Jihočeská univerzita v Českých Budějovicích
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Magisterská práce

Jak ptáci poznávají predátory – význam úplnosti vizuální informace

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Magisterská práce

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Anotace:

Schopnost rozeznat různé druhy dravců a užití „amodal completion“ byly studovány na čtyřech druzích sýkor pomocí preferenčních krmítkových experimentů. Především bylo zjištěno, že chování sýkor je v souladu s „dynamic risk assessment theory“, neboť přítomnost jakéhokoliv predátora snižovala počet příletů na krmítko. Sýkory navíc hodnotily krahujce jako více nebezpečného, protože jeho přítomnost snižovala počet příletů na krmítko více než přítomnost poštolky. Dále byly studovány reakce sýkor na torzo krahujce („amputated“ podnět) a torzo krahujce zakryté ve chvojí („occluded“ podnět). Obě tato torza byla sýkorám nabízena buď spolu s neškodným holubem, nebo s nebezpečným predátorem na alternativním krmítku. Sýkory klasifikovaly obě torza jako plnohodnotné predátory, když měly možnost příjmu potravy na bezpečném krmítku s holubem. Oproti tomu, když byl na alternativním krmítku krahujec, tak sýkory riskovaly přílet k podivnému amputovanému torzu častěji, než k torzu zakrytému ve chvojí. Tato diskriminace jasně dokazuje používání “amodal completion” během rozpoznávacích procesů.

Annotation:

Pair-wise preferential experiments were used to reveal dangerous predator differentiation and ability of amodal completion by four tit species. Firstly was revealed that the tits’ behaviour towards the feeder was in agreement with predictions of the dynamic risk assessment theory. The presence of any predator at the feeder lowered the number of visits to the feeder. Likewise, the tits evaluated the sparrowhawk as more dangerous than the kestrel because its presence lowered the number of visits more than the kestrel. Secondly, we observed tits’ reactions to both partly occluded and amputated dummy of sparrowhawk in two different treatments (torsos vs. complete dummy of pigeon, torsos vs. complete dummy of sparrowhawk). All birds clearly classified both torsos as “full-featured” predators and kept away of them when pigeon on the second feeder. However, when sparrowhawk was presented on the second feeder, number of visits to amputated predator was higher than to occluded one. Birds risked arriving to “utter” amputated torso while the fear of “full-featured” occluded torso stayed without change when second feeder did not provide safe alternative. Such discrimination between torsos needs ability of amodal completion.

Poděkování:

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Obsah

1. Úvod

Schopnost správně rozpoznat a ohodnotit nebezpečnost predátora je základní podmínkou pro fitness volně žijících živočichů (Devereux et al. 2005). Antipredační chování je energeticky náročné (Krams & Krama 2002) a krom přímých nákladů zdržuje od dalších neméně důležitých aktivit, zejména pak od příjmu potravy. Proto jsou zvířata neustále nucena vyhodnocovat, které antipredační chování a kdy se vyplatí. Podhodnocení nebezpečného predátora může být pro jedince fatální. Nadhodnocení aktuálního ohrožení jej ale diskriminuje taktéž (Caro 2005). Podle „risk assesment theory“ (Montgomerie & Weatherhead 1988) by jedinec, který průběžně vyhodnocuje situaci a podle ní mění své chování, měl být ve výhodě před jedincem vykazujícím fixní odpověď na vzniklou situaci.

Schopnost rozpoznat predátora je tedy prvním krokem ke správnému ohodnocení nebezpečí. Tato schopnost byla v minulosti testována zejména v rámci experimentů zaměřených na studium obrany ptačích hnízd (review viz Caro 2005). Ve valné většině prací byla porovnávána pouze reakce na predátora a neškodné objekty typu lahev, krabice apod. (například: Schields 1984; Reyer et al. 1998; Arnold 2000; Radford & Blakey 2000; Rytkönen 2002). Méně často byl porovnáván predátor a neškodný více či méně podobný živočišný druh. Kullberg & Lind (2002) prokázali rozlišování mezi atrapou krahujce a koroptve. Stejně tak Dale et al. (1996) pozorovali u lejska černohlavého (*Ficedula hypoleuca*) rozdílné reakce na vycpaného krahujce (*Accipiter nisus*) a drozda kvíčalu (*Turdus pilaris*). Clemmons & Lambrechts (1992) zjistili, že sýkory (*Parus atricapillus*) reagovaly nejméně na čipmanka (*Tamias striatus*), veverku (*Sciurus carolinensis*) a střízlíka (*Troglodytes aedon*). Naopak na sojku (*Cyanocitta cristata*) a sovu (*Otus asio*) reagovaly silným křikem.

Poměrně intenzivní pozornost byla věnována srovnání reakcí na hnízdní predátory a predátory dospělců, (review viz Caro 2005). Také další práce (Buitron 1983; Knight & Temple 1986; Jacobsen & Ugelvik 1992; Rytkönen & Soppela 1995; Arroyo & Mougeot 2001; Hogstad 2004; Csermely et al. 2006), potvrzují, že ptáci jsou schopni rozlišit hnízdního predátora od predátora dospělců a své chování k nim upravují zejména podle dosavadních investic do hnízdění, šance na náhradní snůšku, typu ohrožení (mláďat a/nebo bránících ptáků) a vzdálenosti predátora od hnízda.

Nicméně jen velmi málo autorů se zabývalo studiem reakcí ptáků na různě nebezpečné druhy predátorů dospělců. Ve většině případů se jednalo o srovnání denního dravce se sovou. Dravcem byl vždy krahujec, zatímco v roli sov se vystřídaly různé druhy. Rytkönen & Soppela (1995) používali atrapu kulíška nejmenšího, Kout (2002) kalouse pustovku a Curio et al. (1983) atrapu puštíka. Všichni tito autoři pozorovali intenzivnější mobbing na sovu, který interpretovali jako důsledek většího strachu z krahujce.

Grubb (1977) a Curio at al. (1983) zjistili rozdíly v reakci ptáků na různé druhy sov, v závislosti na jejich velikosti a potravní specializaci. Naopak Altmann (1956) toto nedokázal, tato práce však metodicky neodpovídá současným požadavkům.

Oproti pokusům s predátory dospělců, jediná práce porovnávající reakce na různé hnízdní predátory žádné rozdíly v chování bránících ptáků nezaznamenala (Jacobsen & Ugelvik 1992).

Alternativu k pokusům založeným na obraně hnízd poskytují krmítkové experimenty. Jestliže ptákovi nabídneme potravu a současně v její blízkosti umístíme predátora, pak návštěva krmítka znamená, že potřeba zisku energie převážila nad vyhodnoceným rizikem.

Většina prací zabývajících se manipulací rizika na krmítku byla prováděna ve voliérách a zaměřila se na studium vztahu mezi fyziologickým stavem testovaných ptáků a jejich ochotou riskovat. Autoři zjišťovali, jak ptáci reagují změnou hmotnosti na přítomnost predátora na krmítku (Lilliendahl 1997, 1998, 2000; Pravosudov & Grubb 1998; Carrascal & Polo 1999). Jiní se zaměřili na studium hladin kortikosteroidních hormonů (Cockrem & Silverin 2001) nebo trade-off mezi ukrýváním se a hledáním potravy (van der Veen 1999; Cressvel et al. 2003; Devereux et al. 2005; Lind et al. 2005). Jen několik prací bylo prováděno v přirozeném postředí (Gentle & Gosler 2001; Desrochers et al. 2002; MacLeod et al. 2005; MacLeod & Gosler 2006; Tvardíkova & Fuchs in prep.). Jejich výsledky především ukazují, že „přírodní“ krmítkové experimenty jsou vhodné pro studium rozpoznávání predátorů a že ptáci rychle a komlexně mění nejen fyziologii ale i chování.

2. Cíle

Stávající studie věnované rozpoznávání predátorů pracovaly s poměrně omezeným počtem „objektů“ Ve své bakalářské práci (Tvardíková & Fuchs in prep.) jsem se rozhodla tento počet podstatně rozšířit. Do svých experimentů jsem zahrnula různě nebezpečné predátory (krahujec, poštolka), více či méně neškodné ptáky (sojka, holub, drozd) a umělý předmět (chomáč vaty). Jako metodu jsem použila přírodní krmítkový experiment a testovanými ptáky byly čtyři druhy sýkor (*Parus major*, *Poecile palustris*, *Poecile montanus*, *Cyanistes cearuleus*).

