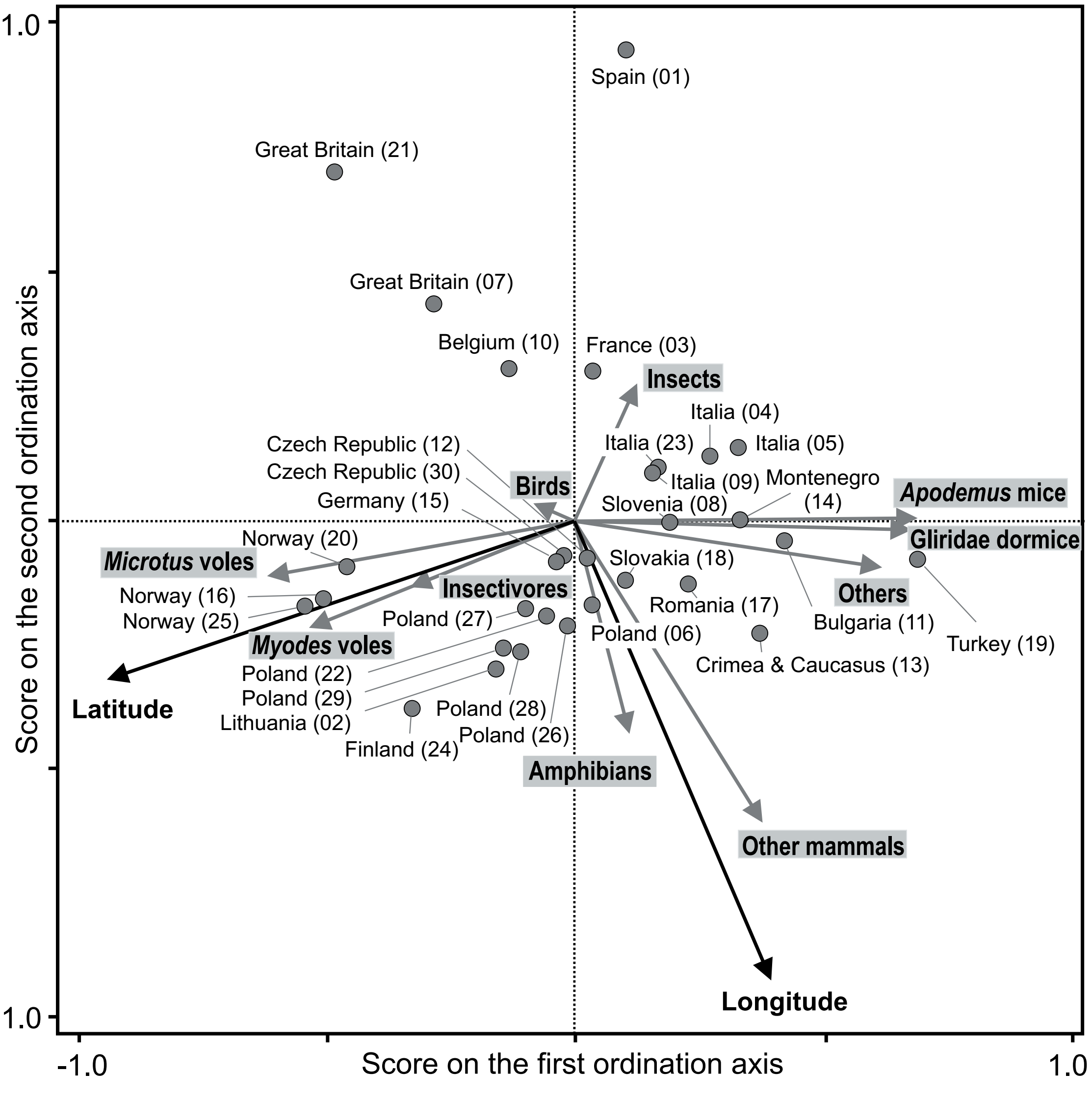
Between the years 2008-2014, we caught 1,267 individual small mammals. *Microtus* voles were the most frequently captured small mammals (87.2%, represented almost exclusively by the common vole *M. arvalis*), other groups of small mammals were less common (*Myodes* voles 4.7%, *Sorex* shrews 4.3% and *Apodemus* mice 3.7%). The total yearly abundance (pooled spring and autumn abundance) of *Microtus arvalis* showed peaks in 2008, 2011 and 2014, while the abundance of *Apodemus* mice and *Myodes* voles showed increased abundances in 2010 and 2012. *Sorex* shrews had low between-year variability in abundance with a maximum in 2012 (Fig. 1).

Diet composition

Meta-analysis of literature data showed that the diet of Tawny Owl in Europe can be divided into four main groups based on their positions within the ordination space (Fig. 2). First, the group including *Apodemus* mice, Gliridae dormice and other groups, proportions of which showed positive correlations with the first ordination axis (regression coefficients; *Apodemus* mice: 0.98, Gliridae dormice 0.97, other groups 0.88). Second, proportions of *Myodes*/*Microtus* voles and insectivores that were negatively correlated with the first ordination axis (regression coefficients; *Microtus* voles -0.90, *Myodes* voles -0.77, insectivores -0.49). Third, other mammals and amphibians, proportions of which were independent of the above mentioned groups and were negatively correlated with the second ordination axis (regression coefficients; other mammals -0.76, amphibians -0.84). Fourth, birds and insects, proportions of which were independent of the above mentioned prey groups and did not correlate with any ordination axis (Fig. 2). Latitude and longitude significantly affected the diet of Tawny Owl within its European range (RDA analysis; latitude: F = 7.80, P = 0.004, longitude: F = 3.10, P = 0.008). Latitude was negatively correlated with the first ordination axis (regression coefficient -0.64) and longitude was negatively correlated with the second ordination axis (regression coefficient -0.47). In Northern Europe, the diet of Tawny Owl is mainly dominated by insectivores, *Myodes* and *Microtus* voles. Towards the South, we recorded an increased proportion of *Apodemus* mice, and Gliridae dormice. Proportions of insects and birds were not related to latitude. Towards the East, we recorded increased proportions of amphibians and other mammals (e.g., *Rattus norvegicus*).

In the diet of our Tawny Owls rodents dominated (84.5%), alternative prey were birds (12.1%), frogs (2.2%) and insectivores (1.2%) represented by three Soricidae species (*Sorex araneus*, *S. minutus* and rarely *Neomys fodiens*). 31.5% of rodents were unidentified. Within determined rodents *Apodemus* mice represented the most dominant prey item (66.9%), *Myodes* (17.3%) and *Microtus* voles (9.4%) were less represented. Other rodents (*Mus* mice, water vole *Arvicola terrestris*, rat *Rattus norvegicus* and Gliridae dormice, mainly *Glis glis* and *Muscardinus avellanarius*) formed a minor proportion of the rodent prey (< 4%). The proportion of main mammal groups varied between years, *Apodemus* mice formed 36.8 - 72.6% of determined mammals. When the proportion of *Apodemus* mice in the diet decreased, the representation of *Microtus* voles (23.3% in 2009 and 2011, yearly median 8.0%), *Myodes* voles (24.1% in 2011, yearly median 16.9%) and insectivores (14.0% in 2009, yearly median 2.2%) increased.

Fig. 2 The effect of latitude and longitude on the diet composition of Tawny Owl in Europe. Meta-analysis of literature data (RDA analysis, I and II ordination axes explain 34.0% of variability). Data taken from: (1) Adánez (2000); (2) Balčiauskiene et al. (2006); (3) Baudvin and Jouaire (2006); (4) Capizzi (2000); (5) Capizzi and Luiselli (1998); (6) Grzedzicka et al. (2013); (7) Kirk (1992); (8) Kuhar et al. (2006); (9) Marchesi et al. (2006); (10) Delmee et al. (1979); (11, 12, 13, 14, 16, 17, 18, 19) Obuch (2011); (15) Uttendörfer (1939, 1952); (20) Overskaug et al. (1995); (21) Petty (1999); (22) Romanowski and Zmihorski (2009); (23) Sergio et al. (2007b); (24) Solonen and Karhunen (2002); (25) Sunde et al. (2001); (26) Wiacek et al. (2009); (27) Zalewski (1994); (28) Zawadzka and Zawadzki (2007); (29) Zmihorski and Osojca (2006) and (30) this study



Representation of birds in the diet was variable with maxima in 2009 (42.4%) and 2011 (38.8%), reaching median 24.2%. The thrush-sized (33.2%) and sparrow-sized birds (37.2%) dominated among bird prey items. The most frequently caught determined species was Blackbird *Turdus merula* (9 ex., 3.3%). We also determined three individuals of Great Spotted Woodpecker *Dendrocopos major*, two individuals of Eurasian Jay *Garrulus glandarius* and one unidentified parrot species (Psittaciformes, Online Resource 1). In two nest boxes, we determined individuals of amphibians (unspecified frogs, Anura) that formed up to 33.0% of the diet by numbers. Finally, we found one maxilla of a small predatory fish.

We found a significant effect of single space predictor on diet composition (PCNM, principal coordinate PCO.4, 2.8% of explained variability, F = 3.3, P = 0.039), but more variability was explained by primary predictor abundance of *Apodemus* mice in the field (16.8% of explained variability, F = 4.01, P = 0.028). Abundance of *Apodemus* mice in the field was negatively correlated with the second ordination axis (regression coefficient 0.96, Fig. 3a). We also found a positive relationship between the proportion of *Apodemus* mice in the diet and their abundance in the field (regression, $R^2 = 0.50$, F = 12.63, beta = 0.23, P = 0.001, Fig. 3b). Proportion of *Apodemus* mice was negatively correlated with the second ordination axis and proportions of birds and insectivores (mainly *Sorex* sp.) showed a positive correlation with this ordination axis. Proportions of *Microtus*/*Myodes* voles and Gliridae were positively correlated with the first ordination axis and unidentified rodents showed a negative relationship with this ordination axis. These two main gradients of diet composition were independent of each other. Proportions of amphibians did not show significant correlation with any ordination axis (Table 2, Fig. 3a).

Table 2. Regression coefficients for the proportions of main diet items with first and second ordination axes based on PCNM analysis of diet composition of Tawny Owl (values above 0.6 are in bold)

Prey item	First axis	Second axis
Birds	0.21	**0.84**
Apodemus mice	0.24	**-0.92**
Microtus/*Myodes* voles	**0.89**	-0.26
Gliridae	**0.65**	0.22
Rodentia unidetermined	**-0.86**	0.26
Insectivora	0.45	**0.85**
Amphibians	0.26	-0.30

Population size

Based on the dataset from seven years, we did not find significant relationships between the number of breeding pairs and the abundance of *Apodemus* mice in the field (regression, $R^2 = 0.30$, F = 2.18, beta = 0.55, P = 0.199), *Microtus*/*Myodes* voles (regression, $R^2 = 0.01$, F = 0.04, beta = 0.09, P = 0.854) nor *Sorex* shrews in the field (regression, $R^2 = 0.01$, F = 0.06, beta = -0.11, P = 0.818).

Table 3. The effect of diet composition and year on laying date and reproductive parameters of Tawny Owl. GLM (F values) and GLMM (Chi values) analyses

Method	Dependent variable	Covariate	Independent variable	df	Percentages of explained variability	Beta	F/Chi	P
GLM	Laying date		Score from second ordination axis	37	16.0	0.66	7.05	0.012
			Year	31	33.6		2.60	0.036
GLMM	Clutch size	Laying date	Score from second ordination axis	37	6.8	-0.45	8.12	0.004
	Brood size	Clutch size	Score from second ordination axis	37	2.4	-0.16	3.15	0.076

Fig. 3 The effect of (a) abundance of *Apodemus* mice on diet composition of Tawny Owls in the Czech Republic. Spatial effects were removed by PCNM analysis, I and II ordination axes explain 60.1% of variability. In the graph we show results after removing spatial effects. (b) The relationship between abundance of *Apodemus* mice in the field and its proportion in the diet of Tawny Owl

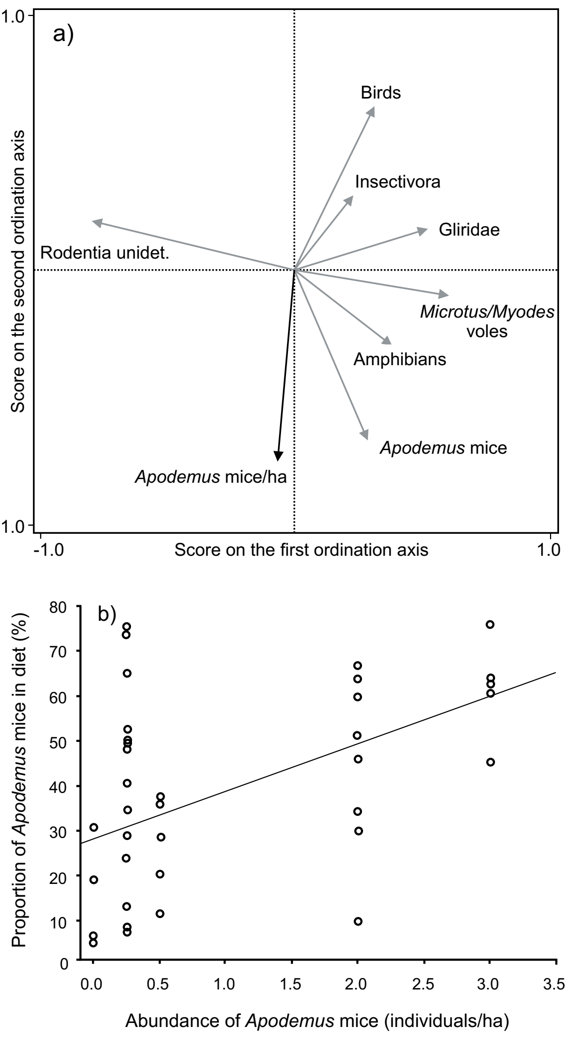
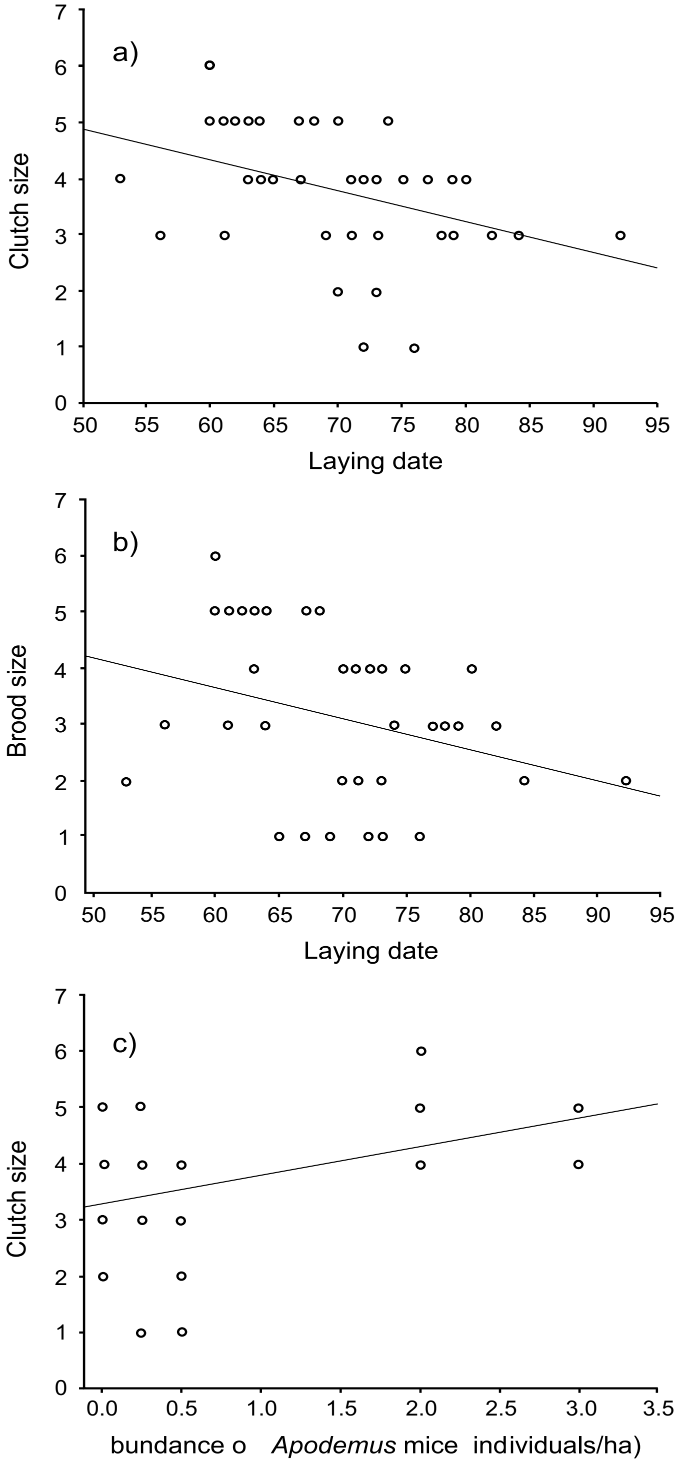


Fig. 4 Regression relationships between laying date (i.e., day from 1 January) and (a) clutch size (P = 0.014) and (b) brood size (P = 0.057) and (c) the relationship between abundance of *Apodemus* mice in the field and clutch size (P = 0.002). For all relationships, n = 39 nesting attempts



Reproduction

During the years 2008-2014, the studied Tawny Owls produced 208 eggs and 127 young (57 breeding attempts). Tawny Owl pairs produced (mean ± SD) 3.7 ± 1.2 eggs, 2.2 ± 1.8 hatchlings and 2.0 ± 1.8 fledglings per nest. The mean clutch size, brood size and number of fledglings varied among years (clutch size 2.7 - 4.7, brood size 1.4 - 3.2 and number of fledglings 1.3 - 2.9 per breeding pair). The largest clutches and broods were produced in 2010 and the highest numbers of fledglings were recorded in 2013. The lowest reproductive parameters were found in 2011 (Table 1).

We confirmed negative relationships between laying date and clutch size (regression, $R^2 = 0.39$, $F = 6.66$, beta = -0.13, $P = 0.014$, Fig. 4a) and brood size (regression, $R^2 = 0.31$, $F = 3.87$, beta = -0.07, $P = 0.057$, Fig. 4b). The relationship between laying date and number of fledglings was indicative (regression, $R^2 = 0.07$, $F = 2.9$, beta = -0.27, $P = 0.094$). Finally, we also found a positive correlation between the abundance of *Apodemus* mice in the field and clutch size (regression, $R^2 = 0.48$, $F = 11.06$, beta = 0.21, $P = 0.002$, Fig. 4c).

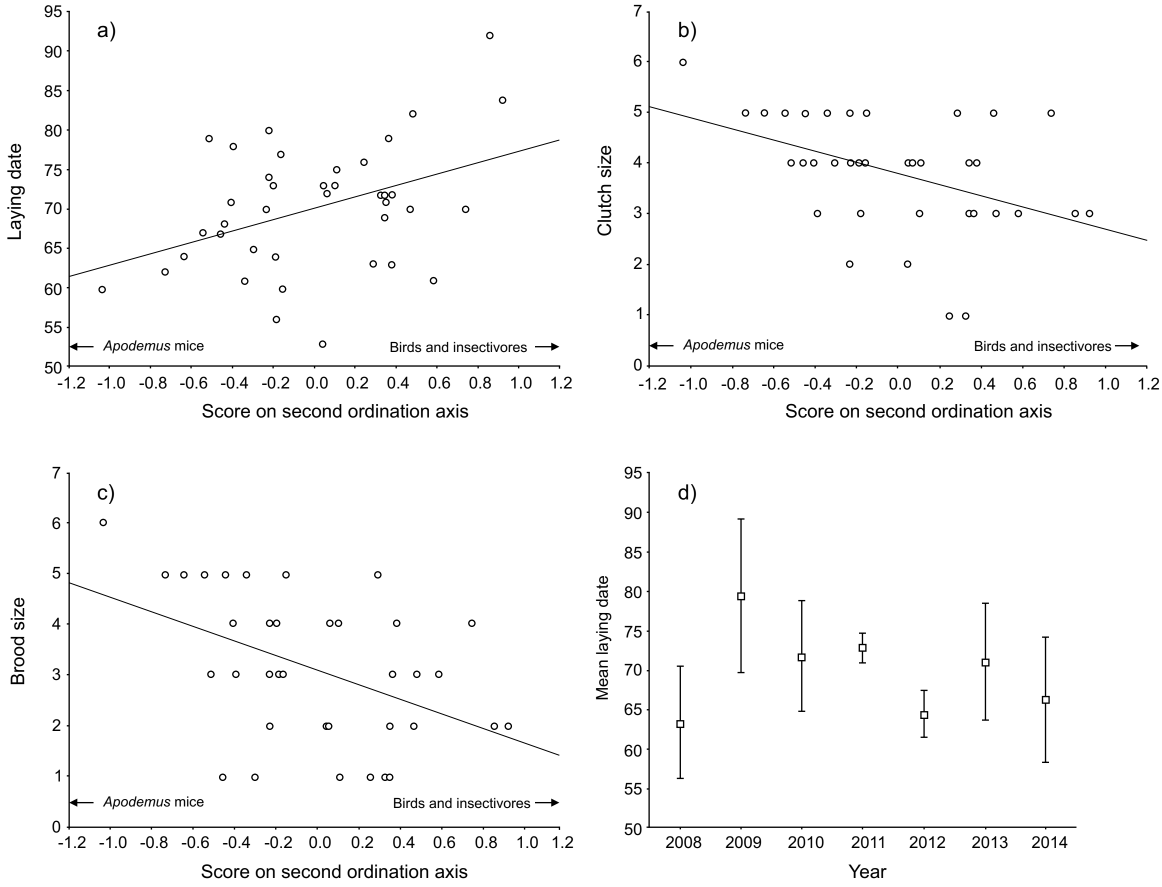
Scores from the second ordination axis of PCNM analysis on diet composition (i.e., gradient of proportions of birds and *Apodemus* mice) showed a positive relationship with laying date (Table 3). Particularly, we recorded a decreasing proportion of *Apodemus* mice and an increasing proportions of birds and insectivores in the diet during the course of the breeding season (Fig. 5a). These scores were also negatively correlated with clutch size (Fig. 5b) and indicatively negatively correlated with brood size (Fig. 5c, Table 3). Laying date also significantly differed among years (Table 3, Fig. 5d). Neither scores from the first ordination axis (i.e., gradient between unidentified rodents and *Microtus*/*Myodes* voles and Gliridae) nor nest box ID had a significant effect. None of the factors affected the number of fledglings.

Discussion

The role of main prey types in the diet of Tawny Owl populations can substantially change with their geographic positions. Within Europe, *Microtus*/*Myodes* voles are common throughout the whole continent, but *Apodemus* mice have their northern range border in Southern Finland. Therefore, Central European populations are more likely to include *Apodemus* mice in their diet compared to northern owls. In agreement, studies from Northern Europe (more than 54°N) consistently show an increased proportion of *Microtus*/*Myodes* voles compared to *Apodemus* mice (e.g., Overskaug et al. 1995; Petty 1999; Sunde et al. 2001). Similarly, Zmihorski et al. (2008) reported an increased proportion of Arvicolidae and a decreased proportion of Muridae in the diet of Tawny Owls along a NE gradient in the area around the Baltic Sea. Also our meta-analysis showed that the proportion of *Apodemus* mice decreases towards northern areas and owls there often feed on shrews and *Microtus*/*Myodes* voles.

In agreement with most others studies (e.g., Capizzi 2000; Balčiauskiene 2005; Balčiauskiene et al. 2005; Gryz et al. 2008), the dominant prey of our owls were rodents (84.5%). Within Europe, rodents in the diet of Tawny Owl are mainly represented by Muridae (mainly *Apodemus* mice) and Arvicolidae (mainly *Microtus* and *Myodes* voles) (e.g., Sunde et al. 2003; Balčiauskiene and Naruševičius 2006; Balčiauskas et al. 2011), which is also supported by our results (*Apodemus* mice 66.9% and *Microtus*/*Myodes* voles 26.7%). Moreover, *Apodemus* mice showed a positive relationship between their proportion in the diet and availability in the field. Such a relationship was not found for *Microtus*/*Myodes* voles nor Sorex shrews. The great importance of *Apodemus* mice in the diet of Tawny Owl has also been recently documented in Switzerland (Roulin et al. 2009). Moreover, it was documented that

Fig. 5 The relationships between scores from the second ordination axis of PCNM analysis on diet composition (i.e., gradient of proportion of birds, insectivores and *Apodemus* mice in the diet as indicated by arrows above horizontal axes) and (a) laying date (regressions, P = 0.012), (b) clutch size (P = 0.004) and (c) brood size (P = 0.076). (d) Mean laying dates (± SD) during the study period (P = 0.036)



within Europe *Apodemus* mice represent the main prey for several owl species. For example, Zárybnická et al. (2013) showed that Boreal Owl diet in the Czech Republic is dominated by *Microtus* voles, but a functional response was found only for *Apodemus* mice. Similar results were also found in Long-eared Owl, a vole specialist in northern latitudes, but often feeding on *Apodemus* mice in Central Europe during vole scarcity (Riegert et al. 2009). Based on these results, we suggest that the availability of *Apodemus* mice drives the diet composition of these owls within their range. The suitability of *Apodemus* mice as a main prey is supported by the following: (1) *Apodemus* mice show mainly nocturnal activity compared to the cathemeral activity of *Microtus* voles (Halle and Stenseth 2000). Therefore, compared to, for example, diurnal vole specialists like Eurasian Kestrel (*Falco tinnunculus*) (Village 1990), owls are more likely to exploit *Apodemus* mice as prey. In agreement, Eurasian Kestrels in Central Europe during vole scarcity feed mainly on insects and *Apodemus* mice are not frequent prey (Riegert and Fuchs 2004). (2) Habitat preferences of *Apodemus* mice for wooded and ruderal habitats (Anděra and Horáček 2005) are consistent with the hunting habitat preferences of Tawny Owl (Kajtoch et al. 2015), Long-eared Owl (Lövy and Riegert 2013) and Boreal Owl (Zárybnická et al. 2015b).

Representations of other components of Tawny Owl diet considerably vary across the European continent, but in general, proportions of birds (12.1%), insectivores (1.2%) and amphibians (2.2%) in the diet of our Tawny Owls are comparable with other studies (e.g., Kirk 1992; Kekkonen et al. 2008; Grzedzicka et al. 2013). Across the years of study, *Apodemus* mice were replaced by different prey including birds, insectivores and *Microtus*/*Myodes* voles in relation to their abundance in the field. Interestingly, in one year we recorded an increased proportion of frogs (11%). In this year (2013), two of six pairs settled nearby water streams. In the territory of one Tawny Owl pair, the water surface developed during the breeding period, which consequently led to the occurrence of frogs in the diet. Similar results were shown by Zmihorski and Osojca (2006) who reported a high proportion of amphibians in the diet of Tawny Owls mainly occurring in pairs breeding near water surfaces. Based on our meta-analysis the proportion of amphibians increases towards the East, but their representation is probably influenced by the presence of an aquatic environment in the home ranges of individual pairs. A similar latitudinal trend was also recorded for other mammals, this was probably caused by the different faunal composition of rodents in Southeast Europe compared to other parts of Europe (e.g., *Chionomys*, *Dinaromys*). The role of Gliridae in the diet of our owls was of rather minor importance, but based on the results of the meta-analysis their proportion in Tawny Owl diet increased at low latitudes.

We did not find a positive relationship between abundance of *Apodemus* mice, *Microtus*/*Myodes* voles or *Sorex* shrews in the field and the number of breeding Tawny Owl pairs. These results are in contrast with some studies in Central Europe (e.g., Roulin et al. 2009), but agree with others (e.g., Zárybnická et al. 2013, 2015a). In our study, we cannot distinguish whether the absence of a numerical response was caused by the breeding strategy of Tawny Owls, low number of caught *Apodemus* mice in the field or relatively short study period (seven years).

We found a negative relationship between the proportion of *Apodemus* mice in the diet and laying date (i.e., the earlier the owl breeds the more *Apodemus* mice occur in its diet) and clutch size that is consistent with the results of a study from Switzerland (Roulin et al. 2009). We also found a positive relationship between the proportion of *Apodemus* mice in the diet (expressed by scores from ordination axis) and breeding parameters (clutch size and brood size). These results suggest that unavailability of the main prey in the late breeding phase forces breeders to switch to alternative prey (i.e., birds or insectivores). As shown by several studies, laying date can be used as a good measure of individual quality (reviewed by Sergio et al. 2007a).

Our results document the great importance of *Apodemus* mice in the feeding ecology of Tawny Owl in Central Europe, independent of the availability of other prey groups. The role of *Apodemus* mice in the diet of Tawny Owl in Central and Southern Europe is also supported by meta-analysis of literature data. *Apodemus* mice availability further influences breeding performance. Although, Tawny Owls are flexible in prey choice, our data suggests that on average the abundance of *Apodemus* mice is important in shaping its breeding performance.

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Electronic Supplementary Material

Apodemus mice as the main prey that determines reproductive output of Tawny Owl (*Strix aluco*) in Central Europe

Population Ecology

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Table S1. Diet composition of Tawny Owls during the years 2008 - 2014. *n* - number of individuals, B - total biomass of the taxon, *n*% - percentages by numbers, B% - percentages by biomass

Taxonomic group	Taxon	*n*	*n*%	B (g)	B%
Insectivora	*Sorex minutus*	19	0.8	76	0.1
	Sorex araneus	7	0.3	63	0.1
	Neomys fodiens	2	0.1	32	0.0
	Insectivora total	28	1.2	171	0.2

Rodentia	*Apodemus* sp.	878	38.7	25023	33.5
	Mus sp.	46	2.0	782	1.0
	Rattus sp.	3	0.1	960	1.3
	Microtus sp.	123	5.4	3752	5.0
	Myodes glareolus	227	10.0	5221	7.0
	Arvicola terrestris	28	1.2	3640	4.9
	Glis glis	2	0.1	235	0.3
	Muscardinus avellanarius	5	0.2	108	0.1
	Rodentia unidetermined	604	26.6	17516	23.4
	Rodentia total	1916	84.5	57236	76.6
Aves	*Columba palumbus*	1	0.0	500	0.7
	Dendrocopos major	3	0.1	240	0.3
	Psittaciformes unidet.	1	0.0	65	0.1
	Oriolus oriolus	1	0.0	72	0.1
	Garrulus glandarius	4	0.2	680	0.9
	Cyanistes caeruleus	1	0.0	11	0.0
	Parus major	2	0.1	40	0.1
	Paridae unidet.	8	0.4	120	0.2
	Aegithalos caudatus	2	0.1	14	0.0

	Sylviidae unidet.	11	0.5	220	0.3
	Sitta europaea	4	0.2	96	0.1
	Phoenicurus phoenicurus	3	0.1	45	0.1
	Turdus philomelos	3	0.1	210	0.3
	Turdus viscivorus	2	0.1	240	0.3
	Turdus merula	9	0.4	863	1.2
	Turdus sp.	9	0.4	863	1.2
	Carduelis spinus	1	0.0	12	0.0
	Fringilla coelebs	8	0.4	185	0.2
	Carduelis chloris	2	0.1	57	0.1
	Coccothraustes coccothraustes	4	0.2	220	0.3
	Loxia curvirostra	1	0.0	94	0.1
	Emberiza citrinella	1	0.0	30	0.0
	Size of *Passer* sp.	102	4.5	2652	3.6
	Size of *Turdus merula*	91	4.0	8645	11.6
	Aves total	274	12.1	16174	21.7
Amphibia		49	2.2	1112	1.5
Osteichthyes		1	0.0	10	0.0
	Total	2268	100.0	74703	100.0

Table S2. Diet composition (percentages by numbers) of Tawny Owl in Europe based on published studies. Number of study refers to its label in the meta-analysis (Fig. 2). *n* – total number of determined prey items

Reference	Study number	Country	Latitude	Longitude	*Apodemus* mice	*Microtus* voles	*Myodes* voles	Insectivores	Gliridae dormice	Other mammals	Birds	Amphibians	Insecta	Others	*n*
Adánez (2000)	1	Spain	41.598	-5.603	11.34	3.92	0.00	3.20	0.73	0.58	3.20	0.58	74.71	1.74	688
Balčiauskiene et al. (2006)	2	Lithuania	55.286	23.978	17.17	37.88	33.09	0.00	0.31	3.75	1.25	5.93	0.62	0.00	961
Baudvin and Jouaire (2006)	3	France	47.305	4.646	51	3.58	20.34	8.33	1.33	0.66	3.52	8.16	2.92	0.04	51734
Capizzi (2000)	4	Italy	43.646	11.495	27.47	17.45	8.94	10.82	9.17	5.24	9.82	1.54	9.40	0.15	2596
Capizzi and Luiselli (1998)	5	Italy	42.417	12.105	37.23	23.69	6.77	2.46	4.31	17.54	6.46	0.00	1.54	0.00	325

Grzedzicka et al. (2013)	6	Poland	50.012	20.986	30.12	10.32	0.00	8.25	0.00	18.02	18.43	7.84	7.02	0.00	727
Kirk (1992)	7	Great Britain	52.475	1.754	18.54	6.83	14.63	0.49	0.00	3.90	27.80	0.00	27.80	0.00	205
Kuhar et al. (2006)	8	Slovenia	46.037	15.594	28.94	6.66	1.73	1.48	7.35	4.19	7.10	3.75	38.17	0.64	2028
Marchesi et al. (2006)	9	Italy	46.067	11.119	21.40	3.97	6.93	0.00	14.40	4.20	44.44	0.00	4.67	0.00	1285
Obuch (2011)	10	Belgium	50.534	3.528	12.74	18.39	16.31	29.50	0.75	2.15	13.19	4.82	1.95	0.19	15450
Obuch (2011)	11	Bulgaria	41.933	24.250	23.33	3.85	0.77	3.85	10.77	11.03	7.95	7.69	4.87	25.90	390
Obuch (2011)	12	Czech Republic	49.817	15.473	35.99	19.30	11.21	9.45	3.12	3.51	11.72	3.94	0.87	0.89	17433
Obuch (2011)	13	Crimea and Caucasus	44.042	37.846	40.52	8.93	0.00	6.14	10.08	7.30	7.30	2.02	3.84	13.87	2083
Obuch (2011)	14	Montenegro	43.233	19.017	22.50	3.97	1.70	2.46	26.28	7.37	9.26	4.35	0.57	21.55	529
Obuch (2011)	15	Germany	51.017	14.741	11.90	56.08	4.65	3.27	0.22	3.08	9.03	5.57	5.23	0.97	8513

Obuch (2011)	16	Norway	63.014	10.349	0.42	43.17	18.54	17.59	0.00	1.67	14.49	3.82	0.00	0.29	27396
Obuch (2011)	17	Romania	46.029	23.881	22.80	3.97	11.09	5.05	17.85	7.03	4.87	9.42	3.15	14.78	2219
Obuch (2011)	18	Slovakia	48.727	19.456	25.27	11.54	9.93	7.20	8.11	6.62	7.48	8.90	3.86	11.10	68070
Obuch (2011)	19	Turkey	37.783	35.562	17.25	2.29	0.47	1.98	0.63	17.96	18.75	30.30	3.01	7.36	1264
Overskaug et al. (1995)	20	Norway	60.887	8.765	13.43	14.93	10.82	6.34	0.00	5.22	7.09	0.37	41.79	0.00	268
Petty (1999)	21	Great Britain	55.194	-2.535	2.67	62.12	2.95	8.78	0.00	0.98	16.30	6.04	0.07	0.07	1423
Romanovski and Zmihorski (2009)	22	Poland	52.329	20.569	14.29	11.08	9.93	38.10	1.23	8.21	10.92	6.24	0.00	0.00	1218
Sergio et al. (2007)	23	Italy	45.741	10.870	32.56	6.98	12.18	0.00	22.85	5.20	13.13	0.00	7.11	0.00	731
Solonen and Karhunen (2002)	24	Finland	60.219	25.272	10.21	20.70	5.98	9.30	0.00	13.18	16.97	17.53	5.98	0.16	3194
Sunde et al. (2001)	25	Norway	63.435	10.398	0.97	43.96	27.05	15.94	0.00	2.90	9.18	0.00	0.00	0.00	207

Wiacek et al. (2009)	26	Poland	51.386	22.559	36.01	9.44	17.48	3.85	2.10	9.79	2.80	13.64	4.20	0.70	286
Zalewski (1994)	27	Poland	53.014	18.599	11.09	11.70	3.34	2.74	0.00	7.45	41.64	13.22	8.81	0.00	658
Zawadzka and Zawadzki (2007)	28	Poland	54.041	23.015	7.83	25.95	11.02	9.91	0.00	11.75	8.08	17.38	7.83	0.24	817
Zmihorski and Osojca (2006)	29	Poland	54.322	22.483	4.44	3.56	15.11	16.67	1.33	13.33	4.67	33.78	7.11	0.00	450
This study	30	Czech Republic	50.501	14.790	38.71	5.42	10.01	1.23	0.31	30.03	12.08	2.16	0.00	0.04	2268

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Příloha VII

Riegert J, Fuchs R. 2004:

Insects in the diet of urban kestrels from central Europe: An alternative prey or constant component of the diet?

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Insects in the diet of urban kestrels from central Europe: An alternative prey or constant component of the diet?

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During the years 1996–1998, the diet composition was assessed from pellets of kestrels in České Budějovice. Within the total number of 5226 prey individuals, insects made up 15.2% by numbers and 0.3% by weight. In the summer and early autumn, the abundance of insects was highest. It was partially caused by including pellets from juvenile kestrels that contained more insect remains than pellets from adults in general. Two main insect groups were found in the diet – beetles (mostly medium-sized Carabidae) and Ensifera (large Tettigoniidae). In the low vole year, the intake of beetles was higher in comparison with high vole year, whereas the intake of Ensifera was rather stable in both years. Our results support the "alternative" role of beetles in the diet of kestrels. However, the beetles are energetically incomparable with voles and are partially at least caught during the hunting on voles. Ensifera were more likely hunted with purpose. Contrary to beetles their proportion at individual roosting sites was balanced.

1. Introduction

The important role of insect prey in the diet of kestrels has been recorded many times before (i. e. Itämies & Korpimäki 1987, Davis 1975), especially in southern latitudes (i. e. Aparicio 1990, 2000, Piatella *et al.* 1999). The significance of this prey also increases when voles (*Microtus* sp.) become rare (i. e. Cavé 1968, Korpimäki 1985). The variation of insects in the diet of kestrels was recorded also within a year, especially the relatively important role of insects during the winter months (Davis 1975, Yalden & Warburton 1979). However, the main peak of insect in the diet comes in late summer or autumn months (Village 1982). This phenomenon was indirectly explained by hunting on insect prey by non-experienced juvenile kestrels (Shrubb 1982).

In central Europe, the role of insect in the diet should be less pronounced (reviewed by Korpimäki 1985). However, we have recorded a relatively high proportion of insects (by number) in the diet of kestrels from České Budějovice (Riegert 2001). Therefore we aimed at a more detailed analysis and tried to discover factors determining occurrence of main insect components.

We tested two null hypotheses: (1) The representation of insects in the diet does not depend on vole availability. (2) The representation of insects in the diet of juvenile and adult kestrels does not differ.

2. Material and methods

2.1. Study population and pellet collecting

We studied the diet composition of kestrels in the medium sized city of České Budějovice (Southern Bohemia, 250 m a. s. l., 49°58'N, 14°29'E; 40 km^2; radius of the city 4 km; 100,000 inhabitants). The population of kestrels in České Budějovice varies between 40 and 50 pairs. The kestrels breed in the centre (in lofts or ventilation shafts) as well as on outskirts (on industrial buildings or in nest boxes). Breeding density is higher in the centre while the number of breeding pairs is more balanced as the area of outskirts is larger. The females disappear from České Budějovice in the course of autumn whereas the males winter there and they leave their breeding ranges for periods with continuous snow cover only.

All kestrels from České Budějovice feed outside the city predominantly and hunting is rarely observable inside the built-up areas. Within a radius of 5 kilometres of the continuously built-up areas, the hunting grounds include ruderal habitats (16%), either cut or not cut meadows (49%) and fields (35%).

The pellet collecting was made at individual roosting sites of kestrels in the centre of the city as well as in the outskirts (during the summer, the temporary roosting sites of juvenile kestrels were included too). In total we made 261 collections at 21 sites, in the period between August 1996 and October 1998, from which 31 collections (11.9%) came from roosting sites of juvenile kestrels in the post-fledgling period. The interval between two pellet controls varied between 8 to 42 days (mean 19.7 ± 8.3 days). The distribution of controls during the year and the number of pellets is shown in the appendix. The August was the only month with low number of collections, therefore it was excluded from statistical analyses.

To make sure of the categorisation of roosting sites between adult kestrels and juveniles, we made irregular night-controls with flashlight (at least one at each site per month). The roosting behaviour of juvenile kestrels was quite different from adult birds, since they tried to spend the night together or close to each other, especially in the early post-fledging period (personal observation). On the other hand adult birds roosted solitary. The juveniles' roosting sites were recorded between June and November, yet the highest number of collections (18 from 35) came from July.

