Artificial dummies as stimuli in field mobbing experiments

Bakalářská práce

Michaela Syrová

Vedoucí práce: Mgr. Michal Němec (PřF JU)

České Budějovice

Syrová, M. (2011): Artificial dummies as stimuli in field mobbing experiments – Bc. Thesis, in English.,19 p, Faculty of Sciences, The University of South Bohemia, České Budějovice, Czech Republic.

Annotation:

Anti-predation behaviour is usually studied using dummies – animal is confronted with a dummy of predator. These dummies are most often stuffed, however stuffed dummies of many species are not available. Dummies made of different (artificial) materials could replace them but their surface is featherless and so is changing general view and impression of dummies. Response of red-backed shrike (*Lanius collurio*) to European jay's (*Garrulus glandarius*) dummy made of different materials has been tested.

Prohlašuji, že svoji bakalářskou práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své bakalářské práce, a to v nezkrácené podobě – v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou - elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

V Českých Budějovicích, dne 3. ledna 2011

Michaela Syrová

Poděkování:

Na tomto místě bych ráda poděkovala svému školiteli Michalu Němcovi za veškerou pomoc jak v terénu, tak při vlastním sepisování, za jeho trpělivost a optimismus. Dále bych chtěla poděkovat Romanu Fuchsovi za supervizi, za jeho podnětné připomínky a ochotu. Chrisu Steerovi děkuji za jazykovou korekturu. Velké dík patří i Simoně Polákové za pomoc se statistikou a všem obyvatelům malého kanclíku na Béčku za to, že se uskromnili a umožnili mi tak obývat pár cm² nevelkého stolu.

V neposlední řadě děkuji svým rodičům, kteří mě podporovali všemi možnými způsoby během celého studia. Barboře Zdvihalové a Kateřině Ungrové děkuji, že si udělaly čas a tuto práci si nejednou přečetly. Janu Chlumskému za veškerou podporu, pomoc i za to, že snášel veškeré výkyvy mojí nálady. A nakonec všem přátelům, kteří mi pomáhali, podporovali mě i rozveselovali.

Obsah:

Introduction1
Material & Methods4
Study area4
Study species4
Experimental design5
Classification of mobbing behaviours6
Statistical analyses
Results7
Discussion11
References14
Enclosures18

1. Introduction

Anti-predation behaviour is usually studied in field experiments. Various stimuli are used to provoke the tested animal to respond to simulated risk. These stimuli may be olfactory, visual or acoustic (see Caro 2005 for review).

In experiments with birds visual stimuli are most often used (see Caro 2005 for review). In certain case live predators are used (e.g. Röell and Bossema 1982, Hakkarainen et al. 1998, Palleroni et al. 2005). Nevertheless the use of living animals has many technical disadvantages such as the danger of injury to the tested birds or mobbing of the predator. Moreover, it is usually difficult to acquire live predators. Most of the studies interested in nest defence behaviour therefore make use of stuffed dummies (see Caro 2005 for review). On rare occasions freeze-dried models are used instead of stuffed dummies (Gill et al. 1997, Burhans 2001).

Knight and Temple (1986) compared reactions to live predators and stuffed dummies in detail. They demonstrated that the red-winged blackbird (*Agelaius phoeniceus*) attacks a stuffed dummy of the American crow (*Corvus brachyrhynchos*) more intensively than the real bird. The opposite finding is demonstrated in the study by Kis et al. (2000). The lapwing (*Vanellus vanellus*) attacks the live European crow more aggressively than its stuffed dummy. Also in the study by Hakkarainen et al. (2001), a live mink was used, because tested owls responded to it more actively than to a stuffed pine marten. Finally, Meilvang et al. (1997) found no difference in the responses of *Turdus philomelos* and *T. iliacus* to stuffed and live European crows (*Corvus corone*). Despite the contradictory results of these few noted studies, it appears that stuffed dummies serve well as stimuli in experimental research of anti-predation behaviour as they were used successfully in dozens of other studies.