Nejvhodnější charakteristikou vlivu atrapy na chování sýkor se ukázal být počet příletů na krmítko. Přítomnost většiny atrap (s výjimkou drozda a umělého předmětu) počet příletů signifikantně snižovala. Jakýkoliv větší pták včetně zcela neškodného holuba tedy zvyšoval opatrnost sýkor. Překvapivě však nerozlišovaly mezi atrapou poštolky a krahujce, přestože krahujec představuje větší nebezpečí, neboť se jedná o specializovaného predátora drobných ptáků (Götmark 2002; Rytkönen et al. 1998).

V magisterské práci jsem tedy na tuto studii navázala. Mým prvním cílem bylo pokusit se prokázat odlišné hodnocení nebezpečnosti poštolky a krahujce pomocí preferenčních krmítkových pokusů. Předpokládala jsem, že pomocí preferenčních experimentů (v nichž pták může volit mezi dvěma možnostmi) bude možné rozlišit i jemné rozdíly v hodnocení nebezpečnosti predátorů, které jsou nepostihnutelné v jednoduchých krmítkových experimentech **(Článek I)**. Můj předpoklad se potvrdil a proto jsem tutéž metodiku použila pro řešení dalšího úkolu – testovat, zda ptáci při rozpoznávání predátorů používají “amodal completion”, nebo se rozhodují pouze na základě klíčových znaků predátorů **(Článek II)**.

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Článek I.

Feeder preferential experiments: Do the birds behave according to dynamic risk assessment theory?

1. ABSTRACT

Pair-wise preferential experiments were used to reveal dangerous predator categorization by four tit species wintering in the Czech Republic. The reactions of tits to more (the sparrowhawk) and less (the kestrel) dangerous predators were compared. The number of visits to a feeder, with a predator present, expressed perceived predator dangerousness. The tits' behaviour towards the feeder was in agreement with predictions of the dynamic risk assessment theory. The presence of any predator at the feeder lowered the number of visits to the feeder. Likewise, the tits evaluated the sparrowhawk as more dangerous than the kestrel because its presence lowered the number of visits more than the kestrel. The results also show the exceptional suitability of preferential experiments for the research of predator differentiation and evaluation.

2. INTRODUCTION

Experiments using a feeder proved productive for the research of antipredatory behaviour in passerines. With a feeder, it is possible to examine the trade-off between the need for predator avoidance and food intake (Gentle & Gosler 2001; Desrochers et al. 2002; MacLeod et al. 2005). In a previous study (Tvardíkova & Fuchs in prep.), we used feeder experiments to examine whether birds specify the antipredatory response according to the differing dangerousness of potential aerial predators and other birds. Two birds of prey differing in prey specialization (the common kestrel *Falco tinnunculus*, the Eurasian sparrowhawk *Accipiter nisus*) were among the tested predators. The sparrowhawk is the most dangerous predator for small passerines (Rytkönen et al. 1998; Götmark 2002), while small mammals predominate in the kestrel's diet (Kubler et al. 2005). We expected that the number of visits to the feeder would be lower in the presence of a sparrowhawk than in the presence of a kestrel because of its different dangerousness for small birds. Our hypothesis was not confirmed statistically. The number of visits to the sparrowhawk was lower than to the kestrel however the difference was not significant.

In this study, we tried a new method to reveal the subtle difference between the evaluation of the kestrel and sparrowhawk. We offered to birds a couple of feeders with various combinations of predators instead of only one. Such an experimental design had never before been applied to study the evaluation of predator dangerousness. However, preferential experiments in birds have already successfully been used to reveal bird food choices. Pair-wise (or "cafeteria") trials, where two (or more) food types are presented, could easily detect food preference (e.g. Willson & Comet 1993; Best & Gionfriddo 1994; Whelan & Willson 1994; Willson 1994). Similarly, we expected that the birds would behave according to risk assessment theory (Montgomerie & Weatherhead 1988), and that confronted with differing risks at the same time they would choose the lesser. We followed Carrascal & Alonso (2006), who found that passerines prefer feeding in safe places in the proximity of protective cover.

We offered the following treatments (combinations of "dangerousness"): a kestrel (or sparrowhawk) vs. an alternative feeder without a predator, a kestrel (or a sparrowhawk) vs. the same predator at an alternative feeder, a kestrel (or a sparrowhawk) vs. the opposite predator at an alternative feeder. We supposed that the birds would prefer feeding in the presence of the less dangerous predator (the kestrel) only in the case of the occupation of the alternative feeder by more dangerous (the sparrowhawk).

3. METHODS

Experimental site and species

The experiment was undertaken during the winter of 2006/2007 at the edge of broad-leaved tree growth near the village of Chodská Lhota (49°21'15", 30°47'25"), West Bohemia, the Czech Republic. Though, the site is 640 meters above sea level and is located in a relatively cold part of Bohemia, this winter was not harsh, being mostly without snow cover. We studied four species of tits, the great tit (*Parus major*), the blue tit (*Cyanistes caeruleus*), and the "marsh" tit, which predominating on feeders. The "marsh" tit was represented by the marsh tit (*Poecile palustris*) and the willow tit (*Poecile montanus*). These two species are indistinguishable on videotape, and so were lumped together as one species.

Experimental design

Two feeders were situated in a field, 7 meters from the edge of tree growth. The feeders were 20 meters apart and the space between them was free of trees. Shrubs and trees in the tree growth edge served as a watching place and as a shelter for the birds. The feeders were square boards (45 cm by 45 cm) lying on the ground with raised edges to avoid the scattering of food. Between experiments, the feeders were covered with a roof. Sun-flower seeds were used as food. To attract the birds, the feeders were filled four weeks before the first experimental series. Any remaining sun-flower seeds were attentively removed and replaced with grated walnuts each time just before the trials started. The tits did not carry the grated walnuts away to consume them under cover as they had done with the sun-flower seeds. Therefore, they had to remain at the feeder for a longer time if they wanted to achieve sufficient food intake.

Stuffed sparrowhawk and kestrel dummies were used as test predators. They were placed on a 75 cm high stake in the outer (from the forest edge) right corner of the feeder and always faced into the centre of feeder. Individual trials lasted 30 minutes. The following combinations of dummies (combination of treatments) were tested: kestrel vs. sparrowhawk, kestrel vs. empty feeder, kestrel vs. kestrel, sparrowhawk vs. empty feeder and sparrowhawk vs. sparrowhawk. Two empty feeders was the reference control. This amounted to six different trials in one series. The sequence of trials within each series was randomly arranged. The placing of the dummy (on the left or on the right feeder) was randomly arranged for each trial as well.

Each series was carried out in one day. There was usually a five or six day break between each series. Each experimental series started 0.5 - 1 hour after daybreak. Feeders were taped constantly during the duration of the experiments. Cameras were set up in a fixed position, facing the feeders, 7 meters away near the edge of tree growth. The snow cover and temperature were noted for each experimental day. Ten series were conducted and amounting to 60 half-hour trials.

As part of this study, birds were trapped using mist-nets to reveal the rate of pseudo replications. Mist-nets were in use the day before each experimental series and the trapping effort was constant (about 30 birds were ringed per day) during the study. Under licence (Czech bird ring association, 1062), each trapped bird was fitted with both a standard metal leg-ring with a unique number and an individual combination of colour-rings. Each bird was thus uniquely identifiable on videotape.

Altogether 265 birds were ringed during the winter. It has been revealed that X+SD = 54.53+4.95 % ringed birds came back to the feeder in the following series (one day after ringing). Only X+SD = 30.39+1.49 % stayed until the second series (approximately 7 days later) and X+SD = 15.11+5.2 % to the third series (approximately 14 days later). Less than X+SD = 1.75+0.7 % of ringed birds dwelled in the locality longer than one month. Individual birds usually visited the feeder in X+SD = 1.46+0.6 trials (at most in 4 trials) during one series. Once appearing during the trial the bird usually arrived at the feeder X+SD = 2.23+0.97 times. These numbers are a little lower than observed by Desrochers et al. (2002) and Tvardíkova & Fuchs (in prep.). This may have been caused by the mild winter.

Statistical analysis

The number of visits at the feeder of individual tit species during the treatment was analysed. The numbers of visits were analysed firstly for each whole trial (half-hour) and secondly for 5 minute long intervals within one trial (to reveal the possible habitualization to the motionless predators). The following explanatory variables were used: the situation at a particular experimental feeder - from which the number of visits were included in the analysis (dummy), situation on the alternative feeder (alternative dummy), the sequence of series during the winter (1-10), tit species (interaction dummy:species), temperature (°C), and snow cover (cm).

