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Přírodovědecká fakulta

**Šelmy v městském prostředí: studium rozšíření, habitatových
preferencí a vybraných aspektů prostorové ekologie**

diplomová práce

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ANOTACE:

This study provides an insight into carnivores' responses to urban conditions. The main goal of this study is to examine changes of population densities and home range sizes of eight mesocarnivore species along the gradient from natural to urbanized habitats by gathering and assessing available data.

Prohlašuji, že svoji diplomovou práci jsem vypracoval/a samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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**Density-dependent variation in home range size of carnivores
along the gradient from natural to urbanized habitats.**

Drahníková L., Tkadlec E., Šálek M.

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Úvod

Člověkem iniciovaná přeměna volné krajiny na urbánní prostředí, tzv. urbanizace, je jeden z nejvýznamnějších krajinnotvorných činitelů současnosti (Pickett 2001, Piorr et al. 2011). Gradace rychlosti rozvoje tohoto trendu je patrná z populačních predikcí, které ukazují, že již v roce 2009 překročil poměr světové populace žijící ve městech hranici 50 % a překonání hranice 60 % se očekává v roce 2030 (WUP 2009). V České republice dosahuje současná míra urbanizace 73,5 % a do roku 2040 se očekává nárůst k 80 % (WUP 2009). Tato přeměna krajiny na obytná, komerční a průmyslově využívaná území významně ovlivňuje strukturu a funkci ekosystému (Niemelä 1999) a vede bezpodmínečně k fragmentaci, degradaci a ztrátě původních habitatů nejen na regionální, ale i globální úrovni (Vitousek et al. 1997, Pickett et al. 2001, Crooks 2002).

V současnosti se proto do popředí dostává obor městské ekologie, který zabývá se distribucí, početností a vzájemnými vztahy druhů městských oblastí a biogeochemickou rovnováhou městských ekosystémů (Pickett et al. 2001). Městský ekosystém se vyznačuje především vysokou populační hustotou obyvatel či vysokým podílem zemského povrchu zakrytého infrastrukturou a zástavbou (McIntyre 2000, Pickett et al. 2001, Shochat et al. 2006). Pojem městská oblast zahrnuje nejen městské jádro, ale i příměstské oblasti, periferie, vesnice propojené dopravními koridory a okolní vesnické oblasti přímo ovlivněné energetikou a produkcí města (Pickett et al. 2001). Z důvodu funkčního propojení dokáže teprve komplexní pojetí popsat plný rozsah, dopady a limity urbanizačních změn. Vliv urbanizace na ekosystém za hranicemi zastavěného území města je navíc značně posílen expanzí příměstských obytných zón do přilehlých zemědělských oblastí (Makse et al. 1995, Gordon & Richardson 1997). Původní kompaktní jednotky měst se vlivem tohoto expanzivního fenoménu tzv. „urban sprawl“, mění v rozlehlá uskupení fraktálního charakteru, díky čemuž větší měrou funkčně hraničí s ekosystémy okolní krajiny (Kasanko et al. 2006) a ovlivňuje je všemi aspekty urbánnímu prostředí, mezi něž patří především pozměněné světelné, povrchové, hlukové, hydrologické a klimatické podmínky (Collins et al. 2000, Kasanko et al. 2006).

Urbanizace jako jedna z hlavních příčin fragmentace a následné ztráty původního habitatu

vede k poklesu biodiverzity jak na lokální, tak globální úrovni (Vitousek et al. 1997, Crooks 2002, McKinney 2002, Riley et al. 2003, Faaborg et al. 2003, Angold et al. 2006, Czech 2005). Zbytkové přirozené a polopřirozené habitaty v městské oblasti jsou obvykle určitou měrou degradovány vlivem znečištění, dopravy a dalších lidských aktivit (McKinney 2008).

Směrem k centru města klesá plocha dochovaných původních habitatů a naopak roste míra fragmentace habitatu (Medley et al. 1995, Blair 1999, McKinney 2002) a lidské aktivity (Niemelä 1999, McKinney 2002), díky čemuž po gradientu urbanizace klesá využitelnost urbánního prostředí pro jednotlivé druhy bioty (McKinney 2002). Směrem k centru města proto obvykle dochází k poklesu diverzity jednotlivých taxonomických skupin (Blair 1996, Blair 1999, Germaine & Wakeling 2001, McKinney 2002).

Rychlý rozvoj urbanizace a velký prostorový záběr urbánního prostředí však v současné době nutí biotu k adaptaci na urbánní podmínky a osídlení města (Luniak 2004). Ačkoliv urbanizace ničí původní habitaty, vytváří ve stejný okamžik škálu nových volných ekologických nik (Luniak 2004), čímž se městská oblast stává v porovnání s přilehlými intenzivně zemědělsky využívanými plochami prostředím s poměrně širokou nabídkou habitatů (Rebele 1994, Cadenasso et al. 2007, Pautasso 2007), které jsou příhodné pro rozličné skupiny bioty (Carrier and Beebee 2003, McFrederick and LeBuhn 2006, Møller 2009, Bateman and Fleming 2012, Møller et al. 2012). Schopnost druhu využít urbánní prostředí závisí na životní strategii, citlivosti k disturbancím a mezidruhových interakcích jednotlivých taxonů (Dickman & Doncaster 1987, Dickman & Doncaster 1989), kdy nezbytným předpokladem pro úspěšnou kolonizaci městského prostředí, je ekologická, demografická a behaviorální plasticita druhu a obzvláště široká tolerance v rámci potravního a habitatového spektra (Luniak 2004). Úspěšná adaptace zvířat na specifika městského prostředí, tzv. synurbanizace (Andrezejewski et al. 1978, Luniak 2004), je z taxonu obratlovců nejčastěji popsána pro ptačí a savčí skupiny (Fleischer et al. 2003, Møller 2008, Herr et al. 2009), ale je známa i pro obojživelníky (Parris 2006) a plazy (Germaine & Wakeling 2001). Proces urbánní adaptace často vede k mnohým změnám ekologických, behaviorálních a morfologických parametrů u urbánních populací v porovnání s populacemi stejného druhu ve volné krajině (Luniak 2004).

Posun aktivity městských populací v průběhu dne směrem k soumravné až noční lze chápat jako snahu vyhnout se zvýšené lidské aktivitě (Ditchkoff et al. 2006). Umělé světlo

ovlivňuje orientaci živočichů způsobem jak matoucím (Ogden 1996, Hill 1990), tak odpudivým (Beier 1995) či jako atraktant (Wiese et al. 2001). Omezené vnímání fáze měsíce může znemožnit živočichům řídit se přirozeným lunárním cyklem (Gehrt 2010). Kumulace kořisti kolem světelného zdroje má pak vliv na prediční vztahy (Svensson & Rydell 1998).

Zvýšená hladina hluku může vést u městských populací ptactva ke změně hlasové frekvence (Slabbekoorn & Peet 2003) či k omezení vokální komunikace (Estes & Mannan 2003).

Obzvláště v zimním období tvoří pro některé urbánní ptačí a savčí druhy významnou složku potravy antropogenní zdroje, což spolu s nezamrzlými zdroji vody a příznivým mikroklimatem podporuje omezené migrační chování (Able & Belthoff 1998, Luniak 2004). Jedinci urbánních populací mívají sníženou útěkovou vzdálenost vůči člověku, či dokonce člověka aktivně vyhledávají za účelem zisku potravy (Luniak 2004).

Absence migrace, bohaté potravní zdroje a mírné klima ovlivňují pozitivně délku života. Nižší výskyt přirozených predátorů v městském prostředí (Etter et al. 2002) však bývá kompenzován vlivem domestikovaných predátorů a celkový urbánní prediční tlak tak může být vyšší než v okolní krajině (Lepczyk et al., 2003, Baker et al. 2008, Koenig et al. 2002). Mezi nejčastější příčiny mortality v městských oblastech patří srážky s motorovými vozidly (Forman & Alexander 1998, Etter et al. 2002), dráty vysokého napětí či prosklenými panely (Luniak 2004). Mortalita vzrůstá i díky vyššímu výskytu endo- i ektoparazitů ve městech (Bradley & Altizer 2006) a četným epidemiím člověkem pozměněných patogenů (Estes & Mannan 2003).

Důsledkem rozvoje adaptací pro urbánní kolonizaci je rychlá mikroevoluce městských populací ve smyslu specifické formy selekce na základě typu disturbancí v městském prostředí (Stockwell et al. 2003) a genetické izolace (Slabbekoorn & Peet 2003). Otázka genetické identity městských populací však není stále dostatečně objasněna.

V porovnání s ostatními taxony jsou šelmy obecně považovány za taxon obtížně reagující na změněné vnější podmínky, a to díky svým vysokým prostorovým nárokům, potravní specializaci, reprodukční strategii a pronásledování člověkem (Woodroffe 2000, Gittleman et al. 2001, Matthiae & Stearns 1981). Přesto některé dostatečně flexibilní druhy mesocarnivorů jsou schopné se adaptovat na urbánní prostředí a využít jeho specifika ve svůj prospěch (McKinney 2002, Fuller et al. 2010, Bateman and Fleming 2012). Mezi těmito

druhy převažují malé nebo středně velké šelmy, které jsou potravními generalisty (Sorace & Gustin 2009, Iossa et al. 2010), tolerantní k fragmentaci habitatu i lidským aktivitám (Crooks 2002, Bateman and Fleming 2012) a schopné lovit samostatně mimo smečku (Iossa et al. 2010). Pro taxon šelem představuje nejpodstatnější výhodu městského prostředí kontinuální nabídka potravy, a to převážně z antropogenních zdrojů (tj. odpadky, úroda, záměrné krmení), ale i v podobě početných městských populací synantropních hlodavců (Doncaster et al. 1990, Saunders et al. 1993, Contesse et al. 2004, Kaneko et al. 2006). Spolu s příznivými mikroklimatickými a hydrologickými podmínkami, nabídkou vhodných úkrytů (Prange et al 2003, Kaneko et al. 2006, O'Donnell and DeNicola 2006) a sníženým pronásledováním člověkem tvoří podněty pro přizpůsobení ekologických charakteristik městských populací, jako je velikost domovského okrsku, populační hustota či rozložení denní aktivity (Bateman and Flemming 2012, Davison et al. 2009).