We can suppose that stuffed dummies (or freeze-dried models) are not fully adequate substitutes for live animals because they do not move. Mathot et al. (2009) studied the importance of movement of the dummy. They tested whether red knots (*Calidris canutus*) adjust the intensity of their anti-predation response to three levels of predatory threat, no predator is present, a perching model of a sparrowhawk (*Accipiter nisus*) is present, and a gliding model of a sparrowhawk is present. In all measured behavioural parameters (e.g. escape flights, vigilance and feeding), red knots appeared to discriminate between the various levels of predation risk. Rotating and moving dummies were also used in a few other studies (e.g. Cockrem & Silverin 2002, Deppe et al. 2003, Zaccaroni et al. 2007) however without

comparison to immovable ones.

Even stuffed dummies are not however suitable to some experiments. Research of predator recognition requires the manipulation of individual traits (e.g. curved heavy bill, strong claws, the colour of eyes or feathers - Deppe et al. 2003), which may be used in discrimination and categorization processes. It is difficult to manipulate these traits on stuffed dummies. Gill et al. (1997) tried to modify their freeze-dried models. They removed the bill of a freeze-dried female cowbird (*Molothrus ater*) substituting it with the bill of a juvenile starling (*Sturnus vulgaris*). They did not however try to modify the colour of feathers or any other features.

Artificial models allow the easy modification of single traits, but it is difficult to create sufficiently believable artificial models. These kinds of dummies are therefore used only sporadically, notable exceptions being rubber snakes (Gottfried at al. 1985, Maklakov 2002, Kleindorfer et al. 2005).

Artificial models of birds have occasionally been used in combination with other types of dummies. Knight and Temple (1988) measured the nest-defence responses of the red-winged black-bird (*Agelaius phoeniceus*) to taxidermy mounts of a raccoon (*Procyon lotor*) and an adult red-tailed hawk (*Buteo jamaicensis*), and a rubber model of the American crow (*Corvus brachyrhynchos*). Arroyo et al. (2001) presented a stuffed fox and plastic models of a crow and eagle owl in proximity to Montagu's harrier (*Circus pygargus*) nests. Deppe et al. (2003) worked with two models of the northern pygmy-owl (*Glaucidium gnoma*) made of balsa wood differing only in the presence or absence of eye-spots on the nape. They augmented the dummy with sounds and movement to evoke mobbing. 2D wooden models of predators were applied in one study. Zaccaroni et al. (2007) confronted rock partridges (*Alectoris graeca*) with the stuffed dummy of a fox and a buzzard-like wooden silhouette.

Some type of anti-predation response emerged in all of those studies. Thus, it seems that the use of artificial models in anti-predation experiments on birds is a valid option. It is notable however that all experiments applying static artificial models combined them with stuffed dummies. We can nevertheless suppose that a more veracious stimulus (a stuffed dummy) may induce reaction to a less veracious one (e.g. a plastic model). In addition no comparison has been done of bird response to a stuffed dummy and an artificial model of the same predator. Only Hartley (1950) wrote that a wooden model of the northern pygmy-owl (*Glaucidium gnoma*) activated the same mobbing response as the stuffed one. He did not however corroborate this conclusion with any statistical analyses.

We compared the reaction of the breeding red-backed shrike (*Lanius collurio*) to various dummies of a nest predator. The birds were exposed to stuffed, plush and silicon dummies of the European jay (*Garrulus glandarius*). The plush model is hairy and bears only a partial resemblance to the living bird. The silicone model has a glossy surface and is the least veracious. We used the silicone model instead of a wooden one to eliminate danger of injury. We supposed that the highest intensity of attacks would be directed at the stuffed dummy, a lower at the plush, and the lowest at the silicone dummy. All of the tested pairs were exposed to all three dummies. In this way we were able to test their mutual effect. We supposed that the response to a less veracious dummy would be stronger following a previous trial with a more veracious dummy.

2. Material and Methods

Study area

The study took place in the Doupovské hory mountains, near the town Karlovy Vary (Western Bohemia; 50°10′N, 13°9′E) in the Czech Republic (Fig. B in enclosures). Experiments were conducted during the breeding seasons (from June to late July) in the years from 2008 to 2010. The study area is situated on the borders of the military area Hradiště. The prevalent landscape is farmlands (old meadows or pastures with many shrubs) and small villages. The red–backed shrike reaches quite high breeding densities (up to 18 pairs/ km²) in the study area (Němec, personal observation).