First, a base line of birds was counted for each series. For that reason, left and right feeders within the reference controls (both feeders without dummy) were compared and found to be nonsignificant (Mann-Whitney U test: U = 47, N1 = N2 = 10, P = 0.819). After that the arithmetic means of arrivals during the reference control were counted for each bird species and each series.

To make comparison of the treatments (within and between trials and series) possible, the relative number of visits at each feeder was counted for each bird species. The numbers of visits to all experimental feeders (to the left as well as to the right) in particular series (with a dummy on at least one feeder) were divided by these means and all the created ratios were entered into the analysis.

We acknowledged the problem of statistical nonidependence as the left and right feeders were in one trial simultaneously. Therefore, to examine which of the explanatory variables had an effect on the number of visits to each experimental feeder, GLM was constructed and the random effect was established for both feeders within one trial. Data had a normal distribution and the link function identity was used. All interactions were originally also included in the model but only particular: dummy:alternative dummy (the only significant) and tit species:dummy (insignificant but important for result interpretation) were mentioned in the results.

Different GLM was constructed to reveal differences between combinations of dummy:alternative dummy. The random effect was set up for both feeders within one trial. Data had normal distribution and the link function identity was used. The ratios of number (from above) of visits were entered into the analysis where the particular combination of dummies on both feeders (for example kestrel – kestrel) was explanatory variable. The sequence of series (1-13), tit species (dummy:species) temperature (°C), and snow cover (cm) were the other explanatory variables. The Tukey post hoc test (Hothorn et al. 2008) was constructed after that.

Repeated measures ANOVA was used for 5 minute long intervals analysis. The number of visits during the experimental trials did not change significantly (dummy: section: $F_{10} = 0.414$, $P = 0.938$). These statistical calculations (and all graphs) were made using STATISTICA 8 for Windows (Statsoft Inc.)

4. RESULTS

Over the winter, 5292 individual visits were recorded at the feeders. The dummy present at the experimental feeder, the situation (kestrel, sparrowhawk or feeder without predator) present at alternative feeder and the temperature were significant predictors of relative change of the number of visits. The interaction between both dummies was also significant. The snow layer, the series sequence, and the interaction between the dummy and the tit species had no significant effect (Table 1).

Table 1. The effects of the dummies, weather and experimental design on the relative change of the number of visits at the feeder (GLM)

Effect	Df	*F*	*P*
Dummy	**2**	**414.056**	**<0.001**
Alternative dummy	**1**	**17.865**	**<0.001**
Temperature	**1**	**9.360**	**0.020**
Snow	1	0.830	0.365
Series	1	0.210	0.648
Dummy : species	10	0.561	0.543
Dummy: Altern. dummy	**4**	**10.016**	**<0.001**

If separate combinations of dummies on experimental and alternative feeder were compared (Tables 2, 3), the kestrel dummies decreased the relative number of visits less than sparrowhawk dummies but only in treatments in which a kestrel was combined with a sparrowhawk or kestrel on the alternative feeder. The decrease in the number of visits did not differ between a kestrel and sparrowhawk in treatments, in which a kestrel was combined with the alternative feeder without a predator (Table 2, Fig. 1).

Table 2. Differences between the relative changes in the number of visits to kestrel and to sparrowhawk in trials with different treatment at the alternative feeder (noted in parentheses)

	SP(SP)	SP(0)	SP(KE)
KE(0)	0.989 *0.952*	0.987 *0.001*	0.978 *0.001*
KE(SP)	**<0.001** *-7.439*	**<0.001** *-7.269*	**<0.001** *-7.267*
KE(KE)	**<0.001** *-7.384*	**<0.001** *-6.981*	**<0.001** *-6.981*

Treatments on both feeders: KE – kestrel, SP - sparrowhawk, 0 – empty feeder (occurs only at the alternative feeder). The Tukey post hoc test results show *P* (above) and *t* (*below*) values.

Table 3. The differences between the relative changes in the number of visits to kestrels, or to sparrowhawks, in trials with different treatment at the alternative feeder (noted in parentheses)

		t	*P*
KE(SP)	**KE(0)**	**7.267**	**<0.001**
KE(SP)	KE(KE)	1.141	0.888
KE(KE)	**KE(0)**	**6.981**	**<0.001**
SP(SP)	SP(0)	0.952	0.989
SP(SP)	SP(KE)	0.952	0.989
SP(KE)	SP(0)	<-0.001	0.987

Treatments on both feeders: KE – kestrel, SP - sparrowhawk, 0 – empty feeder (occurs only on the alternative feeder). Tukey post hoc test results show *P* and *t* values.

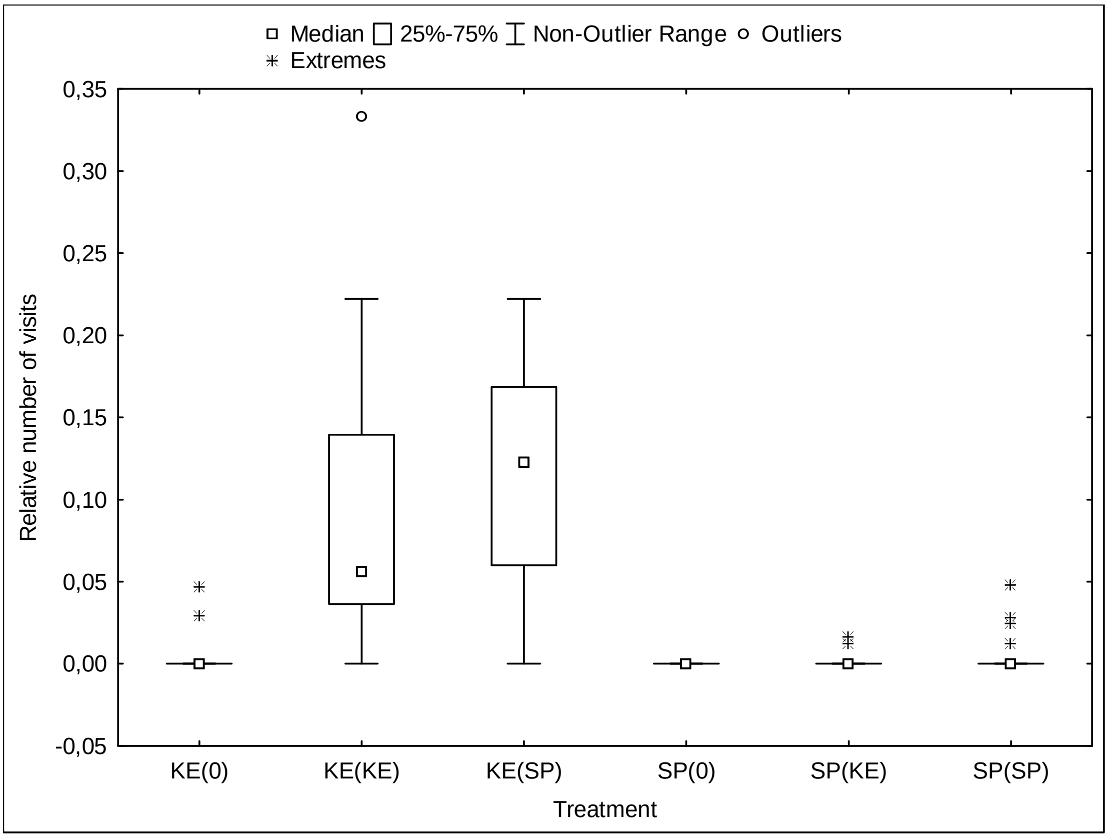

Figure 1. Relative changes (related to reference control) in the number of visits to kestrel and sparrowhawk in trials with different treatment on the alternative feeder (noted in parenthesis). Treatments on both feeders: KE – kestrel, SP - sparrowhawk, 0 – empty feeder (occurs only on the alternative feeder).

The dummy at the alternative feeder also influenced the relative change of the number of visits to the kestrel (Table 3, Fig. 1). A kestrel decreased the number of visits less if it was combined with a sparrowhawk or kestrel than if it was combined with an alternative feeder without a predator. The relative change in the number of visits did not differ in any treatment with a sparrowhawk (Table 3, Fig. 1). Low temperature diminished the decrease in the number of visits to the feeder with a predator (Fig. 2).