Osidlování městského prostředí tak specifickým taxonem, jako jsou šelmy, s sebou nese rozporuplné otázky v tématice dalšího vývoje procesu kolonizace, ochrany, managementu či omezení urbánních populací šelem a pro jejichž rozřešení je nutno dalšího zkoumání. Přiložená studie je komplexním zhodnocením trendů ve vybraných populačních parametrech městských šelem.

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Density-dependent variation in home range size of carnivores along the gradient from natural to urbanized habitats

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Abstract

With rapid development and spread of urbanized land, there is an increasing interest in studying species responses to urban conditions. Carnivores are commonly considered to be sensitive to urbanization; however, there is massive evidence that several mesocarnivores successfully inhabited urban conditions, and human-modified habitats have been recently recognized as an important refuge for several species. Despite increasing number of studies about urban carnivore ecology, no comprehensive cross-species comparisons have been made to assess the effects of urbanization on carnivore spatial ecology and population density. Such a review could provide interesting insight into how some carnivore species respond to urban conditions. In this paper, we examine changes of population density and home range size of eight mesocarnivore species within natural-urban gradient by reviewing 412 articles across their distribution range. In general, we demonstrated that home range size of the carnivore species decreased (significantly in 6 species out of 8 species examined) and population density increased (significantly in 3 species out of 6 species examined) along the natural-urban environmental gradient. This density dependent pattern of variation in home range size was consistent across all species studied. In addition, we reviewed main ideas attempting to explain the observed spatial pattern in carnivore distribution. Our results emphasize the remarkable ability of some carnivores to adapt to novel environment through their behavioural flexibility and life-history modifications. We also outlined further possible research routes that could be useful when addressing this recent phenomenon, namely comparative approaches and detailed studies of biotic and abiotic conditions along natural-urban gradient.

Introduction

The anthropogenic conversion of natural/semi-natural habitats into urbanized land (human-made environments) is a major cause of land-use changes worldwide (Pickett 2001, Piorr et al. 2011) and seriously affects ecosystem structure and function (Niemelä 1999). Expansion of urban habitats to rural landscape is expected to grow during the 21st century, with prediction of increase from current 49 % to 70% of world's human population inhabiting the urban environment by 2050 (United Nations 2004, UN-Habitat 2006, Thomas 2008). The urbanization has critical implications for biodiversity conservation, causing substantial loss, modification and fragmentation of natural habitats, which was identified as a major threat to local and global biodiversity (Vitousek et al. 1997, Crooks 2002, McKinney 2002, Riley et al. 2002, Faaborg et al. 2003, Angold et al. 2006, Czech 2005).

Habitat structure and resource availability for wildlife species change substantially across the urban-natural gradient (McDonnell & Pickett 1990, Blair 1996, McDonnell et al. 1997). When going from the natural or rural areas across suburbia with low-density housing to densely inhabited city centres, the gradient comprises high variation of abiotic factors, such as specific light, noise, hydrologic and climatic conditions (Collins et al. 2000, Kasanko et al. 2006), human intervention/activity/disturbances (Niemelä 1999, McKinney 2002) and/or intensity of habitat loss and fragmentation of natural habitats (Blair 1999, Medley et al. 1995, McKinney 2002). Moreover, the residual natural/seminatural habitats suffer from degradation because of pollution, traffic and other human activities (McKinney 2008), which affect species diversity, structure and ecology. Unlike intensively used agricultural ecosystems, the urban areas could offer higher array of ecological niches, abundant human-related food resources and/or high diversity of natural or novel anthropogenic habitats (Rebele 1994, Cadenasso et al. 2007, Pautasso 2007). Hence, as urbanization rapidly spreads, there is increasing evidence of multiple animal adaptations to specific urban conditions (Andrezejewski et al. 1978, Luniak 2004). As a result, the urban environment has been recently recognized as an important habitat for variety of wildlife taxa (Carrier & Beebe 2003, McFrederick & LeBuhn 2006, Møller 2009, Bateman & Fleming 2012, Møller et al. 2012).

Carnivores represent top mammalian predators commonly considered as sensitive to habitat loss and fragmentation because of their large spatial requirements, low reproduction

rate, diet specialization, or human persecution (Woodroffe 2000, Gittleman et al. 2001). These ecological characteristics makes them particularly vulnerable to human activities associated with urbanization causing their population declines or even local extinctions (Noss et al. 1996, Woodroffe & Ginsberg 1998, Crooks 2002, Crooks et al. 2011). Carnivores' response to urbanization could, however, significantly vary in the ability to live in human-modified habitats, depending on species-specific ecological or behavioural plasticity and life history (McKinney 2002, Fuller et al. 2010, Bateman & Fleming 2012). Successful colonization of urban environments has been recorded especially for mesocarnivores which exhibit high habitat and dietary flexibility and tolerance to human activity (Crooks 2002, Bateman & Fleming 2012) and these features seem to be crucial for carnivores to inhabit urban environments (*sensu* McKinney 2002, Fuller et al. 2010, Iossa et al. 2010).

Habitat composition and structure change importantly along the urban-natural gradient, thus affecting several ecological and demographical characteristics of carnivores at both intraspecific and interspecific level. For example, carnivores are able to exploit increased availability of food and shelter in urban areas by reducing their territoriality, which could reflect in higher population density and smaller home range sizes (Iossa et al. 2010, Bateman & Fleming 2012). Despite increasing numbers of studies focusing on various parts of urban carnivore ecology (Iossa et al. 2010, Bateman & Fleming 2012), no comprehensive cross-species comparison has been made to assess the effect of urbanization on carnivore spatial ecology. To fill this gap in knowledge, we reviewed literature data on home range size and population density of eight mesocarnivore species to explore the major patterns of variations in these parameters along the urban-natural gradient. Focussing on carnivores from Europe, North America and Australia, we show that their responses are uniform, which may have important implications for understanding of changes in carnivore ecology in all continents.

Material and Methods

Literature search

To compare changes in selected ecological parameters within urban-natural gradient we selected eight carnivore species which inhabit urban or suburban areas within their distribution range. In particular, we compiled data on home range size and population density patterns of red fox *Vulpes vulpes*, gray fox *Urocyon cinereoargenteus*, coyote *Canis latrans*, bobcat *Lynx rufus*, raccoon *Procyon lotor*, striped skunk *Mephitis mephitis*, Eurasian badger *Meles meles* and stone marten *Martes foina* (see Appendix 1). The primary search for references was carried out on Web of Science[®] and Google Scholar[™] using the following keywords: urban, suburban, city, rural, natural, home range, population density, (meso)carnivore, and names of carnivore species. We also used reference lists in publications already retrieved as an important information source for seeking out papers published earlier. In total, we collected 412 articles reporting data on home range size, population density and habitat type. We obtained 421 raw data on at least two of these variables for eight carnivores. Among these, there was a subset of 55 data rows with complete information on all 3 variables and 71 data rows with information on both home range size and population density (Table 1).

Table 1: The numbers of studies used for analysis of home range size and population density in eight carnivore species with respect to their habitats.

Species	Home-range studies	Density studies	Both home range and density studies
Red fox	85	39	7
Gray fox	18	7	8
Coyote	46	18	3
Bobcat	70	17	15
Raccoon	38	30	10
Stripped skunk	11	9	1
Eurasian badger	29	52	23
Stone marten	11	7	3

Urbanization gradient

To compare carnivore responses to urbanization we used three broad definitions of environmental habitat groups: urban, suburban and natural (see also McDonnell et al. 1997). Definition of selected habitats in the ecological literature and individual studies about carnivores significantly vary in each study and usually reflect national and cultural differences or even authors' subjective opinion in perceiving of each above-mentioned category (McIntyre et al. 2000). Moreover, we used these broad categories to stress the fact that many studies lack consistent terminology or do not contain any data on habitat composition (natural or artificial land-use) and human population density of the study areas (see also Chamberlain et al. 2008).

In general, human population density, traffic volume and percentage of built-up land increase whereas the proportions of natural habitats decrease in urban-natural gradient (Medley et al. 1995, McKinney 2002). Urban habitats consist mainly of land covered by buildings or impervious surfaces and contain the highest human population density. Suburban habitats are human-dominated areas on the periphery of urban areas forming

transitional zone between urban and natural environment, which are characterized by low or moderate-density development and human population density. Finally natural (rural) habitats are sparsely inhabited by humans and are mainly dominated by rural areas surrounded by an agricultural matrix. Urban and suburban environment, however, may considerably differ in land use and structure (e.g. proportion of green space, residential/industrial/commercial areas) from study to study. Similarly there are differences between non-urban habitats/landscapes due to geographical and regional variations in agricultural intensity and land-use composition. The category “natural habitats” used in our comparison thus contain broad spectrum of agricultural or forest dominated landscapes, which are, however, perceived as closest to carnivores’ original habitat.

Analysis of data

We analysed habitat-related variation in home range sizes by fitting ANOVA model using the categorical variable habitat with three levels as explained above: natural, suburban and urban. We used a function `aov` implemented in statistical program R (R Core Team 2012). Home range size was log-transformed prior to analysis to remove heterogeneity in data. The Fligner–Killeen (median) test of homogeneity of variances did not reject the null that the variances in each of the levels are same for any of the species. The same analytical approach was applied when testing habitat-related variation in population densities. However, lack of population density data over more habitat types prevented us from performing the analysis in the grey fox and bobcat. Because the relationship between home range size and population density was obviously nonlinear, we decided to choose the simplest approach based upon a log-log linear regression model which is the linearized form of a power function. This approach was justified by the analysis of residuals. We did not obtain enough data for fitting the model in the coyote, striped skunk and stone marten. Finally, we lumped together data from all carnivores to estimate the common regression line. Because the structure of data violated the assumption of data independence (data from the same species tend to be correlated), we fitted generalized linear mixed model as implemented in function `lmer` in R (Bates et al. 2012). Identity of species was used as the random effect on both intercept and slope to cope with non-independence of data within a species. We neglected the remaining non-independence of data stemming from phylogenetic relationships assuming that it is effectively small to be important. Both population density and home range size were log-transformed prior to analysis.

