Behav Ecol Sociobiol (2002) 51:466–471
DOI 10.1007/s00265-002-0464-4

ORIGINAL ARTICLE

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Seeing is believing: information about predators influences yellowhammer behavior

Received: 2 August 2001 / Revised: 17 January 2002 / Accepted: 21 January 2002 / Published online: 6 March 2002

Abstract Behavioral decisions based on a trade-off between foraging and vigilance or hiding require information. I studied how the amount of information about predators influenced yellowhammers' (*Emberiza citrinella*) foraging delay and alert perching behavior. Yellowhammers were shown a flying sparrowhawk (*Accipiter nisus*) silhouette, which elicited alarm calls, or a square piece of wood (control), which elicited flight calls. Yellowhammers that could not see the sparrowhawk model, but heard the alarm calls, had less complete information about the predation risk than those that actually saw the sparrowhawk. Hearing alarm calls affected the behavior of yellowhammers. Birds with less complete information about the predator exhibited alert perching more often immediately after the encounter than did birds that saw the sparrowhawk model. Also, birds that saw the sparrowhawk resumed foraging earliest, while birds that heard the alarm calls resumed foraging latest. Although there was a tendency for a significant difference in body mass between dominant and sub-dominant individuals, there was no significant difference in foraging delay. Both the foraging delay and the increase in alert perching caused lost feeding opportunities. Completeness of information and its effect on decision-making may thus affect the fitness of an animal.

Keywords *Emberiza citrinella* · Foraging delay · Incomplete information · Predation risk · Vigilance

Communicated by J.Dickinson

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Introduction

Animals almost continuously face the choice of when and where to forage. The outcome of their decisions depends on their energetic requirements, food availability, and predation risk (reviewed by Lima and Dill 1990). At the same time, the most profitable areas for foraging often have the highest predation risk, forcing animals to trade off energy gain against predator exposure.

Two important behavioral consequences of trading off predation risk against energy gain are a foraging delay due to hiding or waiting to resume foraging, and an increase in vigilance after a predator attack (reviewed in Lima 1998). Both of these behavioral consequences interfere with foraging time and result in lost feeding opportunities. The decision of how long to wait after an attack before resuming foraging may be influenced by the state of an individual (e.g. Koivula et al. 1995), the profitability of the environment (e.g. Dill and Fraser 1997; Sih 1997), and the predatory threat (Lima 1998). In order to make adaptive decisions the forager requires information.

Often, animals do not have complete information about their environment (Stephens and Krebs 1986), making estimation of energetic needs and predation risk less accurate and leading to either over- or underestimation of predation risk (Bouskila and Blumstein 1992; Abrams 1994; Koops and Abrahams 1998). If the animal underestimates the predation risk, it emerges from its refuge while the predator is still present, whereas if it overestimates, it stays in its refuge while the predator has already left the area. The kind of estimation an animal makes will depend on its life history and its state (Abrams 1994). Its state influences the relative costs of losing a feeding opportunity and foraging under predation risk; for example, if an animal has low energy reserves, the fitness costs of a lost feeding opportunity are high and it should leave its refuge soon (Sih 1992). In the non-breeding season, fitness depends mainly on survival, and the fitness cost of one lost feeding opportunity is probably relatively small compared to the fitness cost of feeding while the predator is still around.

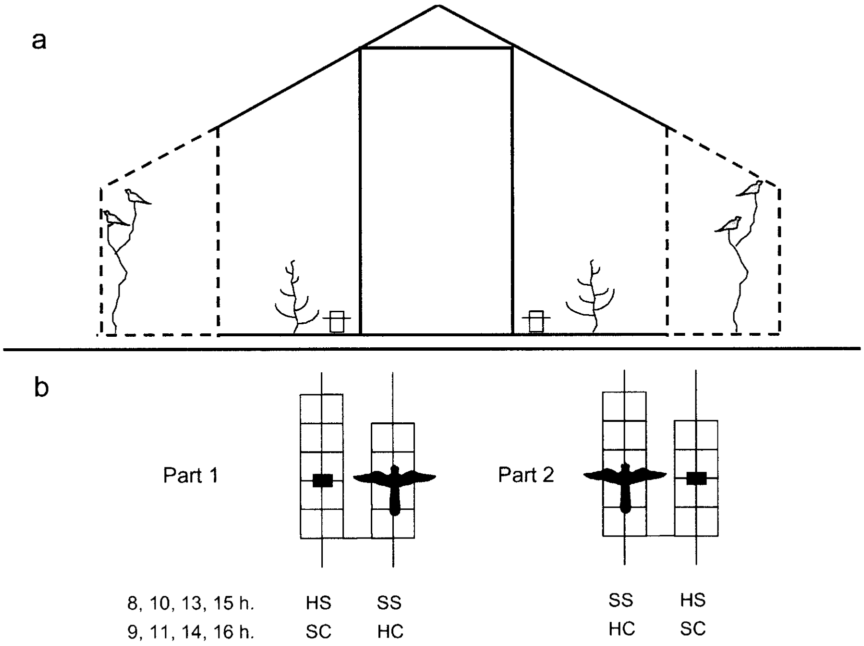

Fig. 1a, b Experimental setup. **a** A cross-section of the cages. Cages were situated on two sides of a corridor. Each cage, containing two yellowhammers, consisted of a protected part covered with wood (*solid lines*) and a part covered with chicken wire (*dotted lines*). The open part contained branches to sit on, while the protected part contained a small pine tree and food and water. **b** An overhead view of the nine cages (five on the left side and four on the right) with the experimental treatments in the first and second segment of the experiment indicated. *SS* See sparrowhawk, *HS* hear alarm calls from birds that saw a sparrowhawk, *SC* see control, *HC* hear calls from birds that saw the control