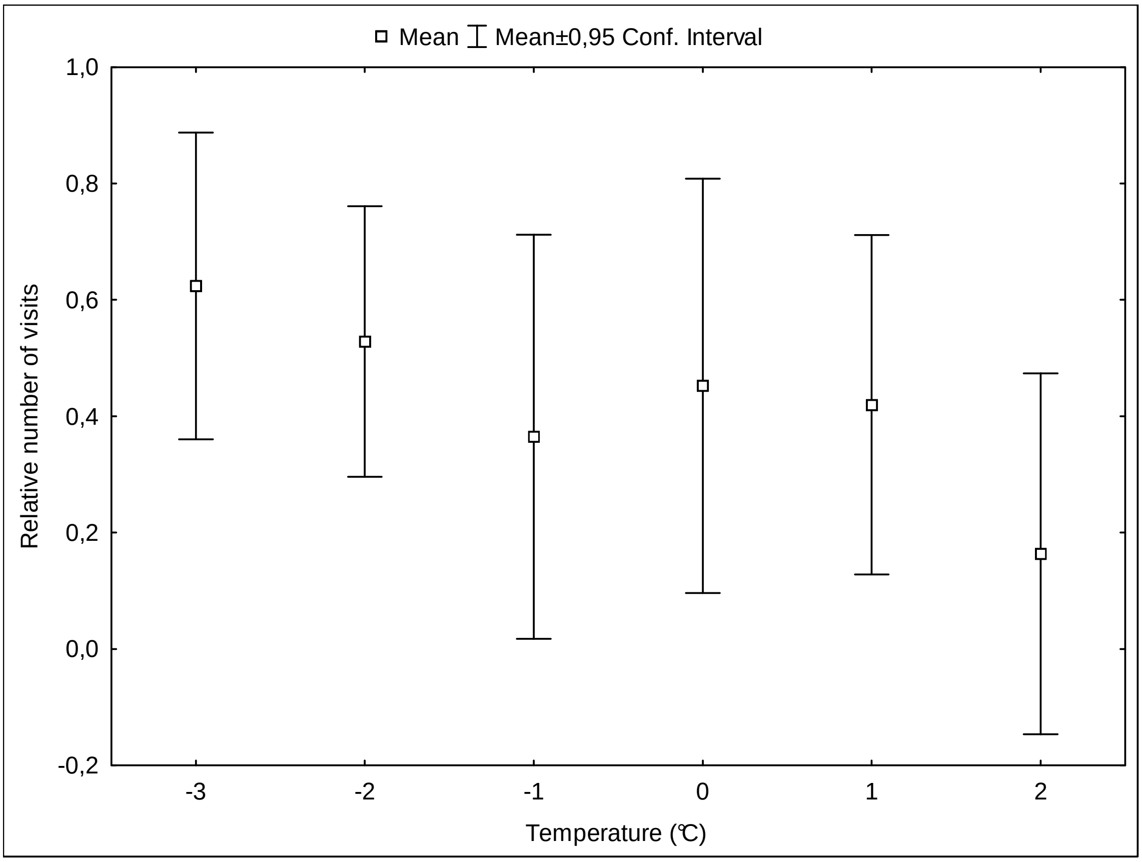

Figure 2. Effect of temperature on the number of visits at the feeder – for experimental trials with a predator

5. DISCUSSION

Tits behaviour at the feeders was in agreement with the predictions of dynamic risk assessment theory (Montgomerie & Weatherhead 1988). The presence of any predator at a feeder lowered the number of visits to the feeder (the number of visits did not get over 35% of reference control in any trial). Likewise, tits evaluated a sparrowhawk as more dangerous than a kestrel because the presence of a sparrowhawk lowered the number of visits more than a kestrel. This difference is in agreement with current knowledge about sparrowhawk and kestrel feeding ecology. Small mammals predominate in the kestrels diet (Kubler et al. 2005). On the other hand, the sparrowhawk is a specialized predator of small passerines (Rytkönen et al. 1998; Götmark 2002) and should represent a bigger threat than the kestrel.

The willingness to risk the visit to the feeder was lowered by the possibility of using an alternative safe feeder. When the alternative feeder was without a predator, tits kept away completely from the kestrel much like the sparrowhawk. When there was a predator (of no matter what species) on the alternative feeder, some tits fed at the feeder with the kestrel while the number of visits to the feeder with sparrowhawk was still negligible. This result proves that the tits' decisions (to visit or not to visit a feeder) depend not only on the general dangerousness of the predator present but also on the possible alternative solutions.

Our preferential experiments allowed us to distinguish whether higher willingness to risk visits to the feeder with a kestrel was caused by its "unrecognition" as a predator or its evaluation as being less dangerous than a sparrowhawk. In the first case, the number of visits during treatments in which the alternative feeder was without a predator should not differ from treatments in which a predator was present.

A new question arises: Where does the tit's ability to differentiate between the more dangerous sparrowhawk and the less dangerous kestrel come from? One possibility is innate predator recognition. The idea of innate recognition has a deep history (see Caro 2005 for review). However, the only study on great tits (Kullberg & Lind 2002) found that young, "naïve", birds did not respond differently to the dangerous sparrowhawk and the harmless grey partridge (*Perdix perdix*). Some studies on other animals (even where predation pressure on newborns is not too high) have also shown that predator recognition is the result of cultural transmission (see Caro 2005 and Kullberg & Lind 2002 for reviews). Therefore, we can presume that most tits visiting at our feeder had previous (at least culturally mediated) experience with both predators and that the tutors' behaviour differed towards variously dangerous animals.

The ability to differentiate dangerous raptors has been discussed in only limited number of studies. Experiments were conducted mostly in the breeding season on birds defending their nests. Rytkönen & Soppela (1995) found that willow tit (*Poecile montanus*) responses towards the pygmy owl (*Glaucidium passerinum*) were generally more intense than those towards the sparrowhawk. Similarly, Curio et al. (1983) revealed that the great tit differentiated not only between different orders of raptors (bird of prey, owl) but also among different genera of owls. They found that the pygmy owl (specialized on birds) was responded to more than the tawny owl (*Strix aluco*, predator of rodents). The black-billed magpie (*Pica pica*) reacted more strongly to falcons (*Falco mexicanus, F. Columbarius*) than to hawks (*Buteo jamaicensis, Circus cyaneus, Accipiter cooperi*) in Buitron's (1983) study. The decision (if any and when) to defend the nest is influenced by the dangerousness of the predator for adults and offspring (this can differ tremendously), past investment in nesting and the chance of renesting in the current breeding season (see Naef-Daenzen et al. 1999 and Caro 2005 for review). Our feeder experiments therefore provide the first unambiguous evidence that birds categorize predators according to dangerousness if only dangerousness for adults is taken into account.

Current study follows in our previous research (Tvardíkova & Fuchs in prep.) on predator recognition where the number of visits to the feeders with kestrel and sparrowhawk did not differ. The only significant difference between them was in the successfulness of the visit to the feeder. Generally, the number of visits to feeders treated with a predator was higher than in the current study. This may have been caused by the conditions (perhaps the closer distance to shrub cover) in which the feeder was placed. That is why we set up a greater distance to cover in the current study. This distance was to prove effective for our experiments. A similar distance was used by Desrochers (2002) who studied changes in the risk perception at feeders separated from tree cover by 6 and 10 metre wide strips of open area when a stuffed merlin (*Falco columbarius*) was present.

In the winter experiments, more simultaneously presented feeders were used to reveal diurnal changes in fat reserves (Koivula et al. 2002; MacLeod et al. 2005; MacLeod & Gosler 2006) or habitat use under the influence of latent predation risk (Carrascal & Alonso 2006). However, although the authors were not interested in preference towards particular feeders; some observations of preferential antipredatory behaviour (MacLeod personal communication) were recorded.

Our results not only confirm that tits behave according to dynamic risk assessment theory but also show the exceptional suitability of preferential experiments for the research of predator recognition and evaluation.

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Článek II

Sign stimuli or amodal completion? Which plays the role in predator recognition?