Study species

The red-backed shrike (*Lanius collurio*) was chosen as a model species for studying antipredation behaviour. It is a medium-size song bird. It occurs in the larger part of Eurasia and migrates to tropical Africa in the winter. It comes back to nest in central Europe during May and leaves in September (Cepák at al. 2008). The red-backed shrike occurs in open habitats with scattered shrubs (especially spiny species like the wild rose - *Rosa canina*, blackthorn -*Prunus spinosa*, hawthorn – *Crataegus spp*. or blackberry - *Rubus spp*.) where it builds an open-cup nest (Kuźniak 1991, Söderström 2001).

The red-backed shrike is an insectivorous species but it is also able to hunt small mammals, birds or lizards (Tryjanowski et al. 2003). It thus possesses a strong bill enabling it in turn to display quite vigorous defensive behaviour. Accordingly, such defence usually involves active mobbing including physical attacks (Tryjanowski and Golawski 2004, Strnad et al. in prep.).

The most dangerous predators for the red-backed shrike's eggs and nestlings are Corvidae, e.g. European jay (*Garrulus glandarius*), European magpie (*Pica pica*), carrion crow (*Corvus corone*), and also some small rodents (Roos & Pärt 2004, Schaefer 2004).

As predator we chose the European jay (*Garrulus glandarius*) because Czech populations of red-backed shrikes are familiar with it and often expel it from their territory (Strnad et al. in prep.). The European jay lives in Europe, Asia and north-west Africa. It is of a similar to a pigeon. There are no differences between male and female in colouration or in size. Its diet is very variable, depending on the food on offer locally during the year (San

Miguel 1983, Förschler et al. 2005). Henze (1979 ex Cramp 1994) found the European jay to be a significant predator of the eggs and nestlings of small passerines – causing up to 85 % of all predated from nests.

The European jay is however probably not dangerous for adult birds as (only rare attacks are documented (e.g. Guex 1986 ex Cramp et al. 1994)). Goodwin (1986 ex Cramp et al. 1994) describes that jays in aviary ignored other breeding passerines in the same cage, damaging only their broods. Holyoak (1968) also describes in his huge comparative study that only birds' eggs, no adult birds, play an important role in the diet of the European jay.

Experimental design

We successively presented three dummies of the European jay in proximity to shrike nests. The dummies were made from different materials – stuffed (the most veracious dummy), plush (the dummy with intermediate veracity as it possesses a surface similar to birds' feathers) and silicone (the least veracious dummy, possessing a glossy surface). All dummies were placed in an upright position with their wings folded, 1m far from the nest on a 1.5 m high pole, facing the nest. During the installation the tested dummies were covered with a cloth to prevent early reactions.

All three dummies were presented to each tested pair in one of six possible sequences. Each sequence was tested on 5 or 6 pairs. Each trial (presentation of one dummy) lasted 20 minutes from the appearance of at least one parent. If the parents did not appear within 20 minutes, the trial was terminated and included into the data set as a zero reaction. The time interval until the presentation of the next dummy was precisely one hour. The defence behaviour was tapped on DV Camera. This video camera was placed on a tripod at c. 50 m from the next to prevent affecting the birds' reactions.

All experiments took place between 10:00 a.m. and 18:00 p.m. CEST as long as the weather was suitable. During the years 2008 to 2010 we examined 27 nests with nestlings at an age of between 4 to 12 days. We categorized the age of nestlings into three groups: the youngest (3-4 days) forming group "a", older (6-9 days) group "b", and the oldest (10-12 days) group "c". These groups were used for an analysis of the influence of the age of nestlings on the number of swoops.

Classification of mobbing behaviours

Female and male behaviour were analysed separately. We focused on the active mobbing (number of swoops with and without physical attack), because it was the best indication that the individual recognized the danger represented by the dummy. A swoop without a physical attack is seen as being a flight over the dummy with obviously reduced height.

Statistical analyses

The dependent variable in all analyses was the number of swoops. In order to meet the demands of normal distribution, data were transferred by logarithmic transformation $[\log (no \text{ of } swoops + 1)].$

Firstly, we tested correlation of the number of swoops between male and female within the pair by nonparametric Kendal tau correlation. The intention of this analysis was to assess the level of mutual influence between individuals in the same pair. Because the correlation was strong (z = 6.9422, P << 0.0001), we decided to use pairs instead of individuals for further analyses.

