

# Do birds behave according to dynamic risk assessment theory? A feeder experiment

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**Abstract** Pair-wise preference experiments were used to reveal predator discrimination by four tit species wintering in the Czech Republic. The reactions of the tits to a more dangerous predator (sparrowhawk) and a less dangerous (kestrel) one were compared. The number of visits to a feeder with a predator present expressed the perceived dangerousness of the predator. The tits' behaviour towards the feeders was in agreement with predictions, according to dynamic risk assessment theory. The presence of any predator at the feeder lowered the number of visits to the feeder. Similarly, the tits were judged to have evaluated the sparrowhawk as being more dangerous than the kestrel, as its presence lowered the number of arrivals more than did the kestrel. The duration of stay and number of pecks of individual birds were also used as measures of predator dangerousness. The results not only confirm that tits behave according to dynamic risk assessment theory, but also show the exceptional suitability of preference experiments for the research of predator differentiation and evaluation.

**Keywords** Common kestrel · Eurasian sparrowhawk · Feeders · Pair-wise experiments · Predator discrimination · Preference experiments · Paridae

## Introduction

In animals, food intake is generally connected with the risk of predation. A repeated daily trade-off is made between the need to search for food and that to avoid predators; this takes place throughout an animal's entire life (Devereux et al. 2006). The animals chose to use the risky feeding site only if the potential additional energy gains outweighed the fitness costs of the additional predation risk; otherwise, it would be better off using a safer feeding site (Abrahams and Dill 1989). Therefore, each animal has to continuously make decisions as to which behaviour has the better net 'pay-off'.

The trade-off between the risk of predation and the energetic gain leads to habitat choices. Each habitat has an associated rate of gain, as well as danger of predation (Houston et al. 1993). However, the choice of habitat could be based not on those qualities alone, but also on the actual state of the animal (Houston et al. 1993) and the time of day, or even time of year (MacLeod et al. 2005). Often, the intake rate that a forager achieves in a habitat also depends on the number of conspecifics also feeding in that habitat. Where there are many competitors, intake rates may decrease, either from interference or exploitation competition (Moody et al. 1996). In such a situation, an animal may do better by moving to a feeding site where there are fewer competitors, even if the overall food quality is lower. This issue has been extensively investigated in what is known as ideal free distribution (Fretwell and Lucas 1970; see Milinski and Parker 1991 for a review). Conversely, a higher number of conspecifics may result in lower levels of vigilance of individuals and, thus, increase the rate of energetic gain for each of them (Houston et al. 1993). Moreover, higher numbers of conspecifics can also decrease the risk of predation through the effects of dilution

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and confusion (Quinn and Cresswell 2005 and references therein). The assumption of dynamic risk assessment is that individuals that continuously assess these trade-offs and dynamically modify their behaviour accordingly will have a fitness advantage (Kleindorfer et al. 2005).

The proximity of a predator does not determine the rate of predation risk in itself. This is principally because of the different feeding specialisations and hunting techniques of individual predator species (Curio et al. 1983). In birds, the ability to discriminate between differentially dangerous predator species has primarily been studied with nest defences within the breeding season (e.g. Patterson et al. 1980; Buitron 1983; Kleindorfer et al. 2005). Until now, predator discrimination in birds has not been studied with respect to the trade-offs between potential food gain and the risks of predation.

The trade-offs between the risk of predation and energetic gain can be studied in preferential experiments where feeding sites which are associated with different danger levels are offered. Abrahams and Dill (1989) measured the influence of the predation risk on patch choice by guppies (*Poecilia reticulata*) using combinations of three risk levels and three diet levels. Similar winter field experiments on a feeder should also perform well with birds. Feeder experiments have been used to assess the willingness of birds to cross an exposed space (Hinsley et al. 1995; Desrochers et al. 2002; Turcotte and Desrochers 2003), or how the birds manipulate their body masses (MacLeod et al. 2005), both under an experimentally manipulated predation risk. More recently, a similar experiment (Jones et al. 2009) was used to assess this trade-off, with regards to the different danger levels of the birds' predators.

We tested the following predictions: (1) The birds will behave according to risk assessment theory and, when confronted with simultaneous risks (differentially dangerous predator species), they will choose the least dangerous. (2) The food intake rate will decrease in those feeders with higher abundances of birds, and visits to a more risky feeder will be compensated with higher food intake by individual birds.