1. ABSTRACT

Amodal completion enables us to perceive whole, meaningful objects and interact appropriately with them. Several studies, based on operant conditioning, have shown that various animals (especially mammals and some birds) can perceive amodal completion. We tested if tits use amodal completion in nature in predator recognition. Reaction of the birds was observed to both partly occluded and amputated dummy of sparrowhawk in two different treatments (torsos vs. complete dummy of pigeon, torsos vs. complete dummy of sparrowhawk). The pairs of dummies were presented on two feeders 25 meters apart. All birds clearly classified both torsos as “full-featured” predators and kept away of them when the pigeon was on the second feeder. This means that birds do not use amodal completion but recognize a predator according to sign stimuli (e.g. eyebrow stripe, hooked bill, eye). However, when the sparrowhawk was present on the second feeder, the number of visits to the amputated predator was three times higher than to the occluded one. Birds risked arriving to an “utter” amputated torso while the fear of a “full-featured” occluded torso stayed without change when the second feeder did not provide a safe alternative. Such discrimination between torsos requires the ability of amodal completion.

2. INTRODUCTION

In a three-dimensional environment, objects frequently occlude parts of themselves and other objects. Yet humans seem to have little difficulty recognizing a person who is sitting in a car and they reach for the visible corner of a book on a messy desk. Casual observations suggest that animals could do the same. For example, a chick can recognize the mother hen if it is partially hidden in grass (Vallortigara 2004).

This adaptive ability is the phenomenon called amodal completion: the psychological completion of one object that has been partially hidden behind another (Kanisza et al 1993). Amodal completion enables animals to perceive whole meaningful objects and behave appropriately to them. Several studies have shown that mammals (mice: Kanisza et al. 1993; rhesus macaques: Bakin et al. 2000; Fujita 2001;

baboons: Duruelle et al. 2000, Fagot et al 2006; squirrel monkeys: Nagasaka & Osada 2000; Japanese macaques: Sugita 1995; and chimpanzees: Sato et al. 1997) can perceive amodal completion. Most recently, the ability to visually complete partly occluded objects was reported in a fish species (Sovrano & Bisazza 2008).

In many bird species evidence for amodal completion has been obtained using traditional training techniques such as filial imprinting or conditioning techniques. Chicks clearly recognized a triangle when faced with a partly occluded triangle and an amputated one (Regolin & Vallortigara 1996; Lea et al. 1996). This confirmed that chicks perceive object uniformity soon after hatching. Similarly, adult hens had the ability of recognition of overlapping squares and circles (Forkman 1998) or chromatically homogenous overlapping figures (Vallotigara & Tommasi 2001).

Evidence surrounding amodal completion for pigeons (the most studied species) is equivocal. Some findings seem to indicate that pigeons can compensate for an incomplete image (Watanabe 1999; Aust & Huber 2006). But there are many experiments suggesting that they are not able to perceive unity and coherence of partly occluded objects. Watanabe & Furuya (1997) concluded that birds did not see the hidden figure in a video image. This finding was supported by DiPietro et al. (2002) and Sekuler et al. (1996).

Typically geometrical shapes were the tested images in experiments and the birds had to complete those simple figures. Recognition of natural stimuli is a different way how to study amodal completion. Natural stimuli tend to offer a large variety of dimensions such as texture, shading, structural information or orientation and their absence can influence results. In nature, animals can use amodal completion to differentiate conspecific, prey and predators.

The ability of birds to differentiate dummies of predators was shown in many studies (see Caro 2005 for review) and these stimuli could be used for amodal completion research. Experiments at a feeder proved to be an effective tool of how to test for the ability of predator dummies differentiation in the field (Gentle & Gosler 2001; Desrochers at al. 2002; MacLeod et al. 2005).

Here, we report on the ability of visual completion of the upper half of an avian predator (*Accipiter nisus*). However, the ability to recognize half of a predator could have two reasons: 1. Birds are able to visually complete a partly occluded predator and they know that it continue behind the view obstruction - or 2. Birds perceive the half of predator as a whole because the half includes sign stimuli of the predator.

Traditional ethologists supposed that just the sign stimuli serve for predator and sexual partner recognition (e.g. Tinbergen 1951; Chantrey & Workman 1984; Carbaugh et al. 1962; Schein & Hale 1957; Shoettle & Schein 1959).

For that reason, we studied bird reactions to both partly occluded and simply amputated predators. There was no view obstruction in the case of an amputated predator and it was clear that the predator does not continue. If the birds a recognize predator only according to sign stimuli, they could evaluate both dummies (amputated and occluded) equally. If they have the ability of visual completion, they could recognize an amputated predator as unnatural (it is not full-featured) and less dangerous than an occluded dummy. The following hypotheses were tested: 1. Birds do not fear an amputated sparrowhawk any more than a harmless bird (pigeon) 2. Birds are not afraid of an amputated sparrowhawk less than an occluded sparrowhawk

3. METHODS

Experimental site and species

The experiment was undertaken during the winter of 2007/2008 in broad-leaved tree growth area near the village of Chodská Lhota (49°21’15”, 30°47’25”), West Bohemia, the Czech Republic. The site is 640 meters above sea level and located in a relatively cold part of Bohemia; the winter of 2007/2008 was quite harsh. We studied four species of tits predominating on feeders: the great tit (*Parus major*), the blue tit (*Cyanistes caeruleus*) and the “marsh” tit. The “marsh” tits was represented by 2 species: the marsh tit (*Poecile palustris*) and the willow tit (*Poecile montanus*). These two species are indistinguishable on videotape, and so were lumped together as one species.

Experimental design

The feeders were positioned in a small clearing, surrounded by mixed deciduous woodland and scrubland, where the shortest distance to cover was ca.4 meters. The two feeders were 25 meters apart and the space between the feeders was free of trees. The feeders were surrounded by shrubs and trees from three sides. Those served as a watching place and shelter for the birds. The feeders were boards (45 cm by 45 cm) lying on the ground with raised edges to avoid the scattering of food. Between experiments, the feeders were covered with a roof. Sun-flower seeds were used as food. To attract the birds, the feeders were filled with sun-flower seeds four weeks before the first experimental series. Any remaining sun-flower seeds were attentively removed and replaced with grated walnuts just before the trial. The grated walnuts were used because of the effort required by the birds forced them to remain longer at the feeder (Desrochers et al. 2002). Tits did not carry grated walnuts away to consume them in cover and stayed on the feeder a longer time to gain sufficient food intake.

Stuffed models were used as tested birds. They were placed on a 75 cm high stake in the outer (from the camera) right corner of the feeder and always faced into the centre of feeder. Throughout the text, the terms occluded (for upper torso hidden in shrubs) and amputated (for upper torso on perch only) sparrowhawk occur. Amputated or occluded sparrowhawk models were tested against to a whole pigeon or complete sparrowhawk respectively. Two empty feeders was the last tested trial (reference control) and it always came after two experimental trials. This amounted to four different [amputated (or occluded) sparrowhawk vs. sparrowhawk, amputated (or occluded) sparrowhawk vs. pigeon] experimental and two reference control trials in one series. The reference control trials had fixed positions within the series (1. and 4. trial). The sequence of pairs of dummies (experimental trials) within each series was randomly arranged. The placing of each dummy (on the left or the right feeder) was randomly arranged within a trial as well.

Individual trials lasted 30 minutes so a series lasted three hours of actual time. Each experimental day started one hour after daybreak. Experimental feeders were taped constantly during the duration of the experiments. The camera was set up in a fixed position, facing the experimental feeder, 8 meters away. Snow cover and temperature were noted for each experimental day. There was usually a six or seven day break between each series. Thirteen series were conducted during the winter of 2007/2008, amounting to 78 half-hours of the trials. A total of 14672 visits of tits were analyzed.

As a part of this study the birds were trapped using mist-nests to reveal the rate of pseudo replications. The experiment was designed so that trapping level was constant (about 50 birds were ringed per day) during the study. Mist-nets were in use one day before each series. A total of 568 birds were ringed during the winter. Each trapped individual was fitted both with a standard metal leg-ring with a unique number and an individual combination of colour-ring was then fitted under the licence (Czech bird ring association, 1062). Each bird was thus uniquely identifiable on videotape.

It was revealed that X+SD = 51.23+2.55 % ringed birds came back to the feeder one day after ringing. Only X+SD = 37.33+2.09 % of them stayed on to the next experiment (8 days later) and X+SD = 18.51+5.2 % to the third experiment (15 days later). Less than X+SD = 1.61+0.7 % of ringed birds appeared four weeks later. The individual bird usually visited the feeder in X+SD = 1.26+0.51 trials (at most in 3 trials) during one series. Once appearing during the trial, bird usually arrived at the feeder X+SD = 1.93+1.08 times.