Secondly we computed residual values for number of swoops after eliminating influence of the pair, because each of them was tested three times. In ANOVA, we use these residuals to test the influence of type of dummy, type of previous dummy, sequence of dummies, age of nestlings, sex of parent and interactions between type of dummy and type of previous dummy, and type of dummy and sequence of dummies. Tukey HSD post hoc tests were used to reveal the particular differences in significant results of the analysis. All graphs were created from raw (not transformed) data, because residual values were not optimal for demonstration.

All statistical analyses were computed in R (http://www.r-project.org) and all graphs in Statistica 9.0 (StatSoft Inc. 2008).

4. Results

Fifteen of the twenty-seven tested pairs attacked all of the dummies at least once. Twenty-one pairs attacked the stuffed dummy, nineteen attacked the plush dummy and sixteen attacked the silicone dummy.

The type of dummy, the age of nestlings and sex of the parent influenced the number of swoops after we had eliminated variability among pairs (Table 1). The red-backed shrikes attacked the stuffed dummy more intensively than the silicone dummy (Fig. 1; Tukey HSD post hoc test, P < 0.01). The number of swoops on the plush dummy was marginally different from the both others dummies (Fig. 1; Tukey HSD post hoc test: stuffed-plush, P = 0.06; silicone-plush, P = 0.13).



Fig. 1 – Intensity of active mobbing against the tested dummies (n = 27).

Neither order of dummy in the sequence of trials nor the type of previous dummy in the sequence of trials influenced the intensity of mobbing (Table 1). However, the interaction of type of previous dummy with type of dummy currently presented was significant. If red-backed shrikes saw silicone dummy as first, they did not attack it (Fig. 2, Table A in enclosures). Silicone dummy as first differed (Tukey HSD post hoc test) from: stuffed as the first (P << 0.001) stuffed after plush (P < 0.05) stuffed after silicone (P < 0.01), plush after stuffed (P < 0.05).

Table 1 - Factors influenced number of swoops to tested dummies (ANOVA, n = 27, residuals of number of swoops without influence of the pair).

	Df	F value	Pr(>F)
Sequence of dummies	2	1.0801	0.34224
Type of dummy	2	10.3997	5.966e-05
Previous dummy	2	1.5298	0.22001
Age of nestlings	2	10.9512	3.686e-05
Sex of parents	1	4.9702	0.02730
Type of dummy: previous dummy	3	2.7248	0.04638
Sequence of dummies: type of dummy	2	0.2712	0.76285
Residuals	147		

Red-backed shrikes defended the youngest nestlings with a lower intensity (Fig. 3, Tukey HSD post hoc test) than older (P < 0.001) and the oldest (with marginally significance, P = 0.09) nestlings. Males defended more intensively than females (Fig. 4) however there was also a strong correlation between partners within the pair (nonparametric Kendalau tau, z = 6.9422, P << 0.001).



Fig. 2 – Intensity of active mobbing against tested dummies dependant on previous trial [stuffed after: n(nothing) = 9, n(plush) = 9, n(silicone) = 9; plush after: n(nothing) = 10, n(stuffed) = 8, n(silicone) = 9; silicone after: n(nothing) = 8, n(stuffed) = 10, n(plush) = 9].



Fig. 3 – Intensity of mobbing dependant on the age of nestlings [n(a) = 6, n(b) = 15, n(c) = 6].



Fig. 4 – Difference between females and males in intensity of active mobbing (n = 27).

5. Discussion

Red-backed shrikes attacked all three dummies - stuffed, plush and silicone. Nevertheless, two artificial dummies (plush and silicone) were mobbed with lower intensity than the most veracity stuffed dummy. The plush dummy (less veracious) was mobbed slightly more than the silicone dummy (the least veracious). The number of tested pairs, attacking the exposed dummy with at least one swoop, also declined with the veracity of the dummy.