2.2. Pellet analysis

In total, we identified 5,226 prey individuals (4,577 pellets) in the diet of kestrels (see Appendix). The pellets were dried and all feather-remains were identified. The rest was dissolved in a solution of NaOH (Schueler 1972). Small mammals were determined by skulls using Anděra and Horáček (1982) and birds by beak and humeri using a reference collection. All beetles' remains were identified according to sculpture, coloration and size of coverts. However, unidentified individuals represent the great part of data on beetles (72.1%), when the remains of coverts were incomplete or milled. Ensifera were identified by the presence of apertures on legs. The presence of earthworms was not proved. Number of heads or mandibles (in Ensifera), coxae and other parts of legs determined the number of individuals. The total number of prey individuals was given by most number of identified parts of the body (i. e. one head and seven legs give two individuals, one head and six legs give one individual). The data on weight of prey groups (Ensifera, beetles, voles, shrews, birds and lizards) were taken from Hudec and Černý (1977), Itämies and Korpimäki (1987) and Carillo *et al.* (1995). Data on lengths of insect prey were taken from Javorek (1968) and Zahradník (1987).

2.3.Vole trapping

From the year 1997 we estimated the vole numbers on hunting grounds used by kestrels from České Budějovice (within a radius of 5 kilometres of the continuously built-up area). We used pitfall traps (plastic bottles with a cut neck and capacity of 2 l), totalling a 100 in number, each year. These traps were installed at 10 kestrel hunting grounds in late July (10 traps made up a trap line). All occurred habitat types were covered (50 traps were installed in meadows, 30 in fields and 20 in ruderal habitats). The traps were filled with a 4% fusion of formaldehyde and exposed for 17 days. In each year the trapping effort was 1700 trap-nights. The numbers of voles caught: 34 (1997), 154 (1998), 45 (1999), 19 (2000), 29 (2001), 79 (2002).

2.4. Observations on hunting behaviour

The data on hunting behaviour were adopted from another authors' project, realised in České Budějovice during 1999–2002. Hunting grounds have been visited during the breeding season, from the late April to half of July. We gathered data on 302 hunting actions of adult birds. Besides the hunting success, we analysed the time, which was spent on ground after landing.

2.5. Statistical analyses

The data from the year 1996 were excluded from analyses, because the abundance of the common vole was not estimated in this year. Before the analyses, we recalculated the data in collections to individuals per one pellet. The changes of abundance were analysed using Generalised Linear Models (GLM, forward selection of factors, logit link function; Mc Cullagh & Nelder 1989). The selection and order of factors in a model was defined by Mallows Cp-statistics (Mallows 1973). We included mean temperature and mean precipitation in the course of control period, summer vole number and month into independent variables. To avoid pseudoreplications by repeating collections at one site, we involved the factor "site" into analyses. As the observed trends had differed for the two main insect components we computed three models that differed in dependent variable: a) all insects together, b) beetles only, c) Ensifera only. Ants or cockroaches were not analysed separately, because their proportions were too small (<2% of all insects). Using GLM analysis we tested the influence of vole abundance and hunting success to time spent on ground by kestrels after landing.

The Multivariate percentage data on diet composition (including vertebrates) were computed by Redundancy Analysis (RDA) in CANOCO (Braak & Šmilauer 1998) and visualised in CANODRAW (Šmilauer 1992). The data from collections were summarised by the month, for both years separately and percentages of each component in the diet were log-transformed. Mean temperature and mean precipitation in the course of control period and summer vole numbers were included into environmental variables. Because the vole proportion in the diet was incomparably higher than proportion of other individuals, its percentages were weighted at 0.011.

The analysis of abundance of prey components between adult and juvenile kestrels was based on Kruskal-Wallis tests using STATISTICA Software (Statsoft, Inc. 1996). We used only data that belong to period when juveniles are present at roosting sites (July–November).

3. Results

3.1. Overall diet composition

The common vole (*Microtus arvalis*) was the most dominant prey in the diet. Its overall proportion was 77.9% by numbers (n = 4073) and 90.7% by weight. Other vertebrates, represented by other mammals, birds and lizards, made only 6.9% by numbers (n = 362) and 9.0% by weight. The insect prey made 15.2% by numbers (n = 796), yet only 0.3% by weight. Within the year (monthly data averaged) the proportion of insect varied between 3.6 and 31.5% (by numbers) or 0.0 and 1.4% (by weight). Other invertebrates were not recorded. The abundance (individuals per pellet) of insect prey showed two decreases during the winters 1996/97 and 1997/98 (Fig. 1). In the year 1998, the followed up increase during the breeding season and summer was less prominent. The abundance of voles in the diet was found to be increasing towards the year 1998 and that of other vertebrates was decreasing.

3.2. Insects in the diet

The remnants of insects were found in 62.1% of collections (162 from 261). Among insects, the proportion of beetles (Coleoptera) was 75,5% by numbers, Ensifera making up 23.9% and ants (Formicidae) and cockroaches (Blattodea) together 0.6%.

The proportion of beetles was high during the months of October and November 1996, and

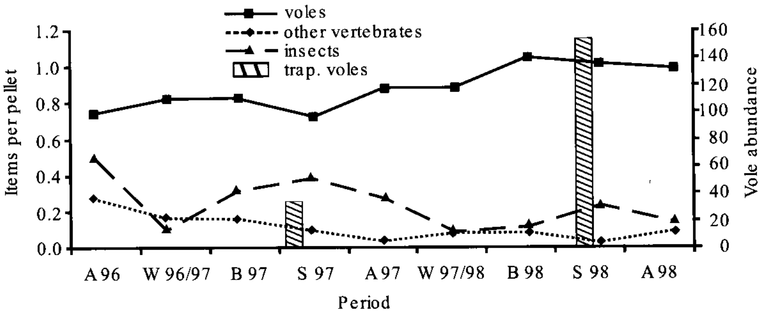

Fig. 1. The changes of abundance (individuals per pellet) of insects, voles and other vertebrates in the diet of kestrels, years 1996–1998. A – autumn (Sep–Nov), W – winter (Dec–Feb), B – breeding season (Mar–May), S – summer (Jun–Aug).

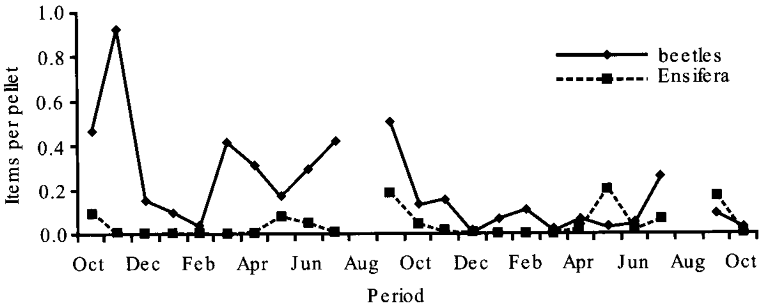

Fig. 2. Seasonal variation in abundance (individuals per pellet) of Ensifera and beetles in the diet. Data from Oct. 1996 to Oct. 1998.

March, July and September 1997 (Fig. 2). The lowest abundance was found in the winters 1996/97 and 1997/98. Among determined beetles (see Appendix), the most dominant groups were Carabidae (56.0%), Scarabeidae (15.7%), Dytiscidae (12.0%) and Curculionidae (8.8%). Carabidae were the only beetles that were found in the diet most of the year through, including the winter months. Their abundance was highest during the summer (June and July) and the same was true for Scarabaeidae. The third most dominant family of beetles, Dytiscidae, became most abundant in March.

The great number of beetles remained unidentified (73.1%), since only coxae and other parts of legs (especially from small species) were found. These could be considered in most cases being from small Carabidae, not true *Carabus* species.

Ensifera were recorded in the period between April and November. Their abundance were higher during the year 1998, with the peak in May and September (Fig. 2). Most of them (>90%), belonged to the family Tettigoniidae. The rest probably belonged to family Gryllidae.

Site, summer vole numbers and mean temperature in the course of control period significantly affected the abundance (individuals per pellet) of insects in the diet whereas the precipitation and the month had no significant effect (Table 1). In the year 1998, when the vole availability increased, the proportion of insect in the diet was lower. With increasing temperature the proportion of insect was higher ($r_s = 0.22$, $P = 0.03$, $n = 261$). When beetles and Ensifera were tested separately, the site and the vole availability had significant effect to the changes in abundance of beetles only. The model containing beetles only explained even

Table 1. Factors affecting the abundance (individuals per pellet) of insect prey in the diet of urban kestrels (only significant relations included). Poisson GLM models, forward selection based on Cp-statistics. For all models, n = 251 collections.

Dep. var.	Indep. var.	Explained var. (%)	β	P
Insects	site	30.9	–	0.0001
	vole numbers	2.8	*	0.0214
	temperature	2.6	0.12	0.0221
Beetles	site	38.2	–	0.0001
	vole numbers	3.3	*	0.0001
	temperature	0.1	0.14	0.0341
Ensifera	temperature	3.1	0.19	0.0042

* The intake was lower in 1998

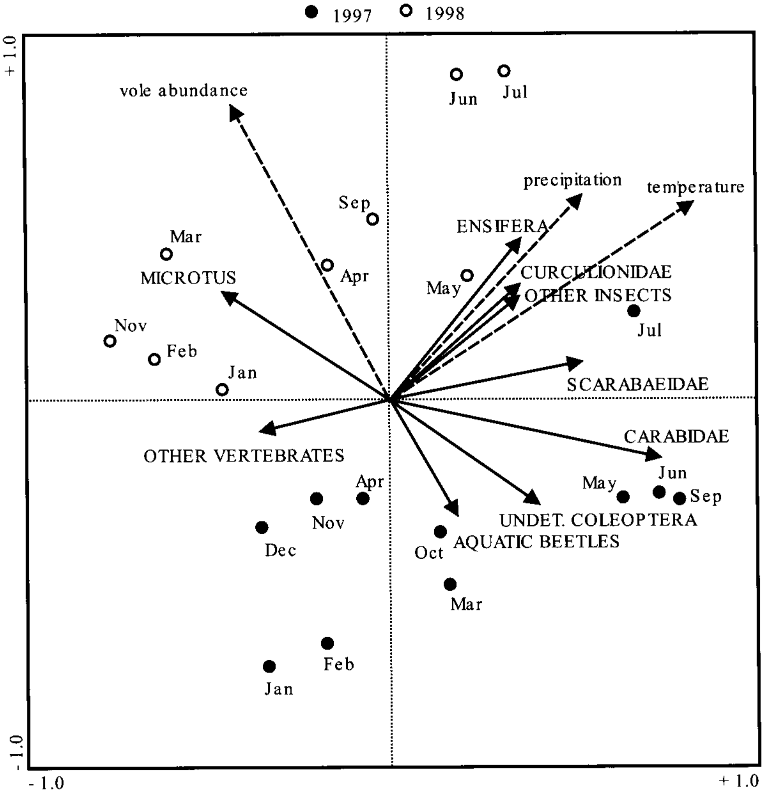

Fig. 3. The projection scores of main recorded invertebrate and vertebrate prey groups (from percentages), related to environmental factors. RDA, I and II canonical axes together 96.2%. Monte Carlo permutation test. Weight given to proportion of voles = 0.011.

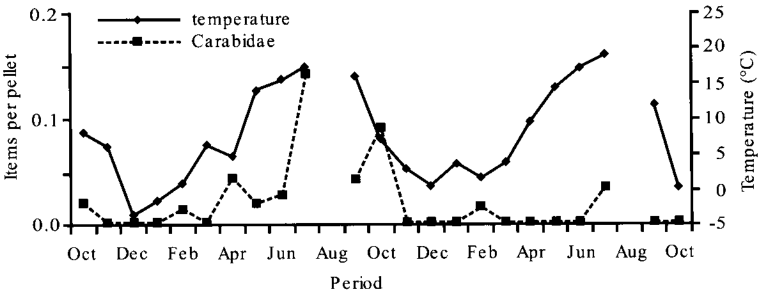

Fig. 4. The changes in abundance of Carabidae in the diet and mean month temperature. Data from Oct. 1996 to Oct. 1998 (n = 89).

more variability than the model with all insects. The mean temperature positively affected the abundance in both, Ensifera and beetles, yet the relationship was more pronounced in Ensifera.

Despite the fact that the influence of environmental factors tested in multivariate analysis (Fig. 3) was only indicative (temperature, P = 0.11; precipitation, P = 0.18; vole numbers, P = 0.10; Monte Carlo permutation tests, RDA), the pattern of data is similar to previous tests. Two independent gradients were found in the data. The first was correlated with the mean month temperature, second with the availability of voles. The precipitation were positively correlated with the temperature ($r_S = 0.71$, $P < 0.05$, $n = 27$). Along gradients, both the collections (sites) and diet components (species) formed well-distinguished groups. The availability of voles markedly separated the years, which apparently differed in the representation of voles and most of beetles (Scarabaeidae, Carabidae, aquatic and unidentified groups) in the diet. The proportion of voles in the diet correlated with the vole availability positively, whereas the proportion of beetles showed a negative relationship. The proportion of other vertebrates, Ensifera, Curculionidae and other insects were correlated with the temperature gradient. The relationship was negative in vertebrates and positive in insects. The border between warm and cold periods was set by the collections from May 1997, March and April 1998.

Carabidae were the only group of beetles that's relatively high numbers enabled detailed analysis. There was a positive correlation between the abundance of Carabidae and mean month temperature ($r_S = 0.51$, $P = 0.012$, $n = 27$). The spring changes of Carabidae abundance clearly followed the changes in temperature, with a one-month delay (Fig. 4). With the single exception of September 1997, the autumn abundance followed actual temperature in the month. In the year 1998, when vole numbers on hunting grounds increased, the relation became less prominent.

3.3. Insect diet of adult and juvenile kestrels

The analysis of diet composition between adult and juvenile kestrels showed that the intake of insects was significantly higher in juvenile individuals (Kruskal-Wallis test, H = 8.44, P = 0.004, n = 123; Fig. 5). The intake of insects by juvenile kestrels did not change between the years (Kruskal-Wallis test, H = 0.47, P = 0.490, n = 31). On the contrary, adult and juvenile kestrels do not differ in the intake of voles (Kruskal-Wallis test, H = 0.82, P = 0.775, n = 123; Fig. 5).

3.4. Size of insect prey

The distribution of insect prey length in the diet is clearly bimodal with the peaks between 10–15 and 30–35 mm (Fig. 6). Medium sized Carabidae, Scarabeaidae and Curculionidae beetles give the first one and Ensifera the second one. Formicidae, Byrrhidae, Hydrophilidae (*Hydrobius fuscipes* only) and Histeridae represent the smallest prey individuals (<10 mm) and Ensifera the largest prey (>30 mm).

3.5. Hunting behaviour

With the increasing vole abundance, the time spent on ground after strike was decreasing (Table 2). After negative strikes, the kestrels spent on ground more time, but the difference was indicative only.

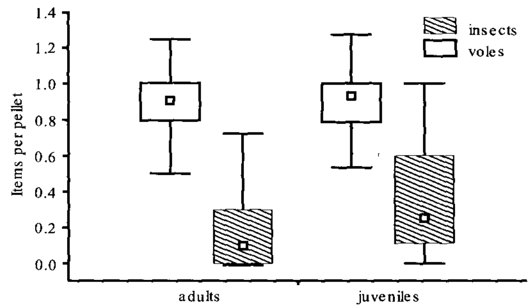

Fig. 5. The intake of voles and insect prey (individuals per pellet) by adult kestrels and post-fledgling juveniles, Kruskal-Wallis median test (H = 8.44, P = 0.004, n = 132,). Median, 25–75%, non-outlier range.

4. Discussion

4.1. The role of insects in kestrel's diet

The role of insect prey in the diet of kestrels increases from north to south and in areas with climates influenced by the Atlantic (Korpimäki 1985, Aparicio 1990, Village 1990). Its proportion in the diet in České Budějovice was quite low, in comparison with southern (Fernández-Alonzo 1985, Aparicio 1990, Carillo *et al.* 1995, Piatella *et al.* 1999) and western Europe (Fairley & McLean 1965, Thiollay 1968, Davis 1975, Village 1982). The proportion of insect was rather similar to other studies from central Europe (9% – Romanowski 1996, 4.7% – Plesník 1992), yet was slightly higher (15.7%).

Among insects, beetles were the most domi-

Table 2. The influence of tested factors to time spent on ground by kestrels after landing (n = 302). Poisson GLM models, forward selection based on Cp-statistics.

Independent var.	Explained var. (%)	β	P
Vole abundance (items)	8.6	–0.84	0.0009
Hunting success (y/n)	1.3	*	0.1012

* The time-delay was longer after non-successful strikes

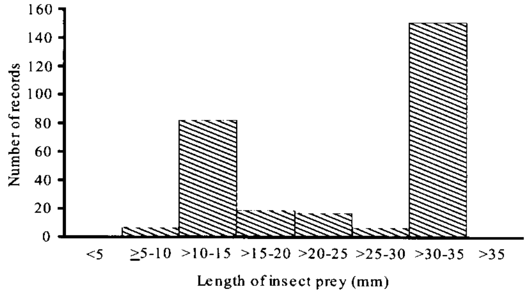

Fig. 6. The distribution of length categories (in mm) of insect prey in the diet, n = 283.

nant group that composed over 75% of the insect remains. This result corresponds well with other works on kestrels diet (i.e. Plesník 1992, Piatella *et al.* 1999). Among beetles, the Carabidae were found in the diet most frequently as showed by other studies at similar and northern latitudes also (i.e. Davis 1975, Itämies & Korpimäki 1987). In the Canary Islands, Carabidae are less numerous and they are substituted for Scarabaeidae and Tenebrionidae (Carillo *et al.* 1995). The importance of Scarabaeidae (genus *Geotrupes*) in the diet of kestrels was also docummented by many studies from islands of United Kingdom (Simms 1961, Fairley & McLean 1965, Davis 1975, Yalden & Warburton 1979, Village 1982). In the recent study, remains of Scarabaeidae were less abundant and in most of cases belonging to genus *Rhizotrogus* (see Appendix). The proportion of the third most numerous group – Dytiscidae – is quite high in comparison with all mentioned studies. This result may have something to do with the large number of fishponds in the surroundings of České Budějovice. However, the family is not represented by large species, but small ones of genus *Colymbetes*, whose occurrence in the diet of kestrels was recorded in western Finland too (Itämies & Korpimäki 1987).

The representation of other insects was nearly restricted to Ensifera (mostly Tettigoniidae), whose overall proportion (3,1%) was similar to other urban studies from central (Plesník 1992) and western (Thiolay 1968) Europe.

We can conclude by saying that the insect component in the diet of kestrels from České Budějovice is similar to other kestrel populations from central Europe. This is not surprising in case that the kestrels from České Budějovice predominately feed in surrounding rural landscape.

4.2. Why kestrels in central Europe prey on insects?

The highest peak of insect prey was found in summer and early autumn. We have no data about insect abundance on the hunting grounds and therefore we are not able reject directly the null hypothesis that the representation of insect prey is determined by its availability only.

Shrubb (1982) explains the increase of insect prey in the diet during the summer and early autumn by the hunting behaviour of juvenile kestrels and our results are consistent with his finding. The pellets from temporary roosting sites of juvenile kestrels contain a higher number of insects than those from adult birds. Moreover, the abundance of insects in the diet of juvenile kestrels did not decreased in the year with high abundance of voles. Therefore juvenile kestrels contribute to the summer and early autumn peak of insect prey at least.

Shrub (l.c.) assigns the higher proportion of insects in the diet of juvenile kestrels to their low hunting ability. However, there are alternative explanations. Juvenile kestrels may be forced out to the worse hunting grounds. We have no indications supporting this hypothesis, as we have not observed any attacks of adult kestrels against juvenile ones. Another explanation is that the juvenile kestrels have less pronounced feeding preferences only. Our finding, that there is no difference in the number of voles in pellets among adult and juvenile kestrels, support this hypothesis. The insects do not substitute the voles in the diet of juvenile kestrels they only supplement them. Therefore the insects in the diet of juvenile kestrels do not represent an alternative prey in the sense of "Optimal Foraging Theory" (Stephens & Krebs 1986).

The abundance of beetles in the pellets differed between sites markedly that indicated great individual variability. Additionally, beetles in diet occurred in low vole year more frequently. The impact of temperature was less pronounced, showing the differences between warm and cold months. The increased abundance of beetles during the summer was prominent in the year 1997 only, when vole availability was lower.

This result supports findings of other studies that beetles play the role of alternative prey in kestrels (i.e.Yalden and Warburton 1979, Village 1982, Korpimäki 1985). However, taking the weight of recorded beetles into consideration, their proportion in the diet is negligible (see also Itämies and Korpimäki 1987, Plesník 1992). The "Optimal Foranging Theory" predicts that prey types are added to the diet in order of their profitability (Stephens & Krebs 1986). However, the profitability of beetles is much lower than that of other potential alternative prey. Especially birds should be attractive for the urban kestrels. However, their representation in the diet remains low and stable. We suppose that minimum hunting costs compensate disadvantage of beetles as alternative prey. Village (1983) and Shrubb (1982) pointed that insects are caught with purpose, from hovering near the ground. We did not observe such hunting behaviour. We suppose that at least some beetles are caught during the hunting on voles. In agreement with the statement, the time spent on ground by kestrels after strike from "normal hovering" was longer during low vole year. We suppose that this time-delay could be used for hunting on beetles. The indicative difference in time-delay was also found between successful and non-successful strikes. This result may indicate that searching for beetles is more intensive if more profitable prey is lost.

In contrast, Ensifera were found in the diet independent to the availability of voles. Their occurrence in the diet is probably limited by temperature only. The representation of Ensifera also did not differ between sites significantly, in contrary with beetles and voles. Ensifera identified in pellets (in most cases large Tettigoniidae) are approximately 6.5 times heavier than beetles. Therefore we suppose that hunting of Ensifera was done with purpose. Moreover the Ensifera represent equally preferred prey as voles do. The similar role of Ensifera was found before, especially in southern and western populations of kestrels (Thiollay 1968, Carillo *et al.* 1995, Piatella *et al.* 1999, Aparicio 2000). Their representation was higher in one order however.

We can reject both null hypothesis formulated in Introduction. In České Budějovice the representation of insects in the diet of kestrel increase with the decreasing vole availability. However, this conclusion is valid for beetles only that form less profitable component of the insect prey. The representation of insect in the diet of juvenile kestrels is higher than that of adult ones. However, the insect prey does not substitute the voles in the diet of juvenile kestrels.

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Hyönteiset tuulihaukan ravinnossa: vaihtoehtosaalista vai pysyvä osa ravintoa?

Artikkelin kirjoittajat analysoivat tuulihaukan ravinnon koostumusta vuosina 1996–1998 České Budějovicen kaupungissa. Kirjoittajat keräsivät oksennuspalloja 21 tuulihaukan levähdyspaikalta 261 eri kertaa. Lisäksi arvioitiin myyrien määrä sekä havainnointiin haukkojen saalistuskäyttäytymistä. Oksennuspallonäytteitä kertyi kaikkiaan 4 577 kappaletta ja niistä määritettiin yhteensä 5 226 saalisyksilöä.

Tuulihaukan pääsaalislajiksi havaittiin kenttämyyrä; saalisyksilöistä kenttämyyriä oli 78 %. Hyönteisten osuus saalisyksilöistä oli keskimäärin 15 %. Saalisyksilöiden painosta hyönteisten osuus oli vain 0,3 %. Suurimmillaan hyönteisten osuus saalisyksilöistä oli kesällä ja alkusyksyllä. Nuorten tuulihaukkojen näytteissä oli enemmän hyönteisiä kuin vanhojen lintujen näytteissä. Pääasiallisia tuulihaukan saalishyönteisryhmiä olivat kovakuoriaiset (erityisesti keskikokoiset maakiitäjäiset) sekä suorasiipisiin kuuluvat pitkäsarviset (erityisesti isot hepokatit). Huonoina myyrävuosina haukat käyttivät ravintonaan enemmän kovakuoriaisia kuin hyvinä myyrävuosina.

Myyräkantojen koon vaihtelu ei sen sijaan vaikuttanut pitkäsarvisten määrään tuulihaukan oksennuspalloissa. Tulosten mukaan kovakuoriaiset näyttävät olevan tuulihaukoille vaihtoehtoista saalista, jota käytetään, kun myyriä on vähän. Kovakuoriaiset eivät kuitenkaan ole energeettisesti rinnastettavissa myyriin ja ilmeisesti tuulihaukka ainakin osittain saalistaa niitä myyränpyynnin yhteydessä. Hepokatteja tuulihaukka näyttää sen sijaan saalistavan tarkoituksellisesti.

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Appendix. The number of prey individuals in the diet of kestrels in České Budějovice during the years 1996–1998 and its annual changes.

Family/Order	taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	total	% by numbers
Byrrhidae	*Byrrhus* sp.	0	0	0	0	0	0	1	0	0	0	0	0	1	0.02
Carabidae	*C. granulatus*	0	0	0	0	2	0	1	0	0	0	0	0	3	0.06
	C. scheidleri	0	2	0	0	0	0	3	0	1	0	0	0	6	0.11
	Carabus sp.	0	1	0	0	3	0	8	0	0	0	0	0	12	0.23
	undet.	0	2	3	6	2	20	13	0	12	10	0	0	68	1.30
Cerambycidae	*Spondylis buprest.*	0	0	0	0	0	0	1	0	0	0	0	0	1	0.02
	Aromia moschata	0	0	0	0	0	0	0	0	1	0	0	0	1	0.02
Curculionidae	*Otiorrhynchus*	0	0	0	0	0	0	11	1	2	0	0	0	14	0.27
Dytiscidae	*Colymbetes fuscipes*	0	0	13	1	3	0	0	0	0	2	0	0	19	0.36
Hydrophillidae	*Hydrobius fuscipes*	0	0	1	0	0	0	0	0	0	0	0	0	1	0.02
Histeridae	*Hister* sp.	0	0	0	0	0	0	0	0	0	1	0	0	1	0.02
Scarabeidae	*Aphodius prodromus*	0	0	0	0	0	0	0	0	0	0	0	0	1	0.02
	Potosia cuprea	0	0	0	0	0	0	1	0	0	0	0	0	1	0.02
	Rhizotrogus sp.	0	0	0	0	0	5	18	0	0	0	0	0	23	0.44
Silphidae	*Necrophorus* sp.	0	0	0	0	0	0	0	0	1	1	0	0	2	0.04
Coleoptera undet.		22	22	35	62	28	25	50	6	65	79	40	8	442	8.46
COLEOPTERA		22	27	52	70	38	51	111	7	82	93	40	8	601	11.50
ENSIFERA		0	0	0	9	28	14	22	2	82	30	3	0	190	3.64
FORMICOIDEA		0	0	0	0	0	0	4	0	0	0	0	0	4	0.08
BLATTODEA		0	0	0	0	0	1	0	0	0	0	0	0	1	0.02
MICROTINAE	*Microtus arvalis*	240	302	365	458	413	356	572	10	339	597	238	183	4073	77.94
OTHER VERT.		21	31	29	54	37	33	29	6	18	65	8	31	362	6.93
Total number		283	360	446	591	516	454	734	25	521	785	289	222	5226	100.00
Number of collections		15	19	21	37	29	28	42	1	15	27	17	10	261	
Number of pellets		279	349	395	480	436	403	625	35	399	690	274	212	4577	

Příloha VIII

Zárybnická M, Kloubec B, Obuch J, Riegert J. 2015:

Fledgling productivity in relation to diet composition of Tengmalm's owl in Central Europe

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FLEDGLING PRODUCTIVITY IN RELATION TO DIET COMPOSITION OF TENGMALM’S OWL *AEGOLIUS FUNEREUS* IN CENTRAL EUROPE

PRODUCTIVIDAD DE VOLANTONES EN RELACIÓN A LA COMPOSICIÓN DE LA DIETA EN EL MOCHUELO BOREAL *AEGOLIUS FUNEREUS* EN EUROPA CENTRAL

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and Jan RIEGERT[3]

SUMMARY.—Based on 52 nesting attempts of Tengmalm’s owl *Aegolius funereus* in the Šumava Mountains (South Bohemia, Czech Republic), in habitats comprised mainly of Norway spruce forests, we investigated the relationships between diet composition and fledgling productivity of this owl. We found that (i) owls feed mainly on *Sorex* shrews (39%), *Microtus* voles (19%), *Apodemus* mice (15%), bank voles *Myodes glareolus* (14%) and birds (6%), (ii) the percentage of *Apodemus* mice, as well as the percentage of *Myodes glareolus*, negatively correlated to the percentage of *Sorex* shrews and birds in the owls’ diet, and (iii) the fledgling productivity of the owls positively correlated to the percentage of *Apodemus* mice in the diet. Finally, (iv) the percentage of *Microtus* voles, the second most common prey, exhibited no close relationships with other prey groups or fledgling productivity of the owls. These results suggest that *Apodemus* mice were an important prey in the diet of the Tengmalm’s owl in our study area, and support the theory that, compared to their northern counterparts, nocturnal raptors in Central Europe may be less dependent on *Microtus* voles due to the increased diversity of available prey species.

Key words: *Apodemus*, boreal owl, diet, *Microtus*, reproductive output, temperate area.

RESUMEN.—Analizamos las relaciones existentes entre la productividad y la composición de la dieta del mochuelo boreal *Aegolius funereus* en las montañas de Šumava (Bohemia del Sur, República Checa), basado en 52 intentos de nidificación de dicha especie en esta área, con hábitats compuestos principalmente por bosques de abetos de Noruega. Encontramos que (i) los mochuelos se alimentan de musarañas *Sorex* (39%), topillos *Microtus* (19%), ratones *Apodemus* (15%), topillo rojo *Myodes glareolus* (14%) y aves (6%), (ii) el porcentaje de *Apodemus*, así como el de *Myodes glareolus* en la

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dieta de los mochuelos mostró una relación negativa con la de *Sorex* y aves, (iii) la productividad se correlacionó positivamente con el porcentaje de *Apodemus* en la dieta de los mochuelos, y (iv) los topillos *Microtus*, que fueron la segunda presa más común, no mostraron relaciones significativas con los parámetros de reproducción analizados. Estos resultados sugieren que los ratones *Apodemus* son una presa importante en la dieta del mochuelo boreal en nuestra área de estudio y apoyan la teoría de que las aves rapaces nocturnas en Europa Central pueden ser menos dependientes de los topillos debido a la mayor diversidad de especies de presas disponibles en comparación con otras zonas del norte.

Palabras clave: *Apodemus*, dieta, *Microtus*, mochuelo boreal, resultado de la reproducción, zona templada.

INTRODUCTION

The optimal diet theory predicts that diet composition should depend solely upon the availability of the main prey (Schoener, 1971; Pulliam, 1974). For some birds of prey, Microtinae voles usually comprise their main prey (e.g., Eurasian kestrel *Falco tinnunculus*: Korpimäki and Norrdahl, 1991; Skierczyński, 2006; Riegert *et al.*, 2007; common buzzard *Buteo buteo*: Skierczyński, 2006; short-eared owl *Asio flammeus*: Korpimäki and Norrdahl, 1991; long-eared owl *Asio otus*: Korpimäki and Norrdahl, 1991; Korpimäki, 1992; Riegert *et al.*, 2009; Dziemian *et al.*, 2012; Ural owl *Strix uralensis*: Korpimäki and Sulkava, 1987). In Northern Europe, where vole populations exhibit regular three to four-year cycles and great multi-annual and intra-seasonal changes of abundance (Korpimäki *et al.*, 2005; Zárybnická *et al.*, 2015a), the percentage of *Microtus* voles in the diets of diurnal raptors and owls closely relates to their availability in the field (Korpimäki, 1986a, b, 1988, 1992). In Central Europe, vole abundance is usually relatively stable across years, showing seasonal changes with low densities in spring and high densities in autumn (Hansson and Henttonen, 1985; Hanski *et al.*, 1991; Zárybnická *et al.*, 2015a). Moreover, as a result of the latitudinal increase in the diversity of small mammals towards southern latitudes (Hansson and Henttonen, 1985), the Central European small mammal community is enriched by other species, for example by *Apodemus* mice. Thereupon the relationship between the percentage of *Microtus* voles in the diet of birds of prey and their availability in the field may not be found in temperate latitudes, whereas the percentage of *Apodemus* mice in the diet may be strongly related to their availability in the field (Zárybnická *et al.*, 2013a).

Tengmalm's owl *Aegolius funereus* is a generalist predator feeding mainly on *Microtus* and *Myodes* voles in northern latitudes (Sulkava and Sulkava, 1971; Korpimäki, 1981, 1988; Hörnfeldt *et al.*, 1990), while *Apodemus* mice also enrich its diet in Central Europe (Schelper, 1972, 1989; Schwerdtfeger, 1988; Kloubec and Vacík, 1990; Pokorný *et al.*, 2003; Zárybnická *et al.*, 2012). When the abundance of the main prey is low, the percentage of alternative prey in the diet (usually *Sorex* shrews and birds) increases in both Northern and Central European owl populations (Zárybnická *et al.*, 2009; Korpimäki and Hakkarainen, 2012). Variation in food abundance is known to affect the reproductive strategies of Tengmalm's owl, mainly breeding density (Korpimäki, 1981), clutch size (Korpimäki, 1987; Zárybnická *et al.*, 2015a), parental care investment (Eldegard and Sonerud, 2009; Zárybnická, 2009), and current and lifetime reproductive success (Korpimäki, 1992; Laaksonen *et al.*, 2002; Zárybnická *et al.*, 2015a). Although there are numerous studies on the diet structure of Tengmalm's owls from both Northern and Central Europe, studies of the relationships between the breeding parameters of Central European owls and food availability in the field or diet composition are still rare.

Based on 52 nesting attempts of Tengmalm's owls in the Šumava Mountains (National Park in South Bohemia, Czech Republic, in habitats composed mainly of Norway spruce *Picea abies* forests), we aim to characterise the relationships between diet composition and fledgling productivity of this owl. In particular, we assess the following two hypotheses: (i) *Apodemus* mice and *Microtus*/*Myodes* voles will be the main prey, i.e., they will negatively correlate with the percentage of *Sorex* shrews and birds (alternative prey) in the owls' diet, and (ii) the percentage of *Apodemus* mice and *Microtus*/*Myodes* voles in the owls' diet will positively correlate with the number of fledglings.

METHODS

Our study was conducted in the Czech Republic during 1992-2002. The study area of approximately 5,000 km^2 is situated in the Šumava Mountains (49° N, 13° E), close to the border with Germany and Austria at an altitude ranging from 500 to 1,100 m.a.s.l. The habitat mainly comprises Norway spruce forests with small pastures, clearings or agricultural fields. During the study period there were 199-582 nest boxes (mean ± SD; 395 ± 134 boxes per year) available for Tengmalm's owls in this area. The annual occupancy of the nest boxes varied between 4% and 8% (mean ± SD; 5.9 ± 1.3%).

The dietary composition of birds of prey is typically determined from prey remains and pellet analyses (Sulkava and Sulkava, 1971; Korpimäki, 1988). Tengmalm's owl males provide nearly all food to the female from egg laying to the fledgling period (Zárybnická *et al.*, 2009, 2013b). The females usually keep their nests clean during incubation and brooding (Kuhk, 1969; Korpimäki, 1981), but they do not remove food remains and pellets during the feeding period. Hence, a layer of pellets and other prey remains accumulates at the bottom of the nest-hole during the nestling period (Sulkava and Sulkava, 1971). Prey remains were collected during nest visits when the young were present in the nest boxes (from late April to the end of July). The remaining material from the nest boxes was collected after the young had fledged, as described in Korpimäki (1981). Small mammals were determined by identifying skulls and mandibles according to the method of Anděra and Horáček (2005), and birds from feather remains, beaks and skulls using a reference collection. The owl pellets or nest lining from each sample were soaked for one hour in a hot 5% sodium hydroxide solution. After the hair and feather debris were dissolved, the sample was rinsed in a dense sieve under running water and washed in a container with water. The washed sample was then dried and sorted into various categories including mammalian jaw bones (maxillae and mandibles, as well as some teeth) and bird beaks, tarsometatarsi, and humeral and metacarpal bones.

During the study period, we recorded a total of 250 nesting attempts of Tengmalm's owls (mean ± SD; 22.7 ± 8.3 nests per year). From this total, the number of fledglings and diet composition was known for 52 attempts (mean ± SD; 4.7 ± 4.1 nests per year) which were then included in the statistical analyses. All 52 nesting attempts were successful –meaning that at least one fledgling was produced– with a total of 193 fledglings being raised (mean ± SD; 3.7 ± 1.3 fledglings per nest). In total, we determined 5,828 prey items (mean ± SD; 112.1 ± 49.6 items per nest box, N = 52 nests), of which 5,483 were of small mammals and 345 were birds. For further analyses, we pooled the prey items into five groups: *Microtus* voles (field vole *M. agrestis*, common vole *M. arvalis*, European pine vole *M. subterraneus*, and *Microtus* spp.), *Myodes* voles (bank vole *M. glareolus*), *Apodemus* mice (yellow-necked mouse *A. flavicollis,* wood mouse *A. sylvaticus*), *Sorex* shrews (common shrew *S. araneus*, pygmy shrew *S. minutus*, Alpine shrew *S. alpinus*), and birds. Other (scarce) species (see table 1), such as the water vole *Arvicola terrestris*, house mouse *Mus musculus*, harvest mouse *Micromys minutus*, northern birch mouse *Sicista betulina*, southern water shrew *Neomys anomalus*,

TABLE 1

Diet composition of Tengmalm's owl (N = 52 nests) in the Šumava Mountains, Czech Republic, 1992-2002.
[Composición de la dieta del mochuelo boreal (N = 52 nidos) en las montañas de Šumava, República Checa, 1992-2002.]

Prey species or group	**Total number of individuals**	**%**	**Mean per nest %**	**SD %**	**Min. %**	**Max. %**
Sorex araneus	2,093	35.9	34.9	15.5	2.0	64.6
Sorex minutus	182	3.1	3.3	3.4	0	14.0
Sorex alpinus	9	0.2	0.1	0.4	0	1.7
Neomys fodiens	17	0.3	0.3	0.7	0	3.8
Neomys anomalus	7	0.1	0.1	0.3	0	2.0
Crocidura leucodon	1	< 0.01				
Myodes glareolus	822	14.1	13.7	10.6	1.3	59.0
Arvicola terrestris	53	0.9	0.9	2.8	0	19.1
Microtus subterraneus	76	1.3	1.4	1.8	0	6.5
Microtus agrestis	770	13.2	12.9	11.5	0	48.2
Microtus arvalis	278	4.8	5.5	9.7	0	52.8
Apodemus flavicollis	710	12.2	12.1	9.5	0	37.4
Apodemus sylvaticus	167	2.9	2.7	3.8	0	15.6
Apodemus spp.	1	< 0.01				
Mus musculus	5	0.1				
Micromys minutus	1	< 0.01				
Eliomys quercinus	1	< 0.01				
Muscardinus avellanarius	218	3.7	4.0	3.3	0	12.2
Sicista betulina	72	1.2	1.3	3.4	0	20.5
Birds	345	5.9	6.7	6.9	0	26.9
Sum	5,828	100				

Eurasian water shrew *N. fodiens*, bicoloured shrew *Crocidura leucodon*, hazel dormouse *Muscardinus avellanarius*, and garden dormouse *Elionomys quercinus* were not included in the analyses.

Using Spearman rank correlations (StatSoft, Inc. 2013), we examined the relationships between the percentages by numbers of particular prey groups in the diet. The unit of data was a nest box (N = 52 successful nests). We applied the Bonferroni correction to avoid autocorrelations. Therefore, results were considered as significant when $P < 0.01$. Using generalised linear models (GLMM, lmer function, poisson model) in R software, we analysed the effect of percentage of each diet item (*Microtus* voles, *Myodes glareolus*, *Apodemus* mice, *Sorex* shrews, birds) to the number of fledglings. The unit of data was represented by each nesting attempt (N = 52). Percentage data on diet composition were arcsine transformed. We used factor year and nest box as random factors. We used the following model formula: lmer (number of fledglings ~ + diet item + (1| year) + (1| nest box)). Statistical significance was obtained by comparing each model with a relevant null model (without factors). Factors were added to the model based on the Akaike information criterion (AIC). Percentages of variability explained by the tested factor were computed as the ratio between deviances of each model and its null model. We also show the values of Chi-squared statistics.

RESULTS

Sorex shrews were the dominant prey animals (39.2%; represented mainly by the common shrew), followed by *Microtus* voles (19.3%; mainly the field and common voles), *Apodemus* mice (15.1%; mainly the yellow necked mouse), bank voles (14.1%), birds (5.9%), hazel dormouse (3.7%) and other rodents (2.7%; table 1).

The percentages of *Apodemus* mice and bank voles in the diet were positively correlated ($r_s = 0.74$, $P < 0.01$). At the same time, the percentage of *Apodemus* mice negatively correlated with the percentage of *Sorex* shrews ($r_s = -0.53$, $P < 0.01$) and birds ($r_s = -0.42$, $P < 0.01$). Also, the percentage of bank voles negatively correlated with the percentage of both *Sorex* shrews ($r_s = -0.60$, $P < 0.01$) and birds ($r_s = -0.51$, $P < 0.01$). The percentage of *Sorex* shrews positively correlated to the percentage of birds ($r_s = 0.36$, $P < 0.01$). No relationship was found between the percentage of *Microtus* voles and the other prey groups ($P > 0.01$).