## 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, Czech Republic. Even though the site is 640 m above sea level and is located in a relatively cold part of Bohemia, this particular winter (mostly without snow

cover) was not harsh. Four species of tits were studied: the great tit (*Parus major*), the blue tit (*Parus caeruleus*), and the "marsh" tit, which predominate at the feeders. The 'marsh' tit was represented by both the marsh tit (*Parus palustris*) and willow tit (*Parus montanus*). As these two species are indistinguishable on videotape, they were lumped together as one species.

### Experimental design

Two feeders were situated in a field, 7 m from the edge of tree growth. The feeders were 20 m apart and the space between them was free of trees. Shrubs and trees at the edge of tree growth served as an observation place and as a shelter for the birds. The feeders were square boards (45 by 45 cm) lying upon the ground, with raised edges (1.5 cm) to avoid scattering of the food. Between experiments, the feeders were covered with a roof. Sunflower seeds were used as food only for the attraction of the birds. The feeders were filled 4 weeks before the first experimental series. Sunflower seeds were carefully removed and replaced with grated walnuts just before the start of trials. The tits were not able to carry the grated walnuts away, to consume them under cover, as they had with the sun-flower seeds. Therefore, they had to remain at the feeder for a longer period of time if they wanted to achieve sufficient food intake. Food gain is thus the direct proportion of undergone risk.

Stuffed sparrowhawk and kestrel dummies were used as the test predators. They were placed on a 75-cm-high stake at the outer (from edge of forest) right corner of the feeder, and always faced into the centre of the feeder. Individual trials lasted 30 min.

The following experimental treatments (combinations of dummies) were tested: kestrel vs sparrowhawk, kestrel vs feeder without predator, kestrel vs kestrel, sparrowhawk vs feeder without predator and sparrowhawk vs sparrowhawk. Two feeders without predator served as the control (reference) treatment. This amounted to six different treatments in one series. The sequence of treatments within each series was arranged randomly. The placing of the dummy (on the left or the right feeder) for each treatment was randomly arranged, as well.

Each series was carried out in a single day. Usually, there was a 5- or 6-day break between each series. Each experimental series started 0.5–1 h after daybreak. Feeders were continuously taped during the duration of the experiments. Cameras were set up in a fixed position 8 m away facing the feeders. The snow cover and temperature were noted for each experimental day. Ten series were conducted and amounted 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

used the day before each experimental series, and the trapping efforts were constant during the study (about 30 birds were ringed per day). Under licence (Czech Bird Ring Association, 1062), each trapped bird was fitted with both a standard metal leg-ring with a unique number plus a unique combination of colour rings. Each bird was thus uniquely identifiable on the videotape.

Altogether, 265 birds were ringed during the winter. It was found that  $54.53 \pm 4.95\%$  of ringed birds stayed on to be in the next series (approximately 1 week after ringing), and  $40.39 \pm 1.49\%$  stayed until the third series (approximately 14 days later). Less than  $1.95 \pm 2.7\%$  of ringed birds dwelled in the locality longer than 1 month. Individual birds usually visited the feeder in  $1.46 \pm 0.6$  trials (at most in four trials) during one series. Once having appeared during the trial, a bird arrived at the feeder an average of  $3.23 \pm 0.97$  times.

### Statistical analysis

Firstly, the number of visits of individual tit species during the trials was analysed. Before the main analysis, the numbers of visits to the left and right feeders within the control (reference) trial were compared and found to be non-significant (Mann–Whitney  $U$  test:  $U=47$ ,  $N_1=N_2=10$ ,  $P=0.819$ ), and thus, the arithmetic means were counted for each series. The numbers of arrivals to the experimental feeders (to the left, as well as to the right) in each experimental trial (with a dummy on at least one feeder) were divided by the number of visits during the reference trial, and all the created ratios (relative change of the number of visits) were included in the analysis as a dependent variable.

The following experimental variables were used: the dummy at an experimental feeder (from which the number of arrivals were included in the analysis), the situation at the alternative feeder (dummy or feeder without predator), the sequence number of the series during the winter (1–10), tit species (interaction of dummy vs species), temperature ( $^{\circ}\text{C}$ ) and snow cover (cm). The temperature was measured at the beginning and at the end of experiment, and the average was rounded off. Snow cover was measured next to the feeder on a pole planted in the ground. We acknowledged the problem of statistical independence, as the left and right feeders were simultaneously in any one trial. Therefore, in order to examine which of the experimental variables had an effect on the relative change of the number of visits to each experimental feeder, generalised linear mixed models (GLMM, function `aov` in library `lme4`) in R 2.9.0 (R DEVELOPMENT CORE TEAM 2008) were modelled, and the random effect was set up for both feeders within one trial. GLMM was modelled for data with a Poisson distribution, using the link function identity. The

results mentioned in the text are the results of step-wise selection. All interactions were also included in the model. Only meaningful interactions, i.e. interaction between experimental dummy and situation at alternative feeder (the only significant one), and interaction between tit species and experimental dummy (insignificant, but important for interpretation of results), were mentioned in the results. The Tukey post hoc test (function `glht` in library `multcomp`, R 2.9.0.) was done to reveal the differences between combinations of dummy and alternative dummy.