At the first sight it seems that the use of artificial dummies in anti-predation and similar experiments is possible without serious problems, although the response of tested animals is lower than to stuffed dummy. However, this conclusion is in conflict with experiments where the least veracious silicone dummy was exposed to shrikes first. Almost none of the tested birds responded in these cases. The active defence reaction against the silicone dummy was conditioned by the presentation of a more veracious dummy (stuffed or plush) in a previous trial. This puts in doubt the validity of using a silicone dummy as the sole dummy in such experiments. There was no similar effect with the plush dummy, when it was presented as the first. Neither dummy order nor previous dummy influenced the intensity of mobbing. Thereby we can exclude potential effects of increasing excitement or habituation, and it seems that plush dummies are suitable for these types of experiments.

Our results are not as positive as the results of previous studies where artificial dummies were used. It is not very surprising that rubber or plastic snakes have been successfully used in such studies (Makkalov 2002, Kleindorfer et al. 2005). Real snakes are covered with keratinous scales and the surface of a silicone dummy is a good imitation of this. However, when Gottfried et al. (1985) exposed nesting American robins (*Turdus migratorius*) to a stuffed blue jay (*Cyanocitta cristatu*) and to a rubber snake model too few robins attacked the snake model to permit a statistical analysis of the data. Robins uttered twice as many vocalizations in response to the jay model as they did to the snake. Of course, we do not know whether the difference was influenced by lesser veracity of the snake dummy or, as the authors suggested the lesser dangerous presented by snake.

The resemblance between real birds and their plastic or wooden models is not as close as in snakes. Even so such models have been successfully used in some studies. The dummies used by Deppe et al. (2003, northern pygmy-owl) and Mathod et al. (2009, sparrow-hawk) where however enhanced by movement, and in the former also by noise, invalidating the trials as tests of the dummies' veracity alone. Moreover, while we analysed only active mobbing, most of the other studies using artificial dummies also monitored less unequivocal responses to presented predators (Knight and Temple 1988, Gill et al. 1997, Burhans 2001, Zaccaroni et al. 2007, Mathot et al. 2009). We may suppose that excited movement or warning calls will also be used in the event of nest defending birds not positively identifying a predator irrespective of its veracity (or even of whether it is living or not), thus similarly invalidating the results of such tests. Cockrem & Silverin (2002) studied the behavioural and physiological responses of the great tit in captivity to a stuffed Tengmalm's owl, a stuffed brambling and a cardboard box in captivity. Great tits changed their behaviour to all three objects (escape flights). Only much faster reaction distinguished response to the owl. In addition only the presence of the owl increased plasma corticosterone levels in the tested birds, indicating that such responses may be precautionary, not an indication of perceived threat.

The most surprising result was that it is necessary to present firstly more veracity (stuffed or plush) dummy to evoke an attack against silicone dummy. A similar effect has not been previously described in any studies of anti-predation experiments with artificial dummies. It is well known however to researchers studying cognitive processes. It is known as matching to sample and was described by Skinner (1950 ex. Ferster 1960). He demonstrated the possibility of maintaining a complex chain of discriminative responses (matching to sample) under intermittent reinforcement. Using of matching to sample has been demonstrated in number of experiments studied how birds (pigeons) categorise various objects (e.g. Farthing & Opuda 1974, Santi 1978, Hollard & Delius 1982, Delius et al. 1999). These studies were based on operant conditioning and usually work with abstract symbols (coloured stripes, squares, circles, etc.). It is interesting that the time between presentation of model and its recognition is much shorter (approximately seconds) in these studies than we observed in our experiments (one hour). Our study firstly shows that matching to sample is used to categorize real objects by non-trained birds in nature.

However, there is the argument that red-backed shrikes do not recognize a jay in the silicone model at all and after being provoked in trial with a more veracious dummy will simply attack any birds. This however has been disproved by the previous study by Strnad et al. (in prep.). They studied the response of nesting red-backed shrikes against predators of adults (sparrowhawk and kestrel) as well as nestlings (jay and magpie) in the same manner as we did. Pigeon was used as harmless control. They demonstrated that red-backed shrikes do not attack the pigeon even when presented after a predator. The intensity of mobbing is slightly higher by males than by females and changes with the age of nestlings too. In the youngest age category it is lower than in the other two. These results are consistent with many previous studies on anti-predation behaviour of nesting birds. It has been proven a number of times that males defend their older nestlings more than females (e.g. Regelmann & Curio 1983, Brunton 1990, Rytkönen et al. 1993). This may be due to the increasing investment made by males during feeding period. For the same reason, the intensity of defence grows also with the age of nestlings (Rytkönen et al. 1993). Our results show newly that red-backed shrikes also optimize their investments in nestlings when artificial dummies are used.