We found a positive relationship between the number of fledglings and the percentage

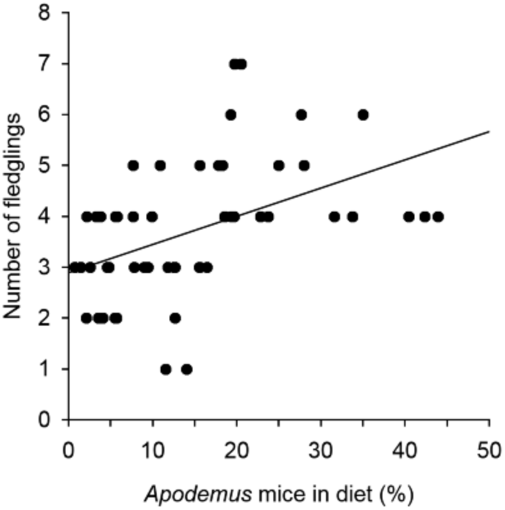

FIG. 1.—Relationship between productivity (expressed by the number of fledglings per individual nest, N = 52) and the percentage of *Apodemus* mice (represented by the yellow-necked and wood mice) in the diet of Tengmalm's owl.
[Relación entre el número de volantones producidos por nido (N = 52) y el porcentaje de ratones del género Apodemus *(representados por ratones leonado y de campo) en la dieta del mochuelo boreal.]*

of *Apodemus* mice in the diet (GLMM, $\chi^2 = 5.46$, $\beta = -0.926$, 21.3% of variance explained, P = 0.019; fig. 1), but other diet items had no effect on fledgling production (GLMM, based on AIC, no other factor was recommended to be added).

DISCUSSION

The diet of Tengmalm's owls in our study area predominantly comprised small mammals (94%). This percentage is similar to those reported in other areas of Central Europe and also from higher latitudes in Northern Europe (reviewed by Korpimäki and Hakkarainen, 2012). In northern populations, voles (mainly *Microtus* spp. and *Myodes* voles) represent 70-90% of the diet (Sulkava and Sulkava, 1971; Korpimäki, 1988; Hörnfeldt *et al.*, 1990), while in Central Europe the diet is enriched with mice (Zárybnická *et al.*, 2013a). The diet of Tengmalm's owls in South Bohemia comprised a lower percentage of *Microtus* voles (19%) and *Apodemus* mice (15%), and a higher percentage of bank voles (14%) and *Sorex* shrews (39%) compared to the owls' diet in Northern Bohemia (47%, 26%, 3%, and 18%, respectively, Zárybnická *et al.*, 2013a). These differences are likely to result from the different habitat structures in the study areas. Old forests of Norway spruce with agricultural fields or pastures predominate in the Šumava Mountains (Vacek and Podrázský, 2003), while small forest fragments of Norway spruce with large open areas, forest clearings, and plantations of secondary growth (formed mainly by non-native blue spruce *Picea pungens*) dominate in the Ore Mountains, Northern Bohemia (Zárybnická *et al.*, 2015b). Thus, the larger extent of spruce forests in South Bohemia could be responsible for the increased percentage of small forest mammals (mainly common shrew and bank vole) in the owls' diet there.

We found that the percentage of *Apodemus* mice correlated negatively with the percentage of alternative prey groups, i.e. *Sorex* shrews and birds and positively with fledgling productivity of breeding owls. However, we found no such relationships for *Microtus* voles. These results largely support the findings from a Tengmalm's owl population in Northern Bohemia, where the percentage of *Apodemus* mice in the diet (26%) followed their availability in the field and positively correlated with the number of fledglings, but these relationships were not found for *Microtus* voles in Northern Bohemia, where they comprised 47% of the owls' diet (Zárybnická *et al.*, 2013a). The absence of such relationships with *Microtus* voles, and in contrast, their occurrence with *Apodemus* mice can result from the different availabilities of mice and voles in the field, due in particular to their different daily activity patterns: *Apodemus* mice being exclusively nocturnal whereas *Microtus* voles show cathemeral activity (Halle and Stenseth, 2000); their different reproductive patterns: mice usually start reproduction during February-March and continue until late summer, while voles usually start in April or May and finish during the autumn (Anděra and Gaisler, 2012; V. Bejček, unpublished data from the study site), and the different habitat structures used: mice select wooded habitats whereas *Microtus* voles select open areas (Anděra and Horáček, 2005). Alternatively, the absence of a functional response in *Microtus* voles in diet and its link to the fledgling productivity could be partly explained by frequent vole prey decapitation, which may cause their under-representation in the sample (Zárybnická *et al.*, 2011). However, no study has yet documented that voles are decapitated by owls more frequently than other prey species.

Bank voles are frequent prey in northern Tengmalm's owl populations, accounting for approximately 30-45% of their diet (Sulkava and Sulkava, 1971; Korpimäki, 1981, 1988; Hörnfeldt *et al.*, 1990). The percentage of this prey in Central Europe is usually much lower (1-25%; Schelper, 1972, 1989; Schwerdtfeger, 1988; Pokorný *et al.*, 2003; Rymešová, 2006; Zarybnická *et al.*, 2013a). In the current study, bank voles represented 14% of the owls' diet, and this percentage positively correlated with the percentage of *Apodemus* mice in the diet. Simultaneously, the percentage of bank voles negatively correlated with the percentages of both *Sorex* shrews and birds. As the optimal diet theory predicts that diet composition should depend upon the availability of the main prey (Schoener, 1971; Pulliam, 1974), the percentage of main prey in the diet of the Tengmalm's owl should depend on its availability in the field, and it should negatively correlate with the other alternative prey species in the diet and positively correlate with fledgling production (Zárybnická *et al.*, 2013a). In our study, we found no significant relationship between the percentage of bank voles in the owls' diet and the number of fledglings, but we have no data on prey availability. Thus, we cannot directly test the relationships between food availability in the field, diet composition and breeding parameters. However, negative/positive relationships between the percentage of *Myodes* voles and alternative (shrews and birds)/main (mice) prey groups indicate that bank voles can be important prey species in the diet of Tengmalm's owls in Central Europe.

CONCLUSION

Our results suggest that *Apodemus* mice are an important component of the diet of Tengmalm's owl in Central Europe, since the percentage of *Apodemus* mice negatively correlated with alternative prey (*Sorex* shrews and birds) in the owls' diet and also positively correlated with fledgling productivity. *Microtus* voles, however, exhibited no such relationships. Our findings also highlight the significance of bank voles in the diet of Czech owls, since their percentage was negatively correlated with the percentage of alternative prey in the owls' diet. These results support the theory that owls in Central Europe are not dependent on only one main prey group (unlike their northern counterparts) but rather that more prey types can figure in their diet.

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Příloha IX

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The effect of elevation and habitat cover on nest box occupancy and diet composition of Boreal Owl *Aegolius funereus*

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The effect of elevation and habitat cover on nest box occupancy and diet composition of Boreal Owls *Aegolius funereus*

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ABSTRACT

Capsule: Diet composition of Boreal Owls *Aegolius funereus* was not affected by habitat cover, but it changed along the elevational gradient.
Aims: To assess the effect of elevation and habitat cover on nest box occupancy and diet composition of a central European population of Boreal Owls.
Methods: A Boreal Owl population was studied in the Šumava Mountains, Czech Republic, at elevations from 500 to 1300 m above sea level (asl), during 1984–2005.
Results: Boreal Owls occupied more frequently nest boxes above 600 m asl, but they did not clearly prefer any elevational band. Habitat cover did not affect the number of nesting attempts. There was also no relationship between habitat cover and diet composition. However, diet composition significantly changed along the elevational gradient. In particular, the proportion of alternative prey of Boreal Owls, i.e. birds and shrews *Sorex* sp., rose with increasing elevation. The proportion of voles *Myodes* and mice *Apodemus* in the diet decreased with increasing elevation. Among bird prey, the proportion of finches Fringillidae positively correlated with elevation.
Conclusions: Central European Boreal Owls did not show a clear preference for any habitat cover or elevational band, but the quality of the owls' diet significantly decreased with increasing elevation.

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Birds represent a suitable model taxa for understanding biogeographic patterns through latitudinal and elevational gradients (reviewed by Martin 2004). Bird species breeding in northern areas show faster life-histories than their tropical and temperate counterparts. In contrast, slow life-history strategies can be found at high elevations (reviewed by Boyle *et al.* 2016). Low fecundity, limited number of nesting attempts and late breeding at high elevations are probably caused by a colder environment, short breeding seasons, low food availability and higher predation risk (Boyle *et al.* 2016). However, the role of some environmental factors in bird life-history strategies is still not clear. For example, predation risk can be increased due to limited vegetation cover and the absence of shelters at higher elevations as a result of severe climatic conditions and low primary production. Simultaneously, the predation risk may be decreased due to lower numbers of predators as a result of low species diversity at high elevations (McKinnon *et al.* 2010, Boyle *et al.* 2016). Food availability and diet variation can also vary in relation to elevation. For example, European Eagle Owls *Bubo bubo* breeding at low elevations in southern France showed significantly higher diet diversity compared to pairs breeding at high elevations (Penteriani *et al.* 2002). However, similar studies of such limitations and their effects on diet composition of birds are rare, and our knowledge of avian life-history changes along elevation gradients is incomplete.

Habitat heterogeneity, that causes great variability in the availability of food resources, nesting sites, shelters and the presence of nest site competitors or predators, can also drive variation in avian life-histories in terms of demographic parameters (Both 1998, Penteriani *et al.* 2002, Pakkala *et al.* 2006), population dynamics (Ferrer & Donazar 1996, Penteriani *et al.* 2002, Pakkala *et al.* 2006) and food webs of many animal populations (Polis *et al.* 1997, Ferger *et al.* 2014). In opportunistic predators, habitat heterogeneity considerably alters diet composition through the availability of food resources, which in turn influences reproductive success and breeding performance (Penteriani *et al.* 2002, Zárybnická *et al.* 2013, Milchev 2015). For example, increased availability of heavier prey species (*Apodemus* mice and *Microtus* voles compared to *Sorex* shrews) reduces costs of reproduction in Boreal Owls

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Aegolius funereus (Zárybnická *et al.* 2009). Although some studies have found individual variability in diet composition or habitat use (Galeotti *et al.* 1991, Riegert & Fuchs 2011), simultaneous data on nest site occupancy, diet composition and habitat cover are scarce (Penteriani *et al.* 2005).

Boreal Owls are nocturnal predators of small mammals and have a circumpolar Holarctic range inhabiting Eurasian and North American coniferous forests (Korpimäki & Hakkarainen 2012). This opportunistic predator feeds on the most available prey, usually voles in northern areas and a mixture of voles and mice in temperate areas (Korpimäki & Hakkarainen 2012, Zárybnická *et al.* 2013, 2015a). Alternatively, it takes shrews and birds when voles or mice are scarce (Zárybnická *et al.* 2009, 2013, Šindelář *et al.* 2015). The distribution of this cavity-nesting species can be limited by the availability of suitable habitats (Hayward *et al.* 1993, Heinrich *et al.* 1999), availability of nesting sites (Heikkinen *et al.* 2007), food availability (Kouba *et al.* 2013), interspecific and intraspecific competition (Vrezec & Tome 2004, Heikkinen *et al.* 2007, Morosinotto *et al.* 2017) and climatic conditions (Castro *et al.* 2008). Food availability and habitat cover also greatly affects other demographic parameters. In particular, food availability is the main determinant of the reproductive strategies of Boreal Owls (Korpimäki & Hakkarainen 2012, Zárybnická *et al.* 2015a), and habitat cover may determine the frequency of nest site occupation and nest predation (Sonerud 1985, Zárybnická *et al.* 2015b, 2016), home range size (Santangeli *et al.* 2012), survival of adults (Hakkarainen *et al.* 2008) and reproductive success (Hakkarainen *et al.* 2003, Zárybnická & Vojar 2013).

In northern Europe, the centre of the Boreal Owls' range, the species frequently inhabits Norway Spruce *Picea abies* forests. More or less isolated populations occur in central and southern Europe where this owl inhabits coniferous, mixed or deciduous forests (Danko *et al.* 2002, Kloubec 2003, Šťastný *et al.* 2006, Castro *et al.* 2008, Broggi *et al.* 2013). It was shown that adult owls and fledglings use dense and high coniferous forests to avoid the risk of being mobbed by small birds or killed by diurnal birds of prey (Bye *et al.* 1992, Korpimäki & Hakkarainen 2012), and the survival of owls increased with the proportion of old forests in their home range (Korpimäki & Hakkarainen 2012). In central Europe, population densities of this owl are usually stable, for example, in Slovakia (Danko *et al.* 2002) and Poland (Sikora *et al.* 2007), or even increasing, for example, in the Czech Republic (Šťastný *et al.* 2006). However, the population densities of northern European Boreal Owl populations, especially in Finland and Sweden, are declining due to the decreasing area of old coniferous forests (Laaksonen *et al.* 2004, Korpimäki & Hakkarainen 2012). Therefore, studies on habitat use and prey use by Boreal Owls are still needed.

In this study, we aim to test the effect of elevation and habitat cover on nest box occupancy and diet composition of the central European Boreal Owl in areas dominated by Norway Spruce forests based on 22-year dataset. In particular, we suggest that (i) the number of nesting attempts will be influenced by elevation and habitat cover, especially the proportion of coniferous forests. Further, we suggest that (ii) the proportion of their main prey (*Microtus* and *Myodes* voles, and *Apodemus* mice) and the proportion of alternative prey (*Sorex* shrews and birds) will change with elevation. We also suggest that (iii) habitat cover will affect diet composition.

Methods

Study area

Our study was conducted from 1984 to 2005 in the Šumava Mountains (49° N, 13°E), the Czech Republic. The study area of approximately 5000 km^2 was situated close to the border with Germany and Austria at elevations from 500 to 1300 m above sea level (asl). The area is classified as a Special Protection Area for the Boreal Owl according EC Directive 79/409/EEC. Two-thirds of the study area was covered by forest that consisted mainly of Norway Spruce (approximately 70%), deciduous forests (dominated by European Beech *Fagus sylvatica*, Mountain Ash *Sorbus aucuparia* and Sycamore Maple *Acer pseudoplatanus*) and mixed forests (dominated by Norway Spruce, European Beech, Mountain Ash, Sycamore Maple and European Silver Fir *Abies alba*). Open areas were mainly represented by meadows, pastures, fields, peat bogs and human settlements (Kloubec 2003, Kloubec *et al.* 2015). A total of 635 nest boxes were available within the study area during the study period, a mean (sd) of 210.8 (184.2) nest boxes each year, totalling 4448 breeding opportunities during the study period. Each nest box was available for a mean (sd) period of 7.0 (3.8) years. A total of 316 nesting attempts by Boreal Owls were recorded in 173 nest boxes (mean ± sd = 14.9 ± 11.2 nesting attempts per year). The annual occupancy of the nest boxes varied between 0.03 and 0.50 nesting attempts per box (mean ± sd = 0.12 ± 0.11) suggesting that nest boxes were not limiting and there were more than enough throughout the study area. All nest boxes were kept in good condition, they were regularly cleaned after breeding and repaired when necessary and the space surrounding the nest box entrance was kept free of vegetation (for details, see Kloubec 2003). The nest boxes were made of wood, with base 20 × 20 cm, height 40–50 cm and with an entrance hole 8.0–8.5 cm in diameter.

Diet analysis

We analysed diet composition for 265 nesting attempts. The remaining material from the nest boxes was collected after the young fledged (Korpimäki 1988). Small mammals were identified by presence of skulls and mandibles, according to Anděra & Horáček (2005), and birds by feather remains, beaks and skulls. The owl pellets or nest bedding from each nest box were soaked for 1 h in a hot 5% NaOH solution. After the hair and feather debris were dissolved, the samples were rinsed using a dense sieve and washed. Samples were then dried and sorted into various categories based on the morphology of jaw bones (maxilla and mandibles, as well as some teeth) of mammals and beaks, tarsometatarsi, humeri and other bones (rostrum, carpometacarpus) of birds, using a reference collection.

For the purposes of diet analyses, we pooled the prey items into six groups: (i) *Microtus* voles (Field Vole *M. agrestis*, Common Vole *M. arvalis*, European Pine Vole *M. subterraneus* and *Microtus* spp.); (ii) *Myodes* voles (Bank Vole *M. glareolus*); (iii) *Apodemus* mice (Yellow-necked Mouse *A. flavicollis* and Wood Mouse *A. sylvaticus*); (iv) *Sorex* shrews (Common Shrew *S. araneus*, Pygmy Shrew *S. minutus* and Alpine Shrew *S. alpinus*); (v) other mammals (Water Vole *Arvicola terrestris*, House Mouse *Mus musculus*, Harvest Mouse *Micromys minutus*, Northern Birch Mouse *Sicista betulina*, Hazel Dormouse *Muscardinus avellanarius*, Southern Water Shrew *Neomys anomalus*, Eurasian Water Shrew *N. fodiens*, Bicoloured Shrew *Crocidura leucodon* and Garden Dormouse *Eliomys quercinus*) and (vi) birds (Table 1). For detailed analysis on bird prey diet composition, we grouped birds into families or subfamilies (for details, see statistical analyses).

Landscape data analyses

Local habitat use was assessed within a radius of 25 and 750 m around each nest box. The radius of 25 m represented the local habitat use of nest sites, while the 750 m radius (177 ha) represented the size of the breeding home range of Boreal Owl males (Kouba 2009, Zárybnická *et al.* 2015b). Habitat categories were defined using geographical information systems (GIS) in ArcGIS version 10.3, (ESRI) from vegetation maps of CORINE land cover 2000. For further analyses, the habitat cover of the study area was divided into the following categories: (i) coniferous forests, where coniferous tree species represented more than 75% of the formation; (ii) deciduous forests, where broad-leaved tree species represented more than 75% of the formation; (iii) mixed forests, where neither broad-leaved nor coniferous tree species were dominant; (iv) open areas (mainly meadows, peat bogs, pastures and fields) and other areas (water and urban areas) (Table 2) (for methodical details see Bossard *et al.* 2000). The proportion of coniferous forest within a radius of 750 m around the available nest boxes significantly increased with altitude (regression, df = 1, 634, $F = 13.2$, beta = 0.143, $P = 0.0003$). This relationship was not found within a radius of 25 m ($P > 0.05$).

Table 1. The diet composition of Boreal Owls divided into prey groups for the purpose of both overall diet analysis ($n = 265$ nests) and bird prey analysis ($n = 60$ nests). The estimate of biomass of each main prey group is shown (calculated after Aulagnier *et al.* 2008).

	Overall diet analysis		Biomass		Bird prey analysis	
Diet group	*n*	%	kg	%	*n*	%
Microtus sp.	4671	24.6	152.8	32.4		
Apodemus sp.	2654	13.9	94.9	20.1		
Myodes sp.	2813	14.8	77.4	16.4		
Sorex sp.	6369	33.5	63.0	13.3		
Other mammals	1182	6.2	43.0	9.1		
Birds	1328	7.0	40.9	8.7		
Prunellidae					10	1.2
Sylviidae					109	13.5
Regulidae					49	6.1
Turdinae					145	17.9
Saxicolinae					117	14.4
Paridae					80	9.9
Sittidae					8	1.0
Certhiidae					10	1.2
Troglodytidae					10	1.2
Emberizidae					13	1.6
Fringillidae					205	25.3
Other birds					54	6.7
Total	19017	100	472.0	100	810	100.0

Statistical analyses

Multivariate data on diet composition and habitat cover surrounding a nest box were calculated using variance partitioning by principal coordinate analysis of

Table 2. Percentages of habitat cover within a buffer radius of 25 and 750 m around the Boreal Owl nest boxes ($n = 635$ available nest boxes).

Habitat cover	Buffer of 25 m Mean percentage	sd	Buffer of 750 m Mean percentage	sd
Coniferous forests	76.3	41.1	67.0	22.8
Mixed forests	8.8	27.4	8.7	13.4
Deciduous forests	2.9	15.8	2.9	8.3
Open areas	11.8	31.1	20.9	20.6
Other areas	0.2	4.3	0.5	3.0

neighbour matrices (PCNM) in Canoco v. 5 software (ter Braak & Šmilauer 2012), the method recommended by Marrot *et al.* (2015). This multivariate analysis enabled us to separate the effect of space predictors (geographical position of the nest box) from the effect of other tested ('environmental') variables (Legendre & Legendre 2012). Simultaneously the analysis enabled us to control the nest box availability during the study period. The analysis included nine steps: test for environmental variables, selection of environmental variables by partial redundancy analysis, principal coordinate analysis (PCoA), PCNM for all space predictors, PCNM selection, spatial effects analysis (effect of spatial autocorrelations), environmental variable effects analysis, joint effects analysis and removing of spatial effects (Šmilauer & Lepš 2014).

The relationships between environmental variables (the number of nesting attempts per nest box and elevation) and space predictors (principal coordinates based on geographical nest box position using a uniform trigonometric cadastral network) and habitat cover of the nest box surrounding within a buffer of 25 and 750 m were analysed using PCNM. Although space predictors were not of ecological interest, we took them into account to remove spatial autocorrelations. For this analysis, each individual nest box was used as a data unit and time of nest box availability (years) as a covariate. Only nest boxes with at least one nesting attempt were used in the analyses ($n = 173$ nest boxes). Proportions of habitat categories were used as response data and were log-transformed prior to analyses as recommended by Šmilauer & Lepš (2014).

The effect of elevation and proportions of main habitats – coniferous forests, deciduous forests, mixed forests, open areas (environmental variables) and space predictors (principal coordinates based on geographical nest box position using a uniform trigonometric cadastral network) to diet composition (i.e. the proportion of each diet item) was analysed using PCNM. For this analysis, we used each nesting attempt ($n = 265$ nesting attempts) as an independent data unit and nest box, the number of all determined prey items and year as covariates. The proportion of each diet group was used as response data and was log-transformed prior to analyses.

The effect of elevation (environmental variable) and space predictors (principal coordinates based on geographical nest box position using a uniform trigonometric cadastral network) to the proportions of bird families in the diet (response variables) was analysed using PCNM. In this analysis, we used individual nesting attempts ($n = 60$ nesting attempts) as the independent data unit and total number of identified bird prey items as a covariate. Prior to this analysis, we excluded all nesting attempts with fewer than 8 bird individuals in the diet, i.e. we included in the analysis a total of 60 nests with 810 bird items (mean ± sd = 13.5 ± 54.9 birds per nest, Table 1). Further, we merged all bird families with fewer than eight individuals to the group 'others'. The Turdidae family was divided into subfamilies Turdinae and Saxicolinae due to their different body sizes. The number of all birds determined in the diet was used as a covariate. For all PCNM analyses, P values of predictor effects were calculated using the Monte-Carlo permutation test. We also used false discovery rate (FDR) to adjust selection of both space and environmental variables and to avoid Type I Errors (Verhoeven *et al.* 2005). In graphs, we show results after removing spatial effects.

Partial relationships between the number of nesting attempts and the proportion of coniferous forest surrounding a nest box, main diet groups, Fringillidae birds and elevation were calculated using regression (StatSoft, Inc. 2013).

The preference for elevation zones was computed using a standardized Manly Bi preference index (Manly *et al.* 2002) by comparing the numbers of available nest boxes and numbers of occupied nest boxes within each 100 m elevational band from 500 to 1300 m asl (upper categories above 1100 m asl were grouped together). We also computed upper confidence limits of Bi standardized indices.

Results

The number of nesting attempts was not significantly affected by habitat cover within a buffer radius of 25 or 750 m around nest boxes ($n = 173$ nest boxes; buffer 25 m: df = 168, $F = 0.4$, $P(\text{adj}) = 0.704$; buffer 750 m: df = 168, $F = 1.6$, $P(\text{adj}) = 0.204$). In both analyses, most variability was explained by space predictors (buffer 750 m: space predictors 6.6%, the number of nesting attempts 0.4%, shared fraction 0.1%; buffer 25 m: space predictors 18.2%, the number of nesting attempts 0.2%, shared fraction 0.1%). However, significant effects of space predictors were found only within a buffer radius of 750 m (buffer 750 m: four principal coordinate variables with maximal $F = 15.6$, maximal $P(\text{adj}) = 0.041$; buffer 25 m: maximal $F = 1.8$, P at least 0.152). Using partial regressions, we found an indicative positive relationship between the proportion of coniferous forests within a buffer of radius 750 m surrounding nest boxes (mean ± sd = 73.0 ± 19.2% coniferous habitat per nest box) and the number of nesting attempts (regression, df = 1, 172, $F = 2.9$, beta =

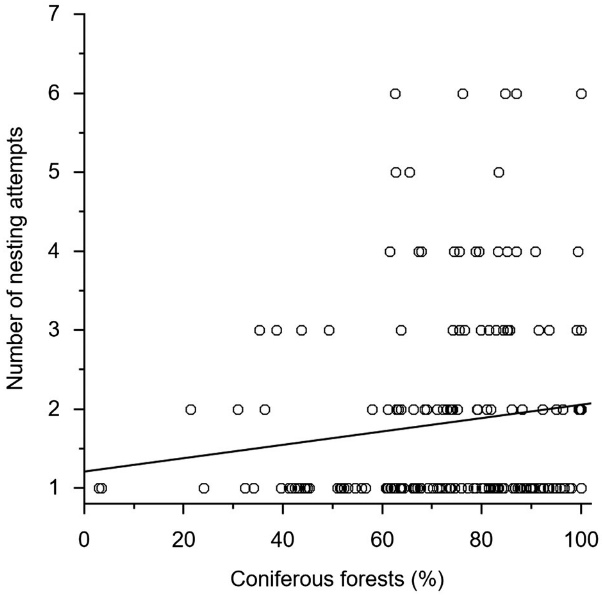

Figure 1. The relationship between the number of nesting attempts (occupied nest boxes) and the proportion of coniferous forests (regression, df = 1, 172, $F = 2.9$, beta = 0.13, $P = 0.09$, $n = 173$ nest boxes).

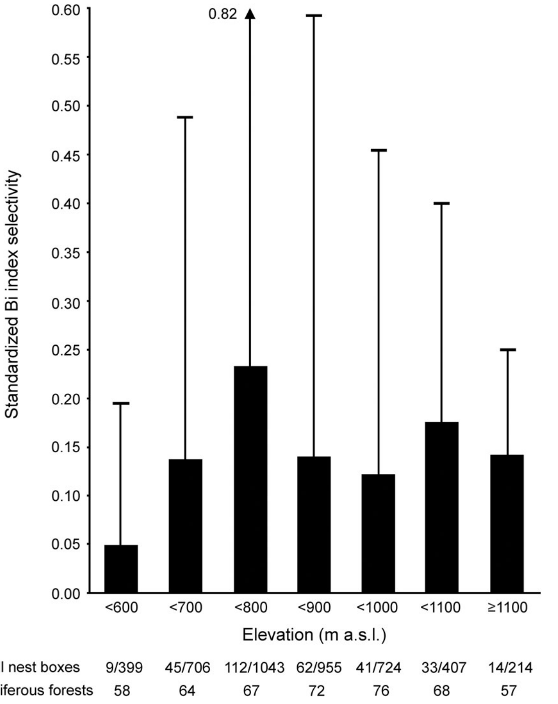

Figure 2. Preference for elevational zones by Boreal Owls based on numbers of occupied and available nest boxes (standardized Manly Bi index selectivity) during the years 1984–2005 in the Šumava Mountains (totalling 4448 breeding opportunities). The upper elevation band limits are shown on the horizontal axis. Numbers below the horizontal axis indicate the number of occupied nest boxes/the number of available nest boxes. On a separate line are indicated the proportion of coniferous forests within 750 m of available nest boxes. Upper confidence limits are shown; note that in one case the confidence limit exceeds the range of the vertical axis.

0.13, $P = 0.090$, Figure 1). No relationship was found between the proportion of coniferous forests within a buffer of radius 25 m (82.9 ± 36.4% coniferous habitat per nest box) and the number of nesting attempts (regression, df = 1, 172, $F = 0.8$, beta = 0.07, $P = 0.380$).

We did not find a significant relationship between the number of nesting attempts and elevation (regression, df = 1, 172, $F = 0.2$, beta = 0.01, $P = 0.902$). Using the Manly preference index based on nest box use and availability, we also did not find a clear preference for any elevational band between 600 and 1300 m asl. However, the owls occupied nest boxes more frequently above 600 m asl compared to lower elevations (Figure 2).

We identified 19 017 prey items from nests (mean ± sd = 71.3 ± 54.5 items per nest), of which 17 689 were small mammals and 1328 were birds (Table 1). We identified 17 424 prey mammals to species ($n = 25$ species), and 265 mammals to genus (*Apodemus* sp. and *Microtus* sp.). We further identified 1106 birds to species ($n = 52$ species), 118 birds to genus (*Luscinia* sp., *Parus* sp., *Certhia* sp., *Phylloscopus* sp., *Turdus* sp. and *Regulus* sp.), 12 bird species to family (Sylviidae) and left 92 birds unidentified. The diet composition of owls was dominated by *Sorex* shrews (33.5%), followed by *Microtus* voles (24.6%), *Myodes* voles (14.8%), *Apodemus* mice (13.9%), birds (7.0%) and other mammals (6.2%) (Table 1). Among birds, the most frequent prey taxa were Chaffinch *Fringilla coelebs* (18.2%), European Robin *Erithacus rubecula* (12.2%), Song Thrush *Turdus philomelos* (10.8%), Goldcrest *Regulus regulus* or Firecrest *Regulus ignicapilla* (6.4%), and Eurasian Blackcap *Sylvia atricapilla* (5.6%). Diet composition was not affected by habitat cover within a buffer radius of 750 m, but it was significantly correlated with elevation (Table 3). Elevation accounted only 1.1% of variability, space predictors 5.1% of variability and the shared fraction was 2.5%.

Table 3. The effect of elevation and space predictors (principal coordinates, PCO, based on geographical nest box position) on a) overall diet composition ($n = 265$ nest boxes) and b) bird prey composition ($n = 60$ nest boxes) in the diet of the Boreal Owl. Statistical significances were obtained by Monte-Carlo permutation tests (*P*) and FDR (*P*(adj)).

Dataset	Tested variable	*F*	*P*	*P*(adj)
Overall diet composition	Elevation (m)	10.0	0.002	0.005
	PCO.2	9.8	0.002	0.042
	PCO.5	9.0	0.002	0.042
	PCO.4	3.4	0.008	0.084
Bird prey diet composition	Elevation (m)	1.5	0.118	0.236
	PCO.4	2.8	0.006	0.078
	PCO.2	2.2	0.024	0.156

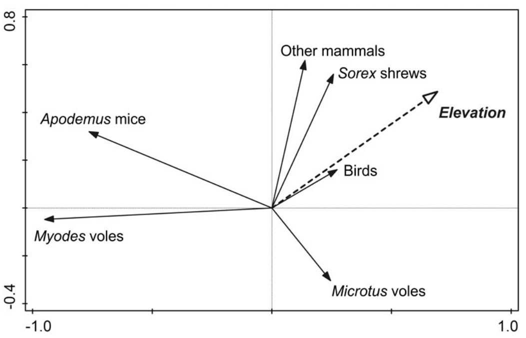

Figure 3. Relationships among proportions of main diet groups of the Boreal Owl and elevation. The first and second axes explained 28.8% and 17.5% of variability, respectively. Geographical variability was eliminated using PCNM analysis.

Proportions of *Sorex* shrews and other mammals positively correlated with the proportion of birds and the proportions of these diet groups positively correlated with elevation (Figure 3). The proportions of *Microtus* voles and *Apodemus* mice were negatively correlated with each other and they were not correlated with proportions of *Sorex* shrews, other mammals or birds (Figure 3). The proportion of *Myodes* voles was positively correlated with the proportion of *Apodemus* mice (Figure 3). Using partial regression, we confirmed that proportions of *Sorex* shrews (regression, df = 1, 264, $F = 17.3$, beta = 0.25, $P < 0.0001$) and birds (regression, df = 1, 264, $F = 4.5$, beta = 0.13, $P = 0.040$) positively correlated with elevation, while proportions of *Myodes* voles (regression, df = 1, 264, $F = 23.2$, beta = −0.28, $P < 0.0001$) and *Apodemus* mice (regression, df = 1, 264, $F = 6.2$, beta = −0.15, $P = 0.010$) negatively correlated with elevation (Figure 4(a–c)).

The effect of elevation on the proportion of bird families in the diet was not significant (Table 3). Elevation accounted only for 0.6% of the variability, space predictors explained 1.5% of variability and the shared fraction was 3.5%. The effect of habitat cover on the proportion of bird families in the diet was also not significant (P at least 0.400). However, using partial regressions, we found a significant positive relationship between the proportion of the most dominant bird family, Fringillidae (Chaffinch represented 98%), and elevation (regression, df = 1, 59, $F = 21.8$, beta = 0.56, $P < 0.0001$, Figure 4(e)).

Discussion

Coniferous forests represent a natural habitat of the Boreal Owl through its whole range, including North America and Eurasia (Korpimäki & Hakkarainen 2012). This habitat offers suitable hunting conditions; for example, it provides numerous hunting patches with low ground vegetation and relatively stable mammal densities.

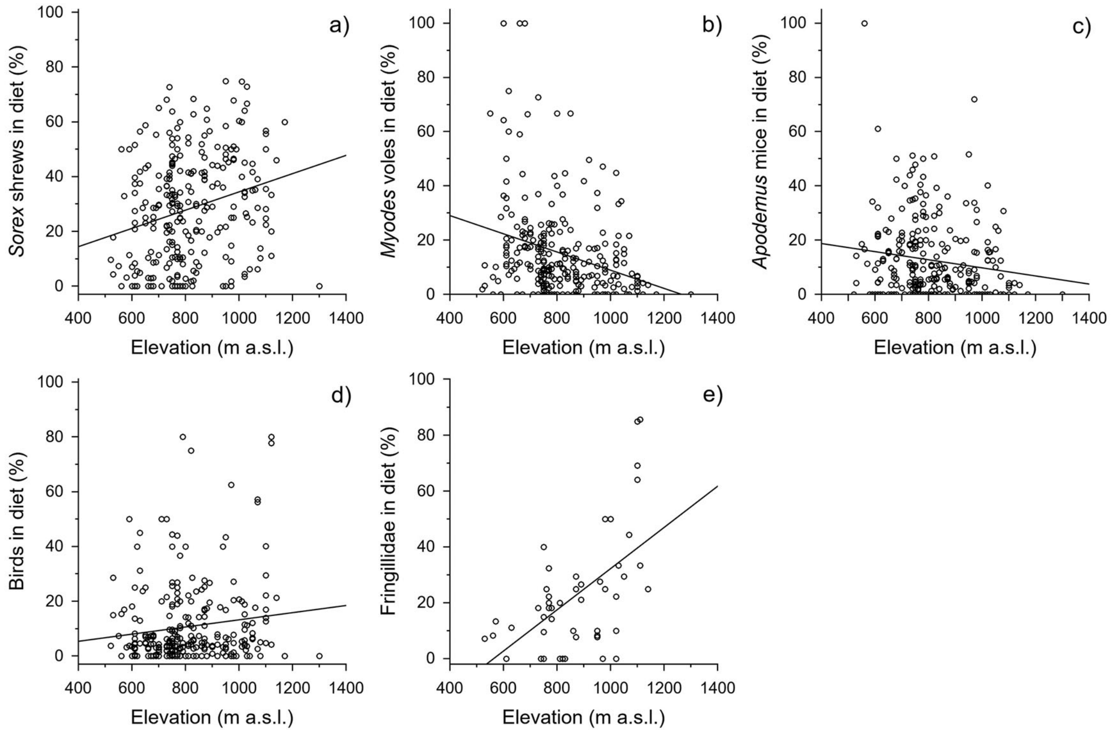

Figure 4. Proportions of (a) *Sorex* shrews (df = 264, $F = 17.3$, beta = 0.25, $P < 0.0001$), (b) *Myodes* voles (df = 264, $F = 23.2$, beta = −0.28, $P < 0.0001$), (c) *Apodemus* mice (df = 264, $F = 6.2$, beta = −0.15, $P = 0.010$), birds (df = 264, $F = 4.5$, beta = 0.13, $P = 0.040$), and (d) Fringillidae birds (df = 59, $F = 21.8$, beta = 0.56, $P < 0.0001$) in Boreal Owl diet along the elevational gradient (regression analyses).

Reproductive success and survival rate of Boreal Owls also increase with increasing portion of coniferous forest area (Hakkarainen *et al.* 2003, 2008, Laaksonen *et al.* 2004). In particular, this habitat provides a safe refuge for fledglings and adult owls against avian and mammalian predators (Bye *et al.* 1992, Korpimäki & Hakkarainen 2012, Zárybnická *et al.* 2015b), and owls nesting in coniferous forests may profit from lower nest predation risk (especially early in the season before tree leafing) compared to owls breeding in deciduous forests (Zárybnická *et al.* 2016). Moreover, some important predators of Boreal Owls, for example the Tawny Owl *Strix aluco*, prefer deciduous and mixed forests rather than coniferous forests (Vrezec 2003, Vrezec & Tome 2004, Obuch 2011, Jensen *et al.* 2012). In our study area, coniferous forests were dominant habitats surrounding occupied nest boxes (83% within a 25 m buffer and 73% within a 750 m buffer), and the number of nesting attempts was not affected by the proportion of habitat cover. These results could be caused by insufficient resolution of Corine vegetation maps, or generally relatively high proportions of coniferous forests in surrounding occupied nest boxes. However, we found an indicative partial relationship between the number of nesting attempts and the proportion of coniferous forest within a buffer of 750 m around nest boxes. These findings suggest that coniferous forests may play an important role in nest box choice by Boreal Owls in the Šumava Mountains, but these results may be also caused by the positive relationship between the proportion of coniferous forest surrounding occupied nest boxes and elevation. Moreover, the effect of changing food availability among years should be considered.

In our study area, where elevations varied from 500 to 1300 m asl, Boreal Owls mainly used nest boxes above 600 m asl, but no clear preference was found for any elevational band above this border. It was shown that more abundant occurrence of Boreal Owls at higher elevations may be connected with the occurrence of other predator species. For example, Hudec *et al.* (2011) mentioned that the occurrence of the Czech Boreal Owl population under 800 m asl was limited due to the occurrence of the Tawny Owl. In Slovenian mountains (Mount Krim, Vrezec 2003) and Czech and Polish mountains (Krkonoše Mountains, Flousek *et al.* 2015), Boreal Owls breed most often at 700–1000 m and 600–1000 m asl, respectively, and the Tawny Owls at 300–600 m and 400–800 m asl, respectively. In alpine European countries, especially in Austria and Switzerland, Boreal Owls mostly inhabit elevations between 800–1800 m and 1000–2000 m asl, respectively, while the Tawny Owls mainly occupy elevations between 100–800 m and 400–1200 m asl, respectively (Dvorak *et al.* 1993, Schmid *et al.* 1998). Using playback methods to census owl territories on Mount Krim, Vrezec & Tome (2004) found that Boreal Owl territories were situated at high elevations, within those of the Ural Owl, while territories of Boreal Owls and Tawny Owls were highly segregated in habitat and space, due to distinctive negative interactions. We suggest an increased frequency of nest box occupancy by Boreal Owls above 600 m asl in our study area could reflect interspecific competition and predation risk from other predators, especially the Tawny Owl.

While Microtinae voles and *Apodemus* mice comprise the main prey of Boreal Owls, alternative prey comprises *Sorex* shrews and birds. This scenario is supported by the weight classes of individual prey species and hunting abilities of the Boreal Owl. *Apodemus* mice, *Microtus* and *Myodes* voles represent similar weight categories (on average 21–30 g), but *Sorex* shrews are considerably lighter (on average 3–9 g, Zárybnická *et al.* 2009). Birds represent a good surrogate for mice and voles (on average 31 g), but the sit-and-wait hunting strategy of the Boreal Owl is not optimal for hunting birds (Zárybnická *et al.* 2009), which were considered as alternative prey. The diet composition of owls, including the Boreal Owl, reflects the spatial and temporal availability of small mammals (Korpimäki 1988, Zárybnická *et al.* 2013, Heisler *et al.* 2016). Moreover, the level of vole specialization increases with latitude (Korpimäki & Marti 1995): in Northern Europe, voles of the genera *Microtus* and *Myodes* constitute the dominant prey of Boreal Owl, while in Central Europe, the diet is enriched with other important prey species, such as *Apodemus* mice (Korpimäki 1988, Zárybnická *et al.* 2013). In contrast to their northern counterparts, Boreal Owls in the temperate zone may benefit from relatively stable prey abundance, a more diverse prey community, longer nights which enable prolonging time for foraging and a lower level of interspecific competition with other vole-eating predators (Zárybnická *et al.* 2015a).

In our study area, the diet composition of Boreal Owls significantly changed with elevation. In particular, proportions of alternative prey, such as birds and *Sorex* shrews (dominated by Common Shrew), were positively correlated with elevation, while the proportion of Bank Voles and *Apodemus* mice decreased with increasing elevation. The distribution and abundance of small mammal species is associated with environmental variables such as vegetation cover and productivity, elevation, local climatic conditions and anthropogenic effects (Jedrzejewski *et al.* 1993, Koerner 2007, Bateman *et al.* 2010, Zhou *et al.* 2011), and it greatly varies among years (Korpimäki & Hakkarainen 2012). Unfortunately, we have no data on small mammal availability in our study area that may significantly affect our interpretations, and it is known that breeding site suitability can change with changing availability of main prey among years (Korpimäki & Hakkarainen 2012, Zárybnická *et al.* 2013). However, it has been shown that Boreal Owl diet reflects availability, and they switch from their main prey to alternative prey only when their main prey becomes scarce (Zárybnická *et al.* 2009). Therefore, we suggest the shift in Boreal Owl diet at higher elevations probably reflected the limited food availability of main prey species (voles and mice).