Statistical analysis

The number of visits at the feeder of individual tit species during treatments was analysed. The number of visits were analysed for three species of tits separately for each whole treatment (half-hour). The following explanatory variables were used: the treatment at a particular experimental feeder (dummy), – from which the number of visits were included in the analysis; treatment on the alternative feeder (alternative dummy); the sequence of series (1-13); tit species (dummy:species); temperature (°C); and snow cover (cm).

First, a base line of birds was counted for each series. For that reason, left and right feeders within the reference controls (both feeders without dummy) were compared and found to be nonsignificant (One-way Anova: F_1 = 0.137, P = 0.713). After that the arithmetic means of arrivals during the reference control were counted for each bird species and each half of series (we had two reference controls per series).

To make comparison of the treatments (within and between trials and series) possible, the relative number of visits on each feeder was counted for each bird species. The numbers of visits to all experimental feeders (to the left as well as to the right) in particular series (with a dummy on at least one feeder) were divided by these means (treatments within first two experimental trials by the first reference control and the treatments within the other two experimental trials by the second reference control) and all the created ratios were entered into the analysis.

We acknowledged the problem of statistical nonidependence as the left and right feeders were in one trial simultaneously. Therefore, to examine which of the explanatory variables had an effect on the number of visits to each experimental feeder, GLM was constructed and the random effect was established for both feeders within one trial. Data had a normal distribution and the link function identity was used. All interactions were originally also included in the model but only particular: dummy:alternative dummy (the only significant) and tit species:dummy (insignificant but important for result interpretation) were mentioned in the results.

Different GLM was constructed to reveal differences between combinations of dummy:alternative dummy. The random effect was set up for both feeders within one trial. Data had normal distribution and the link function identity was used. The ratios of number (from above) of visits were entered into the analysis where the particular combination of dummies on both feeders (for example amputated sparrowhawk – sparrowhawk) was an explanatory variable. The sequence of series (1-13), tit species (dummy:species), temperature (°C), and snow cover (cm) were the other explanatory variables. The Tukey post hoc test (Hothorn et al. 2008) was constructed after that.

Non parametric tests (Wilcoxon) were used when data did not reach normality and when appropriate. These statistical calculations (and all graphs) were made using STATISTICA 8 for Windows (Statsoft Inc. 2007)

4. RESULTS

Over the winter, 14756 individual visits were recorded at the experimental feeders. Both sparrowhawk torsos decreased the number of visits in comparison to the pigeon present on the alternative feeder. (Wilcoxon test, relative number of visits; occluded: T = 75, N = 36, P < 0.001, amputated: T = 107, N = 36, P = 0.001; Fig. 1). However, both sparrowhawk torsos had less of an effect on the number of visits than a complete sparrowhawk presented on the alternative feeder (Wilcoxon test, relative number of visits; occluded: T = 4, N = 36, P < 0.001, amputated: T = 0, N = 36, P < 0.001; Fig. 2).

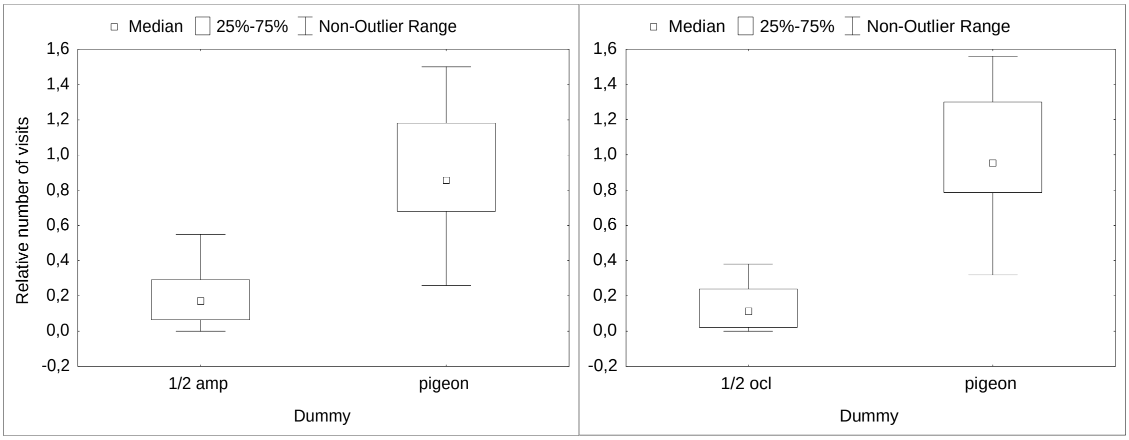

Figure 1. Relative number (related to the reference control) of visits to an amputated (1/2 amp) or occluded (1/2 ocl) sparrowhawk in the trials with pigeon on the alternative feeder

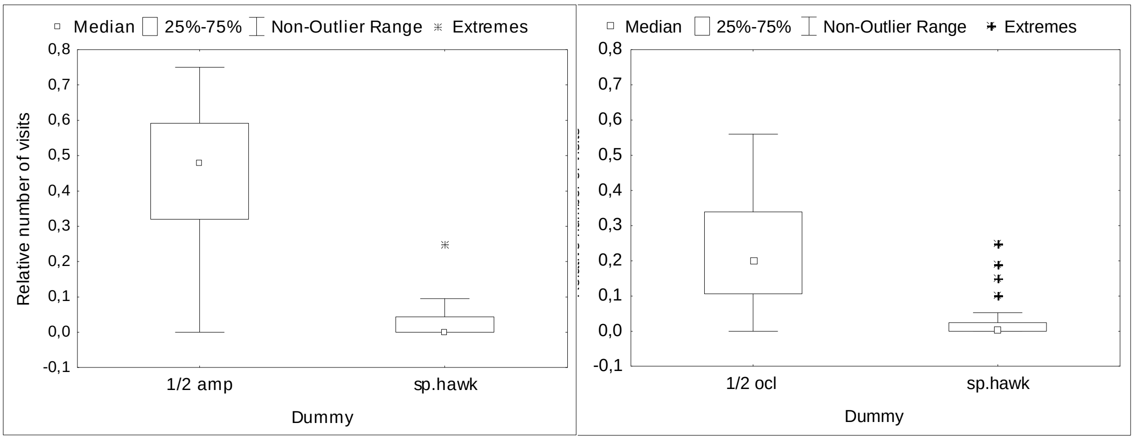

Figure 2. Relative number (related to the reference control) of visits to an amputated (1/2 amp) or occluded (1/2 ocl) sparrowhawk in the trials with sparrowhawk (sp.hawk) on the alternative feeder

The dummy presented on the experimental feeder, the dummy presented on the alternative feeder and temperature were significant predictors of relative change of the number of visits. The interaction between both dummies was also significant. Snow layer, series sequence, and the interaction between the dummy and the tit species did not have significant effects (Table 1). Low temperature diminished the decrease in the number of visits to the feeder with a predator (Fig. 4).

Table 1. Effects of the dummies, weather and experimental design on the relative change of the number of visits to a feeder

	Df	F	P
Dummy	**1**	**7.201**	**0.008**
Alter.dummy	**1**	**4.138**	**0.043**
Temperature	**1**	**6.416**	**0.012**
Snow layer	1	0.946	0.332
Series	1	0.095	0.758
Dummy:alter.dummy	**1**	**13.181**	**<0.001**
Dummy:species	2	0.367	0.693

The results of GLM show Df, F and P values for each predictor and some interactions (see Methods)