Results

Home range size in all investigated carnivores decreased along the natural–urban gradient (Figure 1). This decrease associated with habitat change was significant in 6 species (red fox: $F_{2,82} = 24.18$, $p < 0.001$; coyote: $F_{2,29} = 5.38$, $p = 0.010$; bobcat: $F_{2,49} = 6.72$, $p = 0.003$; raccoon: $F_{2,35} = 4.83$, $p = 0.014$; striped skunk: $F_{1,8} = 7.92$, $p = 0.023$; Eurasian badger: $F_{1,25} = 6.96$, $p = 0.014$) whereas responses of grey fox and stone marten was not so pronounced (grey fox: $F_{1,16} = 0.039$, $p = 0.84$; stone marten: $F_{1,9} = 1.99$, $p = 0.19$). On the contrary, population densities increased with the degree of urbanization in 3 of the 6 species examined (Figure 2) for which we had enough data for analysis (red fox: $F_{2,37} = 13.11$, $p < 0.001$; coyote: $F_{2,13} = 4.40$, $p = 0.035$; raccoon: $F_{2,28} = 12.01$, $p < 0.001$). In badger and stone marten, the pattern was consistent with other species, but not significant (Eurasian badger: $F_{1,50} = 0.51$, $p = 0.48$; stone marten: $F_{1,5} = 3.22$, $p = 0.13$). The opposite pattern observed in the skunk was not supported by statistical analysis (striped skunk: $F_{1,6} = 0.005$, $p = 0.95$).

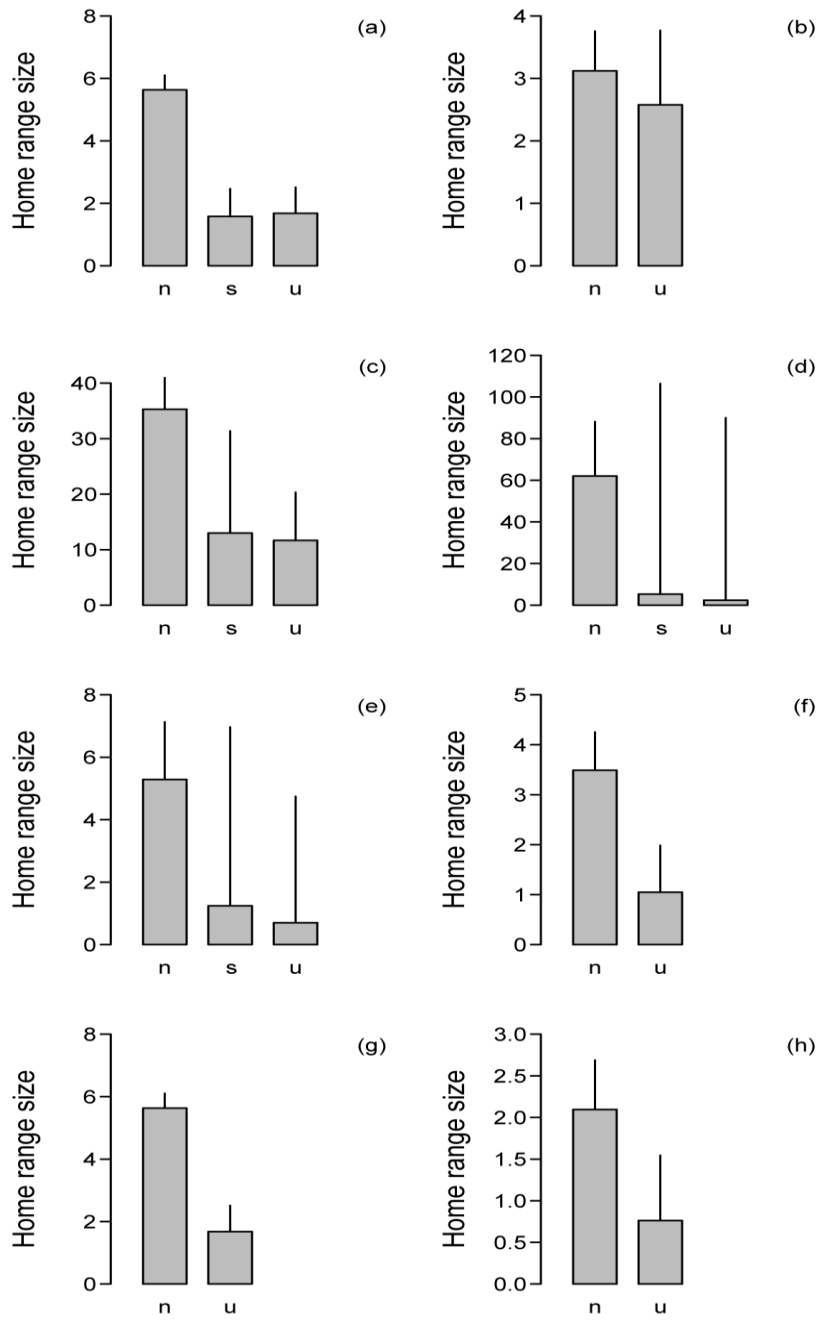


Figure 1. Mean home range sizes (km²) of red fox (a), grey fox (b), coyote (c), bobcat (d), raccoon (e), striped skunk (f), Eurasian badger (g), and stone marten (h) with respect to natural (n), suburban (s) and urban (u) habitats. The precision of estimates is indicated by 1 standard error.

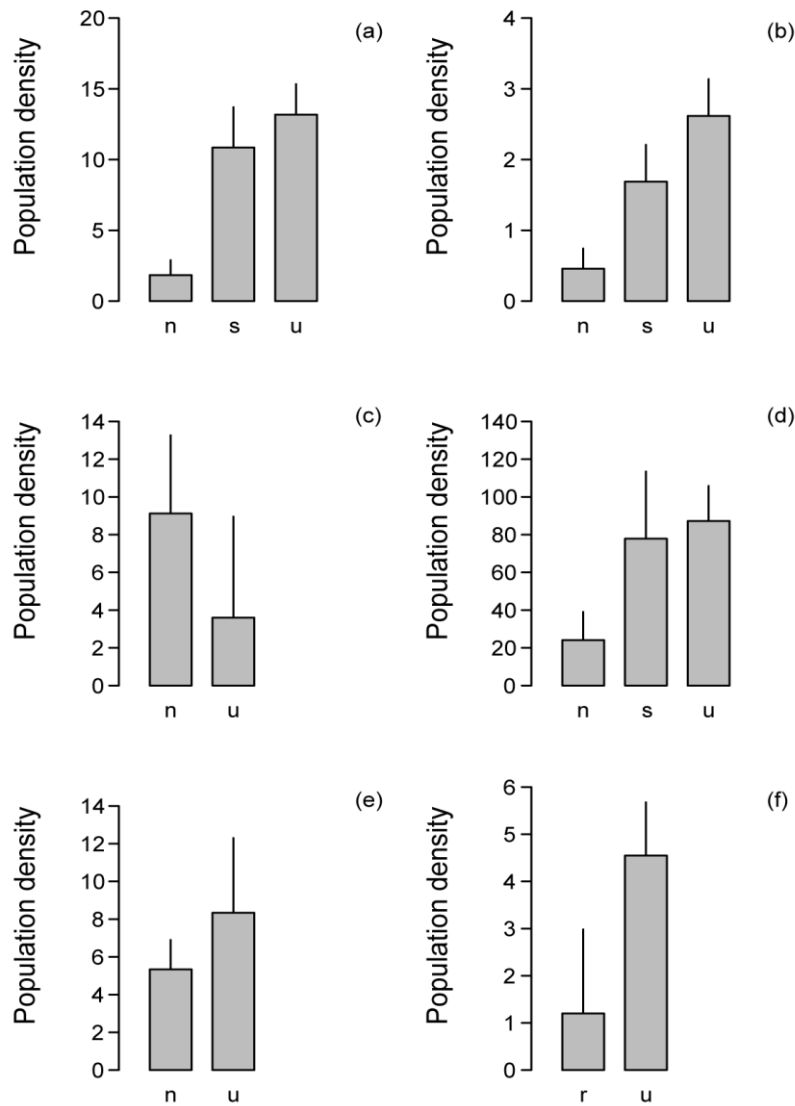


Figure 2. Mean population densities (ind.km⁻²) of red fox (a), coyote (b), , striped skunk (c), raccoon (d), Eurasian badger (e), and stone marten (f) with respect to natural (n), suburban (s) and urban (u) habitats. The precision of estimates is indicated by 1 standard error.

For 5 out of 8 carnivores, we assembled enough literature data to allow us to directly examine the effect of population density on home range size (Figure 3). In all of them, we observed the consistent negative pattern for population density–home range size relationship with statistical evidence for 4 of them (red fox: slope = -0.496 , 95% CI -0.966 to -0.025 ; bobcat: slope = -0.823 , 95% CI -1.134 to -0.511 ; raccoon: slope = -0.923 , 95% CI -1.323 to -0.524 ; Eurasian badger: slope = -0.593 , 95% CI -0.749 to -0.436). Regression slope in

the grey fox did not differ from zero (slope = -0.409 , 95% CI -1.387 to 0.568). When the data points from all carnivores were put together, a significant regression line was obtained (Figure 4) with a common slope of -0.642 (SE 0.0750 , $t = 8.56$).