To determine the possibility of habituation to motionless predators, the number of visits was analysed in 5-min-long intervals (within a half-hour trial). The number of visits during the experimental trials did not significantly change (repeated measures ANOVA, dummy: section:  $F=0.414$ ,  $P=0.938$ ).

Another GLM (function `glm` in basic library, Poisson distribution, R 2.9.0.) model was constructed for the number of pecks, and for the duration of stay of individual birds visiting the feeder during the different experimental situations: (1) feeder with a predator; (2) feeder without predator, when a predator is present at the alternate feeder and (3) feeder without a predator, while the alternate feeder is also without a predator. Results from all feeders with the sparrowhawk or kestrel were clumped together as a feeder with a predator because only a few birds visited the feeders during their presence. The three above mentioned situations at the feeders were used as the explanatory variables together with the sequence of series during the winter, tit species, temperature and snow cover. The Tukey post hoc test (`glht` function in library `multcomp`, R 2.9.0.) was performed in order to reveal the differences between the individual situations at the feeders.

Finally, we compared (ANOVA, Statistica 8) whether the number of pecks of individual birds differed in those situations where a bird was at a feeder alone, as opposed to the situation where at least one other bird is present.

### Results

Over the winter, 5,292 individual visits were recorded at the feeders. The dummy at an experimental feeder, the situation at the alternative feeder (dummy or feeder without predator) and the temperature were predictors of relative changes in the number of visits. The interaction between the experimental dummy and the situation at the alternative feeder 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). Low temperatures lessened the decrease in the number of visits to the feeder with a predator (Fig. 1).

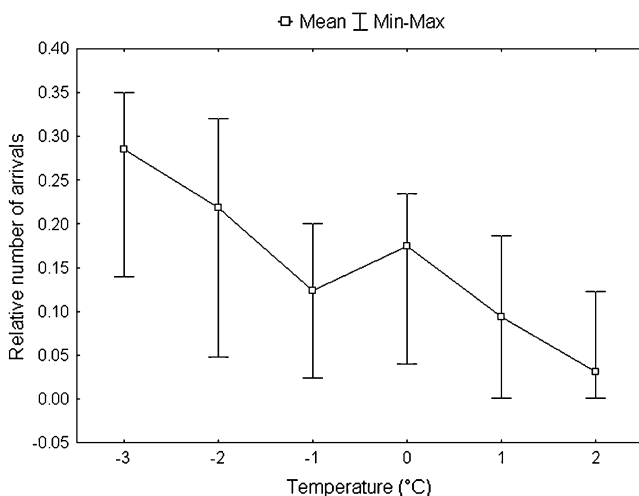
**Table 1** The effects of the predictors on the relative change of the number arrivals to the feeder (step-wise selection, GLMM, only particular interactions mentioned—see “Methods” section)

Effect	Df	F	P
Dummy	2	414.056	<0.001
Situation on alternative feeder	1	17.865	<0.001
Temperature	1	9.360	0.020
Snow	1	0.830	0.365
Species	2	0.316	0.598
Series	1	0.210	0.648
Dummy: species	10	0.561	0.543
Dummy: Altern. feeder	4	10.016	<0.001

The kestrel dummies decreased the relative number of visits less than the sparrowhawk dummies did; however, this was only in those 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 the kestrel and sparrowhawk in those treatments in which a predator was combined with the alternative feeder without a predator (Table 2, Fig. 2).

A kestrel decreased the number of visits less if it was combined with a predator 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. 2).

The duration of stay of individual birds at the feeders was only influenced by snow cover and temperature (Table 4). The duration of stay did not differ under any of the experimental situations: (1) feeder with a predator; (2) feeder without a predator, while a predator was present at the alternate feeder and (3) feeder without predator, while