In this study, I examined the relationship between information about predators, dominance, fat reserves and anti-predator behavior. Since dominant individuals have priority of access to food, they should take fewer risks and can carry fewer fat reserves than sub-dominants when fat reserves are costly in terms of predation risk (see Ekman and Lilliendahl 1993). However, when predation risk is low, one could expect dominants to carry more fat reserves than sub-dominants (see Verhulst and Hogstad 1996). In this study, differences in the amount of information about predators in the environment were created by showing a sparrowhawk (*Accipiter nisus*) silhouette to caged yellowhammers (*Emberiza citrinella*). These birds then gave alarm calls which other yellowhammers, that could not see the predator, could hear. I assumed that the birds that saw the predator had more information about the behavior and location of the predator than the birds that only heard the alarm calls. I studied how completeness of information about the predator affected alert perching behavior and foraging delay of dominant and sub-dominant individuals. I expected birds with less information to be more alert than birds that saw the predator, because the former need to gain more information about the predator. I also expected birds with less information to resume foraging later because they may estimate the risk of predation to be higher due to their increased uncertainty about the predator. Furthermore, the foraging delay may be shorter in sub-dominant birds, because they may value a lost feeding opportunity more than dominant birds and thus they may be willing to take more risks. However, such an effect can also be found when sub-dominant birds are generally younger and are less experienced in assessing risks and adjusting their foraging delay to the prevailing risk.

Methods

Eighteen male yellowhammers were caught in the spring of 1994 and assigned to duos at random; duos were randomly assigned to outdoor aviaries. The aviaries were 2×1.5×2 m (length × breadth × height) each, and situated on both sides of a corridor (Fig. 1). The inner half (facing the corridor) of each cage had wooden walls and contained a small pine tree. Food and water were provided ad libitum in this protected part of the cage. The outer half of each cage was made of chicken wire. The cages were visually isolated from each other with dark plastic, but the birds in different cages were able to hear each other. This could result in synchronization of behavior, which could reduce variance within the data set. However, synchrony of birds that received different treatments would make the statistical tests more conservative.

After apparent habituation to my presence in the corridor, the first segment of the experiment was conducted on 9 days between 12 and 24 February 1995 and the second segment on 6 days between 4 and 12 March 1995. I only used observations from the first 3 days for each segment, because the birds seemed to habituate to the treatments in the course of the first segment (foraging delay: session × see/hear: sparrowhawk: Wilks' $\lambda=0.48$, $F_{2,14}=7.61$, $P<0.01$). Since no differences between the first and second segment of the experiment were found (foraging delay: Wilks' $\lambda=0.97$, $F_{1,15}=0.49$, $P=0.49$; mass: Wilks' $\lambda=0.98$, $F_{1,15}=0.32$, $P=0.58$), data from the first and second segment were lumped.

In the experiment I used nine cages with two birds each. Four cages were situated on the right side, and five on the left side of a corridor. In this experiment, all birds were exposed to all four treatments: see sparrowhawk model (SS), hear alarm calls from birds that saw the sparrowhawk model (HS), see control (SC), and hear calls from birds that saw the control (HC). The exposure to the sparrowhawk model consisted of a silhouette of a sparrowhawk, which was drawn over all the cages on one side of the corridor in alternating directions at subsequent exposures. The exposure to the control consisted of a black square piece of wood, which was drawn over the cages in a similar manner (Fig. 1). When the birds on one side saw a treatment they emitted calls, while the birds on the other side heard those calls, but did not see what happened. When the birds saw the sparrowhawk model, they gave alarm calls, while, when they saw the piece of wood, they gave flight calls. Alarm calls are thought to express strong fear, and flight calls express the intention to fly away (Cramp and Perrins 1994).

On each of the three observation days in February, birds on one side of the corridor saw a sparrowhawk at 0800, 1000, 1300, and 1500 hours (SS), and heard control calls when the birds at the opposite side saw a piece of wood, at 0900, 1100, 1400, and 1600 hours (HC). On the same days, birds on the other side of the corridor saw a piece of wood at 0900, 1100, 1400, and 1600 hours (SC), and heard alarm calls when the birds on the opposite side saw a sparrowhawk, at 0800, 1000, 1300, and 1500 hours (HS). Thus on each day, each side received four times two treatments (SS+HC or HS+SC) at alternating hours. In the second segment of the experiment (in March), the treatments were switched between sides.