Birds were the most common alternative prey in the diet of the owls and these included: Fringillidae (mainly Chaffinch), Turdinae (mainly Song Thrush), Saxicolinae (mainly Robin) and Sylviidae (mainly Blackcap). Similar results have been obtained by other authors from central and northern Europe (Pokorný *et al.* 2003, Korpimäki & Hakkarainen 2012). We further found that the proportion of Fringillidae in the diet of our owls increased with elevation. In our study area, Chaffinch, Song Thrush, European Robin and Blackcap are typical inhabitants of higher elevations, i.e. 700–1400 m asl (Kloubec *et al.* 2015). However, the Chaffinch population reaches substantially higher abundances (100–200 individuals per 100 transect points) compared to other song birds (Blackcap 50–90, Song Thrush 10–40, Robin 40–80 individuals per 100 transect points) (Kloubec *et al.* 2015). We suggest that the high abundance of the Chaffinch population increases its availability for an opportunistic predator such as the Boreal Owl. Additionally, we suppose that Chaffinches are probably easily accessible prey due to their conspicuous behaviour, for example singing openly from high perches, often dwelling on the forest floor and showing increased singing activity during twilight hours (Kloubec & Čapek 2012).

We conclude that Boreal Owls in our study did not show a clear preference for any habitat cover. We also did not find a preference for any elevational band above 600 m asl, but the owls scarcely bred below this elevational border. The diet was not affected by habitat cover. However, the proportion of alternative prey significantly rose with increasing elevation.

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Příloha X

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Diet composition in the Tengmalm's Owl *Aegolius funereus*: a comparison of camera surveillance and pellet analysis

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During a two-year study in Central Europe, we used a combination of pellet analysis and camera recordings to assess the diet composition of Tengmalm's Owls during the breeding season, with regards to availability of the main prey components in the field. The diet of the owls consisted mainly of voles (Arvicolidae), mice (Muridae) and shrews (Soricidae), and their proportion in the diet reflected their local abundances in the field. Pellet analysis allowed us to determine 40.2 (± 6.9 SD)% in 2004 and 46.4 (± 14.7 SD)% in 2006 of all delivered prey items recorded by cameras. We determined 77.1 (± 17.1 SD)% in 2004 and 80.2 (± 12.5 SD)% in 2006 of the prey items recorded by camera monitoring. Pellet analysis underestimated the proportions of all main diet components, but the differences were significant only for the proportion of voles and birds. The underestimation of voles may have been a consequence of their decapitation before delivery to the nest. We regularly recorded decapitated voles and mice in the nest boxes of Tengmalm's Owl, while whole shrews were found more often. Our study highlights that a combination of both methods allows for a more accurate assessment of diet composition in nocturnal raptor species.

1. Introduction

Tengmalm's Owl (*Aegolius funereus*) is a nocturnal avian predator that feeds mainly on voles in Northern Europe (Korpimäki 1981, 1988), and voles and mice in Central Europe (Korpimäki 1986, Pokorný 2000, Pokorný *et al.* 2003). The abundance of small rodents considerably varies from year to year. When their abundance is low, the proportion of shrews and birds in the diet increases substantially (Korpimäki 1981, 1988, Koivunen *et al.* 1996).

Numerous studies on the diet composition of raptors have been based on prey-remain collections and pellet analyses (reviewed by Marti *et al.* 1993). Most dietary studies on Tengmalm's Owl have been based on pellet analyses or stored prey in cavities (Korpimäki 1981, 1988, Sulkava & Sulkava 1971, Schwerdtfeger 1988, Pokorný *et al.* 2003). However, some authors pointed out that such data may be biased due to an underestimation of particular diet components (Redpath *et al.* 2001, Booms & Fuller 2003, Lewis *et al.* 2004, Tornberg & Reif 2007). Such bias can be caused by several factors including unequal preservation of particular prey remains, manipulation of prey by chicks and adult birds at the nest, or prey coloration (Rutz 2003). While pellet analyses usually underestimate the proportion of birds, analyses of prey remains underestimate the proportion of small mammals (Simmons *et al.* 1991).

Cameras can be successfully used to study the breeding behaviour of raptors and their diet composition (e.g., Pierce & Pobprasert 2007, Reif & Tornberg 2006, Grivas *et al.* 2009). This method also produces more reliable data on diet composition and delivery rates (Korpimäki 1981, Rogers *et al.* 2005). For example, the proportion of small mammals in the diet of Common Buzzards (*Buteo buteo*) appeared to be underestimated in an analysis of prey remains (Tornberg & Reif 2007). Another advantage of camera surveillance is a lower disturbance of raptors during breeding, which may lower the risk of nest abandonment (Cain 1985). Finally, due to the nocturnal activity of owls, it is not possible to observe prey deliveries to the nest from a hide or screen. Therefore, camera monitoring remains the only effective method to study owl feeding ecology.

In this study, we assessed the diet composition of Tengmalm's Owl in the Ore Mountains, Czech Republic, by a pellet analysis from nest boxes and using nest recording by continuous camera surveillance (Reif & Tornberg 2006). The aim of the study was to compare the mean delivered numbers of main diet components collected by each method. Furthermore, we assessed the availability of the main components of small mammal prey and compared their abundance with their dietary proportion.

2. Material and methods

2.1. Study area and population

The study area was situated in forests damaged by industrial air pollution in the Ore Mountains (50° N, 13° E) in the Czech Republic at altitudes ranging between 735 to 956 m a.s.l. The study area is covered by fragments of Norway spruce forest, open areas and forest clearings (dominated by Wood Reed *Calamagrostis villosa*), solitary trees (mostly European Beech *Fagus sylvatica*) and plantations of Blue Spruce *Picea pungens*, Birches *Betula* spp., European Mountain Ash *Sorbus aucuparia* and European Larch *Larix decidua*. Within these habitats, 120 nest boxes for the Tengmalm's Owls were placed in an area of 70 km^2. Data on diet composition were collected between May and July 2004 and 2006. We monitored four nests in 2004 (27% of the nest-box breeding population) and six nests in 2006 (25% of the nest-box breeding population). All nests in both study years were successful, i.e., at least one young fledged at each nest.

2.2. Food supply

The abundance of small mammals was assessed using the snap-trap capture method (Pelikán 1971). The captures were carried out in both years at the beginning of June (peak of the small mammal breeding season in the mountains; Dr. Vladimír Bejček, Czech University of Life Sciences, pers. comm.). The traps were laid out in three squares in each year. Each square covered an area of 100 m × 100 m, within which the traps were placed 10 m apart. Thus, a total of 121 traps were laid. The traps were exposed for three nights and checked once a day. The number of caught individuals per night was assessed in each square (number of individuals/hectare*trapping night). All caught mammals (79 individuals in 2004 and 3 individuals in 2006) were determined to species level.

2.3. Camera monitoring

The equipment consisted of a camera (DECAM OBSERVER, version 1.5.136.0, SINIT), a chip reader (PS02, ELVIS), a movement data logger (ZS4, COMET), an infrared motion detector (KS96, KOTLIN) and infrared lighting (IR diodes, SFH 485–2,880 nm; Bezouška *et al.* 2005). Cameras were installed inside the nest box opposite the opening. They were triggered by the infrared detector sensitive to movements in the nest-box opening. The time of detection was recorded by the movement data logger and 1–3 photos were taken for each feeding event. During the night, the opening was illuminated by infrared diodes during

Table 1. The abundance of small mammals captured using snap traps in 2004 and 2006.

		2004		2006	
Family	Species	Ind./ha*night ± SD	*N*	Ind./ha*night ± SD	*N*
Muridae	*Apodemus flavicollis*	6.2 ± 4.8	56	0.0	0
Arvicolidae	*Microtus agrestis*	1.1 ± 1.1	10	0.3 ± 0.7	3
	Clethrionomys glareolus	1.0 ± 0.7	9	0.0	0
Soricidae	*Sorex araneus*	0.4 ± 0.5	4	0.0	0

picture taking. All adult owls and nestlings were marked by chip rings (BR chip ring, BENZING). A chip reader fixed by the nest-box opening detected and archived all movements of chips in the nest opening. Using this equipment, we were able to record most prey items delivered to the nests and determine the genus or family of caught birds and mammals. The nests were continually monitored by the camera system for 24 hours per day from hatching to the fledging phase. Each nest was recorded over a mean period of 28.3 ± 8.5 SD days in 2004 (73.5 ± 24.2 SD% of the chicks' stay in the nest box), and 25.0 ± 8.6 SD days in 2006 (78.9 ± 17.6 SD% of the chicks' stay in the nest box).

2.4. Pellet analysis

Pellets and prey remains were collected twice during the period when most chicks were still present at the nest box (2004: 39.0 ± 3.7 SD days per nest, 2006: 31.2 ± 6.1 SD days per nest). All remaining material was collected after chicks' fledging. The material was moistened with added detergent. Consequently, the material was dissolved in a 5% solution of NaOH (Schueler 1972) and the bony material was blanched using 2–5% solution of hydrogen peroxide. Small mammals were determined by identifying skulls according to Anděra & Horáček (2005), and birds by beak and skulls using a reference collection.

2.5. Statistical analyses

All analyses (Wilcoxon matched-pairs tests, Mann Whitney *U* tests, a *t* test and a Chi-square test) were performed using STATISTICA (Statsoft Inc. 1996). Values below are reported as mean ± SD per nest or trapping site. For the non-parametric tests, we used data pooled for taxonomic families, because of similar body sizes (approximately similar energetic value) of prey species within these groups. One exception to this rule, the European water vole (*Arvicola terrestris*), was very scarce in the diet ($n = 3$) and we considered its impact on the analyses to be negligible compared to the large numbers of other small sized voles (Arvicolidae).

3. Results

3.1. Food supply

The food supply of small mammals changed between the years. The abundance of small mammals was significantly higher in 2004 than in 2006 (8.8 ± 6.2 vs. 0.3 ± 0.7 ind./hectare/night; $t = 4.1$, $P < 0.001$, $n_1 = 9$, $n_2 = 9$). The taxonomic composition of the food supply also differed significantly between the two study years ($\chi^2 = 154.0$, df = 3, $P < 0.0001$). In 2004, the yellow-necked mouse *Apodemus flavicollis* was the dominant prey species (70.9%), while only field voles *Microtus agrestis* were found in traps in 2006 (Table 1).

3.2. Diet composition

In 2004, 300 prey items were determined by pellet analysis (75.0 ± 8.5 individuals per nest). We recorded 754 prey items using camera monitoring, of which we were able to determine 570 items (142.5 ± 15.9 prey items per nest; Fig. 1). Thus, we were able to determine to genus/species 40.2 ± 6.9% of items in the pellet analysis and 77.1 ± 17.1% of items in the camera monitoring. In 2006, 809 prey items were recorded using the camera

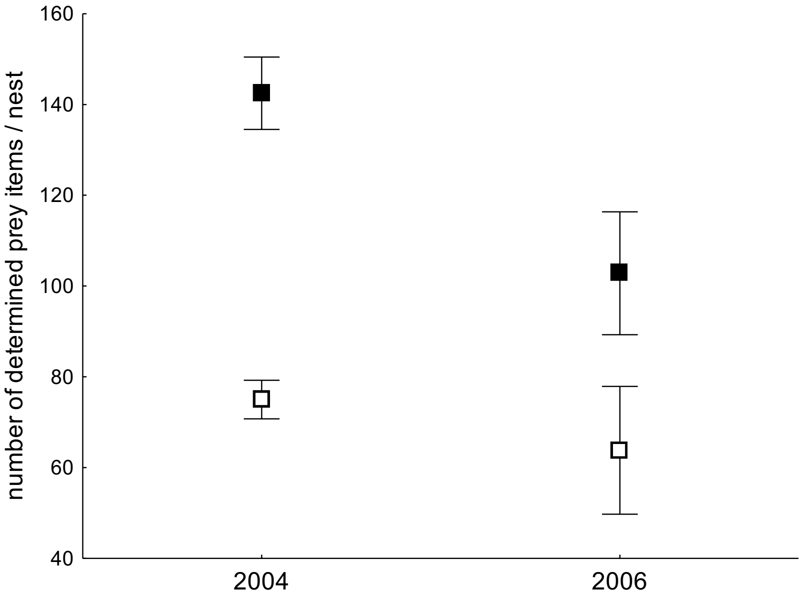

Fig 1. The number of prey items per nest determined by pellet analysis and camera monitoring in 2004 and 2006 (mean ± SD). Open squares – pellet analysis, filled squares – camera monitoring.

system. Of these, we were able to determine 383 prey items to genus/species by pellet analysis (63.8 ± 34.4 prey items per nest) and 617 items (102.8 ± 33.2 prey items per nest; Fig. 1) by camera monitoring. In total, pellet analysis allowed a determination to genus/species in 46.4 ± 14.7% of cases, and camera monitoring for 80.2 ± 12.5% of all delivered prey items.

The main diet component consisted of voles, which made up 56.0% of prey in camera data and 46.6% in pellet data. The identified species were field vole *Microtus agrestis*, common vole *Microtus arvalis*, bank vole *Clethrionomys glareolus* and European water vole. Other important components were mice (28.5% in camera and 36.3% in pellet data; species: yellow-necked mouse and wood mouse *Apodemus sylvaticus*) and shrews (9.6% in camera and 13.3% in pellet data; species: common shrew *Sorex araneus* and Eurasian pygmy shrew *Sorex minutus*). Minor dietary components were song birds (5.2% in camera and 3.4% in pellet data; species: Chaffinch *Fringilla coelebs*, tits *Parus* spp., *Sylvia* and *Phylloscopus* warblers, European Robin *Erithacus rubecula*, pipits *Anthu*s spp., Dunnock *Prunella modularis*, and others) and dormice (0.8% in camera and 0.4% in pellet data; species: hazel dormouse *Muscardinus avellanarius*).

Table 2. Mean numbers of prey items ± SD delivered to Tengmalms' Owl nests recorded by cameras during early and late phases of chick rearing (ages <16 days and ≥ 16 days, respectively).

Taxa	Early	*N*	Late	*N*
Muridae	11.5 ± 16.4	115	21.4 ± 26.6	214
Arvicolidae	25.3 ± 15.1	253	42.7 ± 17.3	427
Soricidae	4.6 ± 3.4	46	7.9 ± 6.5	79
Birds	1.5 ± 1.0	15	3.5 ± 2.2	35
Gliridae	0.2 ± 0.4	2	0.1 ± 0.3	1

Camera monitoring and pellet analysis may be incomparable to some degree because most pellets accumulated at the end of the rearing period, while cameras were used throughout rearing. Therefore, we performed an analysis to compare the similarity in the numbers of delivered prey items recorded by cameras between early and late breeding phases (chicks' age < 16 and ≥ 16 days, respectively). We did not find significant differences between these two phases (Table 2; Wilcoxon matched-pairs test: $Z = 1.7$, $P = 0.079$). Based on these results, we used the whole camera dataset for further comparisons.

Pellet analysis, compared to camera monitoring, underestimated the mean delivered numbers of individuals in all diet groups. However, significant differences were found only for voles and birds (Table 3). For mice, these differences were marginally significant ($P = 0.0506$). Between-year changes in mean numbers of delivered prey were

Table 3. Mean number of items ± SD per nest in the diet of Tengmalm's Owls in 2004 (n = 4 nests) and 2006 (n = 6 nests) recorded by pellet analysis and camera monitoring, and results of statistical analyses. Method comparison was carried out using Wilcoxon matched-pairs test, and between-year comparison was undertaken using Mann-Whitney U test. Significant (P < 0.05) values are marked with an asterisk.

Taxa	Camera	Pellet	Z	P	2004	2006	U	Z	P
Muridae	33.8 ± 41.6	24.8 ± 30.1	2.0	0.0506	69.9 ± 17.2	2.3 ± 2.7	38.4	3.7	0.0002*
Arvicolidae	66.4 ± 25.6	31.8 ± 26.9	2.8	0.0051*	31.4 ± 19.0	60.9 ± 32.6	22.5	–1.9	0.0537
Soricidae	11.4 ± 7.3	9.1 ± 9.9	1.6	0.1097	3.6 ± 2.9	14.7 ± 8.3	11.0	–2.8	0.0048*
Birds	6.1 ± 1.8	2.3 ± 3.3	2.0	0.0469*	2.9 ± 3.4	5.1 ± 3.0	29.5	–1.4	0.1622
Gliridae	1.0 ± 1.2	0.3 ± 0.5	1.6	0.1056	1.0 ± 1.3	0.4 ± 0.7	37.0	0.9	0.3559

significant for mice and shrews. The numbers of delivered mice changed consistently with the availability of mice in the field. In 2006, we recorded low numbers of mice in the field as well as in the diet of Tengmalm's Owls (Tables 1 and 3). A similar pattern was found for shrews and voles; however, their total numbers in the field were low (Table 1).

4. Discussion

The diet composition of vole-eating specialists strongly depends on the abundance of voles, their main prey species (Jaksic & Braker 1983, Recher 1990, Marti *et al.* 1993, Valkama *et al.* 2005). In Northern Europe, the diet composition of Tengmalm's Owl is closely related to the abundance of their main prey in the field (Korpimäki 1981, 1988). In Central Europe, changes in vole abundance do not show regular 3–4 years cycles, but show greater variability between years (Tkadlec & Stenseth 2001). Our two-year data partially supported previous findings in that we confirmed an overall, high significance of voles as the main prey for Tengmalm's Owls. However, we also recorded a high proportion of mice in the diet, and their numbers changed in concert with their availability in the field. In 2006, the availability of mice decreased, and we recorded an increased proportion of voles in the diet. North European Tengmalm's Owls use shrews and small birds as alternative prey (Korpimäki 1981, 1988). In our data, the number of shrews in the diet also increased with increased availability, but the numbers of eaten birds did not change significantly, supporting studies done at similar latitudes (Pokorný 2000, Pokorný *et al.* 2003).

Only a handful of studies can be used for methodological comparisons with our results. Korpimäki (1981) studied Tengmalm's Owl diet and obtained inconsistent results: his camera system tended to overestimate the number of delivered prey items in one year, but underestimate the number in subsequent years. Our results showed that pellet analysis underestimated the number of prey delivered to the nest relative to camera monitoring. These findings agree with earlier studies on Common Buzzard *Buteo Buteo*, Rough-legged Buzzard *Buteo lagopus* and Goshawk *Accipiter gentilis* (Tornberg & Reif 2007). Interestingly, our results support these findings despite the different digestive ability of owls and diurnal birds of prey. Diurnal birds of prey can digest more bones than owls due to lower pH in their digestive tracts (Duke *et al.* 1975). According to our experience, there are marked differences in preservation of bones among complete pellets and material taken from the nests. Bones were scarcer in the material from the nests probably, due to the activity of chicks (J. Riegert, pers. obs.).

The effectiveness of determining prey species to higher taxa (genus or family) was higher for camera monitoring than pellet analyses. In our data, we were able to determine 40.2% (in 2004) and 46.4% (in 2006) of delivered prey items by pellet analysis. Camera monitoring allowed for the determination of a higher proportion of delivered prey items than pellet analyses (77.1% and 80.2%, respectively). When accounting for the time of camera exposition (73.5% in 2004 and 78.9% in 2006 of the chicks' stay at nest), the proportion of determined prey using pellet analysis was further decreased to approximately 30–35%. Similar results were obtained by Tornberg & Reif (2007), but they noted that the exact determination to species level was more difficult using a camera system compared to a prey-remains analysis. Our experience supports this finding. For example, determination of bird-prey items to species was nearly impossible by camera monitoring, and an exact determination was only possible using prey remains and pellet analysis.

Taxonomic diet composition estimation was also affected by the method used. Using pellet analyses, we recorded lower numbers of all main prey groups, but marked differences were found in voles, birds and mice. Similar results were already shown in a study on Common Buzzards, where the proportion of voles was underestimated by pellet analysis (Tornberg & Reif 2007). Contrary to our research, Lewis *et al.* (2004) showed that the proportion of birds in the Goshawk diet was underestimated by pellet analysis and the proportion of mammals was underestimated by camera monitoring. These differences across species may be caused by the size of delivered prey and prey handling behaviour. For example, in the diet of Gyrfalcons (*Falco rusticolus*), the proportion of small passerines was underestimated sevenfold using prey remains, but the proportion of large prey (Rock Ptarmigan *Lagopus mutus*) was underestimated threefold using camera monitoring (Booms & Fuller 2003). The bias can be explained by the prey consumption habits of Gyrfalcons, since Rock Ptarmigans were rarely eaten completely and small prey items were almost always eaten entirely. A similar pattern was found in our data, as the underestimation of voles (and mice) observed by camera monitoring was probably a result of vole decapitation before their delivery to the nest. This is supported by our regular findings of decapitated voles and mice in the nest boxes. Prey decapitation is a well-known feeding behaviour in raptors (hawks Accipitriformes, falcons Falconiformes and owls Strigiformes) and may play several functions such as decreasing the weight of the transported prey items and food preparation for chicks (Glutz von Blotzheim & Bauer 1980, Steen *et al.* 2010). In agreement with Steen *et al's.* (2010) study on Kestrels (*Falco tinnunculus*), we recorded frequent decapitation in voles and mice, but shrews were never decapitated. Furthermore, light conditions and image quality can influence the estimated diet composition assessed by camera monitoring (Booms & Fuller 2003). If the prey is decapitated then its taxonomic determination through pellet analysis based on post-cranial features becomes nearly impossible.

Based on our results, we recommend the use of both pellet analysis and camera monitoring to accurately assess diet composition of breeding raptors and owls. This is especially crucial in owls, where observations from hides or screens are impractical due to darkness.

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Helmipöllön ravinnon koostumus: kameraseurannan ja pellettianalyysin vertailu

Toteutimme Keski-Euroopassa kaksivuotisen seurannan, jossa määritimme pellettianalyysin ja kameraseurannan avulla helmipöllön (*Aegolius funereus*) pesimäkautista ravinnon koostumusta suhteessa maastossa saatavilla olevaan ravintoon. Pöllöjen ravinto koostui enimmäkseen myyristä (Arvicolidae), hiiristä (Muridae) ja päästäisistä (Soricidae), ja näiden osuus ravinnossa heijasteli niiden saatavuutta maastossa. Pellettianalyysissä tunnistimme 40,2 (± 6,9 SD) % vuonna 2004 ja 46,4 (± 14,7 SD) % vuonna 2006 kaikista kameraseurannassa havaituista saaliseläimistä.

Kameraseurannalla tunnistimme 77,1 (± 17.1 SD) % vuonna 2004 ja 80,2 (± 12,5 SD) % vuonna 2006 kaikista kameran tallentamista saaliseläimistä. Pellettianalyysi tuotti kaikista pääsaalisryhmistä aliarvion, mutta erot olivat tilastollisesti merkitseviä vain myyrien ja lintujen osuuksille. Myyrillä tämä voi johtua siitä, että emo usein poistaa saaliilta pään ennen sen tuomista pesälle. Havaitsimme päättömiä myyriä ja hiiriä säännöllisesti helmipöllön pöntöissä, mutta päästäiset olivat useammin kokonaisia. Tutkimuksemme osoittaa, että menetelmien käyttö yhdessä tuottaa tarkemman saaliskoosteen arvion yöaktiivisilla petolinnuilla.

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Příloha XI

Riegert J, Fainová D, Mikeš V, Fuchs R. 2007:

How urban kestrels *Falco tinnunculus* divide their hunting grounds: partitioning or cohabitation?

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How urban Kestrels *Falco tinnunculus* divide their hunting grounds: partitioning or cohabitation?

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Riegert J., Fainová D., Mikeš V., Fuchs R. 2007. How urban Kestrels *Falco tinnunculus* divide their hunting grounds: partitioning or cohabitation? Acta Ornithol. 42: 69–76.

Abstract. The hunting ranges of 34 male urban Kestrels were studied in a small city (40 km^2) in S Bohemia (Czech Republic). It was assumed that males from the city center and periphery hunt for voles mainly on the city's outskirts. The “city-center” males are unable to defend their hunting ranges on the periphery because of aggression on the part of the “periphery” Kestrels. To counter this, they may either 1) invade the hunting ranges of periphery males or 2) establish their own exclusive hunting ranges. Our data supported the first suggestion. Hunting range size varied greatly, from 0.8 to 25.0 km^2 (7.2 ± 6.9 km^2), with large overlaps of between 0.3% and 51.4% (12.5 ± 11.6%). The ranges of city-center males were several times larger than those of the periphery males, and greatly overlapped the ranges of other city center and periphery males. Overlapping of the hunting ranges of periphery males was less extensive. The higher energy costs in terms of flying to distant suitable hunting areas and frequent changes of hunting grounds should decrease the preference for nesting in the city center. Therefore, we suggest that Kestrels derive other advantages from living in the city center (e.g., the high quality of nest sites). Cohabitation, whereby city center males invade the hunting grounds of periphery males, appears to be a more effective strategy than partitioning.

Key words: Kestrel, *Falco tinnunculus*, urban, hunting range

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INTRODUCTION

Among European raptors, the Common Kestrel colonized cities most successfully (Cramp & Simmons 1980). Their breeding densities in cities are higher than farmland populations (Plesník 1992, Salvati et al. 1999). Studies of urban Kestrels in large European cities usually indicate a high proportion of birds in the diet (Yalden 1980, Darolová 1986, Quere 1990, Plesník 1992, Romanowski 1996, Kübler et al. 2005). On the other hand, voles still comprise a considerable part of Kestrel diet in these cities (i.e. Plesník 1992, Romanowski 1996, Rejt et al. 2000). Voles are not available in the city center (Čiháková & Frynta 1996), therefore, Kestrels are forced to hunt voles outside of the urbanized area.

Vole-eating raptors are mainly territorial, due to large energy requirements (Peery 2000). Many factors affect their home range size, especially food conditions (Village 1982, 1987), breeding density (Bowman & Bird 1986, Leary et al. 1998), phase of breeding cycle (Sparks et al. 1994) and relatedness of individuals (Walls & Kenward 2001).

The Kestrel territory is defined as actively defended area, usually within a radius up 100 m from the nest (Cavé 1968). On the other hand, home ranges (~ whole activity ranges) can be several times larger than territories. In general, Kestrel home ranges are always larger than actively defended territories (Village 1990).

Common Kestrels maintain their territories during the breeding season (migratory populations) or throughout the whole year (resident populations, Village 1990), defending them from other Kestrels. Similarly to other falcons, Kestrel males provide most of the food for chicks (Cramp & Simmons 1980). Simultaneously, the males defend their territories more often and more vigorously than females (Wiklund & Village 1992). The hunting ranges of Kestrels may usually surround the nest (Village 1990, Cavé 1968), thus inside of the home range. The size of territory and home range may decrease with the course of breeding season (Cavé 1968) and increase when density of *Microtus* spp. decreases (Village 1990). The hunting range overlap could be a common feature, depending on conditions, included individual factors (Village 1990). However, these results were obtained from farmland populations only; information about spatial activity of urban Kestrels is missing.

The hunting ranges of Kestrel males were studied in a small sized city of 40 km^2 (České Budějovice, Czech Republic) during the time of chick rearing. The Kestrels breed in the city center (continuous urbanized area), as well as on its periphery (mosaic of urban and ruderal habitats). Kestrels in České Budějovice hunt almost exclusively outside of the urbanized area and the common vole *Microtus arvalis* dominated the diet of their chicks (68–88% by numbers, 89–95% within biomass), even during low vole years (Fainová 2005).

Given this, males nesting in the city center seem to have two possibilities of dividing among one another their hunting ranges placed in the city peripheral area: 1) to invade the periphery hunting ranges of other males (cohabitation) or 2) to establish their own exclusive hunting ranges (partitioning). Our predictions are that: a) the hunting ranges of males from the city center are larger compared to those of periphery males and b) the hunting ranges of males from the city center overlap more with those of other males than hunting ranges of periphery males do.

MATERIAL AND METHODS

Study area and Kestrel population

The population of Kestrels was studied in České Budějovice (Southern Bohemia; 49°N, 14°E; 40 km^2; 100 000 inhabitants; 250–300 m a.s.l.) during the breeding seasons 2002–2004. The Kestrels breed in loft-windows of old buildings, factories and churches. A minority of nests were found on trees or in nest boxes, attached to buildings. The population of Kestrels included ca 30–40 breeding pairs each year (Riegert & Fuchs 2004). The hunting grounds are mostly meadows (36%), cereals (35%) and ruderal areas (19%). The rest (10%) were composed of alfalfa, rape or cornfields. The proportion of habitats did not change markedly between years (less than 3% in any of them).

Vole trapping

Pitfall traps (100 plastic bottles with a cut neck and a 2 l capacity) were used each year, following methodology of Anděra & Horáček (1982). The traps were installed on 10 Kestrel hunting grounds (a trap line was composed of 10 traps per hunting ground, span 3 m) in the second half of July. The timing of trapping was determined by the approximate end of the breeding season, when the last Kestrel chicks were reared. This arrangement enabled us to synchronize the trappings among years, since the population hatching span between years also varied (see further). The reason of synchronization of the trapping dates were because the intra-year fluctuations in our area are unknown. The traps were filled with a 4% fusion of formaldehyde as a fixation agent and exposed for 17 days. The trap lines were placed in two types of vegetation cover: meadow (6 lines) and ruderal (4 lines). The vegetation cover of ruderals is not cut; meadows are usually cut at the end of July. The trapping effort was 1700 trap-nights per year. We caught 266 voles in the breeding seasons 2000–2005: 19 in 2000 (1.9 ind./trap line), 29 in 2001 (2.9 ind./trap line), 79 in 2002 (7.9 ind./trap line), 20 in 2003 (2.0 ind./trap line), 21 in 2004 (2.1 ind./trap line) and 98 in 2005 (9.8 ind./trap line). The years 2002 and 2005 seemed to be peak vole years, whereas 2000, 2003 and 2004 were low vole years.

Trapping and tagging of Kestrels

The Kestrels were trapped near nesting holes, using a fake Eagle Owl *Bubo bubo*, without using a tape-recorder (owl decoy induced attack). All the animals were trapped during the incubation stage. A mist-net with a 50 mm mesh was used. For the purpose of this study, only males were tagged since they provide most of the food for the chicks (Cramp & Simmons 1980). Although there were up to 40 pairs in the city, trapping was possible only at approximately 1/3 of all nests in the city. In total, 46 males were trapped (2002: 15, 2003: 20, 2004: 11). The males were equipped with either wing-tags (34) or transmitters (12). The wing tags (2 x 5 cm) were installed on the patagium using a nylon rod (Village 1982). One or two tags of different/same coloration were used. The transmitters were of a standard "back-pack" type (4.5 g, with a TW-4 battery with a lifespan of up to six month). Three-piece Yaggi aerial and wideband receiver AR-8000 were used for telemetry locations.

Hunting range assessment

A total of 34 Kestrel male hunting ranges were assessed (2002: 11, 2003: 12, 2004: 11). The distribution of males on the gradient from city center to its periphery was quite equal (Spearman rank correlation, $r_s = 0.28$, $p > 0.05$, $n = 8$ distance categories). Eight males were radio tagged. We included into analyses only results obtained from 1 male with 12 locations. All 34 males were checked at the nest with visual control during the rearing of chicks. Moreover, all of these males bred successfully. The number of locations for the other 12 excluded males was far below 10. This was caused either by failure of their breeding attempts (8) or they were non-breeding males caught at another male's nest hole (4). The number of locations varied between 12 and 38 (mean 19.1 ± 6.4), totalling 661 locations. We did not include locations of over-flying Kestrel males that did not stop on the hunting grounds. The locations of wing-tagged males were collected during observations on the hunting grounds.

Fights among individuals were recorded during 30–60 min observations on hunting grounds. This parallel project was realized in the years 2000–2005 (2000: 27 hours, 2001: 34 hours, 2002: 28 hours, 2003: 69 hours, 2004: 65 hours and 2005: 67 hours). All the observations took part during rainless days only.

Records were gathered from May to July during the time of chick rearing. The start of observations in each year was set by the first hatching of chicks (4 May 2002, 17 May 2003, 17 May 2004). The mean date ± SD of hatching for the population was as follows: 2002 —15 May ± 7 days (n = 10), 2003 — 27 May ± 6 days (n = 10) and 2004 — 2 June ± 7 days (n = 12). Therefore, observations were continued until the last chick fledged (at least for six weeks). All locations determined by telemetry were verified with visual sightings, using a binocular 7 x 50.

The hunting range area was calculated using the Minimum Convex Polygon Method (Ford & Myers 1981), excluding the nest site. The nest was excluded because of possible effect of "artificial" enlargement of hunting area of Kestrels from city center that do not hunt nearby its nest and just over fly urbanized area. The polygon was assessed using hunting sightings only. The city center was represented by the center of the "old-town", where also lies an approximate geographical centroid of the total urbanized area. We use the terms "periphery" or "city centre Kestrels" (or their modifications) within the text. This means that particular Kestrels that breed close to periphery or center (centroid) polus of the gradient of urbanized area within the city are not two distinctive categories of males. Therefore, our dataset does not have a discrete distribution and both the terms may just approximate the real position of the nest. Hunting range overlap was expressed as a percentage of the shared area between two hunting ranges. The overlap was measured for all overlapping "couples" of males.

Statistical analyses

To control for a potential bias of the method used, ANOVA was computed to compare radio-tagged vs. wing-tagged males (Statsoft, Inc. 1996). Generalized Linear Models (GLM) with a relevant link function were used to analyze an influence of factors on hunting range parameters (McCullagh & Nelder 1989). Factors were incorporated using forward selection, according to Mallow's Cp-statistics (Mallows 1973). The factors included are mentioned for each model. Only three males were observed in more than one year, thus partially removing the effect of pseudoreplications. We used t-tests for comparisons of groups of radio/wing-tagged males, and Kruskal-Wallis test to compare inter-year differences in the hunting range size. Data on male distribution within urbanized area and behavioral data on fights were analyzed using Spearman rank correlations.

RESULTS

Hunting range size and observation method used

The number of locations (wing-tagged males: 19.7 ± 6.9, n = 26; radio-tagged males: 17.1 ± 3.9, n = 8, t-test, d.f. = 1, t = 0.992, p = 0.334) and the hunting ranges (wing-tagged males: 6.2 ± 6.1 km^2; radio-tagged males: 9.4 ± 8.6 km^2, t-test, d.f. = 1, t = -1.14, p = 0.265) did not show any differences between the two groups of males.

Nest location and hunting range size

Hunting range size varied from 0.8 to 25.0 km^2 (7.2 ± 6.9 km^2). The data unit for analysis was represented by an individual male's hunting range. The numbers of locations, distance of the nest from city center and vole abundance were included into the GLM model. The amount of urbanized area within a hunting range was used as a covariate. The hunting range size was not affected by either number of locations or vole abundance. The inter-year differences in the hunting range size (medians for years; 2002: 2.8 km^2, 2003: 4.5 km^2, 2004: 5.0 km^2) were not significant (Kruskal-Wallis median test, $H = 2.08$, $df = 2$, $p = 0.354$). The hunting range size was negatively correlated with the distance of the nest from the city center (Table 1, Fig. 1).

Nest location and hunting ranges spacing

Hunting ranges of "periphery males" usually overlapped each other less than 10% (Fig. 2). Some hunting ranges of "periphery males" showed great overlap (> 50%). However, these couples tended to enlarge one of these hunting ranges (Fig. 2). Hunting ranges of "city center males" often covered most of ranges (up to 100%) of "periphery males" (Fig. 2). Ranges of males from "city center" often showed great overlap (30–50%), but the shared space was mainly represented by urbanized area (Fig. 2).

There was usually a greater overlap among center males than among the periphery ones (Fig. 3). The overlap of two hunting ranges varied from 0.3 to 51.4% (mean 12.5 ± 11.6%). The data unit for analysis represented the intersection between two overlapping hunting ranges.

The sum of nest distances from the city center, calculated for each two males with overlapping hunting ranges, and vole abundance were included into the GLM model. The sum of the distances for a couple of nests indica-tes the position of nests in the area of the city as follows: A minimal value shows that both nests are situated near the city centroid, while a maximal value indicates that both nests lie close to the city periphery polus of the gradient.

The sum of nest distances from the center negatively affected the extent of overlap between hunting ranges (Table 1, Fig. 3). Minimum values of hunting range overlap were typical for "couples" of periphery males, maximum for center ones. Vole abundance did not affect the extent of overlap between hunting ranges.

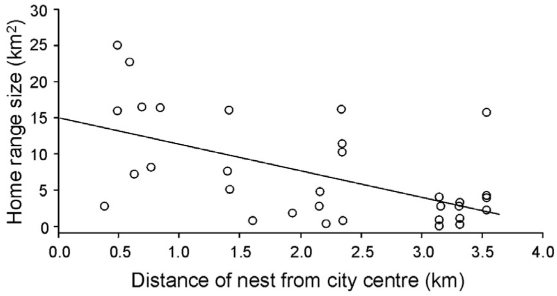

Fig. 1. Hunting range size and distance of the nest from the city center (N = 34).

Fights among hunting individuals

We recorded 91 fights among Kestrels on hunting grounds. The frequency of fights was negatively correlated with vole abundance (Spearman rank correlation, $r_s = -0.93$, $p < 0.05$, $n = 6$ years). We recorded both fights between tagged and non-tagged males (or pairs) from open landscape and also fights between two tagged males (one from periphery and the second from city center). The "intruders" were, as a rule, driven from the hunting ground (or territory) of defending pair.

DISCUSSION

Hunting range size

Although, both the methods used are adequate for studying hunting ranges, they can clearly differ in results obtained. While the data from radio-tracking are "real", those from wing-tagging are dependent on actual position of the observer and what the observer can see (wing-tagged Kestrels were safely distinguished at distance less than 200 m approximately). Therefore, we compared these two datasets. The hunting ranges of radio-tagged males were distinctively larger than those of wing-tagged males, which was caused by a male's nest location. Five radio-tagged males nested up to 2 km from the city centre and only three

Table 1. Statistical analyses of the home range parameters of urban Kestrel males from České Budějovice. GLM, forward factor selection, only factors with significant effect are included. * — covariate: urbanized area.

Dependent variable	N	Model type	Independent variable	% of explained variability	β	p
Home range size (km^2)*	34	Gamma	Distance of nest from center	32.2	-0.90	0.0004
Home range overlap (%)	94	Gamma	Distance of nests from center (sum)	3.9	-0.76	0.0351

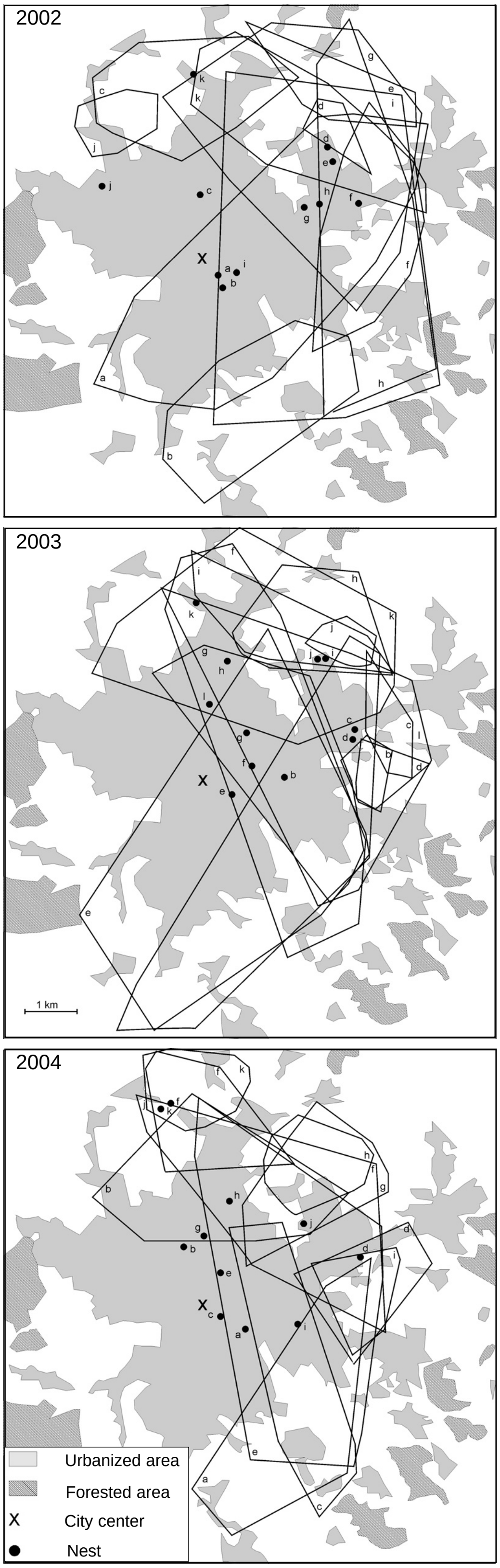

Fig. 2. The distribution of hunting ranges of Kestrel males from České Budějovice in the year 2002–2004.

radio-tagged males were from the city periphery. These results are comparable with those of Village (1982) who did not find significant differences in hunting range sizes between radio- and wing-tagged Kestrels. Unlike Village (1982), we did not find the relationship between number of locations and hunting range size.