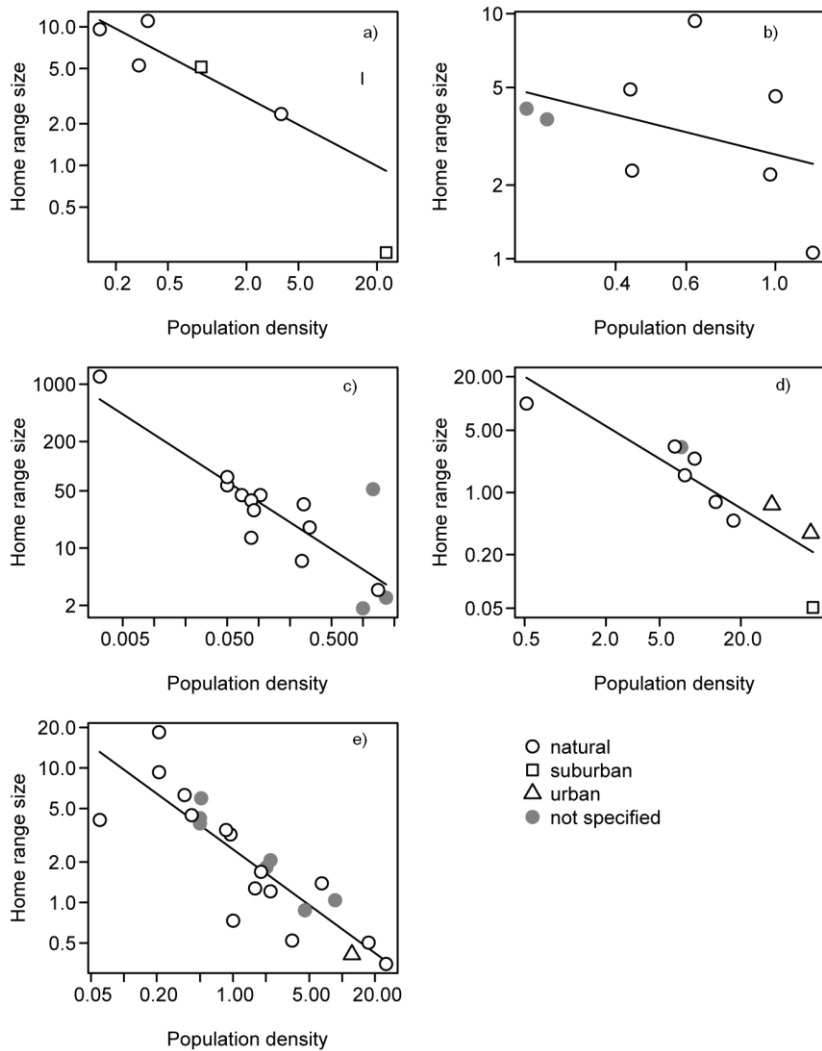


Figure 3. Relationships between home range size (km²) and population density (ind.km⁻²) as modelled in red fox (a), grey fox (b), bobcat (c), raccoon (d), and Eurasian badger (e) by fitting log-log linear regression model. Data are plotted on log scales. Different symbols indicate different habitat types.

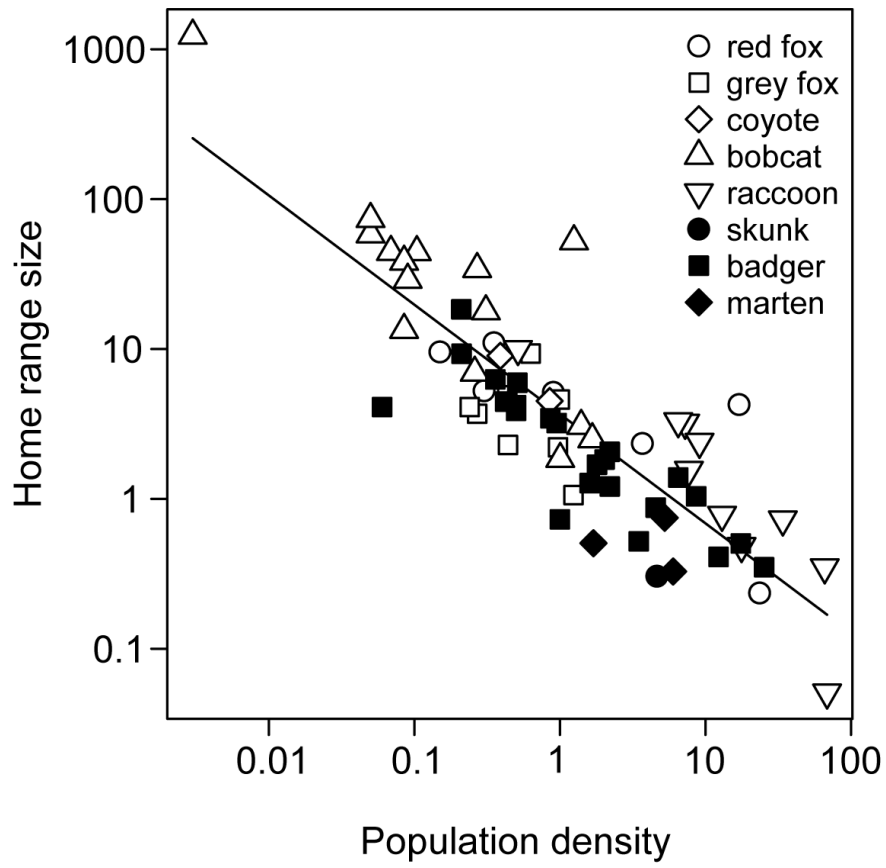


Figure 4. Relationship between home range size (km^2) and population density (ind.km^{-2}) for all carnivores plotted on log scales. Different symbols indicate different carnivores.

Discussion

Although we used data on home range size and population density from several carnivore species from a wide geographical range and broad environmental groups (urban, suburban, natural landscapes), the results of our analysis showed strong and consistent patterns across all species. In particular, we demonstrated that population density of the same carnivore species increased and home range size decreased along the natural-urban environmental gradient. Thus, although urbanization is one of the major causes of habitat loss and fragmentation for several animal species (Vitousek et al. 1997, Crook 2002, McKinney 2002, Riley et al. 2002, Faaborg et al. 2003, Angold et al. 2006) and previous studies considering large carnivores showed them to be particularly vulnerable to these aspects (Noss et al. 1996, Gittleman et al. 2001, Crooks 2002), our results indicates that several mesocarnivore species can successfully adapt to urban conditions through their behavioural flexibility and life-history modifications (see also Ditchkoff et al. 2006, Iossa et al. 2010, Bateman & Fleming 2012).

In accordance with previous studies (Iossa et al. 2010, Bateman & Fleming 2012), the results of our study showed increased population density (significantly in 3 species out of 6 species examined) of carnivores inhabiting urban environment. However, our conclusions are based on stronger evidence because of more comprehensive dataset. Bateman & Fleming (2012) pointed out that coyotes, red foxes, striped skunks, stone martens, Eurasian badgers and raccoons reach higher densities in urban compared to rural landscapes. In particular, carnivores inhabiting urban habitats may attain extremely high population densities as documented for several species, such as the red fox (37 individuals/km², Baker et al. 2001), raccoon (333 individuals/km², Smith & Engeman 2002), Eurasian badger (33 adults/km², Huck et al. 2008) or striped skunk (36 individuals/km², Rosatte et al. 2010). These densities exceed several times those observed in natural or semi-natural habitats. Similarly, despite considerable variation of home range size across studies, our comparison showed a general pattern of smaller home ranges in urban dwelling carnivore species (significantly in 6 out of 8 species examined). In contrast with our results, Iossa et al. (2010) showed species-specific differences in home-range size: some carnivores have smaller, similar or even larger home range in urban areas compared to natural habitats. However, other single-species reviews documented smaller home ranges in urban habitats for carnivores, namely for red fox (e.g.

Trewhella et al. 1988, Adkins & Stott 1998), Eurasian badger (Kowalczyk et al. 2006), bobcat (Riley et al. 2010) or raccoon (Hadidian et al. 2010). Although estimates of home range size and population density can be affected by various factors specific to the study area, including duration of study, model and method used, demographic structure of the population studied, resource distribution or proportion of suitable habitats at different scales (Červinka et al. 2013), there are some general features common to urban environment that have similar effect on carnivore populations. Last but not least, the similar patterns of home range and population density changes in urban environment have been previously reported for birds (Rutz 2006, Møller et al. 2012).

Our results also demonstrate a negative relationship between population density and home range size in urban carnivores, confirming a pattern previously reported for red fox (Trewhella et al. 1988), island fox (Sanchez 2012), Eurasian badger (Kauhala & Holmala 2011) and brown bear (Dahle et al. 2006). High population densities of urban mesocarnivores in connection with increased inter- and intraspecific competition or predation in overlapping home ranges may affect many behavioural and ecological characteristics, such as social organization (Baker et al. 2000, Gloor 2002, Herr et al. 2009), territorial behaviour (Davison et al. 2008), behavioural interactions (Krauze-Gryz et al. 2012, Harrison et al. 2011, Berger & Gese 2007), foraging strategies (diet partitioning) (Krauze-Gryz et al. 2012), or daily activity patterns (Harrison 1997, Quinn 1997, Saunders et al. 1997, Tigas et al. 2002, Riley et al. 2003). Moreover, studies in urban carnivores show that habitat utilization within home ranges is largely associated with limited amount of natural vegetation within urban matrix. This may further enhance competition and finally lead to competitive exclusions (see Lavin et al. 2003, Prange & Gehrt 2004) or segregated spatial distribution/utilization (Connor & Simberloff 1975, Gosselink et al. 2003). For instance, Crooks & Soulé (1999) found negative relationship between visitation rate of coyote and other mesocarnivore species in urban habitat fragments (see also *Gosselink et al. 2003*). Coyotes have been identified as important source of mortality and changes in spatial distribution in smaller subordinate mesocarnivore species (Farias et al. 2005, Cypher & Spencer 1998). On the other hand, other studies indicate a high degree of co-occurrence of smaller mesocarnivore species with the dominant member of carnivore guild, e.g. coyote interactions with striped skunks and raccoons (Gehrt & Prange 2007, Prange & Gehrt 2007,

Crooks et al. 2010) indicating that this subject in urban ecosystems surely deserves further detailed research.

In general, resource availability, lack of natural enemies and the physical environmental conditions are most likely to be three crucial aspects influencing a species' ability to occupy urban environment (Shea & Chesson 2002). Urban carnivores may thrive from a variety of specific characteristics of urban and suburban environment, such as human-related food resources (Doncaster et al. 1990, Contesse et al. 2004, Prange et al. 2004, Herr et al. 2010), non-seasonal water sources (Kaye et al. 2006), convenient microclimatic conditions all year round (Berry 2008), artificial structures as supplemental denning sites and shelters (Hadidian et al. 1991, Prange et al. 2003, Kaneko et al. 2006, Herr et al. 2009), or high habitat heterogeneity (Lucherini & Lovari 1996, Niemala 1999, Pautasso 2007, Cadenasso et al. 2007). Furthermore, urban mesocarnivores may benefit from reduced competition and predation from larger carnivores (Crooks & Soulé 1999, Gehrt 2007, Gosselink et al. 2007) as well as absence (or reduced) of human persecution (Gompper 2002, Gehrt 2007).