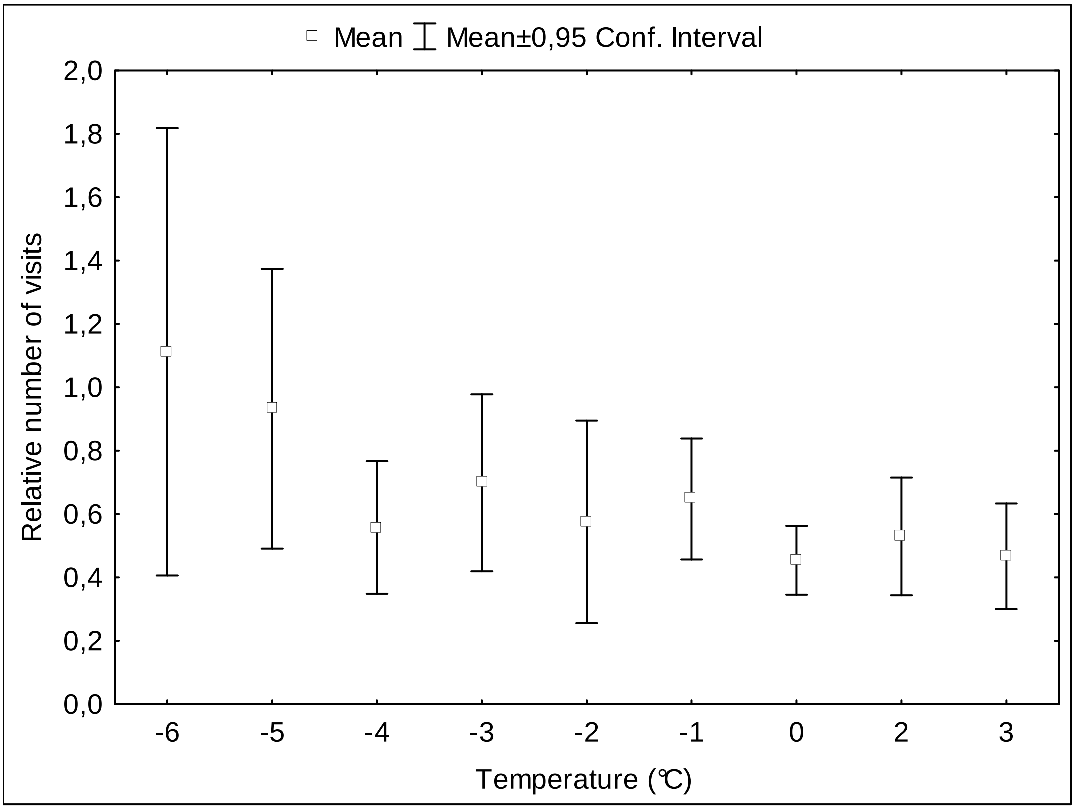

Figure 3. Effect of temperature on the number of visits to a feeder – for experimental trials with dummy

The number of visits was less affected by the amputated sparrowhawk than the occluded sparrowhawk (Table 1, Fig. 4). However, if separate combinations of dummies on experimental and alternative feeder were compared (Table 2, Fig. 4) the difference between both torsos was significant only in treatments when complete sparrowhawk was on the alternative feeder. The decrease in the number of visits did not differ between both torsos in treatments, when the pigeon was on the alternative feeder. The relative number of visits to the occluded torso did not differ between treatments with a sparrowhawk and pigeon, while the relative number of visits was higher in the presence of an amputated torso in the treatments with a pigeon than in the treatments with a sparrowhawk on the alternative feeder.

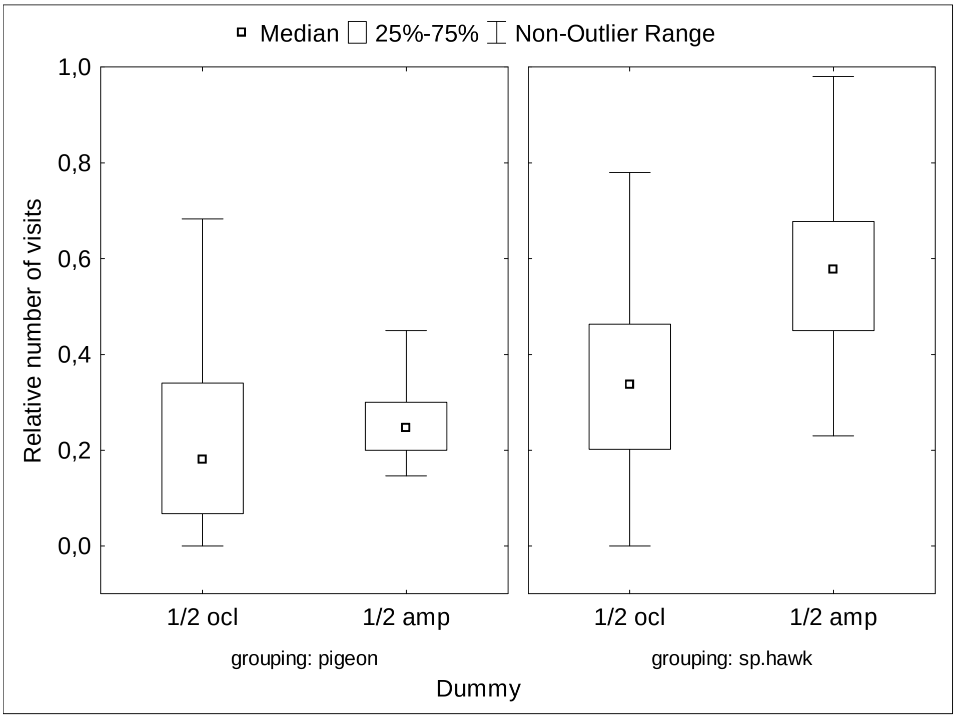

Figure 4. Decrease in the number of visits to a feeder with the occluded (1/2 ocl) and amputated (1/2 amp) sparrowhawk with regard to the dummy present on the alternative feeder (grouping)

Table 2. The differences between the relative changes in the number of visits to both torsos (occluded, amputated) of sparrowhawk, in trials with different treatment on the alternative feeder (pigeon or sparrowhawk - noted in parentheses)

		t	*P*
1/2 ocl(pi)	1/2 amp(pi)	-0.812	0.849
1/2 ocl(sp)	**1/2 amp(sp)**	**4.840**	**<0.001**
1/2 ocl(sp)	1/2 ocl(pi)	-0.809	0.850
1/2 amp(sp)	**1/2 amp(pi)**	**4.753**	**<0.001**
1/2 ocl(pi)	**1/2 amp(sp)**	**4.208**	**<0.001**
1/2 ocl(sp)	1/2 amp(pi)	-0.022	0.099

Treatments on experimental feeder: 1/2 ocl – occluded sparrowhawk, 1/2 amp – amputated sparrowhawk; treatments on alternative feeder: sp – sparrowhawk, pi - pigeon. Tukey post hoc test results show *P* and *t* values

5. DISCUSSION

The tits recognized both sparrowhawk torsos (amputated as well as occluded) as they both decreased the number of visits at the feeder in comparison with the pigeon on the alternative feeder. The decrease in the number of visits did not differ for both torsos. This would mean that tits do not use amodal completion, but they recognize a predator according to sign stimuli (on the head, it can be eyebrow stripe, hooked bill, and eye) and keep away.

However, in the treatments with a sparrowhawk on the alternative feeder, the relative numbers of visits to an amputated sparrowhawk strongly increased, nearly up to 100% of the reference controls in some trials. This must be interpreted as the tits recognizing a predator in both torsos but only the occluded one is perceived as “fully-featured”. On the other hand, the amputated torso is perceived as “utterly”. The birds keep away from both torsos when there is a safe choice at the alternative feeder (pigeon). However, when the alternative feeder offers only a dangerous complete sparrowhawk, they risk visiting the “utter” amputated torso while the fear of a “full-featured” occluded stays without change.

Such discrimination requires the ability of amodal completion. The birds know that an occluded sparrowhawk continues inside the branches, while an amputated sparrowhawk is clearly incomplete.

The only disturbing result is that birds arrived to the occluded sparrowhawk more than to the complete sparrowhawk dummy. There may be some birds that do not recognise the predator in an occluded torso. This could be due to limited experience (e.g. of young birds) or incaution. Several casual observations would support incaution of the birds. Sometimes a bird landed at the feeder, was pecking, suddenly became horrified and emitted an alarm call as he saw the predator too late.

Study of the occlusion phenomena has been extended from infants to nonhuman species and become a popular topic of behavioural psychology in the last few decades. All groups of animals were trained to discriminate between various occluded and amputated objects (see Aust & Hubler 2006, Sovrano & Bisazza 2008 for reviews).

In birds, several comparative studies using operant techniques have yielded inconsistent results. They worked mainly with different geometrical objects (simple basic shapes and geons – the basic perceptual component of objects, Biederman 1987) either occluded by other geometrical objects or structure or amputated (missing corner, half or a middle part). The ability to discriminate between incomplete (amputated) and complete (complete and occluded) shapes was shown in chicks *Galus gallus* (triangle - Regolin & Vallortigara 1995; rod - Lea et al. 1996; square, cross – Regolin et al 2004; triangle, square - Regolin et al. 2007), and hens *Galus gallus* (square and circle - Forkman 1998; ladder and diamond - Forkman & Vallortigara 1999; Vallortigara & Tommasi 2001). Also parrots and parakeets (*Cyanoramphus auriceps* - Funk 1996; *Psittacus erithacus*, *Ara maracana*, *Melopsittacus undulates*, *Nymphicus hollandicus* - Pepperberg & Funk 1990), mynahs *Gracula religiosa* (Plowright et al. 1998) and magpies *Pica pica* (Pollok et al. 2000), could distinguish when an object was partly occluded.