Hunting range size and overlap

The results of the hunting range size and overlap analyses supported our first hypothesis: males from the center had larger hunting ranges than those from the periphery, even when the urbanized area was included into the analysis as a covariate. The hunting ranges of "males from the center" markedly overlapped with each other, as well as with most of those of "males from the city periphery". This finding is evidence that only "periphery males" defend their hunting ranges located within the nest surroundings. The "males from the center" make incursions into the hunting ranges of the "periphery males". It is difficult for males breeding in the city center to defend their hunting ranges, because they have to fly over urbanized areas before reaching their hunting ground. Thus, they can not patrol its hunting ground continually. At the same time, they interact with males that breed near the hunting grounds on the city periphery.

In spite that we did not include the nest site, the mean hunting range size of the Kestrel males in this study was higher than home ranges found in farmland habitats (1.1–5.7 km^2, Village 1982; 0.9 km^2, Mikeš 2003; 7.2 km^2 this study), probably because of different strategies used by males from the center. The home range size of Kestrels could be affected by vole abundance (Village 1982, Bowman & Bird 1986, Dunk & Cooper 1994), but we did not record any correlation between them. The correlation between vole abundance and hunting range was indicative only. Again, this might be due to the particular strategy of the center males. The males have similar area of their hunting range regardless of the vole abundance. The size of hunting range of "males from center" is rather determined by aggressive behaviour of "males from city periphery" and not by food availability. Moreover, we measured hunting ranges, and not home range area, since the nest site was excluded from hunting range. The decreased vole abundance was followed only by increased aggressive behaviour of Kestrels at hunting grounds. This result is in concordance with findings of Village (1990).

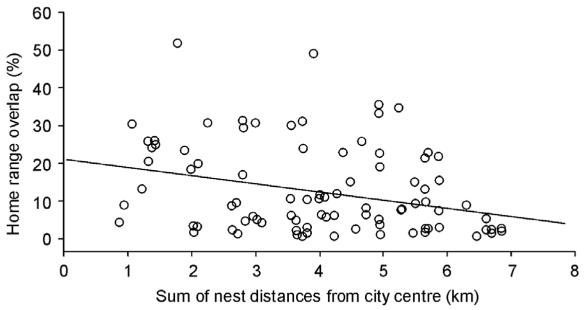

Fig. 3. The hunting range overlap for couples of nests, related to nest position (N = 94 couples).

Our results lead to the question of how the large hunting ranges of "center males" originated. They can visit only one or more hunting grounds per trip. In the first case, the male stays on the ground until the prey is caught. In the second case, if the male does not catch a prey within a particular time, it moves to another hunting ground. The recorded trips of some males (two examples in Fig. 4) and our behavioral data support the second hypothesis. The trip route could be more or less fixed, since males left the nest in a similar direction every day. Fixed daily routines in Kestrels were noted by Rijnsdorp et al. (1981). The changing of hunting grounds within one trip may be due to conflicts with local Kestrels. According to our observations, conflicts with both males and females were quite common. This was probably because the "intruder" male passed the border of territory of periphery pairs, which also partially included hunting range of these Kestrels.

Disadvantageously, males of the city center spent much energy by flying to distant suitable hunting areas and by frequently changing their hunting grounds. Therefore, why do Kestrels nest in the city center? We provide two possible explanations. The nesting possibilities on the periphery could be limited or nest sites in the centre are of higher quality, for example safer sites from predators in the city center. Kestrel densities inside the cities are higher compared to city peripheries (i.e. Hudec et al. 1981, Darolová 1992, Plesník 1992, Salvati et al. 1999, Wassmer 2001). However, the results of this study may support both of the above mentioned hypotheses.

We conclude that Kestrels show partial cohabitation of periphery hunting grounds, but the inter-species aggression probably plays a key role for the use of these grounds. The males from the city centre have to change their hunting grounds because of aggressive attacks of periphery Kestrels. The evidence for cohabitation is indirectly given by great overlap among "central" and "periphery" ranges of males.

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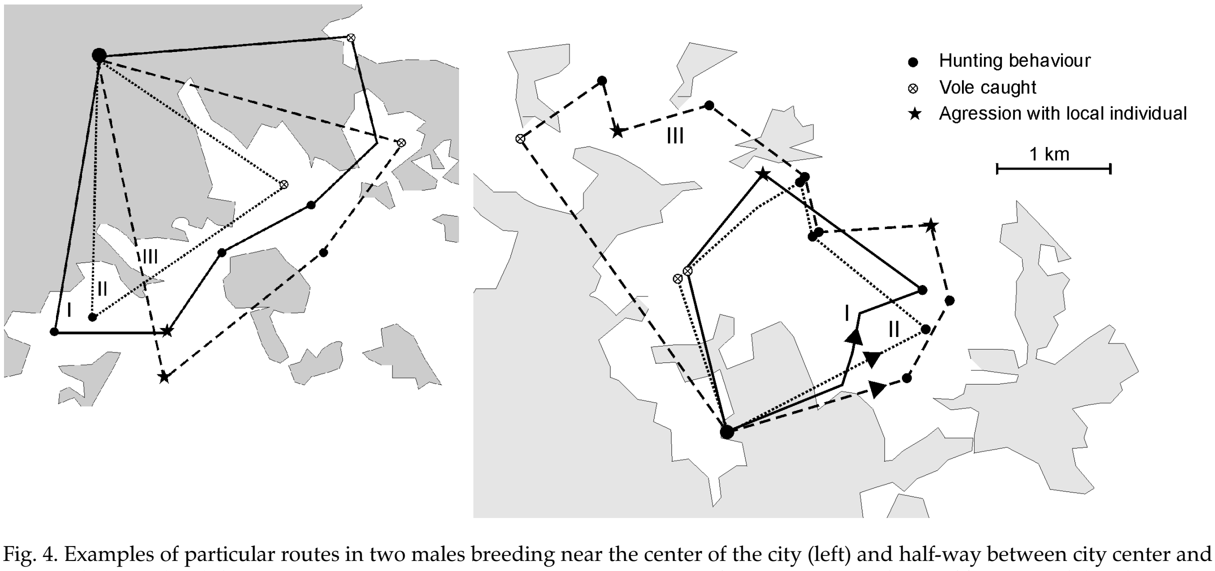

Fig. 4. Examples of particular routes in two males breeding near the center of the city (left) and half-way between city center and its periphery (right): left) 6.6.2003. Routes I (10:36–11:22), II (13:01–13:30) and III (16:05–17:56) finished by successful strike on the last hunting ground; right) 14.6.2002. Routes I (8:28–10:10), II (10:12–10:56) and III (11:10–15:05) finished by successful strike on the last hunting ground.

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STRESZCZENIE

[Sposób użytkowania terenów łowieckich przez miejskie pustułki w Czeskich Budziejowicach]

Pustułka jest jednym z nielicznych gatunków ptaków drapieżnych zasiedlających tereny miejskie. Poszczególne gniazda tych ptaków znajdują się zarówno w centrum miasta (obszar ciągłej zabudowy) jak i na obrzeżach (obszar mozaiki środowisk miejskich i ruderalnych. Badania prowadzono w Czeskich Budziejowicach gdzie liczebność tego drapieżnika sięga 30–40 par, w latach 2002–2004. Przedmiotem badań były zasięgi łowieckie 34 samców pustułek w okresie opieki nad pisklętami.

W celu oszacowania dostępności podstawowej zdobyczy pustułek — norników, co roku w obrębie 10 terytoriów łowieckich rozmieszczono 100 pułapek żywołownych. Pustułki chwytano w sąsiedztwie gniazd wykorzystując imitację puchacza. Schwytane samce były znakowane z wykorzystaniem znaczków naskrzydłowych albo wyposażane w nadajniki telemetryczne. Sposób znakowania ptaka nie wpływał na uzyskiwane wyniki. Wielkość terytorium łowieckiego określano na podstawie 12–28 lokalizacji (z wyłączeniem stanowisk lęgowych) metodą Minimum Convex Polygon. Nakładanie się zasięgów określano jako procent wspólnie użytkowanego obszaru dwóch terytoriów.

Wielkość obszaru łowieckiego wahała się od 0.8 do 25 km^2 (śr. 7.2 ± 6.9 km^2). Zasięg nie był zależny od liczby lokalizacji oraz dostępności ofiar. Stwierdzono natomiast negatywny związek między odległością do gniazda z centrum miasta (Tab. 1, Fig. 1). Nakładanie się terytoriów łowieckich wahało się między 0.3% a 51.4% (śr. 12.5 ± 11.6%). Dostępność norników nie wpływała na stopień nakładania się terytoriów, natomiast najmniejsze wartości nakładania się były charakterystyczne dla "par" samców z terenów peryferyjnych, natomiast największe — dla samców gniazdujących w centrum miasta (Tab. 1, Fig. 2, 3). W oparciu o obserwacje zachowań samców gniazdujących w centrum miasta stwierdzono, że w razie niepowodzenia przenoszą się na inne terytoria (Fig. 4).

Podczas badań stwierdzono, że samce z centrum miasta dokonują penetracji terytoriów łowieckich samców gniazdujących na peryferiach. Same nie mogą stale patrolować swych terenów łowieckich i wchodzą w interakcje z samcami/parami zajmującymi terytoria w sąsiedztwie terenów łowieckich. Pustułki wykazują częściowe współużytkowanie pozamiejskich terenów łowieckich, lecz konflikty między poszczególnymi osobnikami odgrywają prawdopodobnie znaczącą rolę w sposobie ich użytkowania. Samce z centrum miasta muszą często zmieniać miejsca polowań z uwagi na ataki osobników zasiedlający tereny peryferyjne.

Příloha XII

Lövy M, Riegert J. 2013:

Home range and land use of urban Long-eared owls

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HOME RANGE AND LAND USE OF URBAN LONG-EARED OWLS

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Abstract. From 2004 to 2006 we studied the spatial activity of Long-eared Owls (*Asio otus*) breeding in the city of České Budějovice, Czech Republic. Two main factors (size and proportion of home range in developed area) clearly distinguished the owls into two groups: urban ($n = 5$) and suburban ($n = 4$). Urban owls occupied home ranges >50% in developed area; home ranges of suburban owls were <50% in developed area. We obtained 866 radio fixes from nine individuals while they were feeding offspring, when both males and females participated in hunting. The home ranges of urban owls were larger than those of suburban owls (95% kernels: 446 vs. 56 ha, respectively). Urban males and females used home ranges of similar sizes that overlapped greatly with those of the opposite sex and with those of other breeding pairs. In contrast, suburban male owls had home ranges larger than those of suburban females. Wooded areas and meadows were the vegetation types preferred by both urban and suburban owls, and both groups avoided vegetation types associated with human activities. Six of nine owls preferred the edges of open habitats, such as meadows and fields bordering wooded areas. Urban owls used remnant green spaces (refugia) within the city area to hunt small mammals. Long-eared Owls use nests made by other species, and may profit in urban environments from increased nest sites due to the relatively recent colonization of urban areas by the Common Magpie (*Pica pica*) and from suitable hunting grounds within the city.

Key words: Asio otus*, home range, Long-eared Owl, radio-telemetry, urban environment, land use.*

Rango de Hogar y Uso del Suelo de Individuos Urbanos de *Asio otus*

Resumen. De 2004 a 2006 estudiamos la actividad espacial de individuos de *Asio otus* reproduciéndose en la ciudad de České Budějovice, República Checa. Dos factores principales (tamaño y proporción del rango de hogar urbanizado) separaron claramente a los búhos en dos grupos: urbano ($n = 5$) y suburbano ($n = 4$). Los búhos urbanos ocuparon rangos de hogar >50% urbanizados; los rangos de hogar de los búhos suburbanos estuvieron <50% urbanizados. Obtuvimos 866 puntos de radio correspondientes a nueve individuos que se encontraban alimentando a sus pichones, mientras machos y hembras se encontraban participando en actividades de cacería. Los rangos de hogar de los búhos urbanos fueron más grandes que el de los búhos suburbanos, (95% kernels: 446 vs. 56 ha, respectivamente). Los machos y las hembras urbanos presentaron rangos de hogar de tamaños similares, que se superpusieron en gran medida con aquellos del sexo opuesto y con aquellos de otras parejas reproductivas. En contraste, los machos suburbanos tuvieron rangos de hogar más grandes que el de las hembras suburbanas. Las áreas boscosas y de pradera fueron los tipos de vegetación preferidos tanto por los búhos urbanos como por los suburbanos, y ambos grupos evitaron los tipos de vegetación asociados con las actividades humanas. Seis de los nueve búhos prefirieron los bordes de los hábitats abiertos, como los prados y los campos que rodean a las áreas boscosas. Los búhos urbanos usaron los espacios verdes remanentes (refugios) dentro del área de la ciudad para cazar pequeños mamíferos. *Asio otus* utiliza nidos hechos por otras especies y pueden beneficiarse en los ambientes urbanos de un aumento de los nidos debido a la colonización relativamente reciente de las áreas urbanas por parte de *Pica pica* y de sitios de cacería adecuados dentro de la ciudad.

INTRODUCTION

The Long-eared Owl (*Asio otus*) is a widespread holarctic predator that, in Europe, prefers open farmland habitats (Cramp and Simmons 1985) and feeds mainly on small rodents (reviewed by Marti 1977, Birrer 2009). Like other some raptors (Peške 1995, Riegert 2011), the Long-eared Owl has colonized some European cities (Kuźniak 1996, Fuchs et al. 2002, Lövy 2005). In urban environments, however, there are fewer small rodents (Čiháková and Frynta 1996), despite the increased possibilities for nesting and a lack of predators (e. g., the Eurasian Eagle-Owl, *Bubo bubo*).

Until recently, densities of Long-eared Owls breeding in urban areas have remained relatively low. Long-eared Owls began to colonize cities during the last two decades (Kuźniak 1996, Fuchs et al. 2002, Busche 2003, Lövy 2005). Colonization was probably conditioned by the availability of a sufficient number of nests of the Common Magpie (*Pica pica*); the magpie invaded central European cities during the 1980s (Birkhead 1991). In České Budějovice, Long-eared Owls breed in

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old corvid nests, predominantly those of the magpie. The density of breeding birds there (0.3–0.5 pairs km^{-2}, Lövy 2005) is one of the highest reported for the species (cf. 0.01 pairs km^{-2}; Craig and Trost 1979, 0.14 pairs km^{-2}; Wijnandts 1984, 0.03–0.31 pairs km^{-2}; Tome 1997) and is still increasing (Lövy 2005 and unpubl. data).

The spatial ecology and land use of the Long-eared Owl have been studied intensively in farmland habitats (Wijnandts 1984, Craig et al. 1988, Galeotti et al. 1997, Aschwanden et al. 2005). Studies of urban populations have focused on the diet during the winter, when large numbers roost in cemeteries, parks, and orchards (Pirovano et al. 2000, Milchev et al. 2003). In our study area, Riegert et al. (2009) found that the proportion of microtine rodents in a Long-eared Owls' diet increases with the distance of the nest from the city center. This trend probably indicates the owl's different ecological and behavioral responses to the degree of urbanization. Thus a telemetry investigation of the Long-eared Owl in urban environments may reveal novel aspects of its ecology.

To examine the Long-eared Owl's spatial ecology and land use in a predominantly urban area, České Budějovice (Czech Republic), we used radio telemetry on a subset of known breeding pairs to assess (1) size of the home range with respect to the position of the nest in the urbanized area, (2) overlap of home ranges, and (3) land use of radio-tagged Long-eared Owls.

METHODS

STUDY AREA AND LONG-EARED OWL POPULATION

Our study in the city of České Budějovice (Southern Bohemia; 49° N, 14° E; 40 km^2; 100 000 inhabitants; 250–300 m above sea level) encompassed three breeding seasons (2004–2006). The study area covers 154 km^2 and consists of developed area (51%), fields (17%), meadows (12%), wooded areas (7%), orchards (4%), lawns (4%), abandoned areas (2%), and water (4%). The proportion of habitats did not change markedly from year to year. To quantify opportunities for Long-eared Owl nesting, we counted the active magpie nests in two of the quarters around the city's periphery in 2003 (Fig. 1). To describe the degree of urbanization around each magpie nest and also at all Long-eared Owl nests from 2004 to 2006, we defined a radius of 0.5 km (surface area 79 ha) around each, an area corresponding to the maximum core home range of Long-eared Owls in the study area (see Results). On the basis of the proportion of developed area in these circles, we classified nests as either urban (>50% of area developed) or suburban (<50% developed).

At the beginning of each breeding season (first half of March), to locate the owls, we simulated a territorial intrusion by broadcasting a male's territorial call at 350 points throughout the city. We visited sites with positive responses regularly through the breeding season and used only sites where the birds bred successfully for further research.

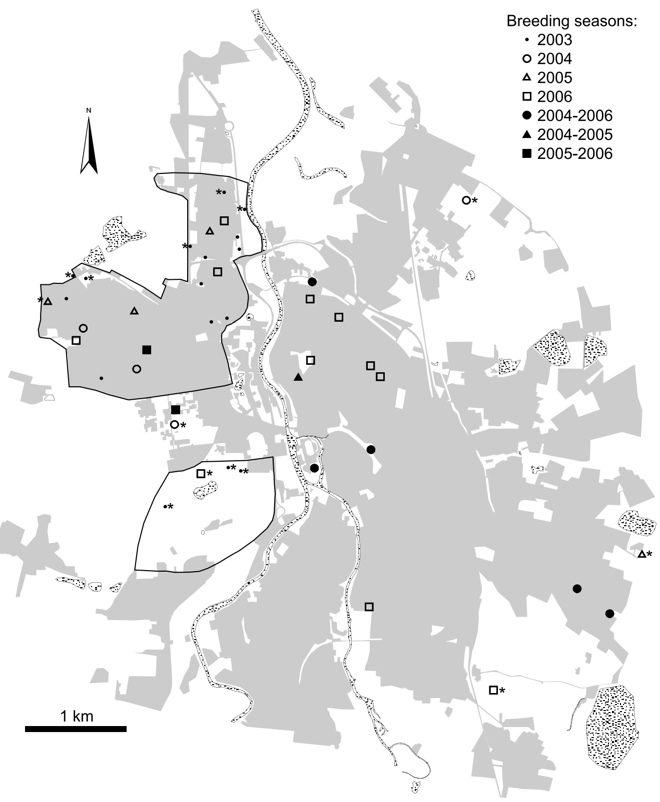

FIGURE 1. Nest sites of the Long-eared Owls and Common Magpie (small dots, magpie nests; black line, area where magpie nests were counted; remaining symbols, nests of the Long-eared Owl; sites marked with an asterisk are suburban; those without an asterisk are urban; filled symbols denote repeated nesting in successive years).

FIELD DATA ON SPATIAL ACTIVITY

Using a stuffed Eagle Owl as a decoy, we captured nine Long-eared Owls (four pairs and one adult male, Table 1) in mist nets (mesh 50 mm) in the vicinity of their nests. We equipped the birds with transmitters (backpack type, 4.5 g, Biotrack UK Ltd.). The weight of the transmitters was <5% of the body weight of the smallest individual captured, and we observed no side effects of the transmitters. Pairs of radio-tracked Long-eared Owls raised on average 3 ± 1 juveniles, a rate of success similar to that across Europe (Cramp and Simmons 1985).

To locate the birds in the field, we used a three-tailed Yagi antenna and a wide-band Icom R20 receiver (Icom America, Inc.). All telemetry surveys took place when the adults were feeding the offspring and both males and females participated in hunting. The survey continued until all juveniles had left the nest, on rainless nights between 19:00 and 01:00. The city's street-lighting system enabled us to precisely locate and follow the owls visually from a distance of up to 100 m. We tracked the pairs cyclically, monitoring only one pair during each night of telemetry. Each individual owl was monitored for a mean of 10 ± 2 nights, totaling 93 nightly sessions of

TABLE 1. Size of home ranges (ha) of Long-eared Owls in České Budějovice, Czech Republic (m, male; f, female; K, B, P, M, and V denote particular nest sites).

Individual	Weight (g)	Period of radio tracking	Degree of urbanization	Developed area (%)	Fixes (*n*)	MCP 95% (ha)	MCP 50% (ha)	Kernel 95% (ha)	Kernel 50% (ha)
K-f	278	25 May–10 Jun 2004	suburban	22	53	23.5	3.7	31.9	3.1
K-m	228	25 May–10 Jun 2004	suburban	5	63	67.2	12.1	76.1	8.7
B-f	268	14 May–16 Jun 2005	urban	25	93	560.8	68.3	491.8	84.6
B-m	232	14 May–16 Jun 2005	urban	40	95	887.6	52.3	545.6	74.1
P-f	>300	15 May–12 Jun 2005	urban	53	79	559.4	28.7	347.0	56.8
P-m	234	15 May–12 Jun 2005	urban	49	96	596.4	35.8	398.4	59.9
M-f	340	1–28 May 2006	suburban	7	44	33.6	4.5	31.1	3.8
M-m	233	1–28 May 2006	suburban	8	150	171.3	26.0	83.7	14.5
V-m	265	30 Apr–24 May 2006	urban	30	193	179.4	23.4	102.5	6.7

radio telemetry. Within a pair, we tracked the male and female successively, one during the first half and the other during the second half of the night of telemetry, then reversed the order during the next session.

ANALYSIS OF SPATIAL ACTIVITY AND LAND USE

We defined a complete home range as the 95% minimum convex polygon (MCP) based on all relocations of the individual tracked. For a more precise assessment of a home range, we used a kernel-density estimator (95% and 50% KDE). For all home-range analyses we used ArcView 3.2 with the extension Animal Movement (Hooge and Eichenlaub 2000). Criteria for estimating home-range size were as follows: kernel—bivariate normal; bandwidth selection—least-square cross-validation method (Silverman 1986). In order to determine the number of radio fixes required for estimation of a home range's size, we calculated its asymptotes with the plug-in HoRAE (Steiniger and Hunter 2012) for OpenJUMP GIS software. In this analysis, we calculated home ranges as the number of locations increased. The home ranges of three owls approached an asymptote at about 20 radio fixes, but one of them increased again at 30 radio fixes. The remaining six home ranges did not approach an asymptote. To assess overlap of home ranges, we used those estimated by the kernel method because these allowed an examination of the space an individual used more precisely than did those estimated by the MCP method.

The study area was defined as a circle with a radius of 7 km around the city center, covering the home ranges of all radio-tracked individuals. For the purposes of the habitat assessment, we divided the study area into eight vegetation types (developed area, orchards, lawns (mowed regularly), meadows, fields, abandoned areas, wooded areas, and water). We identified vegetation types on orthophoto maps and through our own investigation of the area in the field. For all land-use analyses, we used 95% kernel home ranges. We used a compositional analysis (Aebischer et al. 1993) to test vegetation-type preferences at two scales: (1) composition of vegetation types within a home range versus habitat availability in the total study area and (2) the proportion of a vegetation type used, based on the number of radio locations, versus its actual proportion within a home range. For further analyses, we categorized the undeveloped parts of each home range as either wooded (with full-grown trees) or open vegetation. To assess preferences for edge habitats (open habitat bordered with forests or shrubs), we randomly selected a number of control locations within a Long-eared Owl's home range the same as the number of real radio-telemetry fixes in edge habitats.

STATISTICAL ANALYSES

To compare home-range sizes by method and urban versus suburban we used the Mann–Whitney *U*-test in Statistica 9 (StatSoft, Inc. 2010). For the compositional analysis of habitat selection we used the statistical software R (R Development Core Team 2009) with the package adehabitatHR (Calenge 2006). We used a randomization test with 500 repetitions. For habitat not found in a particular home range (values in entry data matrix of zero) we substituted 0.01 (see Aebischer et al. 1993). We considered values of $P < 0.05$ statistically significant. Throughout the text, means ± SD are presented.

RESULTS

URBAN LONG-EARED OWL POPULATION

Over the three years of the study the number of Long-eared Owl nests increased (Fig. 1; 2004—10, 2005—12, 2006—18). While the number of recorded suburban nests remained stable through the study period, the number of urban nests increased from eight in 2004 to 16 in 2006. The nine individuals monitored represented five pairs (Table 1): pairs P, B, and male V were classified as urban owls, pairs K and M as suburban.

HOME-RANGE SIZE

In total, we recorded 866 radio fixes from nine adult Long-eared Owls (Table 1). The home ranges of urban owls were significantly larger than those of suburban ones (95% kernels: 446 ha and 56 ha, respectively; Mann–Whitney *U*-test: $U = 0$, $P = 0.02$, $n_u = 5$, $n_s = 4$). Similar, but only indicative, was the trend for the core home ranges represented by 50% kernels (69 and 8 ha, respectively; Mann–Whitney *U*-test: $U = 2$, $P = 0.066$, $n_u = 5$, $n_s = 4$).

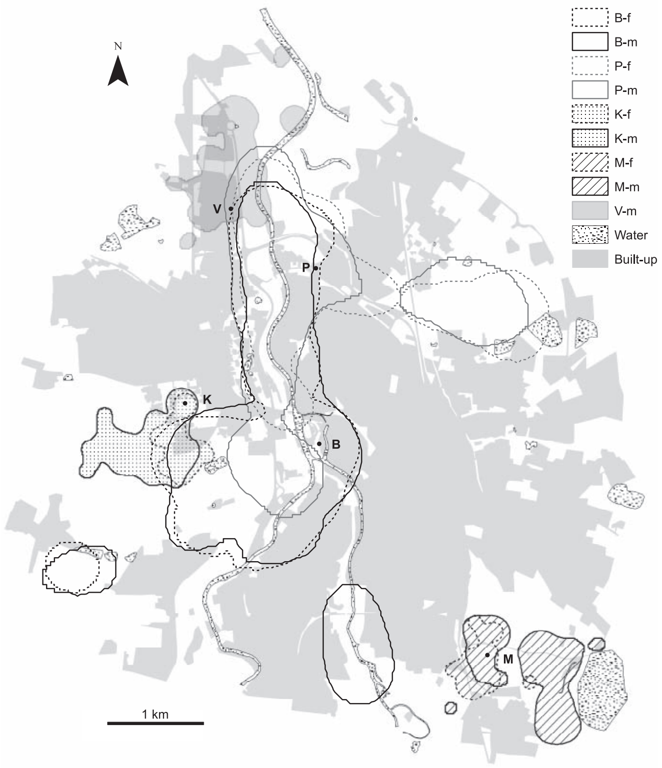

FIGURE 2. Home ranges of all radio-tracked Long-eared Owls (95% kernels). Black dots represent nest sites K, B, P, M, and V.

A smaller home range distinguished the male from locality V from the remaining urban owls (Fig. 2). The mean size of a home range differed according to the method used (Table 1): 95% kernels were smaller (234 ± 209 ha) than those estimated by MCP (342 ± 313 ha), but the difference between the two methods of analysis was not significant (Mann–Whitney *U*-test: $U = 31$, $P = 0.43$, $n = 9$). In contrast, 50% kernels were somewhat larger (35 ± 34 ha) (but not significantly) than MCP ranges (28 ± 22 ha) (Mann–Whitney *U*-test: $U = 39$, $P = 0.93$, $n = 9$).

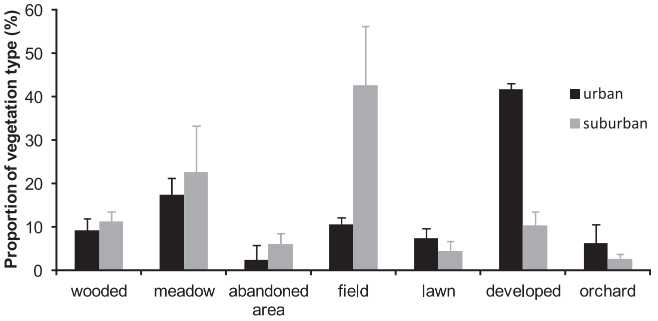

FIGURE 3. Differences in habitat composition (means ± SD) of home ranges of urban and suburban Long-eared Owls.

HOME-RANGE OVERLAPS

Intra-pair comparisons showed that overlaps of 95% kernel home ranges were markedly greater within urban pairs (pair B: 84%; pair P: 74%) than within suburban pairs (pair K: 50%; pair M: 32%). The pattern applied also 50% kernel home ranges (pair B: 59%; pair P: 77% vs. pair K: 40%; pair M: 0%). Also, the home ranges of urban pairs B and P overlapped (46 ± 9% and 19 ± 23% for 95% and 50% kernels, respectively; Fig. 2).

VEGETATION COMPOSITION AND HOME RANGES AND LAND USE BY LONG-EARED OWLS

Over the whole study area Long-eared Owls established home ranges independently of vegetation type (compositional analysis 1: Wilk's $\Lambda = 0.03$, $P = 0.09$). The home ranges of urban owls had a markedly greater proportion of developed area, whereas the home ranges of suburban owls comprised mainly of fields, meadows, and abandoned areas (Fig. 3).

Long-eared Owls, however, showed a preference for some particular vegetation types within their home ranges (Table 2, compositional analysis 2: Wilk's $\Lambda = 0.04$, $P = 0.02$, rank of vegetation types: wooded areas > meadow > abandoned areas > field > lawn > building > orchard). Wooded areas were

TABLE 2. Composition of vegetation types in 95% kernel home ranges and the number of radio fixes within each vegetation type for Long-eared Owls radio-tracked (water is not included because it has been not used by owls; f, female; m, male; K, B, P, M, and V denote particular nest sites).

	Wooded areas		Meadow		Abandoned area		Field		Lawn		Developed area		Orchard	
Individual	Proportion (%)	Fixes (*n*)	Proportion (%)	Fixes (*n*)	Proportion (%)	Fixes (*n*)	Proportion (%)	Fixes (*n*)	Proportion (%)	Fixes (*n*)	Proportion (%)	Fixes (*n*)	Proportion (%)	Fixes (*n*)
K-f	12	11	26	18	5	2	38	18	6	1	12	2	2	1
K-m	11	13	13	4	5	1	59	42	3	1	7	0	2	2
B-f	12	23	14	37	1	4	12	6	9	21	42	2	5	0
B-m	12	24	14	45	1	1	12	5	9	17	41	3	5	1
P-f	6	15	17	36	1	2	10	10	7	10	42	5	11	0
P-m	10	12	19	54	1	6	8	7	9	10	39	3	10	3
M-f	14	15	15	3	5	1	46	23	2	0	14	1	3	1
M-m	9	14	36	104	10	10	26	20	6	0	8	2	4	0
V-m	7	41	23	60	9	26	11	14	4	7	43	44	0	0

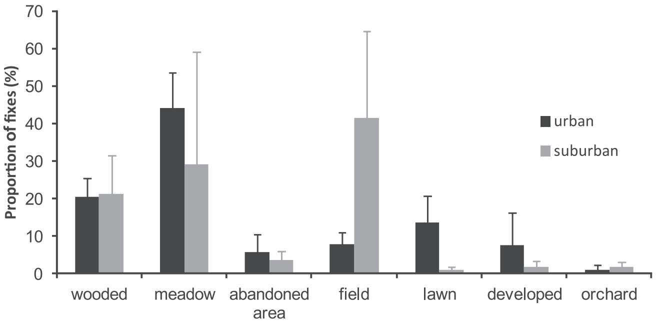

FIGURE 4. Proportion of radio fixes (means ± SD) in different habitats for urban and suburban Long-eared Owls.

the vegetation type most frequently used, by urban and suburban owls equally (Fig. 4). Of the open vegetation types, meadows were preferred primarily by urban owls, but fields were preferred by suburban owls. In general, owls tried to avoid vegetation types associated with human activities such as buildings and orchards. Also, we tested the effect of wooded habitat edge to assess whether owls preferred open vegetation types or only the parts of them that bordered wooded areas, finding a significant preference for edge habitats in six of nine individuals (Bf, Bm, Pf, Pm, Km, and Vm, in all cases $P < 0.01$; Mm, Mf and Kf, $P \geq 0.14$; for abbreviations see Table 1).

DISCUSSION

URBAN LONG-EARED OWL POPULATION

In our study area, urban environments appear to be of superior quality for raptors because of increased opportunities for nesting. Unlike other urban raptors nesting mainly in anthropogenic sites (Cade and Bird 1990, Salvati et al. 2002, Rutz 2008, Riegert 2011), Long-eared Owls depend on the presence of unused nests, predominantly those built by magpies (Cramp and Simmons 1985). Magpies have adjusted their nesting behavior well in response to urbanization (Wang et al. 2008), and their population densities can thus be markedly higher in urbanized areas than in rural environments (Luniak et al. 1997, Jerzak 2001). In České Budějovice, the density of breeding urban and suburban magpies was similar at least within the surveyed part of the city (Fig. 1). However, we assume that the total number of nests available for owls was probably higher, especially in more urbanized areas closer to the city center, as in other European cities (cf. Luniak et al. 1997, Jerzak 2001).

Within the developed area of České Budějovice, the Long-eared Owl population grew in the course of the study, and it is still growing (unpubl. data). While the number of suburban territories remained stable over the years, the number of urban territories increased continuously (Fig. 1). Therefore, we suppose that Long-eared Owls may profit in urban environments from increased potential for nesting and consequently colonize this new ecosystem.

HOME-RANGE SIZE

The mean size of a home range of the Long-eared Owls we studied (342 ha) was smaller than those estimated by other authors (Wijnandts 1984: 2025 ha, Galeotti et al. 1997: 504 ha, Henrioux 2000: 980 ha). Nevertheless, home ranges change in size through the year and are smallest during the breeding season (Exo 1988, Génot and Wilhelm 1993, Zuberogoitia et al. 2007, but see Framis et al. 2011). For example, home ranges of the Long-eared Owl are extensive during the period of winter roosting (Wijnandts 1984, Galeotti 1997) and smaller during the breeding season (Craig et al. 1988, Henrioux 2000; this study). During the winter roosting period, however, Long-eared Owls use intensively only about 25% of large home ranges each night (Wijnandts 1984, Galeotti et al. 1997).

In comparison with other areas of Long-eared Owl use estimated during the breeding season, those we studied were intermediate (Craig et al. 1988: 297 ha, Henrioux 2000: 585 ha, this study: 342 ha). Our tracking owls for only the first half of the night could have affected this result. However, Henrioux (2000) showed that during the breeding season Long-eared Owls are most active from 20:00 to 01:00. Thus we consider our method relevant for describing the spatial activity of Long-eared Owls.

Home ranges of urban owls were much larger than those of suburban ones. Urban territories were probably enlarged by a high proportion of unused developed areas. Riegert et al. (2007) found that the pattern for the Common Kestrel in our study area was similar, and Henrioux (2000) also documented a positive relationship between home-range size and proportion of developed area in farmland. Furthermore, both sexes of urban Long-eared Owl pairs used areas of similar size, but suburban males had home ranges distinctly larger than those of females. The latter is in accordance with findings in farmland (Galeotti et al. 1997, Henrioux 2000, Craig et al. 1988). Unlike males, female owls hunt within a smaller radius around the nest during incubation (Sunde et al. 2009) and during the first two weeks after hatching, when the nestlings are not able to maintain their body temperature (Craig et al. 1988). The size of a home range also depends on food resources (Krebs and Davies 1981, Kenward 1982, Village 1982). Unfortunately, we have no data on prey availability. However, the difference in vegetation composition between urban and suburban environments may affect the availability of small mammals (Mahan and O'Connell 2005). We suspect that the difference between urban and suburban owls in size of each sex's home range may be caused by differences in the availability of suitable hunting grounds, which are sparsely distributed within urbanized areas (Čiháková and Frynta 1996). This is probably the reason for the similar size of home ranges of males and females breeding in more urbanized areas.

LAND USE BY LONG-EARED OWLS

Long-eared Owls established their home ranges within the study area randomly, i.e., the vegetational composition of home ranges and of the study area as a whole were similar. Moreover, all nests were placed in coniferous trees, as Tome (2003) also found. These results imply that nest-site selection is driven primarily by the presence of suitable trees with magpie nests, independent of habitat composition within the area. The great importance of presence of suitable nest sites has also been documented in the Tawny Owls (*Strix aluco*), which to establish breeding territories within urbanized areas requires small woods (Ranazzi et al. 2000).

We observed that Long-eared Owls preferred some vegetation types for hunting and avoided others. Wooded areas, meadows, and abandoned areas were visited most frequently, but areas with increased human activity (gardens, developed areas, lawns) were avoided. These results are consistent with those of Galeotti et al. (1997) and Henrioux (2000). As expected, urban territories had a greater proportion of developed area than did suburban territories. These areas may have been avoided primarily because of difficult access to prey or lack of prey.

Aschwanden et al. (2005) showed that vegetation structure is more important for selection of a hunting ground than is prey abundance. They reported that Long-eared Owls preferred freshly mown meadows and artificial grasslands even their density of voles is 8 times lower. However, these vegetation types bordered strips of herbaceous wildflowers that are associated with a high abundance of small mammals (i.e., refugia) from which they can migrate to adjacent areas (Aschwanden et al. 2005, Briner et al. 2005, Suchomel and Heroldová 2006). In the urban environment we studied, these refugia are represented by strips of herbaceous wildflowers, river banks, flood basins, power-line openings, and road and railway verges. In agreement, six of nine Long-eared Owls (including all of the urban owls) in České Budějovice preferred edge habitats that probably represented refugia for prey. However, the presence of open vegetation types such as meadows and fields bordering those refugia is important, because such habitats allow the owls the use of low scanning flight, the Long-eared Owl's most common hunting technique (Cramp and Simmons 1985). Our findings are in accordance with this assumption since urban owls preferred meadows whereas suburban owls preferred fields, i.e., the most common open habitats in urban and suburban areas, respectively.

HOME-RANGE OVERLAP

We recorded considerable overlap in the home ranges of urban pairs, contrasting with only a small overlap in the home ranges of suburban pairs (for 95% kernel HRs: 79 ± 7% and 41 ± 13%, respectively). Extensive overlap of the sexes' home ranges has been recorded in the Long-eared Owl (Wijnandts 1984, Galeotti et al. 1997) and Little Owl (*Athene noctua*; Zuberogoitia et al. 2007) during the winter. Thus such great overlap may suggest a lack of territorial behavior (Wijnandts 1984, Galeotti et al. 1997) during the period of the year when owls do not defend their nests. Alternatively, it may be explained by the specific distribution of food during the winter (Adams 2001). During the breeding season, owls defend small areas around their nests (Cramp and Simmons 1985, Taylor 1994), and pairs share a core area around the nest site (Craig et al. 1988). Our results agreed with these findings, because within a pair the sexes shared just the core of their home ranges. Males and females of suburban pairs often hunt in different directions from the nest, as reported by Craig et al. (1988). This strategy probably serves to maximize the foraging effort of the pair as a unit.

Compared to those in farmland, urban Long-eared Owls face a low availability of voles (Čiháková and Frynta 1996), and they have to rely mainly on the previously mentioned refugia associated with ecotones. Dickman and Doncaster (1987) showed that such refugia within urbanized areas offer dense populations of small mammals, possibly even higher than in natural environments. Because these refugia are limited within the city, owls are probably forced to exploit them together. We documented this behavior in two urban pairs, which shared a high proportion of their hunting area.

In conclusion, results of our study provide insight into the spatial ecology and land use of Long-eared Owls in a predominantly urban area over multiple breeding seasons. Accordingly, we assumed that both nesting potential and selection of suitable hunting grounds are important factors enabling Long-eared Owls to flourish in urban environments. With respect to directions for future research, we suggest that it would be of interest to clarify raptors' use of habitat networks in urban environments generally, i.e., how fragmentation and/or connectivity of focal habitats influence patterns of the birds' movement.

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Příloha XIII

Zárybnická M, Riegert J, Šťastný K. 2015:

Non-native spruce plantations represent a suitable habitat for Tengmalm's Owl (*Aegolius funereus*) in the Czech Republic, Central Europe

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ORIGINAL ARTICLE

Non-native spruce plantations represent a suitable habitat for Tengmalm's Owl (*Aegolius funereus*) in the Czech Republic, Central Europe

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Abstract Anthropogenic activity can lead to deforestation and subsequent dramatic impacts on forest-dwelling animal species. In this study, we investigated the habitat use of a forest raptor (Tengmalm's Owl *Aegolius funereus*) in an air-polluted area of the Ore Mountains (Czech Republic) that has been restored by non-native spruce. Based on a 14-year Tengmalm's Owl nest-box breeding dataset, we found that the percentage of native Norway Spruce forest was higher for occupied nest boxes than for unoccupied ones within close surroundings of the nest (buffer radius of 25 m). Meanwhile, the percentage of non-native Blue Spruce (originally from Northern America) was higher for occupied nest boxes than for unoccupied ones within the home-range breeding area (buffer radius of 750 m). Moreover, the surroundings of non-predated nests (radius of 750 m) showed a higher percentage of Blue Spruce and a lower percentage of deciduous trees than surroundings of nests predated by Pine Martens. Although small mammal availability was not affected by habitat categories, we found a positive correlation between the percentage of *Apodemus* mice in the diet of owls and the percentages of both Blue Spruce and open forest area within the foraging area radius (750 m). We suggest that adult owls and young fledglings use remnants of tall, old-growth Norway Spruce forests as a safe refuge against avian predators, while secondary stands of non-native Blue Spruce are suitable for hunting both main prey types (*Apodemus* mice and *Microtus* voles), and also ensure good protection against nest predation by Pine Martens.