High availability of anthropogenic and synanthropic food resources has often been identified as crucial factor in explaining the intraspecific variation of home range size and population densities between urban and natural dwelling populations (Smith & Engeman 2002, Prange et al. 2004, Bozek et al. 2007). Spatial dispersion and diversity of anthropogenic food resources result in carnivore accumulation around these concentrated food resources (Prange et al. 2004, Rodewald & Shustack 2008, Wehtje & Gompper 2011) which lead to increased population density (Fedriani et al. 2001). High availability of anthropogenic food resources is also generally considered as important determinant of co-occurrence, home range size and spatial overlap with neighbours through reduced territorial behaviour and aggression on interspecific or intraspecific level (Cresswell & Harris 1988, Mirmovitch 1995, Fedriani et al. 2001, Smith & Engeman 2002, Adams et al. 2006, Davison et al. 2008). Temporal and spatial food distribution in urban environment is strongly influenced by human activity, resulting in high and predictable resource availability, as exemplified by food waste (Lewis et al. 1993, Contesse et al. 2004), crops (Contesse et al. 2004) and the food provided through deliberate feeding (Roper 2010). Although urban mesopredators are known to exploit anthropogenic food efficiently, its proportion in the carnivores' diet may significantly differ at the level of species and population. For example,

the percentage of anthropogenic food resources can account for up to 60% in urban red fox diet (Doncaster et al. 1990, Saunders et al. 1993), 18% in striped skunk diet (Hamilton 1936), 17% in stone marten (Eskreys-Wojcik & Wierzbowska 2007), 2–35% in coyote (Gehrt 2007) and 14–43% in raccoon (Iossa et al. 2010). Likewise, synanthropic rodents, lagomorphs and birds often occur in high densities in cities and sometimes form the most important diet component of several urban carnivores (Contesse et al. 2004, Kaneko et al. 2006, Morey et al. 2007, Iossa et al. 2010). Moreover, urban green areas, such as parks, gardens, orchards, ruderal vegetation or gardening practices, provide a seasonal source of fruits and seeds that can also comprise a large part of mesocarnivores' diet (Harris 1984, Quinn 1997, Lanszki 2003, Contesse et al. 2004).

Although urbanization is often considered as resulting in degraded and fragmented habitats (McKinney 2002, Fahrig 2003, Cadenasso et al. 2007, McDonald et al. 2008), some previous studies documented that suburban areas may offer even higher heterogeneity and diversity of high-quality habitats in comparison to surrounding homogeneous and intensively used agricultural or afforested landscapes (Blair 1996, Niemela 1999, Pautasso 2007). High spatial heterogeneity of anthropogenic and natural habitats can have a favourable effect on wildlife by providing more ecological niches as a result of diverse resource availability (Oehler & Litvaitis 1996, Tews et al. 2004). Moreover, the high habitat heterogeneity and close proximity between food patches and resting sites may result in smaller home range sizes of carnivores (Lucherini & Lovari 1996). Except natural habitats within urban matrix, the urban environment also offers high availability of structurally diverse anthropogenic niches which could be used for shelter and resting. Despite remnants of natural vegetation has been identified as crucial for carnivores' shelter requirements (Baker & Harris 2007, Gehrt 2010), the anthropogenic structures/objects may serve as important shelters and dens for other species (Prange et al 2003, Kaneko et al. 2006, O'Donnell & DeNicola 2006). For example, urban stone martens almost exclusively use buildings (97.1%) in contrast to natural densites for resting (Herr et al. 2010). Importance of artificial structures for denning was also demonstrated for other urban carnivores, such as raccoon (Hadidian et al. 2010) or stripped skunk (Rosatte et al. 2010).

Interaction of favourable abiotic conditions, increased food resources and lower predation rates may importantly affect several ecological and life history characteristics of urban carnivores. Higher ambient temperatures, less snow during winter periods and non-

seasonal water sources make urban microclimatic conditions more convenient compared to the natural ones (Pickett et al. 2001, Berry 2008). For example, milder urban microclimate in combination with anthropogenic food resources may result in reduced migration of urban carnivores during winter period (Rossatte et al. 2010), prolonged breeding season or higher fecundity rates (Beckmann & Lackey 2008). In comparison with populations living in non-urban habitats, the urban carnivores have generally better physical condition (Cypher 2010, Rosatte et al. 2010), higher survival (sensu in Bateman & Fleming 2012, but also see Riley et al. 1999, Gehrt 2007) and reproduction success (Gosselink et al. 2007, Beckmann & Lackey 2008). On the other hand, urban carnivores are exposed to high mortality including road mortality, intoxication and infectious diseases well-spreading within dense urban populations (Bateman & Fleming 2012 and references therein), and thus urban environment may represent “ecological trap” for some species (see Beckmann & Lackey 2008).

In conclusion, our data and subsequent discussion reviewing available evidence not only provide new information on the density-dependent pattern of variation in mesocarnivore home range size, but also show their ecological and behavioural adaptations in highly anthropogenic landscape. Despite increasing bulk of evidence on processes in urban habitats, there are still research areas which did not receive due attention. For instance, we lack comparative approaches applied within natural-urban gradient to examine factors affecting species-specific responses to urbanization. In particular, studies focusing on urban ecology of carnivores from different geographical regions, influence of human activity, historical and current land use intensity (e.g. habitat fragmentation, agricultural intensification) or areas with contrasting habitat characteristics at different spatial scales might provide valuable insights into the coexistence of carnivores and humans in a rapidly urbanizing world.

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Appendix 1: Home range sizes and population densities of eight studied

mesocarnivores along the gradient from natural to urbanized habitats

References	Species	Habitat type	Home range size (ha)	Density (ind/km ²)
Andelt 1976	<i>Canis latrans</i>	natural	1265	NA
Andelt 1982	<i>Canis latrans</i>	natural	450	NA
Andelt 1985	<i>Canis latrans</i>	natural	450	0,85
Andelt & Gipson 1979	<i>Canis latrans</i>	natural	2620	NA
Andelt & Mahan 1980	<i>Canis latrans</i>	urban	370	NA
Andelt & Mahan 1980	<i>Canis latrans</i>	natural	4115	NA
Atkinson & Shackleton 1991	<i>Canis latrans</i>	urban	385	NA
Bekoff & Wells 1986	<i>Canis latrans</i>	natural	3356,5	NA
Bounds & Shaw 1997	<i>Canis latrans</i>	natural	1650	NA
Bounds & Shaw 1997	<i>Canis latrans</i>	suburban	1540	NA
Bowen 1978	<i>Canis latrans</i>	natural	2870	NA
Bowen 1982	<i>Canis latrans</i>	natural	1375	NA
Bradley & Fagre 1988	<i>Canis latrans</i>	natural	304	NA
Crete et al. 2001	<i>Canis latrans</i>	natural	10000	NA
Crete et al. 2001	<i>Canis latrans</i>	natural	3750	NA
Fedriani et al. 2001	<i>Canis latrans</i>	natural	NA	0,35
Fedriani et al. 2001	<i>Canis latrans</i>	urban	NA	2,7
Fedriani et al. 2001	<i>Canis latrans</i>	suburban	NA	1,8
Gehrt et al. 2011	<i>Canis latrans</i>	urban	NA	1,45
Harrison & Gilbert 1985	<i>Canis latrans</i>	natural	4685	NA
Hibler 1977	<i>Canis latrans</i>	natural	1900	NA
Hidalgo-Mihart et al. 2004	<i>Canis latrans</i>	natural	2730	NA
Hidalgo-Mihart et al. 2004	<i>Canis latrans</i>	urban	520	NA
Holzman et al. 1992	<i>Canis latrans</i>	natural	1125	NA
Jantz 2011	<i>Canis latrans</i>	suburban	1061	NA
Jorgensen 1992	<i>Canis latrans</i>	natural	8450	NA
Kamler et al. 2003	<i>Canis latrans</i>	natural	1250	NA
Knowlton et al. 1986	<i>Canis latrans</i>	natural	NA	2,05
Litvaitis 1978	<i>Canis latrans</i>	urban	2145	NA
Litvaitis & Shaw 1980	<i>Canis latrans</i>	natural	5130	NA
McClure et al. 1996	<i>Canis latrans</i>	urban	NA	3,7
Ozoga & Harger 1966	<i>Canis latrans</i>	natural	NA	0,14
Page 2010	<i>Canis latrans</i>	urban	3100	NA
Patterson & Messier 2001	<i>Canis latrans</i>	natural	NA	0,1065
Patterson & Messier 2001	<i>Canis latrans</i>	natural	NA	0,068
Person & Hirth 1991	<i>Canis latrans</i>	natural	1640	NA
Pyrah 1984	<i>Canis latrans</i>	natural	900	0,39

Richer et al 2002	<i>Canis latrans</i>	natural	NA	0,27
Richer et al 2002	<i>Canis latrans</i>	natural	NA	0,05
Riley et al. 2003	<i>Canis latrans</i>	urban	450,5	NA
Sauvajot et al. 2000	<i>Canis latrans</i>	natural	NA	0,3
Springer 198 2	<i>Canis latrans</i>	natural	10780	NA
Sumner et al. 1984	<i>Canis latrans</i>	natural	3060	NA
Tigas et al. 2002	<i>Canis latrans</i>	urban	224,7	NA
Tigas et al. 2002	<i>Canis latrans</i>	urban	165,15	NA
Way 2000	<i>Canis latrans</i>	urban	3135	NA
Way & Timm 2011	<i>Canis latrans</i>	suburban	NA	3,17
Way et al. 2002	<i>Canis latrans</i>	suburban	NA	0,095
Woodruff & Keller 1982	<i>Canis latrans</i>	natural	5495	NA
Anderson 1987	<i>Lynx rufus</i>	natural	5235	1,25
Bailey 1972	<i>Lynx rufus</i>	natural	7375	0,05
Bailey 1974	<i>Lynx rufus</i>	natural	3070	NA
Bailey et al. 1986	<i>Lynx rufus</i>	natural	24650	NA
Benson et al. 2006	<i>Lynx rufus</i>	natural	1342,5	0,085
Berrie 1974	<i>Lynx rufus</i>	natural	1900	NA
Bradley & Fagre 1988	<i>Lynx rufus</i>	natural	230,5	NA
Burton et al. 2003	<i>Lynx rufus</i>	natural	329,7	NA
Cochrane et al. 2006	<i>Lynx rufus</i>	natural	670	NA
Conner et al. 1992	<i>Lynx rufus</i>	natural	2855	NA
Conner et al. 2001	<i>Lynx rufus</i>	natural	1625	NA
Diefenbach et al. 2006	<i>Lynx rufus</i>	natural	1785	0,31
Donovan et al. 2011	<i>Lynx rufus</i>	natural	5730	NA
Fischer 1998	<i>Lynx rufus</i>	natural	347	NA
Fox 1990	<i>Lynx rufus</i>	natural	20605	NA
Fox 1990	<i>Lynx rufus</i>	natural	3350	NA
Fuller et al. 1985	<i>Lynx rufus</i>	natural	4750	NA
Fuller et al. 1985	<i>Lynx rufus</i>	natural	4650	NA
Godbois 2003	<i>Lynx rufus</i>	natural	373	NA
Godbois et al. 2004	<i>Lynx rufus</i>	natural	278	NA
Griffin 2001	<i>Lynx rufus</i>	suburban	685	NA
Hall & Newsom 1976	<i>Lynx rufus</i>	natural	295,6	NA
Hamilton 1982	<i>Lynx rufus</i>	natural	3825	0,085
Chamberlain et al. 2003	<i>Lynx rufus</i>	natural	1291	NA
Janecka et al. 2006	<i>Lynx rufus</i>	natural	705	NA
Kamler & Gipson 2000	<i>Lynx rufus</i>	natural	1375	NA
Kitchings & Story 1978	<i>Lynx rufus</i>	natural	2246	NA
Knick 1990	<i>Lynx rufus</i>	natural	2295	NA
Lawhead 1984	<i>Lynx rufus</i>	natural	695	0,26
Lembeck 1978	<i>Lynx rufus</i>	natural	307	1,4
Litvaitis et al. 1986	<i>Lynx rufus</i>	natural	6345	NA
Lovallo & Anderson 1996	<i>Lynx rufus</i>	natural	4445	0,069
Lyren 2001	<i>Lynx rufus</i>	natural	676	NA