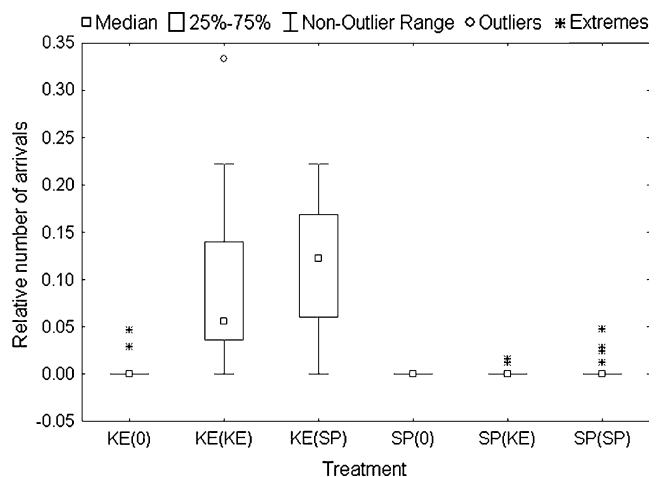
**Fig. 1** Effect temperature on the number of arrivals to the feeder—for experimental trials with predator**Table 2** Differences between the relative changes of the number arrivals to kestrel and to sparrowhawk in trials with different treatment on the alternative feeder (noted in parentheses)

		Sparrowhawk		
		(sp)	(0)	(ke)
Kestrel	(0)	0.989	0.987	0.978
		<i>0.952</i>	<i>0.001</i>	<i>0.001</i>
	(sp)	<0.001	<0.001	<0.001
	(ke)	-7.439	-7.267	-7.267
		<0.001	<0.001	<0.001
		-7.384	-6.981	-6.981

The Tukey post hoc test results show *P* (above) and *t* (below, italic) values

*ke* kestrel, *sp* sparrowhawk, 0 empty feeder

the alternative feeder is also without a predator. On the other hand, the birds pecked much less in the presence of a predator ( $N=1460$ ,  $3.36 \pm 7.868$ ), when compared to its absence ( $N=3832$ ,  $7.56 \pm 11.75$ , Table 4). A Tukey post hoc test revealed that the number of pecks at a feeder with a predator significantly differed from the other experimental situations (a feeder with a predator vs a feeder without a predator, while the alternative feeder is also without a predator:  $St.Er.=0.38$ ,  $Z=-5.251$ ,  $P<0.001$ ; feeder with a predator vs feeder without a predator, while a predator is present at the alternate feeder:  $St.Er.=0.37$ ,  $Z=-5.418$ ,  $P<0.001$ ). The differences between the two experimental situations without a predator were not significant ( $St.Er.=0.06$ ,  $Z=0.882$ ,  $P=0.624$ ). Of the climatic variables, only snow influenced the number of pecks (Table 4).

**Fig. 2** Relative changes on the number of arrivals (the number of arrivals to feeder with dummy/the number of arrivals to feeder during the reference control) to kestrel and sparrowhawk in trials with different treatment on alternative feeder (noted in parentheses). Treatments on both feeders: *ke* kestrel, *sp* sparrowhawk, 0 empty feeder

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

Compared trials	<i>t</i>	<i>P</i>
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

Tukey post hoc test results show *P* and *t* values

ke kestrel, sp sparrowhawk, 0 empty feeder

At a feeder with a predator present, birds always pecked much more ( $\text{Chi}^2=683.17$ ,  $P<0.001$ ) in the presence of at least one other bird (Mean  $\pm$  St.Er.,  $5.7\pm 11.77$ ) than when they were alone ( $1.9\pm 3.3$ ). Although less significant ( $\text{Chi}^2=56.3$ ,  $P=0.046$ ), the same difference was found at a feeder without a predator (alone:  $4.3\pm 11.12$ , accompanied:  $6.22\pm 13.826$ ).

## Discussion

The behaviours of tits at the feeders were in agreement with the predictions of dynamic risk assessment theory (Montgomerie and Weatherhead 1988). The presence of any predator at a feeder lowered the number of arrivals to that feeder. Correspondingly, the tits evaluated a sparrowhawk as more dangerous than a kestrel, as the presence of a sparrowhawk lowered the number of arrivals more than did a kestrel. In the presence of a sparrowhawk, the gain from food only sporadically overrides the risk of predation while as many as 30% of the birds (compared with reference trials) decided to visit the feeder with a kestrel present. This difference is in agreement with current knowledge about sparrowhawk and kestrel feeding ecology. Small mammals

predominate in the kestrel's diet (Kübler et al. 2005). On the other hand, the sparrowhawk is a specialised predator of small passerines (Rytkönen et al. 1998; Götmark 2002), and thus should represent a bigger threat than the kestrel.

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

Our results not only confirm that tits behave according to dynamic risk assessment theory; it also demonstrates the exceptional suitability of field preferential experiments on feeders for research of predator recognition and evaluation. The preference experiment allowed us to distinguish whether the higher willingness to risk visits to the feeder with a kestrel was caused by its “non-recognition” as a predator or by its evaluation as being less dangerous than a sparrowhawk. If the first situation was true, the number of arrivals during treatments in which the alternative feeder was without a predator would not have differed from treatments in which the kestrel was present there.