Keywords *Aegolius funereus* · Habitat use · Air pollution · Non-native habitat · Reproductive success · Nest predation · *Martes martes*

Zusammenfassung

Plantagen nicht-heimischer Fichten sind geeigneter Lebensraum für den Rauhfußkauz (*Aegolius funereus*) in der Tschechischen Republik, Zentraleuropa

'Entwaldung durch menschliches Einwirken kann schwerwiegende Auswirkungen auf waldlebende Tierarten haben. In dieser Studie untersuchten wir die Raumnutzung eines waldlebenden Beutegreifers (Rauhfußkauz *Aegolius funereus*) in einem luftverschmutzten Gebiet des Erzgebirges (Tschechien), das durch nicht-heimische Fichten aufgeforstet wurde. Anhand eines 14 Jahre umfassenden Datensatzes von in Nistkästen brütenden Raufußkäuzen, fanden wir bei bewohnten Nistkästen einen höheren Anteil der einheimischen Gemeinen Fichte im direkten Umfeld des Nestes (Pufferradius: 25 m) als bei unbewohnten. Der Anteil der nicht-heimischen Stech-Fichte (ursprünglich aus Nordamerika stammend) war hingegen im gesamten Aktionsraum (Pufferradius: 750 m) um bewohnte Nistkästen höher als um unbewohnte. Des Weiteren waren im Umfeld um nicht geräuberte Nester (Radius: 750 m) ein größerer Anteil Stech-Fichten und ein geringerer Anteil Laubbäume zu verzeichnen, als im Umfeld von Nestern, die von

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Baummardern geräubert wurden. Obwohl die Baumzusammensetzung keinen Einfluss auf die Verfügbarkeit von kleinen Säugetieren hatte, stellten wir einen positiven Zusammenhang zwischen dem Anteil an Waldmäusen im Nahrungsspektrum der Käuze und dem Anteil an Stech-Fichten sowie offenen Waldgebieten im Aktionsraum (750 m) fest. Wir nehmen an, dass erwachsene Käuze und junge Flügglinge die Überreste großgewachsener Altbestände Gemeiner Fichten als sicheren Rückzugsort vor größeren Beutegreifern nutzen, während neuere Bestände nicht-heimischer Stech-Fichten als gutes Jagdrevier für ihre beiden häufigsten Beutegruppen (Waldmäuse und Feldmäuse) und auch als Schutz gegen Nesträuber wie den Baummarder dienen.

Introduction

Landscape changes and habitat fragmentation are the most important threats to the global biodiversity of several taxonomic groups (Sala et al. 2000; Foley et al. 2005). These processes are of special interest to conservation biologists (Haila 2002; Fazey et al. 2005) due to the increasing need to investigate the impact of anthropogenic changes on habitat quality and the viability of natural populations (Hanski and Gilpin 1997). Good examples are species inhabiting old-growth forests: where this habitat type is in decline as a result of anthropogenic activity, habitat specialist bird populations are decreasing while populations of generalists are increasing (Esseen et al. 1997; Bunnell 1999).

At present, changes in the biogeochemistry of terrestrial ecosystems are primarily associated with three major factors: land-use, climate change, and chemical atmospheric deposition (Norton and Veselý 2004). The latter is closely associated with emissions of pollutants into the atmosphere and transboundary transportation of those pollutants (Thunberg and Hanneberg 1993), especially in mountainous and remote areas. During the 1980s, the Czech Republic was a significant Central European source of sulfur and nitrogen oxides emitted from point sources, most of which were situated in the so-called “Black Triangle” (Germany–Poland–Czech Republic border), known for its large coal resources and numerous power plants (Kopáček and Veselý 2005). Due to the emissions in this region, soils became acidified, which led to deforestation and dramatic impacts on animal communities (Šťastný and Bejček 1999; Flousek 2000). The resultant landscape mosaic is composed mainly of clear-cut areas, remnants of old-growth Norway Spruce (*Picea abies*) forest, and young stands of native (e.g., Birch *Betula* spp., European Mountain Ash *Sorbus aucuparia*, Norway Spruce) and non-native (mainly Blue Spruce *Picea pungens*, originally found in Northern America; Špulák 2009) tree species.

Young forest habitats of areas damaged by air pollution have been found to be suitable for Tengmalm’s Owl—a threatened nocturnal predator (see the Czech Directive 395/1992 and the Council Directive 79/409/EHS) with a wide Holarctic breeding range. This suitability is probably due to higher food availability and the absence of most avian predators (mainly Northern Goshawk *Accipiter gentilis* and Tawny Owl *Strix aluco*; Drdáková-Zárybnická 2004) from such areas. Tengmalm’s Owl primarily nests in natural tree cavities, but also readily accepts nest boxes (Korpimäki and Hakkarainen 2012). The breeding female incubates eggs and broods, and the male provides nearly all the food for the female and the young (Zárybnická 2009a, b). Tengmalm’s Owl is a sit-and-wait generalist predator (Bye et al. 1992), feeding mainly on small mammals (especially Microtinae voles) and birds (Korpimäki and Hakkarainen 2012). In Northern Europe, it inhabits boreal coniferous forests with low tree species diversity, dominated by Norway Spruce and Scots Pine (*Pinus sylvestris*) (Korpimäki and Hakkarainen 2012). In Central Europe, the main breeding habitats of this owl are coniferous, mainly Norway Spruce-dominated forests at high elevations and mixed forests of mainly Norway Spruce and European Beech (*Fagus sylvatica*) or pure beech stands at lower elevations (Schwerdtfeger 1984; Schelper 1989; Šťastný et al. 2006).

In the study reported in the present paper, we investigated the habitat use of Tengmalm’s Owl in air-polluted areas of the Ore Mountains, Czech Republic. We analyzed a 14-year time series on breeding habitats, diet composition, reproductive success, and the probability of nest predation by Pine Marten (*Martes martes*). In particular, we aimed to answer the following questions. (1) Does Tengmalm’s Owl use a particular habitat within a buffer zone of radius 750 m more frequently than expected (i.e., foraging area selection)? (2) Does Tengmalm’s Owl use a particular habitat within a buffer zone of radius 25 m more frequently than expected (i.e., nest site selection)? We also evaluated the relationships between habitat composition and (3) small mammal availability, (4) diet composition, (5) nest-predation probability, and (6) reproductive success (expressed as the number of fledglings).

Methods

Study area

The study was conducted in the north of the Czech Republic (50°N, 13°E), on the Ore Mountain plateau (elevation: 730–960 m a.s.l.; area: 70 km^2) from 1999 to

Table 1 Percentages of habitat categories within radii of 25 and 750 m around the nest boxes ($n = 229$ nest box sites, including overlaps), and percentages of individual habitat categories grouped according to tree height

Habitat category	Radius 750 m ± SD (%)	Height of growth until 5 m (%)	Radius 25 m ± SD (%)	Height of growth until 5 m (%)
Norway Spruce	32.6 ± 12.4	24.0	49.6 ± 32.0	14.0
Blue Spruce	26.3 ± 13.6	47.2	18.0 ± 25.1	41.2
Other coniferous trees	11.0 ± 9.7	66.3	7.5 ± 14.8	51.0
Other deciduous trees	13.1 ± 8.5	20.6	10.6 ± 17.5	43.8
European Beech	2.6 ± 4.6	12.1	3.4 ± 12.6	9.1
Open forest	10.0 ± 7.1		3.2 ± 10.3	
Other areas	4.4 ± 7.4		7.7 ± 11.8	
Total (%)	100		100	
Total (ha)	40,264		44.7	

2012. During the second half of the twentieth century, emissions from factories located in the foothills caused the destruction of the forest environment, and was followed by intensive logging of dead trees (Kopáček and Veselý 2005). The consequent restoration process was hindered by the high acidity of the soil, harsh mountain weather, and extensive damage to young plantations, caused mainly by cervids (Kula and Rybář 1998; Hruška et al. 1999). Today, the study site is characterized by a mosaic of open areas (formed mainly by clear-cutting and creating pasture patches for cervids), fragments of young secondary forests (i.e., the forest habitat which has regrown after a major disturbance; Tabarelli et al. 2012), and small patches of tall old-growth Norway Spruce forests. The vegetation of the open areas is dominated by Wood Reeds (*Calamagrostis villosa*). Secondary stands are dominated by non-native Blue Spruce, which shows a strong tolerance of atmospheric pollution, adverse climatic conditions, and damage caused by game species (Špulák 2009). In contrast to Norway Spruce, Blue Spruce typically does not form forest habitat (Podrázský 1997). Blue Spruce trees occur scattered in open habitats, they do not reach the height of Norway Spruce (50 % of Blue Spruce stands reach no more than 5 m in height; Table 1), and their branches reach the ground (Fig. 1a, b). In our study site, the seedlings of Blue Spruce were hand-planted, usually in a 2 × 2 m span (A. Kilb, in verb.). Other tree species besides Blue Spruce were also used during restoration—mainly birch, European Mountain Ash, and European Larch (*Larix decidua*). Norway Spruce was also planted, but more than 70 % of Norway Spruce stands are made up of old-growth trees (Table 1). These stands are chiefly concentrated in small patches (up to 1 ha) scattered within the study area. Only the northern part of the area is characterized by compact old-growth forest patches of Norway Spruce (ca 15 % of the whole area). In addition, old-growth and solitary European Beech trees occur rarely within the study area (Table 1), and there is only one forest patch of European Beech (ca 1 ha).

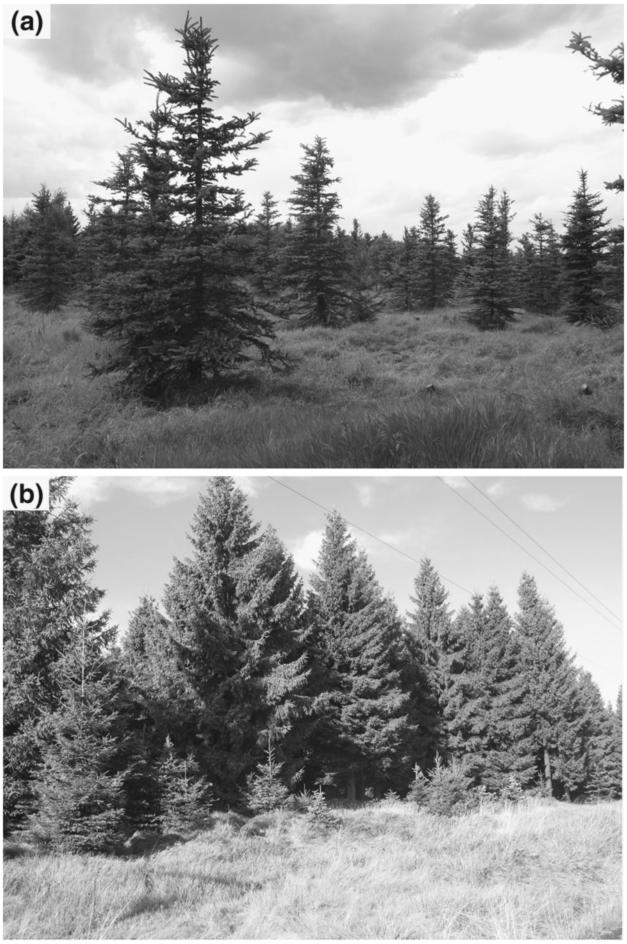


Fig. 1 Examples of **a** a secondary stand of non-native Blue Spruce (a 20-year-old stand) used by Tengmalm's owl as a hunting habitat, and **b** a stand of native Norway Spruce (a 50-year-old stand) used for resting during the day in the Ore Mountains, Czech Republic

Tengmalm's Owl population

In the study area, Tengmalm's Owl breeds primarily in nest boxes (>90 % nests), as natural cavities can only be found in rare solitary beech trees. The population reaches 10–26 breeding pairs per 70 km^2 each year (mean ± SD:

Table 2 Numbers of nests found, nests predated by martens, successful nests (i.e., at least one young fledged), nests with known reproductive success, and nests with known diet composition in each year of the 1999–2012 study period

Year	No. of nest boxes	No. of nests	No. of nests predated by martens	No. of successful nests	No. of nests with known number of fledglings	No. of nests with known diet composition
1999	100	10	1	7	0	9
2000	100	10	5	4	4	5
2001	100	22	10	9	7	12
2002	100	26	3	16	16	18
2003	100	14	4	4	4	7
2004	120	15	1	9	9	9
2005	119	20	7	8	8	8
2006	116	24	3	15	15	18
2007	131	11	1	8	8	9
2008	132	14	4	7	7	7
2009	164	17	5	8	8	8
2010	166	13	3	8	8	11
2011	167	25	11	9	9	0
2012	158	13	2	7	7	0
Sum	1,773	234	60	119	110	121
mean	126.6	16.7	4.3	8.5	8.5	10.1
SD	26.8	5.6	3.1	3.4	3.5	4.1

16.7 ± 5.6; Table 2), which is above average within the Czech Republic (Drdáková-Zárybnická 2004; Šťastný et al. 2006). The number of deployed nest boxes varied yearly between 100 and 167 (mean ± SD: 126.6 ± 26.8; Table 2), and were evenly distributed within the study area. The boxes were usually placed at the edges of forest patches. All nest boxes were kept in good condition (they were regularly repaired). and their entrances and close surroundings were kept free of branches. The bottom of each nest box was square-shaped, with an inner width of between 20 and 22 cm, a height of 40 cm, and an 8-cm diameter entrance. They were usually installed 3–5 m above the ground.

Reproductive parameters

Basic breeding data were collected by inspecting all nest boxes during the onset of the breeding season (Zárybnická et al. 2012). From 1999 to 2012, a total of 234 breeding attempts by Tengmalm's Owls were recorded, of which 119 were successful (i.e., at least one fledgling was produced), and the number of fledglings in each of 110 nest boxes was determined (Table 2). A total of 60 nests were predated by martens. Marten predation was identified via the signs left behind in the nests: scat, hairs, broken eggshell remains (either inside or near the nest box), and killed or absent nestlings (smaller nestlings usually disappeared all at once; larger nestlings were typically killed by neck strangulation).

Pellet analyses

The diet composition during 1999–2010 was analyzed for 121 nesting attempts (103 successful nesting attempts and 18 failed nesting attempts or abandoned nests; Table 2). Prey pellets and food remains were collected during the period when the most chicks were present in the nest box (from late April to the end of July) during regular nest visits (Zárybnická et al. 2013). In total, 8,537 prey items were determined (mean ± SD: 70.7 ± 31.5 items per nest box), of which 8,233 were small mammals and 304 were birds. The majority of small mammals were determined to species level (63.2 %), and the remainder to genus level (*Apodemus* or *Microtus*). Of the birds, 262 individuals (86.2 %) were determined to species or genus level. To allow further analyses, we divided the prey items into four groups: *Microtus* voles (Field Vole *M. agrestis*, Common Vole *M. arvalis*, European Pine Vole *M. subterraneus*, and *Microtus* spp.), *Apodemus* mice (*Apodemus* spp.), *Sorex* shrews (Common Shrew *Sorex araneus*, and Pygmy Shrew *S. minutus*), and birds. Other, more scarce, species were not included in the analyses (for details see Zárybnická et al. 2013).

Small mammal availability

To facilitate habitat-use analysis we assessed the abundances of small mammals during 1999–2012 using the snap-trap capture method in three 1-ha areas (100 × 100 m squares with a 10 m spacing; $n = 121$ traps per square). Trapping areas were situated in the core of the study area in young secondary forests. Trapping was carried out each year at the start of June. The traps were left out for three nights and checked daily in the morning. We calculated the number of captured individuals per 100 trap nights each year. All captured mammals ($n = 327$) were identified to species level and grouped into three small mammal categories: *Microtus* voles, *Apodemus* mice, and *Sorex* shrews. Although *Myodes* voles were present among the captured individuals ($n = 99$), they formed only 3 % of the diet of Tengmalm's Owl (Zárybnická et al. 2013). Therefore, we did not include *Myode*s voles in the analyses.

To enable comparisons of food availability in different habitats, we used data from four lines (100 traps per line; 5 m span) in the period 2002–2012. Trapping lines were deployed in different habitats, which included forest clearings, young stands of Blue Spruce, other coniferous and deciduous trees, and small patches of old-growth Norway Spruce forest. Captures were conducted during spring (early June) and autumn (early October). The traps were left out for three nights and checked daily in the morning. The percentage of habitat categories for each line was evaluated within a buffer zone of radius 25 m using GIS. In the spring captures, 227 individuals were caught and identified to species level; in the autumn captures, the number was 381.

Landscape data analyses

Habitat composition was quantified within radii of 25 m and 750 m around each nest box (totaling 1,773 boxes during 1999–2012 across 229 individual sites; Table 2). A radius of 25 m represented local habitat use of nest sites, while the 750-m radius (177 ha) approximately represented the size of the breeding home range of Tengmalm's Owl males in the study area (90 % kernel density estimation = 187 ha, $n = 10$ males; Kouba 2009). We also recorded the number of other buffers overlapping with the particular nest box buffer.

The habitat categories for both the 25-m and 750-m radius buffer zones were quantified using GIS. The vegetation maps used were originally developed for the purposes of the Forestry Institute in 2008, and cover 79.2 % of the study area. We mapped the remaining forest-free areas (20.8 %) using Google Earth (habitat mapping layer: Czech Republic). For analyses, the habitat of the study area was divided into the following categories: (1) Norway Spruce; (2) Blue Spruce; (3) other coniferous trees; (4) other deciduous trees; (5) European Beech; (6) open forest (dominated mainly by clearings but also including pasture patches for cervids, wetlands, grazed lands, and meadows); and (7) other areas (water surfaces and built-up areas) that do not impact on the occurrence of Tengmalm's Owl.

Statistical analyses

Firstly, we performed compositional analysis of habitats for real and randomly generated nest boxes (R Development Core Team 2011, R version 3.0.2 2013) using the command "compana." This analysis was carried out in two steps. First, the significance of habitat use was tested (using a Wilks lambda). Then a ranking matrix was built, indicating whether the habitat category in the rows is used significantly more or less than the habitat type in the columns (Aebischer et al. 1993). This analysis was performed for both buffer radii. Data on the relationship between habitat characteristics (percentage area of each habitat category within a buffer zone; response variable) and the probability of nest box use (0/1), the probability of nest box predation (0/1), diet composition (% by number), and reproductive success (number of fledglings) (explanatory variables) were analyzed using redundancy analysis (RDA) in the Canoco (version 5.0) software (ter Braak and Šmilauer 2012) to avoid autocorrelations among habitat percentages. Using this method allowed us to test the influences of both binary and continuous explanatory variables using multivariate data on habitat characteristics (Lepš and Šmilauer 2003). Percentages of areas for habitat categories were log transformed, as well as covariates with continuous distributions. The use of covariates is specified in Table 3; the covariate "buffer nest overlap" was expressed as the number of overlapping buffers for a particular nest box. Monte Carlo permutation tests with 499 permutations were used to determine the significance of each explanatory variable using forward selection. Instead of using small mammal availability directly (Fig. 2), we used year as a covariate to avoid pseudoreplications. All of the abovementioned analyses were performed for both the 25-m and 750-m radius buffer zones. Partial analyses of the relations between each habitat category and tested factors were performed using Mann–Whitney *U* tests or multiple regressions in Statistica version 9.0 (StatSoft Inc 2010). The relationships between small mammal availability as an explanatory variable (obtained by line trapping) and habitat categories as response variables were analyzed using RDA. This analysis was only performed for the 25-m radius buffer zones. Percentages were log transformed. We only present significant results in the present work.

Results

Habitat use

Compositional analyses of both buffer zone sizes showed significant differences in habitat categories from the surroundings of randomly generated nest boxes. Within a buffer

Table 3 Relationships between habitat categories (response variables) and nest box occupancy, nest predation by martens, and the diet composition of the owls

Topic	Buffer radius	No. of year–nest boxes	Year	Nest box ID	Buffer–nest overlap	Prey number	I and II axes	Explanatory variable	*F*	*p*
Habitat use	25	1,773	[a]	[a]			30.70	Nesting (0/1)	4.49	0.0040
Habitat use	750	1,773	[a]	[a]	[a]		39.60	Nesting (0/1)	13.11	0.0020
Predation	750	234	[a]	[a]	[a]		67.22	Predation (0/1)	3.30	0.0160
Diet composition	25	121	[a]	[a]		[a]	50.85	*Apodemus*	2.61	0.0280
								Sorex	3.18	0.0140
Diet composition	750	121	[a]	[a]	[a]	[a]	71.14	*Apodemus*	3.40	0.0140

Results of RDA analyses and Monte Carlo permutation test results are shown

[a] Covariates were used. Axes I and II indicate the percentages of variability explained by the first two ordination axes. Only significant results are shown

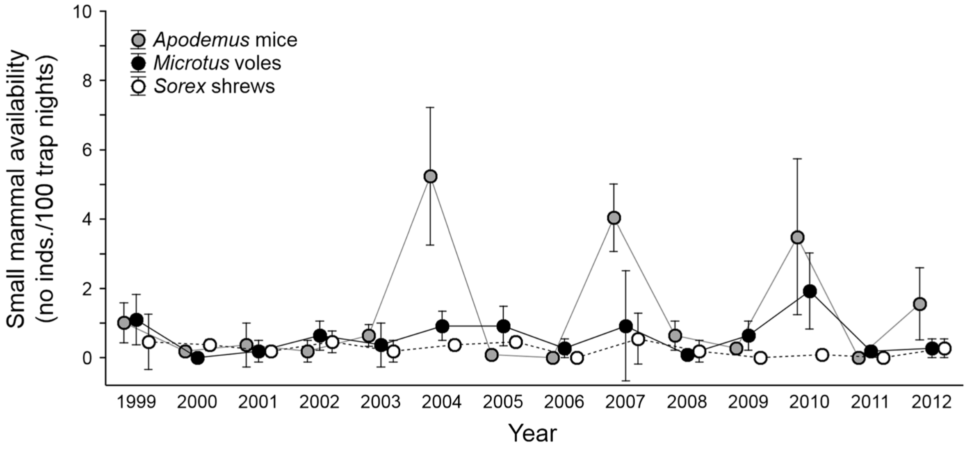


Fig. 2 Changes in the spring abundances of *Microtus* voles, *Apodemus* mice, and *Sorex* shrews in the study area in the Ore Mountains, Czech Republic from 1999 to 2012. Data are shown as mean ± SD

radius of 25 m, the owls used Norway Spruce more frequently than expected ($\lambda = 0.7515$, $p = 0.0020$; habitat ranking in descending order: Norway Spruce > European Beech > open forest areas > other areas > Blue Spruce > other deciduous trees > other coniferous trees). Within a buffer radius of 750 m, the owls used Blue Spruce more frequently than expected ($\lambda = 0.6545$, $p = 0.0020$; habitat ranking in descending order: Blue Spruce > open forest areas > Norway Spruce > other deciduous trees > European Beech > other areas > other coniferous trees).

Based on the results of RDA analysis using Monte Carlo permutation tests, nest box occupation was significantly affected by habitat categories within both buffer zone sizes (Table 3). Within a buffer radius of 25 m, the percentage of Norway Spruce was negatively correlated with the percentage of other deciduous and coniferous tree species, and also partially with the Blue Spruce percentage (Table 3; Fig. 3a). We found a significantly higher percentage of Norway Spruce around occupied nest boxes than unoccupied ones (Mann–Whitney *U* test: $U = 133{,}518.5$, $p = 0.0160$; Fig. 3c). The differences were not significant for Blue Spruce, European Beech, and other deciduous and coniferous species percentages (Mann–Whitney *U* tests: $p > 0.3$). Within a buffer radius of 750 m, we found a negative correlation between the percentage of Blue Spruce and other tree species (RDA analysis and Monte Carlo permutation tests; Table 3; Fig. 3b). Independently, the Norway Spruce percentage was negatively correlated with the beech percentage (Fig. 3b). A significantly higher percentage of Blue Spruce was found for occupied nest boxes than for unoccupied ones (overall RDA analysis, Fig. 3b; Mann–Whitney *U* test: $U = 120{,}363.0$, $p < 0.00001$, Fig. 3d). Percentages of Norway Spruce, beech, and other deciduous and coniferous species did not show significant differences (Mann–Whitney *U* tests: $p > 0.2$).

Small mammal availability and diet composition

The availability of small mammals (*Microtus* voles, *Apodemus* mice, *Sorex* shrews) did not significantly differ among the studied habitats (RDA analysis, Monte Carlo

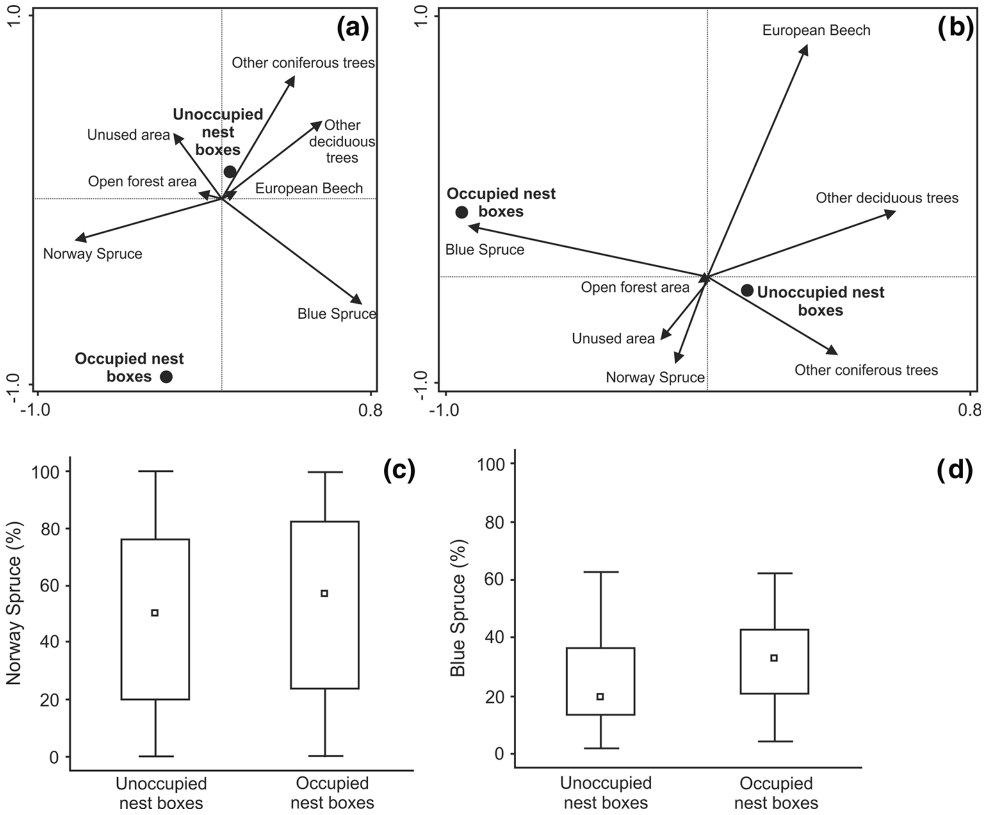


Fig. 3a–d The projection scores of habitat categories (defined by percentage of area) related to nest box occupancy by Tengmalm's Owl within a buffer radius of **a** 25 m and **b** 750 m around the nest (RDA analysis). Within a buffer of 25 m, the percentage of Norway Spruce was negatively correlated with the percentage of other tree species and partially with the percentage of Blue Spruce. Within a buffer of 750 m, a negative correlation was found between the percentage of Blue Spruce and the percentage of other tree species. Percentages of **c** Norway Spruce within a buffer radius of 25 m (M–W U test, $p = 0.0160$) and **d** Blue Spruce within a buffer radius of 750 m (M–W U test, $p < 0.00001$) around the nest related to the occupancy of nest boxes. Box-and-whisker plots: *small squares* medians, *boxes* 25–75 % of data; *whiskers*, non-outlier range

permutation tests: $p > 0.2$). Diet composition of owls was significantly affected by habitat categories for both buffer zone sizes (RDA analysis, Monte Carlo permutation tests). Within a buffer radius of 25 m, percentages of *Apodemus* mice and *Sorex* shrews in the diet of owls were significantly affected by overall habitat categories (Table 3), but no partial relationship was significant (multiple regressions: $p > 0.1$). Within a buffer radius of 750 m, a significant effect of habitat categories on the percentage of *Apodemus* mice in the diet was found (Table 3; Fig. 4a). The percentage was positively related to the percentage of Blue Spruce (multiple regression: beta = 0.208, $t = 2.28$, $p = 0.0230$; Fig. 4b) and open forest areas (multiple regression: beta = 0.272, $t = 3.99$, $p = 0.0027$; Fig. 4c).

Nest predation by Pine Martens and reproductive success

Habitat categories within a buffer radius of 25 m showed no differences between nests that were predated by martens and nests that were not predated by martens. However, significant differences were found for a buffer radius of 750 m (RDA analysis, Monte Carlo permutation tests: Table 3; Fig. 5a). A negative correlation was found between the percentage of Blue Spruce and other deciduous trees (RDA analysis, Monte Carlo permutation tests: Table 3; Fig. 5a). The large-scale surroundings of nonpredated nests were characterized by a higher percentage of Blue Spruce (Mann–Whitney U test: $U = 4{,}326.0, p = 0.0480$; Fig. 5b) and a lower percentage of other deciduous trees (Mann–Whitney U test: $U = 4{,}193.0$, $p = 0.0230$; Fig. 5c) compared to nest boxes predated by Pine Martens. The number of fledglings (controlled for laying date) was not affected by habitat categories within a buffer radius of either 25 or 750 m (Table 3).

Discussion

Habitat use in nest surroundings

A slightly higher but significant percentage of Norway Spruce was found around occupied nest boxes than

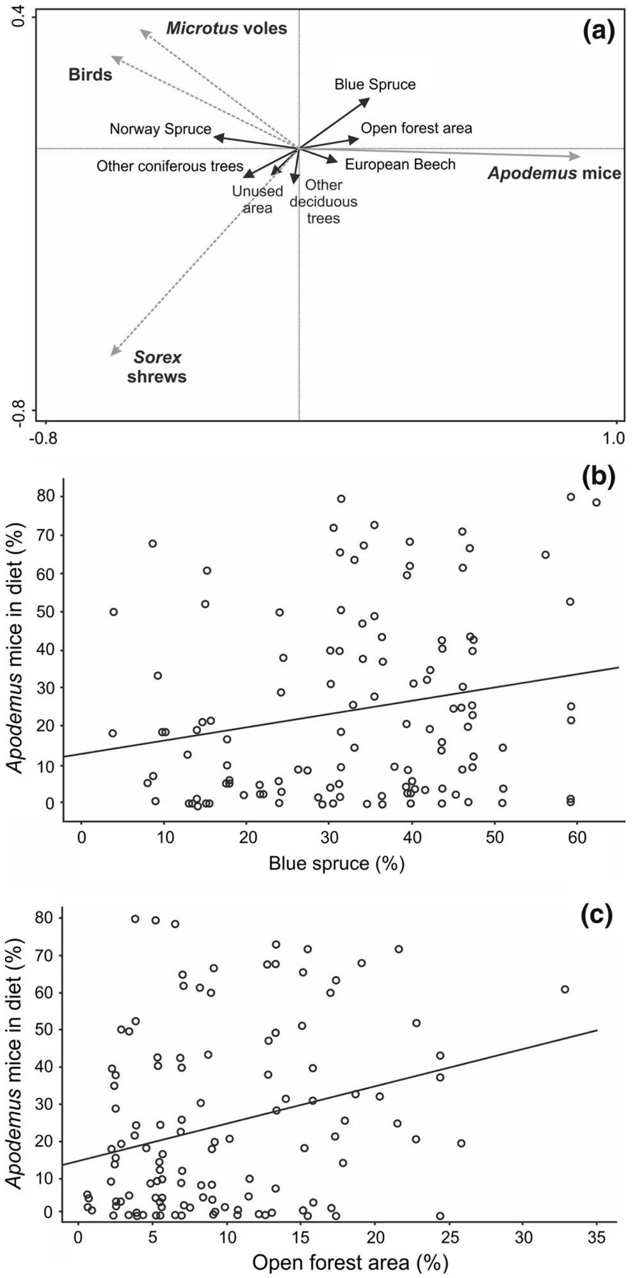
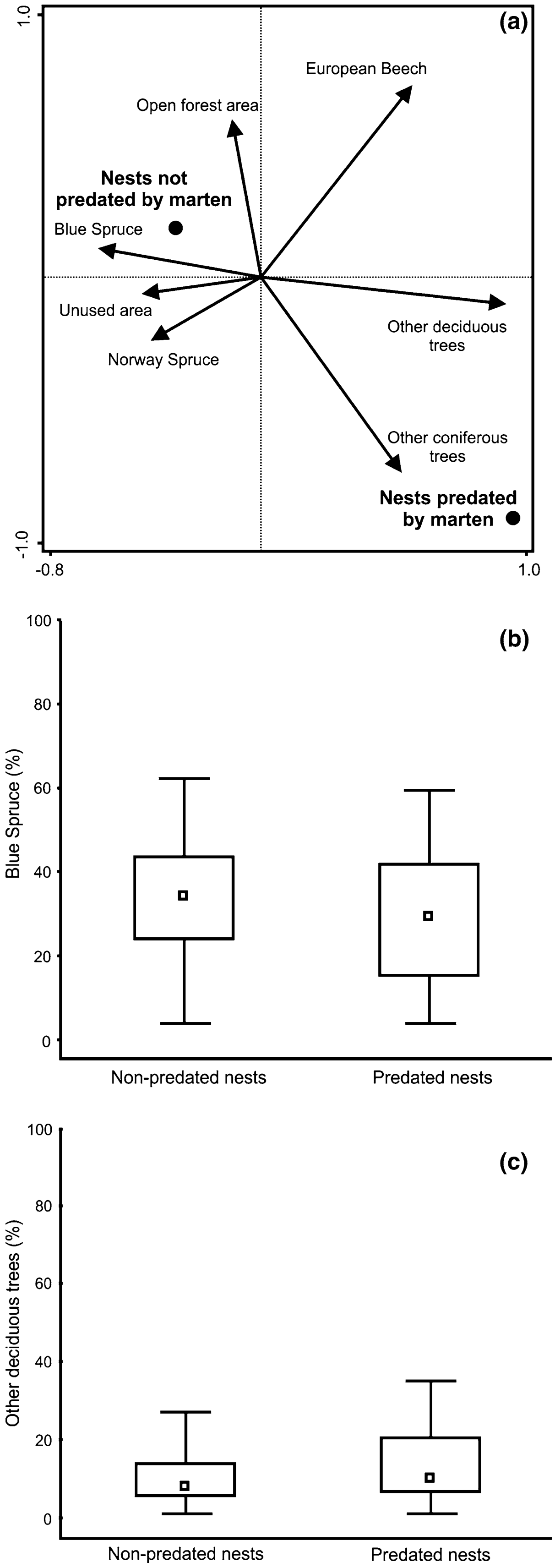


Fig. 4a–c **a** Projection scores of habitat categories (defined by percentage of area) within a buffer radius of 750 m around the nest related to percentages (% by numbers) of main diet components (RDA analysis, Monte Carlo permutation tests: *gray solid arrows* $p < 0.05$, *gray dashed arrows* $p > 0.05$). Regression relationships between the percentage of *Apodemus* mice in the diet of Tengmalm's owl and the percentages of **b** Blue Spruce (regression, $p = 0.0230$), and **c** open forest area (regression, $p = 0.0027$)

around unoccupied ones within a buffer radius of 25 m (median 56.7 vs. 49.5 %, respectively). Kouba (2009) showed that 13 radiotracked males during the period 2006–2008 preferred old Norway Spruce forests for resting during the day (88 % of all locations) in our



◀**Fig. 5** **a** The projection scores of habitat categories (defined by percentage of area) within a radius of 750 m around the nest (RDA analysis); a negative correlation between the percentage of Blue Spruce and the percentage of other deciduous trees was found. The percentages of **b** Blue Spruce (M–W *U* test, $p = 0.048$) and **c** other deciduous trees (M–W *U* test, $p = 0.023$) related to nests predated by Pine Martens. Box-and-whisker plots: *small squares* medians, *boxes* 25–75 % of data, *whiskers* non-outlier range

study area. Similar preferences for dense coniferous forests for roosting have been reported in Northern America (Bondrup-Nielsen 1984; Hayward et al. 1993). In Colorado, all roosts were found to be located on steep slopes in relatively dense coniferous forests dominated by Engelmann Spruce (*Picea engelmannii*). This tree species appeared to offer good conditions for roosting (i.e., protection against enemies from above) but less cover below, facilitating easier attacks on prey towards the ground surface (Palmer 1986; Ryder et al. 1987). High tree density seems to be an important factor for protecting against enemies during resting for other owl species too; for example, Screech Owl *Megascops watsonii* (Barros and Cintra 2009), Spotted Owl *Strix occidentalis* (Ganey and Balda 1994; May et al. 2004), or Tawny Owl *Strix aluco* nonbreeding adults that usually roost in less exposed locations than adults with young and newly independent juveniles (Sunde et al. 2003).

During the breeding season, Tengmalm's Owl males often roost far from their nests to avoid attracting mobbing birds and predators to the vicinity of their nests, and do not defend their broods against enemies during the daytime (Korpimäki and Hakkarainen 2012). On average, males roost 626 m from their nests in our study area (Kouba 2009). Furthermore, males bringing food to the nest often perch in dense Norway Spruce stands while communicating with females (M. Zárybnická, unpublished data). Moreover, females incubating eggs and broods typically leave the nest for a few minutes each night to defecate, regurgitate pellets, and preen (Korpimäki 1981; Zárybnická 2009a). After the brooding period, females may help males with the provisioning of food for the young (Eldegard and Sonerud 2009, 2010, 2012; Zárybnická 2009a), and they also use old-growth Norway Spruce forest during prey delivery (M. Zárybnická, unpublished data). Meanwhile, fledglings roost close to the nest box during their first days after fledging (Kouba et al. 2013) and they often sit in dense, tall and old-growth Norway Spruce forests (M. Kouba, unpublished data). We suggest that tall, old-growth Norway Spruce forests with dense structure in the vicinity of nests are used more frequently than expected by Tengmalm's Owl individuals due to the protection they provide against avian (mainly Goshawk and Tawny Owl) predators during the rearing and fledging period.

Habitat use within a foraging area

A higher percentage of Blue Spruce was found within a buffer radius of 750 m for occupied nest boxes than for unoccupied ones (33.1 vs. 19.2 %, respectively), but no relationship was found for other habitat groups. Kouba (2009) showed that radiotracked Tengmalm's Owl males in our study area often hunt in Blue Spruce stands. Males are frequently observed to hunt from Blue Spruce trees, and show no sign of difficulty with sitting on the prickly needles. Several studies have shown that open areas such as forest clearings, meadows, or young tree stands are characterized by a wide variety of small mammals, and provide good foraging opportunities for some avian predators, for example Common Kestrel *Falco tinnunculus* (Village 1990), Sparrowhawk *Accipiter nisus* (Šálek et al. 2010), Ferruginous Pygmy Owl *Glaucidium brasilianum* (Sarasola and Santillán 2014), or Tengmalm's Owl breeding in northern areas (Hakkarainen et al. 1996). In our study site, the main components of the diet of Tengmalm's Owl are *Microtus* voles and *Apodemus* mice (Zárybnická et al. 2009, 2013). We found that the abundances of both *Apodemus* mice, *Microtus* voles, and *Sorex* shrews are comparable in all basic habitat types within our study area (including secondary stands of Blue Spruce, other coniferous and deciduous trees, forest clearings, and small patches of old-growth Norway Spruce forest). This is probably caused by the open nature of most habitats and the dominance of Wood Reed vegetation throughout the study area. We suggest that Blue Spruce stands provide a suitable habitat for the occurrence of both main prey types of Tengmalm's Owl (*Apodemus* mice and *Microtus* voles), whilst they also offer good hunting opportunities for the sit-and-wait tactic employed by this owl.

It was also found that the surroundings within a buffer radius of 750 m in nonpredated nests showed a somewhat higher percentage of Blue Spruce (median 34.2 vs. 29.4 %, respectively) and a slightly lower percentage of deciduous trees (median 8.3 vs. 9.6 %, respectively) than the surroundings of nests preyed upon by Pine Martens. The 750-m radius buffer zone roughly equates to the home range area of Pine Martens (approximately 200 ha) (Zalewski et al. 1995; Pereboom et al. 2008). In some years, martens predated up to 50 % of all nests. In Central Europe, Pine Martens prefer woodlands (hedgerows, edges, groves, and forests), but also use other areas such as fields and human settlements (Pereboom et al. 2008). Sonerud (1985) showed that the predation rate of Tengmalm's Owls' nests by Pine Martens was higher in closed mature spruce forests than in the open forest landscape. As a result, nest boxes in closed mature spruce forest were avoided. In agreement with this observation, Pereboom et al. (2008) found that Pine Martens moved faster in closed forests compared to open areas. In our study site, Blue Spruce forest is generally difficult to walk through because it does not form a natural forest habitat, i.e., individual trees are formed separately, they are low (compared to Norway Spruce trees), and their branches reach the ground. Moreover, Blue Spruce growth contains the remains of dead trees and snags, and field bumps originating during restoration (each seedling was located on the top of a soil bump of height 0.5–0.7 m made by an excavator; V. Bejček, in verb.). In this habitat, Black Grouse *Tetrao tetrix* can find suitable protection against mammalian predators: dense cover may reduce the visual and olfactory cues of nests for predators or serve as an impediment to mammalian movements (Svobodová et al. 2004). We suggest that the high percentage of Blue Spruce growth within the home range of Tengmalm's Owl may provide good protection of owl nests against predation by Pine Martens. Moreover, deciduous trees may offer a good foraging habitat for Pine Martens, particularly due to the occurrence of Mountain Ash, the fruits of which are often found in its diet (Jedrzejewski et al. 1993). In agreement, we found a lower percentage of deciduous trees in surroundings of nonpredated nests.