Major 1983	<i>Lynx rufus</i>	natural	9770	NA
Major & Sherburne 1987	<i>Lynx rufus</i>	natural	8305	NA
Marshall & Jenkins 1966	<i>Lynx rufus</i>	natural	350	NA
Miller & Speake 1979	<i>Lynx rufus</i>	natural	185	1,005
Nielsen & Woolf 2001	<i>Lynx rufus</i>	natural	3420	0,27
Plowman et al. 2006	<i>Lynx rufus</i>	natural	1212	NA
Provost et al. 1973	<i>Lynx rufus</i>	natural	250	1,67
Riley 2006	<i>Lynx rufus</i>	urban	386,75	NA
Riley 2006	<i>Lynx rufus</i>	natural	943,25	NA
Riley et al. 2003	<i>Lynx rufus</i>	urban	238	NA
Roberts 2007	<i>Lynx rufus</i>	suburban	573,9	NA
Roberts 2007	<i>Lynx rufus</i>	suburban	329,5	NA
Rolley 1985	<i>Lynx rufus</i>	natural	2900	0,09
Rollings 1945	<i>Lynx rufus</i>	natural	3250	NA
Rucker et al. 1989	<i>Lynx rufus</i>	natural	4435	0,104
Ruell et al. 2009	<i>Lynx rufus</i>	urban	NA	0,335
Shiftlet 1984	<i>Lynx rufus</i>	natural	800	NA
Sunde et al. 2000	<i>Lynx rufus</i>	natural	123350	0,003
Thornton et al. 2004	<i>Lynx rufus</i>	natural	920	NA
Tigas et al. 2002	<i>Lynx rufus</i>	urban	198,35	NA
Tigas et al. 2002	<i>Lynx rufus</i>	urban	137,5	NA
Whitaker et al. 1987	<i>Lynx rufus</i>	natural	3205	NA
Zezulak 1980	<i>Lynx rufus</i>	natural	5825	0,05
Bissonette & Broekhuizen 1995	<i>Martes foina</i>	urban	45	NA
Genovesi et al. 1997	<i>Martes foina</i>	natural	361	NA
Hermann 2004	<i>Martes foina</i>	natural	71,5	NA
Hermann 2004	<i>Martes foina</i>	urban	32,75	6
Herr et al. 2009	<i>Martes foina</i>	urban	74,8	5,25
Lachat Feller 1993	<i>Martes foina</i>	natural	50,625	1,7
Lopez-Martin et al. 1992	<i>Martes foina</i>	natural	52,5	NA
Müskens & Broekhuizen 2005	<i>Martes foina</i>	urban	152	NA
Nicht 1969	<i>Martes foina</i>	urban	NA	8
Santos & Santos-Reis 2010	<i>Martes foina</i>	natural	310,07	NA
Serafini & Lovari 1993	<i>Martes foina</i>	natural	NA	0,7
Simon & Lang 2007	<i>Martes foina</i>	natural	522,5	NA
Skirnisson 1986	<i>Martes foina</i>	natural	99	NA
Šálek et al. 2005	<i>Martes foina</i>	urban	NA	2,5
Toth et al. 2009	<i>Martes foina</i>	urban	NA	1
AarisSorensen 1987	<i>Meles meles</i>	urban	NA	0,1
Bartmanska & Nadolska 2003	<i>Meles meles</i>	natural	1075	NA
Bicik et al. 2000	<i>Meles meles</i>	natural	NA	0,224
Bicik et al. 2000	<i>Meles meles</i>	urban	NA	0,121
Bock 1986	<i>Meles meles</i>	natural	505	NA
Broseth et al. 1997	<i>Meles meles</i>	natural	540	NA
Broseth et al. 1997	<i>Meles meles</i>	natural	NA	0,5

Cresswell & Harris 1988	<i>Meles meles</i>	urban	25	NA
Davison et al. 2009	<i>Meles meles</i>	urban	4,91	NA
Do Linh San et al. 2007	<i>Meles meles</i>	natural	320,5	0,95
DoLinhSan et al. 2007	<i>Meles meles</i>	natural	169	1,8
Feore & Montgomery 1999	<i>Meles meles</i>	natural	50,4	17,5
Feore & Montgomery 1999	<i>Meles meles</i>	natural	127,4	1,6
Feore & Montgomery 1999	<i>Meles meles</i>	natural	345	0,86
Frantz et al. 2010	<i>Meles meles</i>	natural	76,5	NA
Goszczynski 1999	<i>Meles meles</i>	natural	NA	0,59
Goszczynski & Skoczynska 1996	<i>Meles meles</i>	natural	NA	1,85
Graf et al. 1996	<i>Meles meles</i>	natural	387	0,5
Harris & Cresswell 1987	<i>Meles meles</i>	urban	NA	5,95
Harris & Cresswell 1988	<i>Meles meles</i>	urban	NA	3,4
Heydon et al. 2000	<i>Meles meles</i>	natural	NA	2,43
Heydon et al. 2000	<i>Meles meles</i>	natural	NA	1,305
Hofer 1988	<i>Meles meles</i>	natural	52,1	3,48
Hofmann 1999	<i>Meles meles</i>	natural	138,9	6,5
Huck et al. 2008	<i>Meles meles</i>	urban	NA	32,5
Cheeseman et al. 1981	<i>Meles meles</i>	natural	NA	22
Cheeseman et al. 1981	<i>Meles meles</i>	natural	NA	6,5
Cheeseman et al. 1981	<i>Meles meles</i>	natural	NA	5,8
Cheeseman et al. 1981	<i>Meles meles</i>	natural	NA	30,7
Cheeseman et al. 1985	<i>Meles meles</i>	natural	104	8,64
Ivanter 1973	<i>Meles meles</i>	natural	NA	0,46
Johansen 1993	<i>Meles meles</i>	urban	760	NA
Kanda 1993	<i>Meles meles</i>	urban	NA	4
Kaneko et al. 2006	<i>Meles meles</i>	urban	25,65	NA
Kauhala & Holmala 2011	<i>Meles meles</i>	urban	134	NA
Kauhala & Holmala 2011	<i>Meles meles</i>	natural	306	NA
Kauhala & Holmala 2011	<i>Meles meles</i>	natural	949	NA
Kauhala et al. 2006	<i>Meles meles</i>	natural	1840	0,21
Kowalczyk 2003	<i>Meles meles</i>	natural	930	0,211
Kowalczyk et al. 2000	<i>Meles meles</i>	natural	NA	1,57
Kowalczyk et al. 2000	<i>Meles meles</i>	natural	NA	0,16
Kruuk & Parish 1982	<i>Meles meles</i>	natural	183	2,03
Kruuk & Parish 1982	<i>Meles meles</i>	natural	206	2,2
Kruuk & Parish 1987	<i>Meles meles</i>	natural	121	2,2
Lobachev 1976	<i>Meles meles</i>	natural	NA	1,52
Macdonald & Newman 2002	<i>Meles meles</i>	natural	NA	44,3
MacDonald et al. 1996	<i>Meles meles</i>	natural	NA	3,18
Macdonald et al. 2004	<i>Meles meles</i>	natural	NA	38
Martin-franquelo & Delibes 1985	<i>Meles meles</i>	natural	422	0,5
Matyastik & Bicik 1999	<i>Meles meles</i>	natural	NA	0,118
Molina-Vacas et al. 2009	<i>Meles meles</i>	natural	NA	1,9
Molina-Vacas et al. 2009	<i>Meles meles</i>	natural	NA	0,6