6. References

- Arroyo B, Mougeot F & Bretagnolle V (2001) Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). Behavioral Ecology and Sociobiology 50, 109-115.
- Brunton DH (1990) The effects of nesting stage, sex, and type of predator on parental defense by killdeer (*Charadrius vociferous*): testing models of avian parental defense. *Behavioral Ecology and Sociobiology* 26 (3), 181-190.
- Burhans DE (2001) Enemy recognition by field sparrow. *The Wilson Bulletin* 113 (2), 186-193.
- Caro TM (2005) Antipredator defenses in birds and mammals. University of Chicago Press.
- Cepák J, Klvaňa P, Škopek J, Schröpfer L, Jelínek M, Hořák D, Formánek J & Zárybnický J (2008). *Czech and Slovak bird migration atlas*. Praha: Aventinum.
- Cramp S, Perrins CM, Brooks DJ, Dunn E & Gillmor R (1994) Handbook of the Birds of Europe the Middle East and North Africa. The Birds of the Western Palearctic. Oxford, New York: Oxford university press.
- Cockrem JF & Silverin B (2002) Sight of a predator can stimulate a corticosterone response in the great tit (*Parus major*). *General and Comparative Endocrinology* 125, 248 255.
- Delius JD, Emmerton J, Hörster W, Jäger R & Ostheim J (1999) Picture-object recognition in pigeons. *Current Psychology of Cognition* 18, 621–656.
- Dennis JE & Schnabel RB (1983) Numerical Methods for Unconstrained Optimization and Nonlinear Equations. Prentice-Hall, Englewood Cliffs, NJ.
- Deppe C, Holt D, Tewksbury J, Broberg L, Petersen J & Wood K (2003) Effect of northern pygmy-owl (*Glaucidium gnoma*) eyespots on avian mobbing. *The Auk* 120(3), 765–771.
- Farthing GW & Opuda MJ (1974) The role of physical identity of the sample and correct comparison stimulus in matching-to-sample paradigms. *Journal of the Experimental Analysis of Behavior* 21, 199-213.
- Ferster CB (1960) Intermittent reinforcement of matching to sample in the pigeon. *Journal of the Experimental Analysis of Behaviour* 3, 259-272.

- Förschler MI, Borras A, Cabrera J, Cabrera T & Senar JC (2005) Inter-locality variation in reproductive success of the citril finch *Serinus citronella*. *Journal of Ornithology* 146, 137–140.
- Gill SA, Neudorf DL & Sealy SG (1997) Host responses to cowbirds near the nest: cues for recognition. *Animal Behaviour*, 53, 1287–1293.
- Gottfried MM, Anedrews K & Haug M (1985) Breeding robins and nest predators: effect of predator type and defence strategy on initial vocalization patterns. *Wilson Bulletin* 97, 183–190.
- Hakkarainen H, Ilmonen P, Koivunen V & Korpimäki E (1998) Blood parasites and nest defence behaviour of Tengmalm's owls. *Oecologica* 114, 574 577.
- Hakkarainen H, Ilmonen P, Koivunen V & Korpimäki E (2001) Experimental increase of predation risk induces breeding dispersal of Tengmalm's owl. *Oecologia* 126, 355–359.
- Hartley PHT (1950) An experimental analysis of interspecific recognition. *Symposium for the Society of Experimental Biology* 4, 313–336.
- Hollar VD & Delius JD (1982) Rotational invariance in visual pattern recognition by pigeon and humans. *Science* 218, 804-806.
- Holyoak D (1968) A comparative study of the food of some British Corvidae. *Bird Study* 15 (3), 147.
- Kis J, Liker A & Székely T (2000) Nest defence by lapwings: observations on natural behaviour and an experiment. *Ardea* 88 (2), 155-163.
- Kleindorfer S, Fessl B & Hoi H (2005) Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. *Animal Behaviour* 69 (2), 307-313.
- Knight R & Temple S (1986) Methodological problems in studies of avian nest defence. *Animal Behaviour* 34, 561-566.
- Knight R & Temple S (1988) Nest-defense behavior in red-winged blackbird. *The Condor* 90, 193-200.
- Kuźniak S (1991) Breeding ecology of the red-backed shrike (*Lanius collurio*) in the Wielkopolska region (western Poland). *Acta Ornitologica* 26, 67-84.
- Mathot KJ, Van den Hout PJ & Piersma T (2009) Differential responses of red knots, *Calidris canutus*, to perching and flying sparrowhawk, *Accipiter nisus*, models. *Animal Behaviour* 77, 1179-1185.