Diet composition

Because we did not find differences in small mammal availability among habitats, one might expect no effect of habitat categories on diet composition. However, a positive correlation was found between the percentage of *Apodemus* mice in the diet of Tengmalm's Owl and the percentage of Blue Spruce and open forest habitats within a buffer radius of 750 m (i.e., hunting range). No such relationship was found for the percentage of the second main prey type, *Microtus* voles. The availability of *Apodemus* mice in the field positively affected its percentage in the diet (26 %), but no such relationship was found for *Microtus* voles despite its high percentage in the owls' diet (47 %) (Zárybnická et al. 2013). The results of this study support the notion in related work that mice are a more vulnerable prey type in general than *Microtus* voles, especially during years of high abundance. (1) *Apodemus* mice show similar night activity to Tengmalm's Owls, while voles usually exhibit a mixture of day, dusk, and dawn activity (Wójcik and Wołk 1985; Halle and Stenseth 2000). (2) The timing of mice reproductive activity is well synchronized with that of Tengmalm's Owls, as compared to the relatively late reproductive activity of voles. Mice usually start reproducing in February to March and continue until late summer, while voles usually start in April or May and finish in autumn (Anděra and Gaisler 2012; V. Bejček, 20-year unpublished dataset from our study area). (3) The social behavior of mice differs from that of *Microtus* voles. *Apodemus* mice are not social animals and have larger home ranges (ca. 5,000 m^2) than *Microtus* voles, which are social animals and have small home ranges (ca. 20 m^2) (Sládek and Mošanský 1985; Halle and Stenseth 2000). However, note that the absence of a functional response to the availability of *Microtus* voles can be partially explained by the frequent records of decapitated vole prey, which may reflect an underestimation of them in the diet (Zárybnická et al. 2011, 2013).

Reproductive success

No relationship between habitat categories and the reproductive success of owls (expressed as the number of fledglings) was found. In Finland, the production of young and the nestling survival of Tengmalm's Owl have been reported to be negatively correlated with the proportion of farmland area during the decreasing phase of the vole cycle, while breeding performance was not affected by landscape composition during the low and increasing phases of the vole cycle (Hakkarainen et al. 2003). The authors suggested that this phenomenon may have resulted from an earlier decline in vole densities in luxuriant farmland habitats where predator density was higher than in barren hinterland (Hakkarainen et al. 2003). These results were not supported by our findings. We suggest that the differences are mainly caused by the different cycles of prey, low competition for prey with other raptors, and completely different habitats. (1) Food availability of small mammals in Central Europe is relatively stable from year to year, and there is simultaneously a higher diversity in the prey community (both mice and voles) compared to northern areas (Korpimäki and Hakkarainen 2012; Zárybnická et al. 2012, 2013). (2) There is low competition with other vole-specialized predators (the abundances of other birds of prey and owls in the study area are very low: only Tawny Owl and Eurasian Pygmy Owl *Glaucidium passerinum* breed in densities of 1–2 pairs/100 km^2 within old beech and spruce forest remnants; Šťastný et al. 2006; M. Zárybnická, unpublished data), and thus there is a low impact of specialized predators on vole availability. (3) There are only small patches of old-growth Norway Spruce forests in our study site, and most foraging habitats of Tengmalm's Owl contain open areas of Blue Spruce and open forest habitats (including clearings) compared to the more compact forest habitats of Northern Europe.

Conclusions

Forest habitats in the Ore Mountains have been changed radically due to anthropogenic activity, but—paradoxically—they have become suitable for the threatened

Tengmalm's Owl. We have shown that the European population of Tengmalm's Owls is able to accept non-native spruce (originally from Northern America) within its home range, and uses this habitat at the scale of its hunting range. We suggest that the Blue Spruce stands provide a suitable environment because (1) both of its main prey types (*Apodemus* mice and *Microtus* voles) can be found in them, (2) the stands permit the use of the owl's favoured sit-and-wait hunting strategy, and (3) they provide good protection against nest predation by Pine Martens. Meanwhile, forests of native Norway Spruce were found to be a necessary component of the close surroundings of the nest, suggesting that adult owls and young fledglings can use this habitat type as a safe refuge against avian predators. These findings indicate that Tengmalm's Owl is able to cope with anthropogenic impacts on the environment and even respond positively to these changes. However, populations of other predators show lower abundances; thus, from a broader perspective, anthropogenic pressure in the Ore Mountains has resulted in an unstable raptor community.

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Conflict of interest The authors declare that they have no conflict of interest.

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Příloha XIV

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THE SOCIETY OF POPULATION ECOLOGY

ORIGINAL ARTICLE

Seasonal habitat-dependent change in nest box occupation by Tengmalm's owl associated with a corresponding change in nest predation

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Abstract We investigated the nest-site settlement of the forest-dwelling Tengmalm's owl (*Aegolius funereus*) in the temperate zone of Central Europe (Czech Republic) over a 14-year period. We analysed the effect of changes in nest-site suitability (expressed as the proportion of deciduous forest) within the immediate surroundings of the nest boxes (a buffer radius of 25 m) in relation to nest box occupancy, the mean standardized laying date (further the laying date), occurrence of nest predation, and breeding density. In line with the predictions of the site dependence model, we found a positive relationship between the laying date and the proportion of deciduous trees in the nest box surrounding. Further, we found the interactive effect of the laying date and the proportion of deciduous forest surrounding a nest box on the occurrence of breeding attempts predated by pine martens. A higher proportion of deciduous forest was found in the surroundings of predated than non-predated breeding attempts, and a steeper positive relationship between the laying date and the proportion of deciduous forest was found in the surroundings of non-predated than predated breeding attempts. The change in the owls' habitat utilization can be explained by the process of tree leafing which makes the deciduous forest a less suitable habitat with high risk of nest predation before tree foliage and a more suitable habitat with low risk of nest predation after tree foliage. We conclude that our results are in agreement with the site dependence model, and that the degree of foliage of deciduous forest in the nest surrounding of Tengmalm's owl is a key factor determining site suitability due to predation risk from pine martens in Central Europe.

Keywords *Aegolius funereus* · Anti-predation strategy · Habitat selection · Laying date · Temperate area · Tree foliage

Introduction

Habitat selection is a key process determining distribution and abundance in wild animal populations. Formerly, two main hypotheses for animal distribution have been proposed. The ideal free distribution model predicts that animals occupy habitats in proportion to the availability of resources within habitats and no competitive asymmetries among individuals exist (Fretwell and Lucas 1970; Fretwell 1972). However, this model seems to be inappropriate for territorial animals, due to their limitations of movements among suitable habitats, and also because territorial behaviour precludes high densities that would lead to decreased fitness. Thus, the model gained only little support in empirical studies (reviewed by Newton 1998). More often, territory occupancy patterns have been found to be selective (e.g., Halama and Dueser 1994; Kostrzewa 1996). Dominant individuals usually secure territories of higher quality early in the spring while subordinate individuals or young are consequently forced into unfavourable or lower quality habitats. Such a settlement pattern is known as the ideal despotic distribution (Fretwell and Lucas 1970; Fretwell 1972). Since the above-mentioned models are relevant for discrete habitats patches, they were consequently modified with new ideas to be more realistic for

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natural populations of living animals. In this paper, we focus mainly on the relevancy of the site dependent model evaluating the continuum of variability among different sites (Rodenhouse et al. 1997, 2000). Contrary to the former hypotheses, the site dependence model predicts that individuals occupy the territories from best to worst, in terms of changing site suitability over the years and in the course of the breeding season. Site suitability is defined by complex of environmental factors that affect reproductive performance and the survival of individuals. Laying and arrival date have been found to be good surrogates of individual quality and reproductive performance in many species (reviewed by Sergio et al. 2007). Although not all predictions of this model were usually tested, the empirical data seems to give a support for site dependent model (Sergio et al. 2007).

Territory quality is usually related to the availability of food resources, which in turn increases reproductive success (e.g., Franklin et al. 2000; Penteriani et al. 2004). In some species, however, it has been documented that food resources play a minor role in quality of territory (e.g., Suárez et al. 2000; Tome 2003; Martínez et al. 2007), and that rather other factors may be the main determinants of reproductive output, such as the risk of predation (Tome 2003; Martínez et al. 2006), availability of nest-sites (Both and Visser 2003; Tome 2003), or competitive interactions (Hakkarainen and Korpimäki 1996). Most studies concerning habitat selection and animal distribution have focused on habitat quality within the entire territory of the studied species, but local nest-site quality has been neglected. Moreover, habitats may change considerably during the breeding season which may have serious implications for habitat selection (Wilson et al. 1997; Donald et al. 2002; Brambilla and Pedrini 2011).

Tengmalm's owl (*Aegolius funereus*) is a small nocturnal bird of prey, feeding mainly on voles and mice (Korpimäki 1988a; Zárybnická et al. 2013), with a Holarctic distribution that corresponds well with the natural range of Norway spruce (*Picea abies*). The availability of voles and mice determines the owls' reproductive success, which decreases over the course of the breeding season (Zárybnická et al. 2015a). More or less isolated populations occur in Central and Southern Europe where they inhabit mainly Norway spruce forests, mixed forests of spruce and European beech (*Fagus sylvatica*), or non-native blue spruce (*Picea pungens*) forests (Šťastný et al. 2006; Zárybnická et al. 2015b). Adult owls and fledglings use dense and tall coniferous forests to avoid the risk of being mobbed by small birds or killed by diurnal birds of prey (Bye et al. 1992; Korpimäki and Hakkarainen 2012). The effect of environmental heterogeneity can vary within the geographic range of a species. For example, the proportion of Norway spruce forests and farmland can be positively correlated with the survival and breeding success of the Tengmalm's owl population in Finland (Korpimäki 1988b; Hakkarainen et al. 2008), while a higher proportion of non-native blue spruce can decrease the rate of nest predation by pine martens (*Martes martes*) in the Tengmalm's owl population in the Czech Republic (Zárybnická et al. 2015b). In Norway, the owls preferred to occupy boxes installed in clear-cuts and avoided those installed in old coniferous forest because of higher predation risk from pine martens (Sonerud 1985). In Central Europe, coniferous stands are the most common habitat type for Tengmalm's owl, although deciduous forests also represent a considerable part of Tengmalm's owl territories (Korpimäki and Hakkarainen 2012; Zárybnická et al. 2015c). Despite this fact, the role of deciduous forest in the distribution of Tengmalm's owl is not well understood. In particular, the degree of tree foliage of deciduous forests changes dramatically throughout the breeding season of Tengmalm's owl (i.e., from March to August), but little is known about the impact of these seasonal changes on nest-site selection by these forest-dwelling predators.

In this study, we investigated the distribution of the Central European Tengmalm's owl population in the Ore Mountains (Czech Republic) where both coniferous and deciduous forests form important habitats for this owl. Based on the site dependent model, we predicted that the proportion of deciduous forests in the immediate surroundings of the nest box would differ between (1) occupied and unoccupied nest boxes, i.e., the owls would more frequently breed in coniferous forests and (2) predated and non-predated breeding attempts, i.e., the proportion of deciduous forest would be higher in the surroundings of predated than non-predated breeding attempts. Since clutch size and fledgling production of Tengmalm's owl was negatively correlated with laying date (Korpimäki and Hakkarainen 2012; Zárybnická et al. 2015a) we used the mean standardized laying date as a surrogate of individual quality and predicted that (3) the proportion of deciduous forest would positively correlate with the laying date. We also tested the relationship between (4) the mean annual proportion of deciduous trees per breeding attempt and annual breeding density.

Materials and methods

Study species and area

The study was conducted in the northern part of the Czech Republic (50°N, 13°E), in the forests of the Ore Mountains (elevation 730–960 m a. s. l.; area 70–100 km^2), from 1999 to 2012. In our study site, foliage cover develops during April and May when the mean monthly temperature is 5.4 and 10.1 °C, respectively (data from the Czech

Hydrometeorological Institute). The main habitat is characterized by a heterogeneous mosaic of old Norway spruce forests, fragments of young secondary forests dominated by non-native blue spruce, native deciduous trees (mainly European beech, European larch *Larix decidua*, mountain ash *Sorbus aucuparia*, European hornbeam *Carpinus betulus*, alders *Alnus* sp., and birches *Betula* sp.), and open areas with solitary beeches. In this study site, the owls breed primarily in nest boxes (>90% of nests), as the availability of natural cavities is low (for details, see Zárybnická et al. 2015c). Nest boxes have been evenly distributed within the study area and were fixed onto trees, 3–5 m above the ground. The total number of nest boxes in the study area annually varied between 100 and 167 (mean ± SD, 126.6 ± 26.8 boxes, $n = 14$). All nest boxes were kept in good condition (they were regularly cleaned after breeding and repaired when necessary) and the surroundings of the nest box entrance were kept free of vegetation.

Basic breeding data (i.e., laying date, fledgling production, and predation events) was collected during regular inspections of all nest boxes during the breeding season (for details, see Zárybnická et al. 2012). From 1999 to 2012, a total of 234 breeding attempts (i.e., at least one egg was laid) of Tengmalm's owls was recorded, of which 119 were successful (i.e., at least one young fledged) and 115 unsuccessful. Of the latter, 60 were predated by pine martens and 55 nesting attempts failed due to unknown reasons (one of which could be for example the death of adults, see also Zárybnická and Vojar 2013). Tengmalm's owls in our study area usually breed from March to July, and their residence in the cavity from egg laying to fledging lasts about two months (Eldegard and Sonerud 2012; Zárybnická et al. 2015d). The laying date of the first egg was known for 207 breeding attempts (mean ± SD, 16th April ± 23.4 days, range 4 March–29 June). Each year, we also assessed the breeding density of owls as the number of breeding attempts per 100 nest boxes and the number of breeding attempts per 100 km^2, respectively.

Landscape data analyses

Habitat structure was assessed within a radius of 25 m around each nest box (Zárybnická et al. 2015c). Habitat categories were defined using GIS (ArcGIS version 10.3, ESRI, Inc.) from vegetation maps that were originally developed for the purposes of the Forestry Institute (for details, see Zárybnická et al. 2015c). For further analyses, the habitats of the study area were divided into following categories: (1) evergreen coniferous forests (dominated by Norway and blue spruce); (2) deciduous forests (dominated by European beech, European larch, mountain ash, European hornbeam, alders, and birches), and (3) unused areas (dominated mainly by clearings, meadows, and pasture patches for cervids).

Statistical analyses

For all the nest boxes available to the owls during 14-year study period ($n = 1777$), the relationship between nest box occupancy (0/1) and the proportion of deciduous forest within a buffer radius of 25 m around the nest box (%) was analysed using GLMM model (*lmer* function) in R software. Nest box occupancy was used as dependent variable with binomial distribution and the proportion of deciduous forest as independent variable. Year and nest box were used as random factors to eliminate the effect of changing food supply and the occurrence of pseudo-replications (owls nested repeatedly in some nest boxes, mean ± SD, 1.9 ± 1.1 breeding attempts per nest box).

We further performed analyses only for occupied nest boxes with known laying date ($n = 207$ breeding attempts). Due to the occurrence of pseudo-replications in our dataset, we used a nest box as a data unit ($n = 111$ nest boxes). Laying date of each nest box was in each year standardized to mean zero and variance 1. We used the mean standardized laying date of all breeding attempts for each nest box. This recalculation of raw data allowed us to eliminate the effect of food supply or weather conditions on laying date in particular years. We built a GLM model with the mean standardized laying date as dependent variable and the proportion of deciduous forest in the nest box surrounding as independent variable. Because the distribution of dependent variable did not differ from Gaussian distribution (Kolmogorov–Smirnov test, $P = 0.13$), we used identity link function. The effect of the proportion of deciduous forest (independent variable) on the occurrence of predation (dependent variable) was calculated by binomial GLM model. Numbers of predated/non-predated breeding attempts in the nest box were used as separate columns. We used *cbind* function in R to aggregate these two variables. We also included the interaction between the mean standardized laying date and the proportion of deciduous forest in the model. Percentages of explained variability were calculated after recommendations of Nakagawa and Schielzeth (2013).

The relationship between breeding density (the number of nesting attempts per 100 boxes and per 100 km^2, respectively) and the mean annual proportion of deciduous forest ($n = 14$ years) were calculated using a simple regression in Statistica v. 12.0 (StatSoft, Inc. 2013).

Results

The proportion of deciduous trees in the nest box surrounding was marginally non-significantly higher in unoccupied nest boxes than occupied ones (GLMM, 2.6% of explained variability, beta ± SE, −1.9 ± 0.12;

Chi = 3.14, $P = 0.08$; occupied vs. unoccupied boxes: median, range 25–75%: 7.3%, 0.1–22.8% vs. 10.9%, 1.4–38.5%, $n = 1777$ nest boxes of which 234 were occupied and 1543 were unoccupied). Using the dataset for occupied nest boxes only, we found that the mean standardized laying date was positively correlated with the proportion of deciduous forest (GLM, 14.1% of explained variability, beta ± SE, 0.22 ± 0.05, $P = 0.01$, $n = 111$, Fig. 1a). Further, we found a significant effect of the interaction between the mean standardized laying date and the proportion of deciduous forest surrounding a nest box on the occurrence of predation events (GLM, 3.3% of explained variability, $P = 0.03$, beta ± SE, proportion of deciduous forest: 0.02 ± 0.01, standardized laying date 0.55 ± 0.29, interaction −0.05 ± 0.02). In general, a higher proportion of deciduous forest was found in the surroundings of predated than non-predated breeding attempts (Fig. 1b). We also found a steeper positive relationship between standardized laying date and the proportion of deciduous forest in the surroundings of non-predated than predated breeding attempts (Fig. 1c, d). Finally, we did not find a significant relationship between annual breeding density and the mean annual proportion of deciduous forest (a simple regression: nest density per 100 boxes: beta ± SE −0.20 ± 5.76, $F = 0.51$, $P = 0.49$, $n = 14$ years, or nest density per 100 km^2: beta ± SE −0.17 ± 5.68, $F = 0.36$, $P = 0.56$, $n = 14$ years).

Discussion

For birds inhabiting an agriculture landscape in a temperate zone, it has been shown that habitat utilization may change considerably over the season (e.g., Wilson et al. 1997; Donald et al. 2002; Brambilla and Pedrini 2011), but these patterns are poorly known for forest-dwelling birds. However, it has been documented that early nesting long-eared owls (*Asio otus*) and hooded crows (*Corvus corone*) prefer to settle in coniferous forests as a result of the higher predation risk in deciduous forest before the development of tree foliage (Loman 1975; Tome 2003). As predicted, the proportion of deciduous forest tended to be lower in the immediate surroundings of occupied nest boxes (7%) than non-occupied nest boxes (11%). The result was probably altered by the fact that young and inexperienced individuals tried to breed in suboptimal habitats. Furthermore, we found more deciduous forests around nests initiated later in the season. Therefore, we suggest that the proportion of deciduous trees can be a useful measure of site suitability. Consequently, we found that a higher proportion of deciduous forest surrounded predated breeding attempts, and a steeper positive relationship between the laying date and the proportion of deciduous forest in the surroundings of non-predated than predated breeding attempts. Thus, site suitability probably changed in term of predation risk and our results support the site dependence model proposed by Rodenhouse et al. (1997).

Many terrestrial vertebrates, and in particular birds and mammals, prefer habitats with dense vegetation cover to reduce predation risk (e.g., Kaufman et al. 1983; Franklin et al. 2000). For example, dense forests habitats offering good vertical and horizontal concealment were preferred by roosting tawny owl fledglings (Overskaug et al. 1999). Similarly, Tengmalm's owl in both Europe and Northern America prefers dense coniferous forests as a refuge against a number of bird and mammalian predators (Bye et al. 1992; Hayward et al. 1993; Korpimäki and Hakkarainen 2012). The survival rate of adult Tengmalm's owl males in Finland even increased with the proportion of old forests within their home-ranges (Korpimäki and Hakkarainen 2012). Moreover, it has been documented that the mortality of tawny owl fledglings was the highest early after leaving the nest, when fledglings were small and had poorly developed locomotion (Overskaug et al. 1999; Sunde 2005). Deciduous forests (birches *Betula* sp. and aspen *Populus tremula*) usually comprise only a marginal share (<5%) in Tengmalm's owl territories without any effect on owl reproduction or adult survival (Korpimäki and Hakkarainen 2012), whereas our study site was located in the southern margin of species range where deciduous forests (e.g., European beech, European hornbeam, European larch, mountain ash) regularly occur because of their increased temperature requirements (Úřadníček et al. 2001). Therefore we suggest that the proportion of deciduous trees in nest surrounding cannot be a universal measure of site suitability through the entire range of Tengmlam's owl occurrence.

We did not find a relationship between the proportion of deciduous forest and annual breeding density. This finding is not surprising in light of the site dependence model which suggests negative feedback even for small populations (Rodenhouse et al. 1997). For example, the breeding density of Tengmalm's owl can be locally influenced by small mammal availability that can considerably alter nest-site suitability. In Finland, low-quality nest sites are more frequently occupied by European Tengmalm's owls during increased density of bank voles (Korpimäki and Hakkarainen 2012).

To conclude, we found that the nest-site distribution of the Central European Tengmalm's owls was influenced by temporal changes in deciduous forests. Breeding attempts predated by pine marten were associated with more deciduous forest in the nest box surrounding early in the

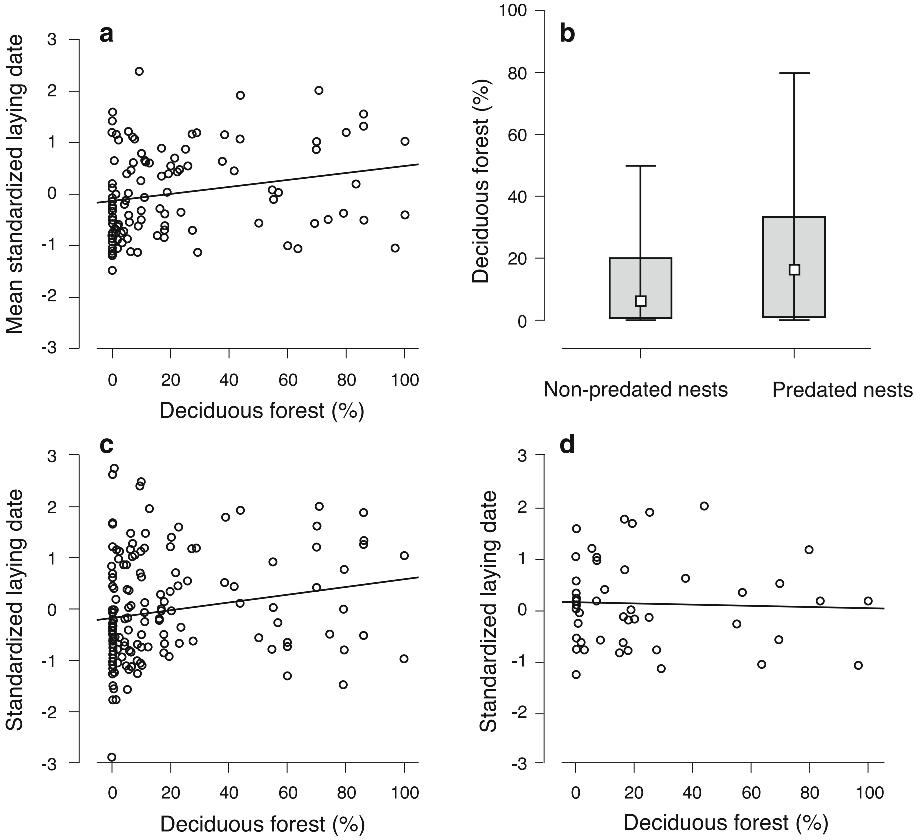

Fig. 1 The relationship between **a** the mean standardized laying date of Tengmalm's owl and the proportion of deciduous trees in the nest box surrounding (a buffer radius of 25 m, $n = 111$ nest boxes), **b** the comparison of the proportion of deciduous forest in the surrounding of predated and non-predated breeding attempts (point: median, *box* 25–75% of data, *whiskers* non-outlier range, $n = 207$ breeding attempts), and relationships between the proportion of deciduous forest and standardized laying date of **c** non-predated ($n = 160$) and **d** predated breeding attempts ($n = 47$)

season. The main factor affecting Tengmalm's owl nest distribution in our study site is therefore actual site suitability which is in line with the site dependence model.

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Příloha XV

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Indirect food web interactions affect predation of Tengmalm's Owls *Aegolius funereus* nests by Pine Martens *Martes martes* according to the alternative prey hypothesis

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Although population cycles of rodents are geographically widespread and occur in a number of rodent species, higher-order food web interactions mediated by predator–rodent dynamics have primarily been described from boreal and arctic biomes. During periods of low rodent abundance, predators may switch to alternative prey, which may affect other predators directly or indirectly. Using a long-term dataset, we assessed the frequency of Pine Marten *Martes martes* predation on the nests of Tengmalm's Owl *Aegolius funereus* during periods of fluctuating rodent abundance in Central Europe. The number of nests predated by Pine Martens was positively correlated with the annual number of nests available. The probability of predation by Pine Martens on Tengmalm's Owl nests decreased with increasing spring abundance index of *Apodemus* mice, but was not related to the abundance index of *Myodes* and *Microtus* voles, pooled rodent abundance or age of the nestbox. Additionally, we found no relationship between the breeding frequency (i.e. the number of nesting attempts per nestboxes available) and an abundance index of *Microtus* and *Myodes* voles, *Apodemus* mice or overall rodent abundance. Our results demonstrate, for the first time in a temperate area, that during periods of low *Apodemus* mouse abundance, the switching response of an opportunistic mammalian predator can lead to indirect food web interactions through an increase in nest predation on a sympatric avian predator.

Keywords: *Apodemus* mice, birds of prey, Boreal Owl, mammalian predator, *Microtus* voles, nest predation, predator–rodent dynamics, temperate area.

Annual variation in the breeding success of ground-nesting birds in boreal and arctic areas depends on cyclical changes in the abundance of small mammals (Summers 1986, Underhill *et al.* 1993, van Impe 1996, Bêty *et al.* 2001, Ackerman 2002). According to the alternative prey hypothesis, this relationship is caused by variable annual predation pressure on alternative prey resulting from the functional and numerical responses of predators to the density of their main prey (Lack 1954, Angelstam *et al.* 1984, Bêty *et al.* 2001). When small mammals are abundant, the majority of vertebrate predators feed primarily on those, i.e. they respond functionally to small mammals (Angelstam *et al.* 1984, Sonerud 1992). However, during periods of decline in small mammal populations, these same vertebrate predators must switch to alternative prey, which often includes the eggs and young of birds (Pienkowski 1983, Underhill *et al.* 1993, Wilson & Bromley 2001). As a result of these dynamics, alternative prey species suffer higher predation during the decline and low phase of the rodent cycle. This relationship was found between lemming (Arvicolinae) population densities and the frequency of predation by Arctic Fox

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Alopex lagopus, gulls (Laridea) or skuas (Stercorariidae) on nests of geese *Branta* sp. and *Anser* sp. and wader species (Charadriidae) in artic areas (e.g. Summers 1986, Martin & Baird 1988, Underhill *et al.* 1993, Bêty *et al.* 2001, Wilson & Bromley 2001), as well as between microtine rodent density and predation by mammals on nests of grouse (Phasianidae) in boreal areas (Angelstam *et al.* 1984, 1985, Wegge & Storaas 1990, Small *et al.* 1993). To date, such indirect food web interactions have been described almost exclusively in northern areas, although several studies have shown a correlation between predation pressure on ground nesters (Ackerman 2002, Saniga 2002, Šálek *et al.* 2004) or cavity nesters (Dunn 1977) and small mammal abundance in temperate areas. To our knowledge, no long-term study has shown such interaction between predation intensity on cavity nesters and small mammal abundance as a form of indirect competition between two predators feeding on the same resource.

Tengmalm's (or Boreal) Owl *Aegolius funereus*, weighing on average during breeding 170 g (female) and 102 g (male) (Korpimäki 1981), is a nocturnal avian predator, feeding primarily on *Microtus* and *Myodes* voles and *Apodemus* mice (Korpimäki 1988, Zárybnická *et al.* 2013). It nests for the most part in cavities made by Black Woodpecker *Dryocopus martius*, but it also willingly occupies nestboxes (Korpimäki & Hakkarainen 2012). The Pine Marten *Martes martes*, weighing 600–2200 g (Aulagnier *et al.* 2009), is an opportunistic forest-dwelling predator, feeding mainly on small mammals (Storch *et al.* 1990). In Central Europe, it occupies a similar range to the Tengmalm's Owl and, as with the Owl, *Microtus* and *Myodes* voles and *Apodemus* mice make up 60–80% of its diet from March to July (Jedrzejewski *et al.* 1993). In addition, Pine Martens also take alternative prey including small birds, their eggs and nestlings, fruit, beetles and ungulate carcasses (Helldin 2000, Sidorovich *et al.* 2005). The Pine Marten is also a significant predator of Tengmalm's Owl nests (Korpimäki 1981, Sonerud 1985a,b, Drdáková-Zárybnická 2003). In both Central and Northern Europe, only martens *Martes* sp. are documented as mammalian predators of Tengmalm's Owl nests (Korpimäki & Hakkarainen 2012). The proportion of Tengmalm's Owl nests predated by martens varies between areas from 5 to 59% based on an average over several years (Sonerud 1985b, Vacík 1991, Drdáková-Zárybnická 2003, Mayer 2003, Korpimäki & Hakkarainen 2012). Marten predation on fledglings soon after leaving the nest has also been occasionally recorded in Central Europe (Kouba & Šťastný 2011). The proportion of Tengmalm's Owl nests predated by martens, however, does not seem to differ between natural cavities and artificial nestboxes (Mayer 2003, López *et al.* 2010). As nest predation by Pine Martens in a box increases with time (Sonerud 1985b), the predation risk of Tengmalm's Owl nests can be reduced by nestbox relocation (Sonerud 1989, 1993).

We analysed a 14-year dataset on predation of Tengmalm's Owl nests by Pine Martens in the Czech Republic, Central Europe, in relation to the availability of small mammals and Tengmalm's Owl nests. Due to the opportunistic feeding strategy of martens (Storch *et al.* 1990) we predicted that the annual number of nests predated by Pine Martens would correlate positively with the number of nests available. Simultaneously, we predicted that the annual frequency of nest predation by Pine Marten would not correlate with breeding frequency of Owls, because the number of Owl nesting attempts does not correlate with the density of nestboxes in our study area (Zárybnická *et al.* 2015b). Furthermore, in light of the alternative prey hypothesis (Lack 1954), we predicted that the probability of nest predation by Pine Marten would decrease with increasing abundance of the usual primary prey of Pine Martens (*Microtus* and *Myodes* voles, *Apodemus* mice, and pooled rodent abundance), but it would not be related to functional age of the nestbox due to selective relocation of predated nestboxes. Finally, we assessed the relationship between breeding frequency of Tengmalm's Owl and an index of abundance of *Microtus* and *Myodes* voles, *Apodemus* mice, and pooled rodent abundance.

METHODS

Study species and area

Our study was conducted in a northern part of the Czech Republic (50°N, 13°E), on the Ore Mountain plateau (730–960 m a.s.l., area 70 km^2) from 1999 to 2012. The study site is characterized by a mosaic of small patches of mature Norway Spruce *Picea abies* forests, fragments of young secondary forests and open areas with no trees; such a pattern results from significant impacts of air pollution towards the end of the 20th century (Zárybnická *et al.* 2013). Pine Marten and Tengmalm's Owl occur together at this study site. Tengmalm's Owls breed mainly in nestboxes (> 90% of breeding pairs), as natural holes are infrequent and usually confined to rare solitary European Beech *Fagus sylvatica* trees. The nestboxes were lined with wood chips and were square-shaped in cross-section, with an inner width between 20 and 22 cm, a height of 40 cm, the distance from the top of the layer of wood chips to the box entrance was 22–24 cm, and the opening diameter was 8 cm. They were usually installed 3–5 m above the ground. Nestboxes were evenly distributed within the study area and their numbers varied between 100 and 167 (mean ± se, 126.6 ± 7.2) in different years. On an irregular basis we relocated old boxes and boxes with occurrence of nest predation to new places and installed new boxes (5.1 ± 2.8 new boxes per year). The average life of each nestbox in any given location was 7.7 ± 0.2 years (range = 3–14 years, median = 7 years). All nestboxes were kept in good condition (they were cleaned regularly after breeding and repaired when necessary) and the area surrounding nestbox entrances was kept free of vegetation, with any branches obstructing the entrance being cut.

In our study area, Tengmalm's Owls usually breed from March to July and the nesting period takes about 2 months (26–32 days of incubation and 27–38 days of brooding; Zárybnická *et al.* 2012, Kouba *et al.* 2014). They exhibit similar daily activity patterns to those of Pine Marten (both are active between 20:00 and 06:00 h; Zalewski 2001, Zárybnická 2009a). Females incubate the eggs and brood the young (they leave the nest several times each night to defecate, regurgitate the remains of food and preen; Korpimäki 1981, Zárybnická 2009b). Males provide food for females and young from egg-laying to independence of fledglings (i.e. 5–9 weeks after fledging; Zárybnická 2009b, Eldegard & Sonerud 2012, Kouba *et al.* 2013). Tengmalm's Owl females are usually nomadic outside the breeding season, whereas males are resident throughout the year (Korpimäki & Hakkarainen 2012).

Field procedures

Each year, all nestboxes were inspected from the onset of the breeding period (late March) to the end of the breeding period (July) within intervals of 1–3 weeks to detect new breeders. Nestboxes found to be occupied were subsequently re-visited once per week. A nesting attempt was considered successful when at least one young fledged; otherwise the nesting attempt was considered to be unsuccessful. Nest predation by Pine Martens was identified according to the signs left in the nest or near the nestbox, i.e. scat or hairs together with the presence of broken eggshell remains (with evidence of tooth marks, Supporting Information Fig. S1a), dead nestlings or their remains, or when recorded on a camera installed in the entrance of some nestboxes (Supporting Information Fig. S1b). If the Marten predated a nest before our first nestbox visit and removed all eggs without any signs, we could not determine that nest predation has occurred. Therefore, the frequency of nests and nest predation may have been underestimated. It is possible that the frequency of nest predation could be affected by our own visits (Bart 1977). However, we visited the nestboxes during a period without snow cover and so left no tracks that a potential nest predator could follow. Other failed nesting attempts were caused by nest abandonment during the incubation phase or during the nestling phase with signs of food shortage (no stored prey in the nestbox and disappearance of the youngest nestlings during regular nest visits; Zárybnická & Vojar 2013).

Both Pine Martens and Stone Martens *Martes foina* occur in the Czech Republic; however, the Pine Marten is a typical inhabitant of forest areas (Zalewski *et al.* 1995, Pereboom *et al.* 2008), whereas Stone Martens inhabit urban and suburban, rock cliffs, and agriculture landscapes (Šálek *et al.* 2005), which are very rare at our study site. Furthermore, we have observed only Pine Martens in our study site during 1999–2014 (e.g. Fig. S1b) and we assume that all nest predations were caused by this species.

Prey abundance

The abundance of small mammals was assessed using snap-traps. Trapping was carried out at the beginning of June each year from 1999 to 2012 by setting up snap-traps (baited with roasted flour-covered bacon) in three 1-ha areas (100 × 100 m squares, 11 × 11 trap grid, span 10 m, 121 traps in total for each square). The traps were left out for 3 days and checked every morning. We calculated the abundance index of small mammals as the number of captured individuals per 100 trap nights in each trapping area. All captured mammals ($n = 425$) were identified to species level and grouped into three categories according to main prey of Pine Marten (after Jedrzejewski *et al.* 1993): *Microtus* voles (Field Vole *Microtus agrestis*, Common Vole *Microtus arvalis* and European Pine Vole *Microtus subterraneus*), *Myodes* voles (Bank Vole *Myodes glareolus*) and *Apodemus* mice (Yellow-necked Mouse *Apodemus flavicollis* and Wood Mouse *Apodemus sylvaticus*).

Statistical analysis

Autocorrelation analysis on prey population fluctuations of *Apodemus* mice, and *Microtus* and *Myodes* voles was performed using STATISTICA v. 9.1. (StatSoft 2010). Positive correlation coefficients with 95% confidence limits that did not span zero were taken to indicate peak periodicity.

The occurrence (0/1) of predation events (dependent variable with binomial data distribution) in nestboxes was analysed in R software v. 3.0.2 (R Development Core Team 2011) using generalized linear mixed models (GLMM, lmer function) with logit link function (McCullagh & Nelder 1989). The unit of input data was each independent breeding attempt. Year was fitted as a random effect and laying date (calculated as the number of days from 1 January in each year) as a covariate. We used abundance indices of main prey (*Microtus* and *Myodes* voles, *Apodemus* mice, and pooled abundance of voles and mice) and functional age of the nestbox (i.e. the length of time a nestbox had remained in a given location) as independent variables. We used forward selection of factors based on the Akaike information criterion (AIC). First, we built a null model with random factors only. Then we built alternative models with tested factors (only one factor added) and compared AIC values with the null model. Finally, we added factors with the lowest AIC value to the null model. Significant relationships between abundance index of *Apodemus* mice and the predation frequency based on GLMM analysis were assessed by non-linear estimation in STATISTICA software.

We conducted regressions between the annual number of nests preyed upon (dependent variable) and the number of nests available (independent variable), the annual frequency of nest predation (dependent variable) and breeding frequency (i.e. the number of nesting attempts per the number of nestboxes available) (independent variables), as well as between breeding frequency and the abundance index of *Apodemus* mice, and *Microtus* and *Myodes* voles and pooled rodent abundance as independent variable, computed in STATISTICA software v. 9.1. (StatSoft 2010).

RESULTS

The estimated index of abundance for different prey groups varied between years; *Apodemus* mice were the most abundant small rodent prey group overall and had the most pronounced between-year fluctuations (mean ± se, 1.27 ± 0.46 animals), followed by *Myodes* voles (0.65 ± 0.27) and *Microtus* voles (0.62 ± 0.14) (Fig. 1). There was significant 3-year periodicity in *Apodemus* mouse fluctuations ($P = 0.03$, Fig. 2), but no periodicity was found in *Microtus* ($P \geq 0.230$) or *Myodes* voles ($P \geq 0.223$).

We recorded a total of 234 breeding attempts by Tengmalm's Owls over the period 1999–2012 (mean 16.7 ± 1.5 nests per year) of which 119 were successful. In total, 60 nests (4.3 ± 0.8 nests per year) were predated by Pine Martens during the 14 years of our study and 55 nests failed for other reasons (abandoned during incubation or failed due to food shortage).

The annual predation frequency reached 25.0 ± 3.9% (Fig. 1). Predation on eggs dominated (76.7%, $n = 46$) over predation on chicks (23.3%). We did not record any case of Pine Martens killing the adult female Owl inside the nestbox.

The annual number of nests predated by Pine Martens was positively correlated with the annual availability of Owl nests ($\beta = 0.56$, $F = 5.65$, $P = 0.036$; Fig. 3), but the annual frequency of nests preyed upon was not correlated with Owl breeding frequency ($\beta = 0.074$, $F = 0.07$, $P = 0.80$). The probability of nest predation (0/1) was significantly affected by the abundance index calculated for *Apodemus* mice (GLMM, df = 1, explained variability = 1.8%, $F = 4.75$, $P = 0.029$, means ± se, non-predated nests: 1.17 ± 0.13, predated nests: 0.61 ± 0.14), but was not affected by indices of abundance for *Microtus* and *Myodes* voles or pooled rodent abundance, or by functional age of the nestbox (based on AIC values these latter factors were not supported for inclusion in the

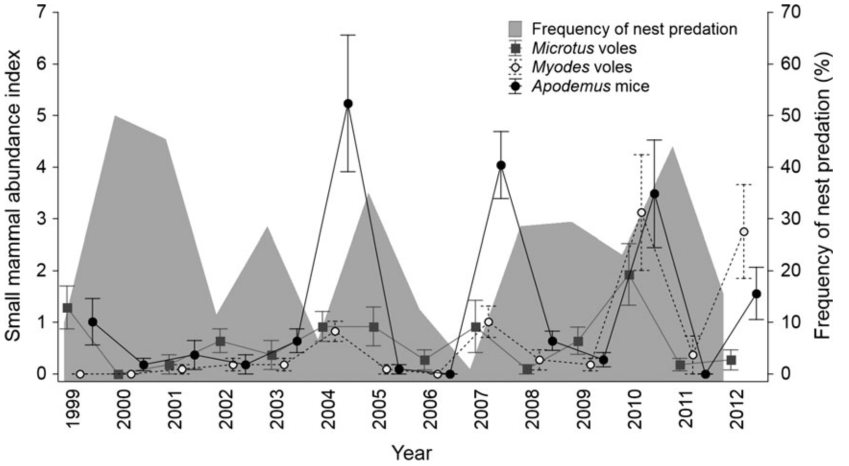

Figure 1. Population fluctuations of the main prey groups of Pine Marten estimated by June snap-trapping expressed as the numbers of individuals per 100 trap-nights (abundance index) and the annual predation rate of Tengmalm's Owl nests during 1999–2012 (means ± 1 se).