OCorryCrowe et al. 1993	<i>Meles meles</i>	natural	87,4	4,55
Packham 1983	<i>Meles meles</i>	urban	41	12,3
Palphramand et al. 2007	<i>Meles meles</i>	natural	NA	4,9
Pelikan & Vackar 1978	<i>Meles meles</i>	natural	NA	0,98
Pigozzi 1987	<i>Meles meles</i>	natural	73	1
Remonti et al. 2006	<i>Meles meles</i>	natural	383	NA
Revilla & Palomores 2002	<i>Meles meles</i>	natural	412	NA
Revilla et al. 1999	<i>Meles meles</i>	natural	NA	0,45
Revilla et al. 2001	<i>Meles meles</i>	natural	NA	0,67
Rodgers et al. 1997	<i>Meles meles</i>	natural	35	25,3
Rodriguez et al. 1996	<i>Meles meles</i>	natural	627	0,36
Rosalino et al. 2004	<i>Meles meles</i>	natural	446	0,42
Seiler et al. 1995	<i>Meles meles</i>	natural	NA	1,3
Seiler et al. 1995	<i>Meles meles</i>	natural	NA	3
Schley et al. 2004	<i>Meles meles</i>	natural	NA	0,78
Sidorovich et al. 2011	<i>Meles meles</i>	natural	410	0,06
vanApeldoorn et al. 2006	<i>Meles meles</i>	natural	NA	1,3
Woodroffe.Macdonald 1993	<i>Meles meles</i>	natural	595,5	0,51
Zejda & Nesvadbová 1983	<i>Meles meles</i>	natural	NA	0,35
Zoss 199 2	<i>Meles meles</i>	natural	NA	0,3
Bailey 1971	<i>Mephitis mephitis</i>	natural	30,35	4,63
Bartelt et al. 2001	<i>Mephitis mephitis</i>	natural	NA	0,94
Bixler & Gittleman 2000	<i>Mephitis mephitis</i>	natural	108	NA
Bjorge 1977	<i>Mephitis mephitis</i>	natural	NA	1,45
Broadfoot et al. 2001	<i>Mephitis mephitis</i>	urban	NA	1,7
Ferris & Andrews 1967	<i>Mephitis mephitis</i>	natural	NA	19,5
Frey & Conover 2006	<i>Mephitis mephitis</i>	natural	300	NA
Gehrt 2005	<i>Mephitis mephitis</i>	urban	NA	4
Greenwood et al. 1985	<i>Mephitis mephitis</i>	natural	275	NA
Greenwood et al. 1997	<i>Mephitis mephitis</i>	natural	200	NA
Hansen et al. 2004	<i>Mephitis mephitis</i>	natural	NA	0,405
Lariviere & Messier 1998	<i>Mephitis mephitis</i>	natural	765	NA
Prange & Gehrt 2007	<i>Mephitis mephitis</i>	urban	NA	5,1
Rosatte et al. 1991	<i>Mephitis mephitis</i>	urban	51	NA
Rosatte et al. 2011	<i>Mephitis mephitis</i>	urban	90	NA
Ruffino 2008	<i>Mephitis mephitis</i>	urban	190,5	NA
Shirer & Fitch 1970	<i>Mephitis mephitis</i>	natural	NA	23,3
Storm 1972	<i>Mephitis mephitis</i>	natural	444,75	NA
Weissingner et al. 2009	<i>Mephitis mephitis</i>	urban	87,5	NA
Barding & Nelson 2008	<i>Procyon lotor</i>	natural	45,35	NA
Bartelt et al. 2001	<i>Procyon lotor</i>	natural	NA	3,65
Bartoszewicz et al. 2008	<i>Procyon lotor</i>	suburban	285	NA
Bartoszewicz et al. 2008	<i>Procyon lotor</i>	natural	640	NA
Bartoszewicz et al. 2008	<i>Procyon lotor</i>	natural	5786	NA
Beasley et al. 2007	<i>Procyon lotor</i>	natural	61	NA

Bellrichard 2011	<i>Procyon lotor</i>	urban	18,6	NA
Blackwell et al. 2004	<i>Procyon lotor</i>	natural	NA	23,5
Bozek et al. 2007	<i>Procyon lotor</i>	natural	229,5	NA
Bozek et al. 2007	<i>Procyon lotor</i>	suburban	83	NA
Bozek et al. 2007	<i>Procyon lotor</i>	urban	128	NA
Broadfoot et al. 2001	<i>Procyon lotor</i>	urban	NA	23,5
Butterfield 1944	<i>Procyon lotor</i>	urban	NA	21
Byrne & Chamberlain 2011	<i>Procyon lotor</i>	natural	175,67	NA
Fisher 2007	<i>Procyon lotor</i>	natural	131,5	NA
Fisher 2007	<i>Procyon lotor</i>	natural	199,1	NA
Frantz et al. 2005	<i>Procyon lotor</i>	natural	340	NA
Frey & Conover 2006	<i>Procyon lotor</i>	natural	360	NA
Fritzell 1978	<i>Procyon lotor</i>	natural	1683	NA
Gehrt & Fritzel 1997	<i>Procyon lotor</i>	natural	303,75	NA
Glueck et al. 1988	<i>Procyon lotor</i>	natural	134	NA
Gross et al. 2011	<i>Procyon lotor</i>	urban	34,9	66
Gross et al. 2011	<i>Procyon lotor</i>	urban	72,85	34
Hoffmann & Gottschang 1977	<i>Procyon lotor</i>	suburban	5,1	68,5
Hohmann et al. 2001	<i>Procyon lotor</i>	urban	NA	100
Chamberlain et al. 2000	<i>Procyon lotor</i>	natural	208,25	NA
Chamberlain et al. 2000	<i>Procyon lotor</i>	natural	127	NA
Chamberlain et al. 2003	<i>Procyon lotor</i>	natural	171	NA
Juen 1981	<i>Procyon lotor</i>	natural	1922,3	NA
Lehman 1984	<i>Procyon lotor</i>	natural	375	NA
Lotze 1979	<i>Procyon lotor</i>	natural	52	NA
Michler et al. 2004	<i>Procyon lotor</i>	urban	123	NA
Pitt et al. 2008	<i>Procyon lotor</i>	natural	999	0,515
Prange et al. 2003, 2004	<i>Procyon lotor</i>	natural	NA	8,85
Prange et al. 2003, 2004	<i>Procyon lotor</i>	urban	NA	54,6
Prange et al. 2003, 2004	<i>Procyon lotor</i>	suburban	NA	67,05
Ratnayeke et al. 2002	<i>Procyon lotor</i>	natural	78,2	13
Rees et al. 2008	<i>Procyon lotor</i>	natural	240,1	9,1
Riley et al. 1998	<i>Procyon lotor</i>	urban	NA	172
Rosatte 2000	<i>Procyon lotor</i>	urban	42	NA
Rosatte et al. 1992	<i>Procyon lotor</i>	urban	NA	140
Rosatte et al. 2010	<i>Procyon lotor</i>	natural	322	7,25
Rosatte et al. 2010	<i>Procyon lotor</i>	natural	NA	10,3
Rosatte et al. 2010	<i>Procyon lotor</i>	urban	NA	12,1
Rosatte et al. 2010	<i>Procyon lotor</i>	natural	NA	11,7
Rosatte et al. 2010	<i>Procyon lotor</i>	natural	NA	9
Rosatte et al. 2010	<i>Procyon lotor</i>	natural	NA	6,9
Rosatte et al. 2010	<i>Procyon lotor</i>	natural	NA	10,4
Rosatte et al. 2010	<i>Procyon lotor</i>	natural	329,5	6,5
Rosatte et al. 2010	<i>Procyon lotor</i>	natural	NA	3,4
Shirer & Fitch 1970	<i>Procyon lotor</i>	natural	43,45	NA

Schinner 1969	<i>Procyon lotor</i>	urban	NA	98
Schinner & Cauley 1974	<i>Procyon lotor</i>	suburban	NA	98
Smith & Engeman 2002	<i>Procyon lotor</i>	urban	NA	238
Sonenshine & Winslow 1972	<i>Procyon lotor</i>	natural	NA	17,2974
Stuewer 1943	<i>Procyon lotor</i>	natural	156	7,7
Suzuki et al. 2003	<i>Procyon lotor</i>	natural	171,5	NA
Totton et al. 2004	<i>Procyon lotor</i>	natural	74,8	NA
Twichell & Dill 1949	<i>Procyon lotor</i>	natural	NA	250
urbann 1970	<i>Procyon lotor</i>	natural	48,4	17,7
Wehtje & Gompper 2011	<i>Procyon lotor</i>	natural	250,5	NA
	<i>Urocyon</i>			
Bowles 1975	<i>cinereoargenteus</i>	natural	111	NA
	<i>Urocyon</i>			
Fuller 1978	<i>cinereoargenteus</i>	natural	107,5	NA
	<i>Urocyon</i>			
Haroldson & Fritzell 1984	<i>cinereoargenteus</i>	natural	299	NA
	<i>Urocyon</i>			
Harrison 1997	<i>cinereoargenteus</i>	natural	549	NA
	<i>Urocyon</i>			
Harrison 1997	<i>cinereoargenteus</i>	urban	384	NA
	<i>Urocyon</i>			
Jeselnik 1981	<i>cinereoargenteus</i>	natural	106	1,24
	<i>Urocyon</i>			
Labisky & Progluske 1982	<i>cinereoargenteus</i>	natural	370	0,27
	<i>Urocyon</i>			
Lord 1961	<i>cinereoargenteus</i>	natural	NA	1,3
	<i>Urocyon</i>			
Nicholson 1982, Nicholson & Hill 1984	<i>cinereoargenteus</i>	natural	933	0,63
	<i>Urocyon</i>			
Progluske 1982	<i>cinereoargenteus</i>	natural	460	1
	<i>Urocyon</i>			
Riley 2006	<i>cinereoargenteus</i>	urban	73,55	NA
	<i>Urocyon</i>			
Riley 2006	<i>cinereoargenteus</i>	natural	63,75	NA
	<i>Urocyon</i>			
Rountree 2004	<i>cinereoargenteus</i>	urban	408	NA
	<i>Urocyon</i>			
Sawyer 1988	<i>cinereoargenteus</i>	natural	229	0,44
	<i>Urocyon</i>			
Sawyer & Fendley 1990	<i>cinereoargenteus</i>	natural	156	NA
	<i>Urocyon</i>			
Sunquist 1989	<i>cinereoargenteus</i>	natural	550	NA
	<i>Urocyon</i>			
Temple 2010	<i>cinereoargenteus</i>	natural	91,42	NA
	<i>Urocyon</i>			
Tucker et al. 1993	<i>cinereoargenteus</i>	natural	491	0,435
	<i>Urocyon</i>			
Weston 2001	<i>cinereoargenteus</i>	natural	221	0,97
	<i>Urocyon</i>			
Willingham 2008	<i>cinereoargenteus</i>	urban	165,3	NA
Wooding 1984	<i>Urocyon</i>	natural	410	0,24