The ability of birds to differentiate between various dangerous raptors has only been discussed in a limited number of studies. Experiments have mostly been conducted during the breeding season on birds defending their nests. Rytkönen and Soppela (1995) found that 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 not only differentiated between different orders of raptors (bird of prey, owl), but also among different genera of owls.

**Table 4** The effects of the predictors on the duration of stay at feeder and number of pecks (step-wise selection, GLMM, quasi-Poisson distribution, only particular interaction mentioned—see “Methods” section)

Effect	Duration of stay				Number of pecks		
	Df	Dev	Res. Dev	<i>P</i>	Dev	Res. Dev	<i>P</i>
Situation on feeder	2	135	34,064	0.065	102	28,245	<0.001
Temperature	1	181	33,884	0.007	1	28,163	0.400
Snow	1	411	33,473	0.001	131	28,350	<0.001
Species	2	27	30,205	0.869	2	28,150	0.501
Series	1	45	32,016	0.127	46	28,112	0.432
Species: situation at feeder	4	35	31,439	0.789	54	28,011	0.061

They found that the pygmy owl (*G. passerinum*, specialised on birds) was responded to more than the tawny owl (*Strix aluco*, a predator of rodents). In Buitron's (1983) study, the black-billed magpie (*Pica pica*) reacted more strongly to the falcon (*Falco mexicanus* and *Falco columbarius*, predators of birds) than to the hawk (*Buteo jamaicensis*, *Circus cyaneus* and *Accipiter cooperi*, predators of small rodents). The decision (if any, and how intensively) 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 (for review, see Caro 2005). Therefore, our feeder experiments represent unambiguous evidence that birds categorise predators according to the perceived danger to themselves. This evidence corresponds with the findings of Templeton et al. (2005), who showed that intensity of mobbing calls is related to the size and threat of a potential predator.

In the situation with many conspecifics, an animal may do better by moving to a patch where there are fewer competitors, even if the overall risk of this patch is higher, but might be compensated with a higher food intake for any individual bird (Moody et al. 1996). We were not able to confirm this theory, as our birds did not stay longer in patches with fewer competitors, and even pecked fewer times in the presence of a predator. The lower number of pecks during the same length of stay shows that the birds increased their vigilance. Presumably, this is caused by the lower number of birds at a feeder at that time (the total number of birds visiting a feeder with a predator did not reach over 25% of the birds visiting a feeder during control trials). The decrease in both the collective probability of detecting attack (group size effect) and numerical dilution of risk (dilution effect) with a decreasing group size can cause an increase in the individual levels of vigilance, as well as a decrease in the time devoted to feeding (see McNamara and Houston 1992; Cresswell 1994; Bednekoff and Lima 1998). This is supported by our findings that all birds pecked more times in the cases when some conspecific was present at the same feeder, even in the situation without a predator at the feeder. This could indicate that a bird felt safer when accompanied by others. Conditions always agreeing with an ideal free distribution at our feeder would be the simplest explanation of the unchanged duration of stay for birds at the feeder. However, the decreased interference competition being compensated by a decreased dilution effect cannot be ruled out.

We cannot confirm the differences in the behaviour of individual bird species. The significance of explanatory variable "species" indicates that different numbers of individual species visited the feeder. Only the interaction between species and an explanatory variable (e.g. dummy) would indicate that a bird species behaved differently from

another. This was not true in any of our analyses. Individual tit species have different abilities in their competition for food (Dhondt and Eyckerman 1980). The Blue Tit is limited by the Great Tit but the smallest and least forcefulness is the Marsh Tit. The tits with lower competitive abilities should be more willing to visit feeders with a predator present. Our failure to support this hypothesis could again be caused by the ideal free distribution of birds at our feeder, without regard to the experimental situation.

Maintenance of a constant high body temperature becomes increasingly difficult in colder conditions, especially for small birds (e.g. Caraco et al. 1990). Thus, many birds should be expected to exploit less profitable (including more dangerous) sources of food. We demonstrated that lower temperatures did cause a much higher number of arrivals (greater willingness to risk) at the feeder. A decrease of the temperature from 2 to  $-3^{\circ}\text{C}$  increased the mean proportion of birds visiting the feeder with a predator from 5 to nearly 30% (in comparison with the control trial). This result is in concordance with the findings of previous studies (Walther and Gosler 2001; Carrascal and Alonso 2006; Desrochers et al. 2002).

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