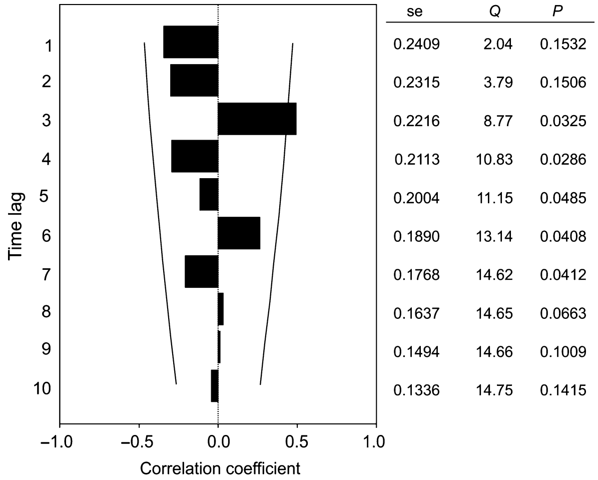

Figure 2. Results of autocorrelation analysis on population fluctuations of *Apodemus* mice showing a significant 3-year peak periodicity. Lines indicate 95% confidence intervals; standard errors are white-noise estimates.

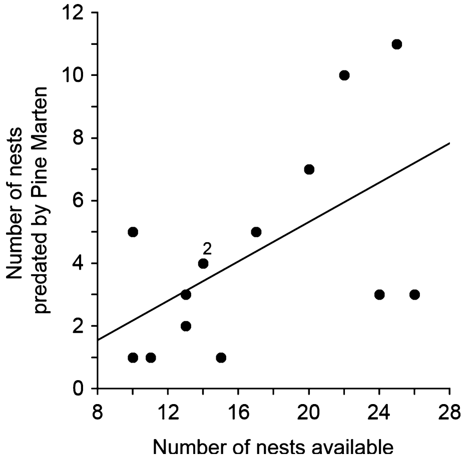

Figure 3. The relationship between the number of nests available in a given year and the number of nests predated by Pine Martens during the period 1999–2012 ($\beta = 0.56$, $F = 5.65$, $P = 0.036$). In two years, we recorded the same value (indicated by number beside the point).

model). The relationship between the annual frequency of nest predation and the abundance index of *Apodemus* mice was best described by a non-linear hyperbolic function: predation frequency = 75.04/(2.22 + *Apodemus* mouse abundance index) (non-linear estimation, $R = 0.58$, Fig. 4). The highest annual frequency of predation (> 25%) was recorded during the years with an *Apodemus* mouse index lower than 1 (Fig. 4).

We found no significant association between the number of nesting attempts per available nestbox and the abundance index of *Microtus* voles ($\beta = -0.29$, $F = 1.07$, $P = 0.320$). These relationships were marginally non-significant for *Myodes* voles ($\beta = -0.50$, $F = 4.02$, $P = 0.068$) and *Apodemus* mice ($\beta = -0.47$, $F = 3.48$, $P = 0.087$). In the dataset pooled for voles and mice, this relationship was close to being significant ($\beta = -0.53$, $F = 4.65$, $P = 0.052$).

DISCUSSION

In agreement with the opportunistic predation strategy of Pine Martens (our first prediction), we found a clear relationship between the number of

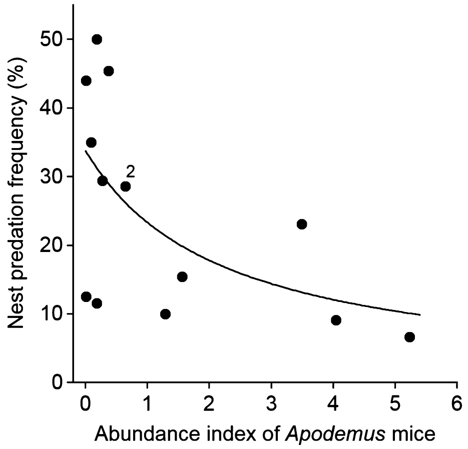

Figure 4. The relationship between the annual predation frequency on Tengmalm's Owl nests by Pine Martens and the annual abundance index of *Apodemus* mice (individuals per 100 trap-nights) estimated by June snap-trapping. Data from 1999–2012. Non-linear estimation, $R = 0.58$, formula: predation frequency = 75.04/(2.22 + *Apodemus* mouse abundance index). In two years, we recorded the same value (indicated by number beside the point).

nests predated and the number of nests available in any year. A similar relationship was found by Dunn (1977) between predation by Least Weasels *Mustela nivalis* and tit nest density. Vickery *et al.* (1992) also suggested that nest predation by Striped Skunk *Mephitis mephitis* on grassland birds is opportunistic because of a positive relationship between foraging activity of skunks and predation rate, the absence of skunk foraging behaviour consistent with active nest searching, and the absence of a relationship between nest success and vegetation cover. However, we did not find a relationship between nest predation frequency and breeding frequency, suggesting that Pine Martens foraged for owl nests at random. Moreover, we found that Pine Martens preyed upon nests with eggs more frequently than nests with chicks, suggesting that owl nests are usually detected by Martens soon after egg-laying. Similarly, Sonerud (1985b) documented a strong bias towards predation on Tengmalm's Owl eggs (94%) rather than nestlings in boreal areas. Collectively, we suggest that these results can be explained by the opportunistic nature of predation by Pine Martens.

In accordance with our second prediction, we found that the probability of nest predation was significantly affected by the abundance of *Apodemus* mice. Similarly, Jedrzejewski *et al.* (1993) found that spring biomass of rodent prey in Pine Marten diet in Poland was related to the abundance of *Apodemus* mice, but not to the abundance of *Myodes* or *Microtus* voles. In our study area, the proportion of *Apodemus* mice in the diet of Tengmalm's Owls increased with the abundance of *Apodemus* mice (Zárybnická *et al.* 2013) and with the proportion of hunting habitat suitable to catch mice (Zárybnická *et al.* 2015a); however, we found no such relationships for the abundance of *Microtus* or *Myodes* voles. These findings support the predictions of the alternative prey hypothesis between a mammal predator and a cavity bird nester, two predators that compete for the same small mammal resource in temperate areas. However, the functional response of Pine Marten towards Tengmalm's Owl nests was found only during periods of *Apodemus* mice scarcity, and it was emphasized when *Apodemus* mice reached an abundance below one prey per 100 trap nights. To our knowledge, this is the first study showing such a relationship for two predators feeding on *Apodemus* mice.

We found no relationship between the frequency of nest predation by Pine Marten and functional age of the nestbox (the length of time any nestbox had remained in a given location), which agreed with our third prediction. In contrast to our results, Sonerud (1985b) found that predation risk increases with age of the nestbox. It has been shown that Pine Martens regularly search for food through all habitats within their territories (Pereboom *et al.* 2008) and have long-term memory for places and food caches, which can result in re-visits of nestboxes found previously (Dow & Fredga 1983, Sonerud 1985b, 1989). They may also rest in non-occupied Tengmalm's Owl boxes during the day and even raise their own young there (Sonerud 1985a, M. Kouba & M. Zárybnická unpubl. data). These behaviours could lead to an increased ability of Martens to detect owl nests located in older nestboxes. We suggest the absence of a relationship between age of the nestboxes and predation rate in our study may be due to relocation of some older boxes, particularly boxes which had suffered nest predation on a previous occasion.

As Tengmalm's Owls breeding in Central Europe respond to *Apodemus* mouse abundance by increasing the proportion of mice in the diet with the abundance of mice in the field (Zárybnická *et al.* 2013), it could be expected that they would also show a numerical response with an increase in the number of nests in relation to increasing availability of mouse prey, which fluctuates in our study site with a 3-year periodicity. Such relationships often exist in northern latitudes between predatory bird community and vole availability (e.g. Korpimäki 1984, reviewed by Poulin *et al.* 2001). In Central Europe, however, these relationships are not pronounced and other factors may influence raptor densities (e.g. climatic conditions or the availability of breeding sites; Kostrzewa & Kostrzewa 1991). In agreement with this, we did not find clear evidence of a numerical response of nesting Tengmalm's Owls (expressed as the number of nesting attempts related to nestbox availability) to prey abundance in the field. Numerical responses for each prey separately were non-significant (*Microtus* voles) or marginally significant (*Myodes* voles, *Apodemus* mice), while the relationship was nearly significant for pooled data for all prey types. However, all regression coefficients were negative (see also Zárybnická *et al.* 2013). Therefore, we do not consider these results evidence of numerical response but rather an artefact of several other influences in our population (e.g. high overall predation frequency leading to replacement broods). Despite the absence of a relationship between owl breeding frequency and food availability, the Central European owl populations respond to increased food availability by having larger clutch sizes and increased reproduction output (Zárybnická *et al.* 2013, 2015b).

Hakkarainen and Korpimäki (1994) found that both male and female Tengmalm's Owls defend their nests with warning calls, beak snaps and direct attacks against a caged American Mink *Mustela vison* placed on the roof of the nestboxes. However, under real life conditions, nest defence by males is not likely because they spend most of the daytime far from the nest (on average 626 m; Kouba 2009), and during the night they are actively hunting (also away from the nest); and they increase their hunting effort during times of food scarcity (Zárybnická *et al.* 2009). Furthermore, during incubation and brooding, female Tengmalm's Owls leave the nestbox as soon as possible when a Marten attacks their nest (Sonerud 1985a). In addition, Pine Martens have substantially higher body mass compared with Tengmalm's Owls. Based on the above, we suggest that male or female Tengmalm's Owls are not able to defend nests against Pine Martens effectively, leaving nests open to predation.

We conclude that Pine Martens use nests of Tengmalm's Owls as an alternative food resource when small mammals are scarce, even in Central Europe where vole population cycles are not regular or as marked compared with Northern Europe (Hansson & Henttonen 1985, Korpimäki *et al.* 2005). However, the functional response of Pine Martens to Tengmalm's Owl nests was found only during periods of *Apodemus* mouse scarcity, suggesting that these indirect food web interactions can be less pronounced in temperate areas compared with arctic and boreal biomes due to more stable rodent populations and increasing prey diversity with decreasing latitude (Zárybnická *et al.* 2015b). Our results also document for the first time that switching behaviour in a mammalian predator can influence the breeding success of an avian predator feeding on the same prey.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. (a) Tengmalm's Owl eggs predated by Pine Marten. (b) Pine Marten front leg in the opening of a nestbox recorded by camera.

Příloha XVI

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RESEARCH ARTICLE

Factors Affecting Growth of Tengmalm's Owl (*Aegolius funereus*) Nestlings: Prey Abundance, Sex and Hatching Order

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Abstract

In altricial birds, energy supply during growth is a major predictor of the physical condition and survival prospects of fledglings. A number of experimental studies have shown that nestling body mass and wing length can vary with particular extrinsic factors, but between-year observational data on this topic are scarce. Based on a seven-year observational study in a central European Tengmalm's owl population we examine the effect of year, brood size, hatching order, and sex on nestling body mass and wing length, as well as the effect of prey abundance on parameters of growth curve. We found that nestling body mass varied among years, and parameters of growth curve, i.e. growth rate and inflection point in particular, increased with increasing abundance of the owl's main prey (*Apodemus* mice, *Microtus* voles), and pooled prey abundance (*Apodemus* mice, *Microtus* voles, and *Sorex* shrews). Furthermore, nestling body mass varied with hatching order and between sexes being larger for females and for the first-hatched brood mates. Brood size had no effect on nestling body mass. Simultaneously, we found no effect of year, brood size, hatching order, or sex on the wing length of nestlings. Our findings suggest that in this temperate owl population, nestling body mass is more sensitive to prey abundance than is wing length. The latter is probably more limited by the physiology of the species.

Introduction

In altricial birds, phenotypic characteristics of nestlings such as body mass and wing length can affect sibling competition [1,2], nestlings' survival [3,4] and at which age each individual fledges [5]. During the post-fledgling period, the body characteristics affect fledgling survival, behavioural performance and recruitment into the breeding population [6–8]. Energy supply, which is determined by natural food availability and parental effort [9,10], is the main factor determining individual fledglings' body mass [3,4,11–13] and enhances feather growth [13–15]. In species where asynchronous hatching seems to be an adaptation to unpredictable changes in food supply, the youngest nestling usually dies first due to its poor body condition (i.e. brood reduction theory; [16–20]). This effect is more pronounced during food scarcity [16,19,21]. Simultaneously, nestlings from enlarged broods usually reach a lower body mass and shorter wings compared to those from smaller broods, due to increased sibling competition [22–25]. Moreover, the larger sex usually grows faster than the smaller sex and reaches a higher body mass [26–29]. However, across bird species, particular factors can play different roles. For example, the body condition of Montagu's harrier *Circus pygargus* fledglings does not vary according to sex and food abundance [30], the larger sex of marsh harrier *Circus aeruginosus* nestlings has no reduction effect on the smaller sex [28], and brood size in common grackles *Quiscalus quiscula* has no effect on nestling body mass [31]. Moreover, despite the reasonable amount of existing experimental studies on the differential quantity and quality of fledglings, observational studies remain scarce.

The Tengmalm's owl *Aegolius funereus* is a nocturnal avian predator with a wide Holartic breeding range [32], feeding mainly on voles in northern areas, and voles and mice in temperate areas [33–36]. As in other raptors and owls, eggs are laid at an interval of 1–2 days, and incubation begins after the first or second egg has been laid. Consequently, the nestlings hatch asynchronously and the youngest nestlings usually suffer from a higher mortality risk due to a combination of starvation and sibling aggression [32,37]. The nestlings stay on the nest usually 32 days (range 27 – 38 days) from hatching [5]. In Tengmalm's owl, reversed size dimorphism reaches approximately 30–40% in terms of body mass during the breeding season due to female body reserves for egg production and successful incubation, although the difference is only 4% in body mass and 2.5% in wing length outside the breeding season [38,39]. Hipkiss et al. [3] found that female nestlings in northern populations attained 5% higher asymptotic mass than males, and that experimentally fed nestlings were heavier than control nestlings, suggesting that the females' larger size gave them a competitive advantage against their male siblings during food scarcity. On the other hand, Kouba et al. [5] demonstrated that wing length is important measurement of individual quality in Tengmalm's owl young because it determines the duration of the nestling period (i.e., duration of stay of individual nestlings at the nest box from hatching to fledging). However, between-year observational data on this topic are scarce, as well as no long-term study has focused on the effect of extrinsic factors such as prey abundance, brood size, hatching order, and sex on body mass and wing length in nestlings of raptors in general and Tengmalm's owl in particular.

In this study, we analyse a seven-year observational data on nestling conditions from a central European population of the Tengmalm's owl. Specifically, we examine the effect of year, brood size, hatching order, and sex on nestling body mass and wing length, as well as the effect of prey abundance on parameters of growth curve. We hypothesise that (i) body mass and wing length of nestlings (controlled for age) vary among years due to between-year variation in prey abundance, and growth parameters (i.e. asymptote, inflection point, and growth rate) increase with prey abundance, (ii) nestlings in smaller broods, as well as (iii) early-hatched brood-mates, attain a higher body mass and wing length (both controlled for age) than nestlings in larger broods and later-hatched brood-mates, and (iv) females attain a higher body mass than males, but not longer wings. To support our results, we also compare main growth parameters (asymptote, inflection point and growth rate) among years, hatching order groups and sexes.

Materials and Methods

Ethics statement

The project (evaluating small mammal abundances and handling with Tengmalm's owl chicks) was approved by the Ministry of the Environment of the Czech Republic (permit No. 35016/

02-OOP/8751/02, 530/758 R/08-Abt/UL, 01220/LP/2008, and 48429/ENV/14-2831/630/14). Owl chicks were handled and ringed under the Ringing Centre of the National Museum in Prague permit No. 329 and 942. Maximum effort was made to reduce handling time.

Study area

The study was conducted in the northern part of the Czech Republic (50°N, 13°E), on the Ore Mountain plateau (elevation: 730–960 m a. s. l.; area: ca 100 km^2), from 2006 to 2014, except 2007 (blood of nestlings not available) and 2013 (no nestlings hatched). The study site is characterized by a mosaic of small patches of mature Norway Spruce *Picea abies* forests, fragments of young secondary forests, and open areas with no trees; such a pattern resulted from significant impacts of air pollution towards the end of the 20th century (for details see [40]). In this study site, Tengmalm's owls breed mainly in nest boxes (> 90% of breeding pairs), as naturally occurring cavities for nesting are scarce [40]. The nest boxes were evenly distributed within the study area, and their numbers varied between 116 and 212 (mean ± SE; 159.3 ± 11.5) in different years.

Field procedures

Each year, all nest boxes were inspected from the onset of the breeding period (late March) to the end of the breeding period (July) in intervals of one to three weeks to detect new breeders. Nest boxes found to be occupied were subsequently revisited at a sufficient frequency to assess the number of eggs, hatchlings and hatching date (± 1 day). During the study period of 2006–2014 (except 2007 and 2013) we found a total of 116 nesting attempts from which 301 nestlings hatched. We weighed, measured and identified the sex of a total of 137 nestlings from 43 nests (Table 1). Owl nestlings were measured at age from 1 to 42 days after hatching (n = 418 measurements). Each nestling was measured and weighted on average 3.1-times (SE = 0.1, n = 137 nestlings) during its stay on the nest. The body mass and wing length of the nestlings were measured usually at intervals between one to two weeks. The nestlings were mostly identified according to their rings. When they were too small to be ringed, they were identified according to colour marks under wings or on legs. Number of measurements was during early phases of ontogeny lower compared to late phases (mean chick age during measurement was 21.4 days, SE = 0.4). This was a consequence of tactful research approach during early phase of nestling ontogeny when female often exhibit disturbed behaviour, especially during cold days. Blood samples for molecular sexing (see below) were taken from each nestling by brachial vein puncture under the wing, around 14–21 days after hatching.

Prey abundance

The abundance of small mammals was assessed using snap-traps (baited with flour roasted on bacon). Trapping was carried out at the beginning of June each year by setting up snap-traps in

Table 1. Prey abundance index (expressed by number of trapped individuals per 100 trap nights) of separate prey groups, number of nests and number of nestlings measured in each study year. Means (per one hectare trapping area or nest) ± SE are shown.

Year	*Apodemus* mice	*Microtus* voles	*Sorex* shrews	Pooled prey abundance	No. nests	No. nestlings per nest
2006	0.00	0.28 ± 0.16	0.00	0.28 ± 0.16	9	3.33 ±0.29
2008	0.64 ± 0.24	0.09 ± 0.09	0.18 ± 0.18	0.92 ± 0.37	6	3.17 ± 0.48
2009	0.28 ± 0.00	0.64 ± 0.24	0.00	0.92 ± 0.24	7	2.00 ± 0.22
2010	3.49 ± 1.30	1.93 ± 0.64	0.09 ± 0.09	5.51 ± 1.88	6	5.83 ± 0.75
2011	0.00	0.18 ± 0.09	0.00	0.18 ± 0.09	5	2.00 ± 0.55
2012	1.56 ± 0.60	0.28 ± 0.16	0.28 ± 0.16	2.11 ± 0.72	2	5.00 ± 0.00
2014	0.28 ± 0.28	0.09 ± 0.28	0.09 ± 0.09	0.46 ± 0.24	8	2.38 ± 0.46

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three one-hectare areas (11 × 11 trap grid; span of 10 m). The traps were left out for three days and checked every morning. We calculated the abundance index of small mammals as the number of captured individuals per 100 trap nights in each trapping area. All captured mammals (n = 186 individuals, 7 years) were identified to species level and grouped into three prey categories according to the Tengmalm's owl diet: *Microtus* voles (field vole *M*. *agrestis*, common vole *M*. *arvalis* and European pine vole *M*. *subterraneus*), *Apodemus* mice (yellow-necked mouse *A*. *flavicollis* and wood mouse *A*. *sylvaticus*), and *Sorex* shrews (common shrew *S*. *araneus* and pygmy shrew *S*. *minutus*) (for details see [34,41]).

Laboratory work

Sex identification from blood samples was carried out using molecular biology techniques involving PCR with primers related to the CHD gene [42]. Genomic DNA from blood samples was extracted by alkaline lysis following a neutralization step [43]. A small amount (3–5 μl) of blood suspension in 96% ethanol was briefly spun down, alcohol was decanted and samples were dried out at room temperature. Into each sample, 50 μl of alkaline lysis buffer (25 mM NaOH, 0.2 mM disodium EDTA, pH 12) was added and heated to 96°C for 10 min. The samples were then cooled down on ice and 50 μl of neutralization buffer (40 mM Tris-HCl, pH 5) was added. As a template for PCR, 1–2 μl of mixture was used. Alternatively, the Chelex100 Resin (BioRad) DNA extraction method can also be used [44]. The 150 μl of 5% Chelex100 solution in sterile water was mixed in a microcentrifuge tube with the blood sample, briefly vortexed and incubated at 56°C for 30 min. After another vortexing followed an 8 min incubation step at 96°C, and samples were then vortexed again. The final step was centrifugation at 10 000 g for 10 min. The supernatant was directly used as a template for PCR. Each PCR reaction was performed in 20 μl. We used the primers 2550F(5'-GTTACTGATTCGTCTACGAGA-3') and 2718R (5'-ATTGAAATGATCCAGTGCTTG-3'), as described by Fridolfsson and Ellegren [42]. The PCR mastermix was prepared according to the Taq DNAPolymerase (NewEngland Biolabs) manufacturer's guidelines. The PCR conditions were optimized to initial denaturation for 5 min at 95°C, followed by 29 cycles of denaturation at 95°C for 30 s, annealing at 60°C for 40 s, an extension at 72°C for 1 min 10 s, and a final extension at 72°C for 5 min. At the end of the PCR program, the amplified samples were loaded into wells on agarose gel (1% w/v) stained with ethidium bromide. Bands along the DNA molecular marker were detected and photographs taken under UV light. In Tengmalm's owl, this pair of primers produces a single Z-band (700 bp) in males, and Z- (700 bp) and W- (1200 bp) bands in females [45].

Statistical analyses

We ran GLMM Gaussian models with an identity link function for testing the effect of (i) year, (ii) brood size, (iii) hatching order and (iv) sex on body mass and wing length (dependent variables) data using R software, version 3.02 [46]. The distribution of dependent variables did not differ from the Gaussian distribution (Kolmogorov-Smirnov tests, *P* at least 0.4). A data unit was represented by each measurement; we used nestling individual (n = 137 individuals; categorical data) and nest (n = 43; categorical data) as random factors, and age of nestling (1–42 days; continuous data) as a covariate. Hatching order (1–2, 3–4, 5–8; categorical data), sex (male/female; categorical data), brood size (1–8; continuous data) and year (n = 7; categorical data) were used as independent (tested) variables. We used factor year in GLMM analysis instead of direct prey abundances to eliminate pseudoreplications and more detailed analyses on our first prediction are described below. We used the following model formula: lmer (dependent variable ~ age of nestling + tested factors + (1| nestling individual) + (1|nest box)). Statistical significance was obtained by comparing each model with previous model using the anova command, starting with comparison of first model with factor with null model without factors. We used forward selection, factors were added to the model based on Akaike's information criterion (AIC) using Akaike's weights. Percentages of variability explained by the tested factors were computed as the ratio between decrease of deviance of each model and previous model. We also show the values of the Chi-squared statistic. Because body mass was not meaningful to show standing alone, we present results of above mentioned analysis as body mass increase per day (g/day). Post-hoc comparisons of changes in daily increase of body mass among years and hatching order categories were calculated in R software using glht function.

To support above mentioned models, we also calculated growth and showed parameters for each year, hatching order group and sex using logistic growth curves fitted by non-linear regression based on the formula $y = A / (1 + e ^ (-K \times (x - T_i))$ (Starck and Ricklefs [47], where y is nestling body mass, x is nestling age, A is an asymptotic—maximal—value, K is growth rate, and T_i is the inflexion point). Iterations were carried out using non-linear estimation in Statistica v. 12. 9 [48]. Using this software, we also calculated linear regressions for particular relationships between the above-mentioned parameters of the growth curve and prey abundance (*Microtus* voles, *Apodemus* mice, and pooled prey abundance index, which included *Microtus* voles, *Apodemus* mice and *Sorex* shrews). We present all relevant data used in the analyses in (S1 Dataset).

Results

The abundance index of the most frequent prey groups of Tengmalm's owl in our study area varied among years: *Apodemus* mice were the most abundant prey group overall and had the most pronounced between-year fluctuations (mean ± SE; 1.14 ± 1.57 individuals per 100 trap nights), followed by *Microtus* voles (0.48 ± 0.59 individuals per 100 trap nights), and *Sorex* shrews (0.14 ± 0.18 individuals per 100 trap nights) (Table 1).

We found that nestling body mass, controlled for age, significantly varied among study years, hatching order groups and sexes (Table 2). Daily increase of body mass among years varied between 4.4 and 6.5 (mean ± SE, 5.4 ± 0.2, Post-hoc Tukey test, minimal $p < 0.01$ between maximum and minimum in the years 2008 and 2011, respectively). Within a brood, the older nestlings reached a larger daily body mass increase (min-max: 5.2–5.5, mean ± SE; 5.4 ± 0.1, Post-hoc Tukey test, minimal $p = 0.07$ between first and last age categories). Body mass increase was higher in females compared to males (5.7 ± 0.1 and 5.2 ± 0.1, respectively). These results can be also supported by comparing growth parameters between above mentioned categories; early hatched young showed higher asymptote and inflexion point, and lower growth rate than late hatched young (Table 3). Similarly, females reached higher asymptote and inflection point, and lower growth rate than males (Table 3). After hatching (1–3 d after hatching), females were on average 2.1 g (n = 11 individuals) heavier than males, and they were also 8.2 g (n = 52 individuals) heavier during the fledging period (i.e., 30–36 d after hatching; Fig 1). Brood size was not recommended to be added to the model using the AIC criterion. Similarly,

Table 2. Effects of the tested factors on nestling body mass, based on Gaussian GLMM models with nestling age as covariate and nestling individual and nest as random factors (n = 137 nestlings from 43 broods). Explained variability is shown in cumulative way.

Model	Explained variability (%)	DF	Chi	p
Mass ~ Year	0.6	236	24.1	< 0.01
Mass ~ Year + Sex	0.7	235	7.3	< 0.01
Mass ~ Year + Sex + Hatching order group	0.9	233	8.3	0.02

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Table 3. Parameters of the growth curve for Tengmalm's owl nestlings related to year, hatching order and the sex of nestlings. The asymptote (maximal body mass), inflection point and growth rate are shown (n = number of nestlings measured; n_m = number of measurements).

	Asymptote (g)	Inflection point (days)	Growth rate	n	n_m
Hatching order					
1–2	131.7	10.1	0.24	80	229
3–4	126.9	9.6	0.23	41	137
5–8	123.6	9.4	0.28	16	52
Sex					
Female	134.6	10.1	0.22	62	195
Male	124.8	9.6	0.27	75	223
Year					
2006	135.0	9.8	0.21	30	100
2008	150.4	10.8	0.23	19	26
2009	142.7	11.1	0.20	14	42
2010	125.8	13.5	0.78	35	116
2011	115.4	11.1	0.26	10	28
2012	123.7	14.3	0.45	10	32
2014	130.1	10. 7	0.25	19	74

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no factor was recommended to be added to the model when nestling wing length was a dependent variable.

Further analyses on growth parameters showed that growth rate was positively correlated with *Apodemus* mouse index (regressions, n = 7 years: beta = 0.979, $F = 114.25$, $p < 0.01$; Fig 2A), *Microtus* vole index (beta = 0.862, $F = 14.464$, p = 0.01; Fig 2B) and pooled prey abundance index (beta = 0.980, $F = 119.94$, $p < 0.01$; Fig 2C). Inflection point was positively correlated with *Apodemus* mouse index (beta = 0.799, $F = 8.818$, p = 0.03; Fig 2D) and pooled prey abundance index (beta = 0.864, $F = 14.764$, p = 0.01; Fig 2F). No relationship was found between inflection point and *Microtus* vole index (beta = 0.521, $F = 1.862$, p = 0.23; Fig 2E) or *Sorex* shrew index (beta = 0.645, $F = 3.556$, p = 0.12), nor growth rate and *Sorex* shrew index (beta = 0.314, $F = 0.546$, p = 0.50). Finally, the yearly asymptote of body mass was not related to the abundance of any prey group index (*Apodemus* mice, beta = –0.22, $F = 0.244$, p = 0.64; *Microtus* voles, beta = –0.16, $F = 0.14$, p = 0.73; *Sorex* shrews, beta = 0.058, $F = 0.017$, p = 0.90; pooled prey abundance index, beta = –0.30, $F = 0.486$, p = 0.52).

Discussion

Body mass

In accordance with our first hypothesis, we found that the body mass of nestlings controlled for age varied among years. Simultaneously, the yearly growth rate and inflection point increased (i.e., nestlings grew faster and for a longer period) with increasing prey abundance index. This effect was most pronounced during the peak years of *Apodemus* mice and *Microtus* voles. No relationship was found between the asymptote of nestling body growth (i.e. maximal nestling mass) and prey abundance index. Eldegard & Sonerud [10] documented that supplemental feeding led to parental allocation of food for self-maintenance rather than to higher body mass of Tengmalm's owl nestlings. On the other hand, Hipkiss et al. [3] showed that the asymptote of Tengmalm's owl nestling body mass increased in experimentally fed broods, but no relationship was found between the rate of mass gain and food supplementation. In this light, Kouba et al. [49] demonstrated that Tengmalm's owl parents produced nestlings with

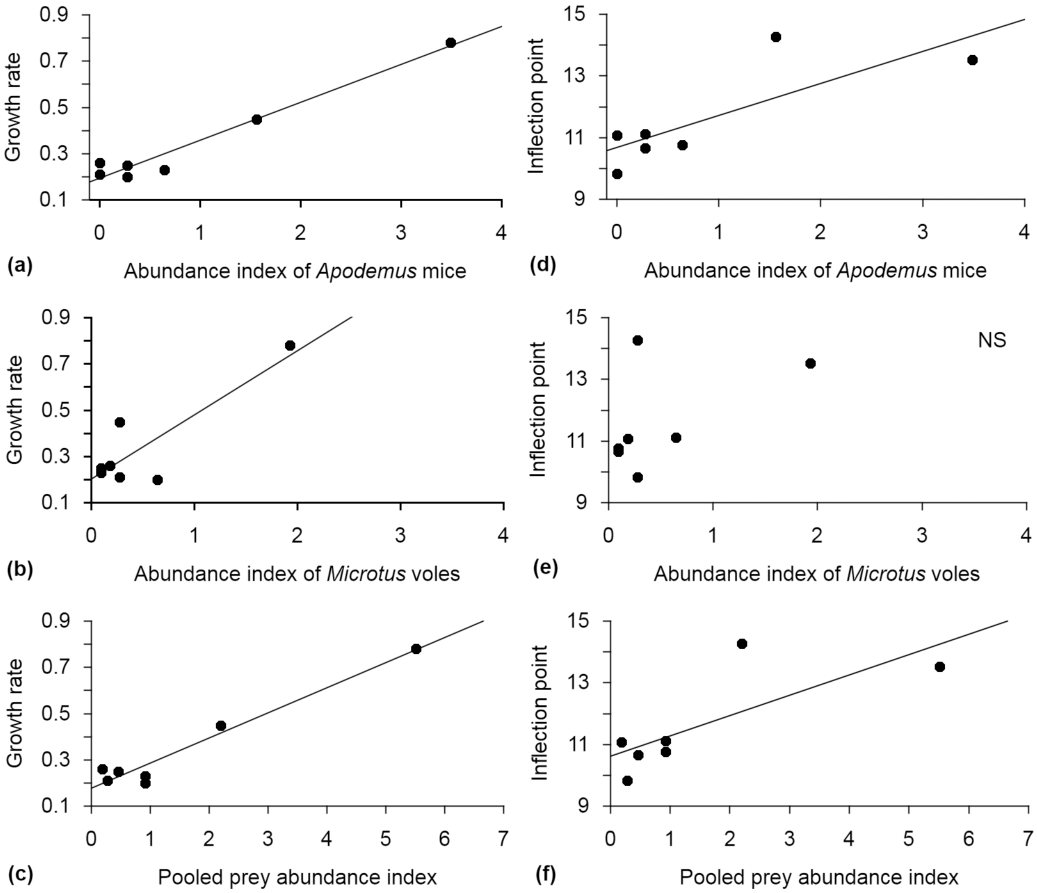

Fig 1. Relationships between the growth rate of Tengmalm's owl nestlings and prey abundance index (number of individuals per 100 trap nights) of Apodemus mice (a), Microtus voles (b) and index of pooled prey abundance (c), and the relationship between the inflection point of Tengmalm's owl nestlings and prey abundance index of Apodemus mice (d), Microtus voles (e) and index of pooled prey abundance (f). Lines denote curves fitted by regression.

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different body mass during a two-year period with extremely different prey abundance (*Apodemus* mouse peak compared to a poor rodent year), but Valkama et al. [16] found that the body condition (expressed by residuals of the regression between body mass and wing length) of fledged Tengmalm's owlets was not associated with the phase of the vole cycle. Similarly inconsistent results were documented in other owl species, e.g. supplementary food resources have been found to affect the growth rate of little owl *Athene noctua*, burrowing owl *Athene cunicularia* or Ural owl *Strix uralensis* nestlings [4,12,19], however, the body condition of Montagu's harrier *Circus pygargus* during fledging (expressed by the difference between measured body mass and the asymptotic body mass) did not vary according to vole cycles [30]. We suggest that the body mass of the Tengmalm's owl nestlings in a temperate areas varies under natural prey abundance, but other factors, such as clutch size adjustment by females [50,51], the feeding effort of males [52,53], or variable environmental conditions (e.g. the night length which can limit foraging time of owls, as well as the level of interspecific competition with other vole-eating predators [50,54]), may play important roles.

The body mass of nestlings can be affected by brood size. For example, Eurasian kestrel *Falco tinnunculus* nestlings showed increased mortality and reduced growth rate when broods were experimentally enlarged, even when parents increased their hunting effort [22]. Similarly,

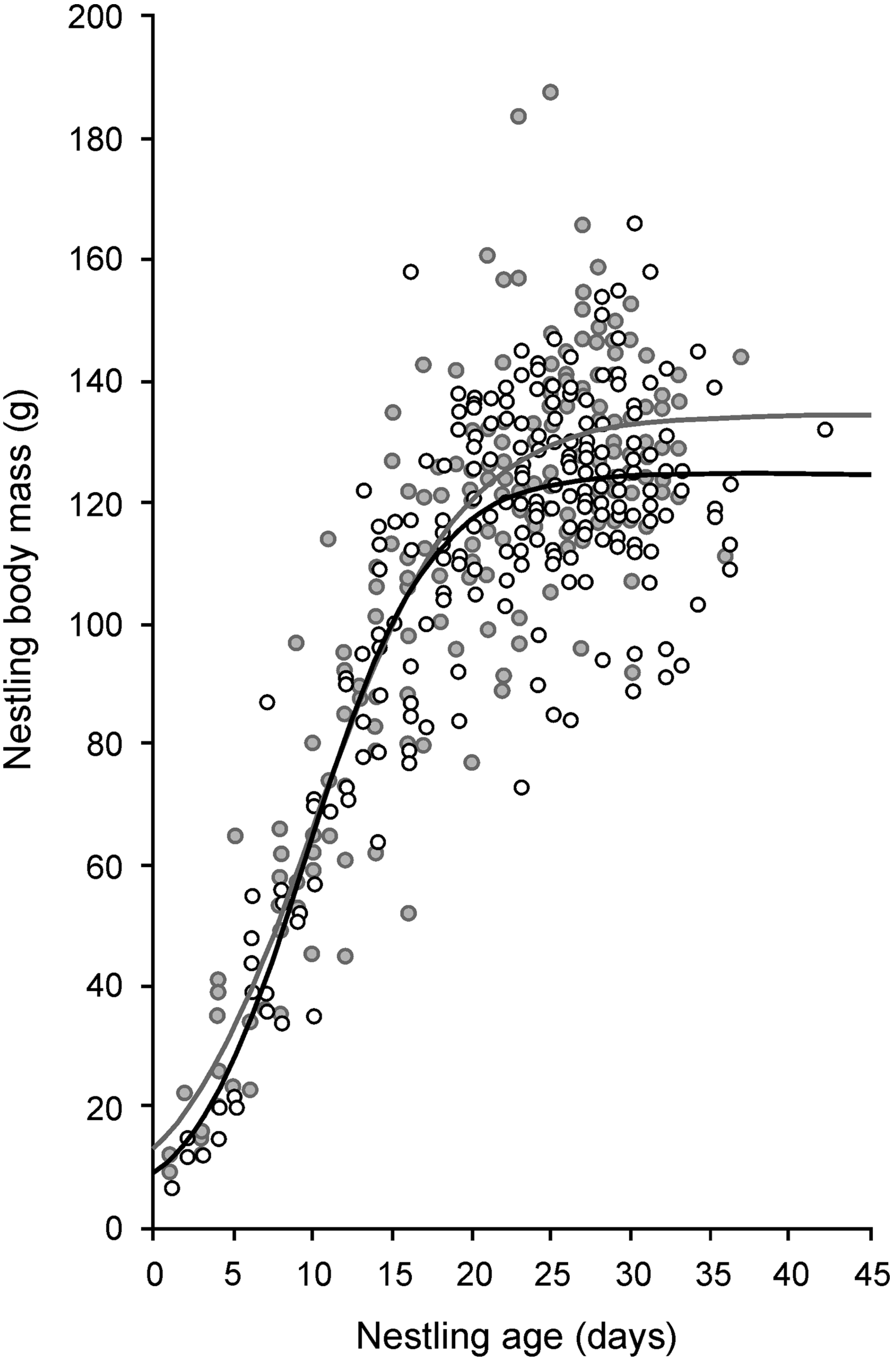
Nestling body mass (g)
0
20
40
60
80
100
120
140
160
180
200
Nestling age (days)
0
5
10
15
20
25
30
35
40
45

Fig 2. Logistic growth curve for body mass of male (n = 75 individuals) and female (n = 62 individuals) Tengmalm's owl nestlings. Open circles and black line represent males; filled circles and grey line represent females. Formula for females: $y = 134.62 / (1 + e^{\wedge} (-0.22 \times (x - 10.19)))$; formula for males: $y = 124.80 / (1 + e^{\wedge} (-0.27 \times (x - 9.61)))$.

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experimental brood enlargement in barn owl *Tyto alba* led to increased nestling mortality and decreased body mass of the surviving male and female nestlings [24]. Also, in a northern population of Tengmalm's owl, nestlings in larger broods suffered from higher mortality and fledglings from larger broods tended to reach a lower mass than those in reduced or control broods [16,55]. We found no effect of brood size on nestling body mass in the natural environments of this temperate Tengmalm's owl population, thus rejecting our second hypothesis. Tengmalm's owl females in temperate areas adjusted their clutch size better than females in northern areas, where prey availability is less predictable, which can lead to a clutch size larger than optimal and increased nestling mortality [50]. In light of the mentioned effect of latitude, we suggest that no effect of brood size on nestling body mass was found in our study population because females adjusted their clutch and brood size depending on prey availability.

In agreement with our third hypothesis, we found that early-hatched nestlings reached a larger body mass, and showed higher asymptote and inflection point, compared to late-hatched nestlings. Similarly, in Montagu's harrier, Arroyo et al. [30] found the poorest fledgling condition in the youngest nestlings. Also, in other owl species (e.g., little owl, burrowing owl, Ural owl), hatching order has been found to affect growth rate [4,12,19]. In our study, late-hatched nestlings suffered from poor body condition, supporting that hatching asynchrony in Tengmalm's owl is an adaptive way to optimize brood size under varying environmental conditions (see also [16]).

In keeping with our fourth hypothesis, we found that female nestlings reached a higher body mass than male nestlings during their time in the nest, and thus a higher asymptote and inflexion point was found in females compared to males. This finding corresponds with the results of Hipkiss et al. [3], who suggested that the female's larger size gives them a competitive advantage over their male siblings during fights over food items [56].

Wing length

Despite adult female Tengmalm's owls having slightly longer wings than males, no male-female difference in wing length was found in nestlings. Similarly, in marsh harrier *Circus aeruginosus*, Krijgsveld et al. [28] found no difference between the sexes in wing length, although female fledglings were heavier than males. Our results also agree with the finding of Hipkiss et al. [3] that juvenile Tengmalm's owl females require more time to fully develop their wings than males. Furthermore, we found no effect of year, brood size, hatching order or prey abundance index on the wing length of nestlings. These findings are in contrast to the two-year study performed in the same study area by Kouba et al. [49], in which owl parents produced nestlings with longer wings during an *Apodemus* peak year (2010), compared to a poor rodent year (2011). In our seven-year dataset (2006–2014, excluding 2007 and 2013), we recorded no occurrence of extremely high prey abundance, except in one year (2010). The disunity of these results indicates that wing length can differ under extremely different food conditions, but the differences are not pronounced when food availability is relatively stable. This finding is quite unexpected, because the individual duration of nestling periods is related to wing length rather than body mass, sex, prey abundance index or weather conditions [5].

Conclusions

No factor affected wing length growth, while the body mass of nestlings controlled for age varied among years, hatching order groups and sexes. Growth parameters were affected by prey abundance and also differed between sexes and with hatching order. Thus, the body mass of nestlings seems to be more sensitive than wing length to environmental factors. The latter is probably controlled more by the physiology of the species.

Supporting Information

S1 Dataset. Relevant data used in the analyses.
(PDF)

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Author Contributions

Conceived and designed the experiments: MZ. Performed the experiments: MZ JR. Analyzed the data: JR MZ. Contributed reagents/materials/analysis tools: MZ JS MK JH AP PM VT KS. Wrote the paper: MZ JR. DNA analyses: LB.

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