cinereoargenteus

Ables 1969	<i>Vulpes vulpes</i>	suburban	237	NA
Ables 1969	<i>Vulpes vulpes</i>	natural	590,8	NA
Adkins & Stott 1998	<i>Vulpes vulpes</i>	suburban	56	NA
Algar & Thomson, pers. com. in Saunders et al. 1995	<i>Vulpes vulpes</i>	natural	340	NA
Algar & Thomson, pers. com. in Saunders et al. 1995	<i>Vulpes vulpes</i>	natural	NA	0,75
Baker et al. 2000	<i>Vulpes vulpes</i>	urban	NA	32,8
Baker et al. 2000, 2007	<i>Vulpes vulpes</i>	suburban	23,5	23,5
Boitani et al. 1984	<i>Vulpes vulpes</i>	natural	195	NA
Bubela 1993	<i>Vulpes vulpes</i>	natural	550	NA
Bubela 1994	<i>Vulpes vulpes</i>	natural	NA	1,8
Cavallini 1992	<i>Vulpes vulpes</i>	natural	494	NA
Cavallini 1996	<i>Vulpes vulpes</i>	natural	188,9	NA
Cavallini & Lovari 1994	<i>Vulpes vulpes</i>	natural	282	NA
Coman et al. 1991	<i>Vulpes vulpes</i>	suburban	100	NA
Coman et al. 1991	<i>Vulpes vulpes</i>	natural	NA	3,9
Coman et al. 1991	<i>Vulpes vulpes</i>	natural	610	NA
Coman et al. 1991	<i>Vulpes vulpes</i>	natural	490	NA
Dekker et al. 2001	<i>Vulpes vulpes</i>	natural	NA	NA
Doncaster & Macdonald 1991	<i>Vulpes vulpes</i>	suburban	54,3	NA
Doncaster & Macdonald 1991	<i>Vulpes vulpes</i>	urban	38,8	NA
Doncaster & Macdonald 1991	<i>Vulpes vulpes</i>	urban	93,4	NA
Doncaster & Macdonald 1996	<i>Vulpes vulpes</i>	urban	NA	NA
Englund 1980.Lindstrom 1982	<i>Vulpes vulpes</i>	natural	525	0,3
Fallier 2008	<i>Vulpes vulpes</i>	natural	12,95	NA
Frafjord 2004	<i>Vulpes vulpes</i>	natural	525	NA
Frey & Conover 2006	<i>Vulpes vulpes</i>	natural	350	NA
Gloor 200 2	<i>Vulpes vulpes</i>	urban	NA	10,5
Goldyn et al. 2003	<i>Vulpes vulpes</i>	natural	NA	2,2
Gosselink et al. 2003	<i>Vulpes vulpes</i>	urban	379,5	NA
Gosselink et al. 2003	<i>Vulpes vulpes</i>	natural	1404	NA
Gosselink et al. 2003	<i>Vulpes vulpes</i>	urban	547,5	NA
Gosselink et al. 2003	<i>Vulpes vulpes</i>	natural	503	NA
Goszczyński 1989	<i>Vulpes vulpes</i>	natural	412	NA
Goszczyński 1999	<i>Vulpes vulpes</i>	natural	NA	0,27
Harris 1980	<i>Vulpes vulpes</i>	urban	45	NA
Harris 1981	<i>Vulpes vulpes</i>	urban	NA	8,5
Harris & Rayner 1986	<i>Vulpes vulpes</i>	urban	NA	NA
Harrison et al. 1989	<i>Vulpes vulpes</i>	natural	1470	NA
Heydon et al. 2000	<i>Vulpes vulpes</i>	natural	NA	0,9
Heydon et al. 2000	<i>Vulpes vulpes</i>	natural	NA	2,62
Heydon et al. 2000	<i>Vulpes vulpes</i>	natural	NA	0,59
Insley 1977	<i>Vulpes vulpes</i>	natural	NA	0,75

Iossa et al. 2008	<i>Vulpes vulpes</i>	urban	NA	23,6
Iossa et al. 2008	<i>Vulpes vulpes</i>	urban	NA	4,75
Janko et al. 2012	<i>Vulpes vulpes</i>	natural	76,6	NA
Jones & Theberge 1982	<i>Vulpes vulpes</i>	natural	1611	NA
Kamler et al. 2003	<i>Vulpes vulpes</i>	natural	760	NA
Kauhala et al. 2006	<i>Vulpes vulpes</i>	natural	1100	0,35
Keenan 1981	<i>Vulpes vulpes</i>	natural	674	NA
Kolb 1984	<i>Vulpes vulpes</i>	suburban	200,5	NA
Kolb 1986	<i>Vulpes vulpes</i>	suburban	100	NA
Lewis et al. 1993	<i>Vulpes vulpes</i>	suburban	425	17
Lewis et al. 1993	<i>Vulpes vulpes</i>	natural	1002	NA
Lewis et al. 1993	<i>Vulpes vulpes</i>	suburban	284	NA
Lewis et al. 1993	<i>Vulpes vulpes</i>	suburban	81	NA
Lewis et al. 1993	<i>Vulpes vulpes</i>	urban	46	NA
Lloyd 1980	<i>Vulpes vulpes</i>	natural	235	3,7
Lovari et al. 1994	<i>Vulpes vulpes</i>	natural	330	NA
Macdonald 1981	<i>Vulpes vulpes</i>	suburban	71	NA
Major & Sherburne 1987	<i>Vulpes vulpes</i>	natural	1990	NA
Marks & Bloomfield 1999	<i>Vulpes vulpes</i>	urban	NA	9,5
Marks & Bloomfield 2006	<i>Vulpes vulpes</i>	urban	28,65	NA
Marks et al. 2009	<i>Vulpes vulpes</i>	natural	NA	3,3
Marlow 1992	<i>Vulpes vulpes</i>	suburban	513	0,9
Maurel 1980	<i>Vulpes vulpes</i>	natural	517	NA
Mulder 1985	<i>Vulpes vulpes</i>	natural	152,5	NA
Newsome & Catling 1992	<i>Vulpes vulpes</i>	natural	NA	0,2
Newsome & Catling 1992	<i>Vulpes vulpes</i>	suburban	NA	2
Niewold 1980	<i>Vulpes vulpes</i>	natural	263	NA
Page 1975	<i>Vulpes vulpes</i>	urban	NA	2,6
Page 1981	<i>Vulpes vulpes</i>	urban	165	NA
Pandolfi et al. 1991	<i>Vulpes vulpes</i>	natural	NA	2,345
Pandolfi et al. 2009	<i>Vulpes vulpes</i>	natural	112,6	NA
Panek & Bresinski 2002	<i>Vulpes vulpes</i>	natural	NA	1,325
Phillips & Catling 1991	<i>Vulpes vulpes</i>	natural	330	NA
Phillips & Catling 1991	<i>Vulpes vulpes</i>	natural	416	NA
Pils & Martin 1978	<i>Vulpes vulpes</i>	natural	558	NA
Pouille et al. 1994	<i>Vulpes vulpes</i>	natural	200	NA
Rau 1987	<i>Vulpes vulpes</i>	natural	NA	1,7
Reynolds & Tapper 1995	<i>Vulpes vulpes</i>	natural	272	NA
Rosatte & Allan 2009	<i>Vulpes vulpes</i>	urban	324,8	NA
Rountree 2004	<i>Vulpes vulpes</i>	urban	334	NA
Sargeant 1972	<i>Vulpes vulpes</i>	natural	513,5	NA
Sargeant et al. 1987	<i>Vulpes vulpes</i>	natural	1190	NA
Saunders et al. 1993	<i>Vulpes vulpes</i>	urban	30	NA
Saunders et al. 2002	<i>Vulpes vulpes</i>	natural	275	NA
Saunders et al. 2002	<i>Vulpes vulpes</i>	natural	433	NA

Saunders et al. 2002	<i>Vulpes vulpes</i>	natural	398,33	NA
Saunders et al. 2002	<i>Vulpes vulpes</i>	natural	289,67	NA
Scott 1943	<i>Vulpes vulpes</i>	natural	400	NA
Silva et al. 2009	<i>Vulpes vulpes</i>	suburban	137,25	NA
Silva-Opps & Opps 2011	<i>Vulpes vulpes</i>	urban	132,03	NA
Storm et al. 1976	<i>Vulpes vulpes</i>	natural	960	NA
Sunquist 1989	<i>Vulpes vulpes</i>	natural	961	0,15
Takeuchi & Koganezawa 1992	<i>Vulpes vulpes</i>	natural	624,75	NA
Thompson & Fleming 1994	<i>Vulpes vulpes</i>	natural	NA	5,9
Travaini et al. 1993	<i>Vulpes vulpes</i>	natural	218	NA
Tullar & Berchielli 1980	<i>Vulpes vulpes</i>	urban	390	NA
VanEtten et al. 2007	<i>Vulpes vulpes</i>	natural	988,5	NA
Voigt & MacDonald 1984	<i>Vulpes vulpes</i>	natural	234	NA
Voigt & MacDonald 1984	<i>Vulpes vulpes</i>	natural	900	NA
Voigt & MacDonald 1984	<i>Vulpes vulpes</i>	urban	86	NA
Voigt & MacDonald 1984	<i>Vulpes vulpes</i>	suburban	45	NA
Voigt & Tinline 1980	<i>Vulpes vulpes</i>	natural	900	NA
Vos 1995	<i>Vulpes vulpes</i>	natural	NA	0,59
Vos 1995	<i>Vulpes vulpes</i>	natural	NA	1,77
Webbon et al. 2004	<i>Vulpes vulpes</i>	natural	NA	0,99
Webbon et al. 2004	<i>Vulpes vulpes</i>	natural	NA	0,79
Webbon et al. 2004	<i>Vulpes vulpes</i>	natural	NA	2,23
Webbon et al. 2004	<i>Vulpes vulpes</i>	natural	NA	1,88
Webbon et al. 2004	<i>Vulpes vulpes</i>	natural	NA	1,39
Webbon et al. 2004	<i>Vulpes vulpes</i>	natural	NA	0,82
Webbon et al. 2004	<i>Vulpes vulpes</i>	natural	NA	0,21
Weber & Meia 1996	<i>Vulpes vulpes</i>	natural	197,75	NA
White et al. 2006	<i>Vulpes vulpes</i>	suburban	44,6	NA
White.Saunders & Harris 1996	<i>Vulpes vulpes</i>	urban	27,6	NA
Woollard & Harris 1990	<i>Vulpes vulpes</i>	urban	55	NA
Zabel & Taggart 1989	<i>Vulpes vulpes</i>	natural	NA	9,5
Zimen 1984	<i>Vulpes vulpes</i>	natural	473	NA
Zimen 1984	<i>Vulpes vulpes</i>	urban	133	NA

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