Above mentioned results of the occlusion tests stand in contrast to all findings of related research in pigeons, which were studied most intensively. After training pigeons to respond a triangle, Cerella (1980) found that responses to an amputated triangle exceeded those to a partially occluded triangle suggesting that they did not amodally complete the visual stimuli. Similarly, in Sekuler et al. (1996), pigeons responded equally to both an incomplete circle and a circle occluded by a rectangle. Fujita (2001) concluded that feeding habit may be related to the ability for amodal completion. He mentioned that grain eaters (pigeons) do not need to search for obstructed grain as grains are abundant.

DiPietro et al. (2002) tried to reveal whether shaded and textured stimuli can improve visual object recognition. In each case, recognition was weak and appeared to require special training. The recognition of occluded objects requires pigeons to learn to first discriminate the object from the occluder.

On the other hand, Nagasaka et al. (2005) showed that pigeons can see perceptual transparency and discriminate partially occluded objects without using local features. The most recent results (Nagasaka & Wasserman 2008) suggest that motion may facilitate amodal completion by pigeons, perhaps by enhancing the figure. In that study, the birds were presented with a partially occluded and amputated or complete moving shape.

From the above studies (and others: Ushitani & Fujita 2005; Lazareva et al 2005; Aust & Hubler 2006), it appears that pigeons can perceive partly occluded objects as complete only under appropriate conditions.

The results of our study demonstrate for the first time that amodal completion is used as a part of object recognition in natural discriminating and categorization processes. The results show that field experiments, in which the predicted reaction (e.g.

escape) of birds to real objects (e.g. predator) is used, are a suitable alternative for conditioning techniques.

At the same time, our results show that discrimination and categorization is not a simple process and that amodal completion is only part of it. Birds recognize predators according to sign stimuli. Therefore, both occluded and amputated torsos of a predator are judged as danger, and the incompleteness (and lesser dangerousness) of an amputated torso appears only when it is compared with a complete predator. Complexity of the recognition processes should be taken into account even in conditioning experiments.

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4. Závěry

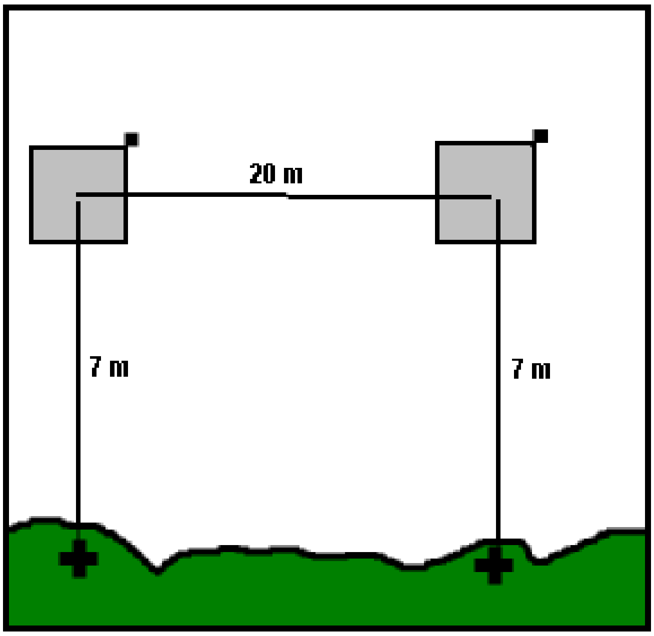
1. Preferenční krmítkové pokusy se osvědčily ve výzkumu jemných rozdílů v hodnocení predátorů ptáky.
2. Sýkory se nepřibližovaly ke krmítku s jakýmkoliv predátorem v případě, že jim bylo nabídnuto krmítko bez predátora.
3. Sýkory snižovaly počet příletů na krmítko ke krahujci více, než na krmítko k poštolce v případě, že mohly volit jen mezi těmito predátory.
4. Toto hodnocení obou predátorů odráží jejich potravní specializaci a současně jejich nebezpečnost, kterou by pro sýkory měly znamenat.
5. Chování sýkor na krmítcích je v souladu s „dynamic risk assesment theory“.
6. Preferenční krmítkové pokusy se osvědčily i při studiu kognitivních schopností sýkor – zejména schopnosti „amodal completion“.
7. Sýkory rozpoznaly predátora v obou nabízených variantách torz („amputated“ a „occluded“) a na krmítko přilétaly v jejich přítomnosti méně, než v přítomnosti neškodného holuba.
8. Sýkory snižovaly počet příletů k „occluded“ krahujci více než k „amputated“ krahujci v případě, že nabízenou alternativou byl jen nebezpečný celý krahujec.
9. Toto hodnocení torz predátorů znamená, že sýkory jsou schopny „amodal completion“, které je součástí kognitivních procesů v přirozených podmínkách.

5. Obrazové přílohy

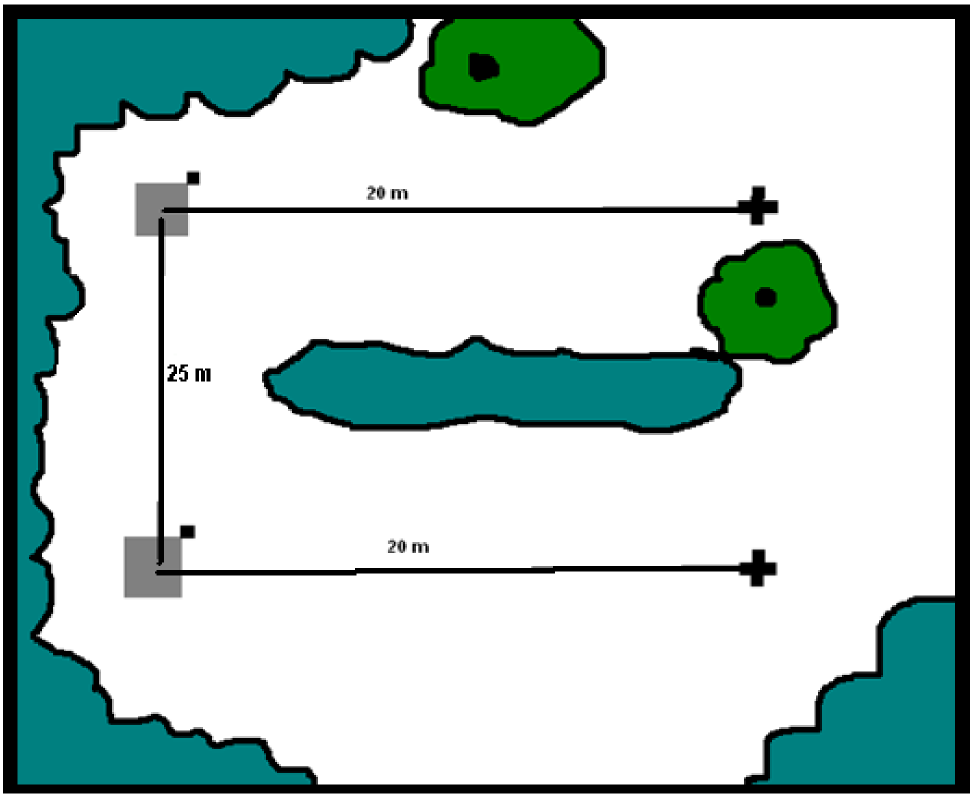
Seznam obrazových příloh

1. Mapa pokusného místa pro obě studie

2. Situační plánek pokusného místa v roce 2006/2007



3. Situační plánek pokusného místa v roce 2007/2008



4. Atrapy krahujců používané v sezóně 2006/2007

5. Atrapy poštolek používané v sezóně 2006/2007

6. Atrapa nezakryté poloviny krahujce 2007/2008 – „amputated“

7. Atrapa zakryté poloviny krahujce v sezóně 2007/2008 – „occluded“

8. Atrapa celého krahujce používaná v sezóně 2007/2008

9. Atrapa celého holuba používaná v sezóně 2007/2008