- Meilvang D, Moksnes A & Roskaft E (1997) Nest predation, nesting characteristic and nest defence behaviour of Fieldfares and Redwings. *Journal of Avian Biology* 28, 61-68.
- Palleroni A, Hauser M & Marier P (2005) Do response of galliform birds vary adaptively with predator size? *Animal Cognition* 8, 200-210.
- Röell A & Bossema I (1982) A comparison of nest defence by jackdaws, rooks, magpies and crows. *Behavioral Ecology and Sociobiology* 11 (1), 1-6.
- Maklakov AA (2002) Snake-directed mobbing in a cooperative breeder: anti-predator behaviour or self-advertisement for the formation of dispersal coalitions? *Behavioral Ecology and Sociobiology* 52, 372-378.
- Regelmann K & Curio E (1983) Determinants of brood defence in the great tit Parus major L. *Behavioral Ecology and Sociobiology* 13, 131-145.
- R Development Core Team (2010). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org
- Roos S & Pärt T (2004) Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). *Journal of Animal Ecology* 73, 117–127.
- Rytkönen S, Orell M & Koivula K (1993) Sex-role reversal in willow tit nest defence. *Behavioral Ecology and Sociobiology* 33, 275 – 282.
- San Miguel A (1983) Contribution to the study of feeding habits of jays (*Garrulus glandarius* L. 1758) in Spain. *Boletin de la Estacion Central de Ecologia* 12 (23), 77-82.
- Santi A (1978) The role of physical identity of the sample and correct comparison stimulus in matching-to-sample paradigms. *Journal of the Experimental Analysis of Behavior* 29, 511-51
- Schaefer T (2004) Video monitoring of shrub-nests reveals nest predators: Capsule Jays *Garrulus glandarius* are the most common predators, but carnivorous mammals and some other species also predate nests. *Bird Study* 51 (2), 170.
- Schnabel RB, Koontz JE & Weiss BE (1985) A modular system of algorithms for unconstrained minimization. ACM Trans. *Math. Software* 11, 419–440.
- Söderström B (2001) Seasonal change in Red-backed Shrike *Lanius collurio* territory quality the role of nest predation. *Ibis* 143 (3), 561-571.

- StatSoft, Inc. (2010) Electronic Statistics Textbook. Tulsa, OK: StatSoft. WEB: http://www.statsoft.com/textbook/.
- Strnad M, Němec M, Veselý P, Poláková S & Fuchs R (in prep.) Is the nest defence of red-backed shrike (*Lanius collurio*) adjusted to peril for parents of offspring? Submitted to *Behavioural Ecology and Sociobiology*.
- Tryjanowski P, Karg MK, & Karg J (2003) Diet composition and prey choice by the red-backed shrike *Lanius collurio* in western Poland. *Belgian Journal of Zoology* 133 (2), 157-162.
- Tryjanowski P & Golawski A (2004) Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season. *Journal of Ethology* 22 (1), 13-16.
- Zaccaroni M, Ciuffreda M, PaGanin M & Beani L (2007) Does an early aversive experience to humans modify antipredator behaviour in adult Rock partridges? *Ethology, Ecology* & *Evolution* 19, 193-200.

7. Enclosures

Fig. A – Dummies of European jay – stuffed, plush and silicone.



Fig. B – Map of the study area.





Table A – Differences between orders of dummies (Tukey HSD post hoc test).