On each of the three observation days in each segment of the experiment I observed three focal cages at a time: two cages situated on one side of the corridor and one cage on the other side of the corridor. In that way, all cages were observed once after 3 days. The cages that were observed on the same day I call a group of cages. The order in which I observed the groups of cages was randomized in each segment of the experiment.

On each observation day, without interfering with the birds, I measured morning mass, evening mass, and daily mass increase, by means of a balance placed under the feeding tray. Observations on body mass started as soon as it was light enough to see the color rings of the birds and ended when the birds stopped feeding and sat on their roosting sites. Foraging delay was measured as the time from exposure to the first feeding event on the feeding tray. For foraging delay, I only used data from the first three (of four) exposures per day, because the last exposure was too close to dusk. In 6 of 204 observations (3%), the bird had not resumed foraging within an hour after the exposure and in those cases foraging delay was set at 60 min. This will have caused a slight underestimation of the actual foraging delay. Foraging delays were square root transformed in order to normalize the right-skewed data. I also monitored alert perching in three intervals at each exposure: 6 min before each exposure, the first 6 min after each exposure and 13–18 min after each exposure. In these intervals, observations were made every second minute in one of the focal cages, so that over each of these 6-min intervals the behavior of all six birds in the three focal cages had been recorded once. Behavior was measured as time-point measurement (Altmann 1974) and categorized as alert perching time when the bird was sitting on a branch in the outer part of the cage. For each interval, alert perching time was calculated as the number of times perched as a percentage of the four observations (one observation at each of the four exposures during a day). Because this percentage was only based on four observations, alert perching time was analyzed nonparametrically with sign tests for differences between the sparrowhawk and control treatment, between seeing or hearing, and between the three intervals.

Dominance hierarchy within each pair of birds was obtained by observing aggressive interactions (11.1±1.6 SE interactions per pair) at the feeding trays. The individual in each pair that won most interactions was classified as dominant (average difference in number of interactions won 6.7±2.0 SE per pair).

Analyses

Since all birds were observed in all treatments once, analyses on foraging delay were based on within individual changes between treatments, and performed with multivariate repeated measures ANOVAs (O'Brien and Kaiser 1985). The first within-subject factor I included was 'treatment', which had four levels: SS, HS, SC, and HC.

Since the two birds within each cage may have influenced each other's foraging at the feeding tray, they cannot be treated as independent data points. Therefore, I performed the analyses on the level of the cages. Since in each cage a dominance hierarchy had developed, which could influence the bird's behavior and mass, I divided the birds within each cage in two categories, dominant and sub-dominant. Thus, I included the within cage factor 'dominance' in the statistical model. This factor may, for example, indicate differences in risk-proneness between dominant and subdominant individuals.

The third factor I included in the model is the between-subject factor 'side'. Since the birds on the same side of the corridor were exposed to the same microclimate and received the same treatments on the same days, they may have been more alike than birds from different sides of the corridor.

I also included 'group' as a between-subject blocking factor. Since the cages in each group (note that each group of cages includes cages from both sides of the corridor, and thus cages that received different treatments) were measured on the same day, there may have been similarities between those cages due to, for example, weather conditions. The interaction between side and group was never significant and was therefore removed from all the models.

Differences between the treatments were investigated with contrast analysis between the SS treatment and all other treatments. Wherever I performed multiple testing in other analyses, I adjusted the α-levels by means of a sequential Bonferroni procedure (Sokal and Rohlf 1995). Those adjusted levels are given in brackets.

Body mass could not be analyzed for effect of treatment, because on each day all individuals were exposed to two different treatments. Therefore I analyzed the effect of dominance on body mass in another multivariate repeated measurement ANOVA model. In this model, the within-subject factor 'dominance' and the between-subject factors 'side' and 'group' were included as described for foraging delay. Furthermore I included the within-subject factor 'segment' (the first vs the second segment of the experiment) and also the within-subject factor 'time' (dawn vs dusk).

In one of the cages, one of the individuals fed only sporadically on the balance, and this cage was removed from analyses of foraging delay and body mass.

Results

Body mass

Differences in body mass between dominant and sub-dominant birds may indicate a difference in state between the two categories of birds. A difference in state may in turn influence risk-taking after a predator attack. Dominant birds seemed to maintain lower body mass than sub-dominant birds (Fig. 2); however, this was not significant (dominance: Wilks' λ=0.38, $F_{1,4}$=6.62, P=0.06). This effect seemed to be strongest in birds on the left side of the corridor; however, this was also not significant (dominance × side: Wilks' λ=0.39, $F_{1,4}$=6.14, P=0.07). There was a significant difference between dawn and dusk mass (time of day: Wilks' λ=0.01, $F_{1,4}$=276.27, P<0.0001); however, this daily mass increase did not differ significantly with dominance (time of day × dominance: Wilks' λ=1.00, $F_{1,4}$=0.02, P=0.90).

There were no overall significant differences in body mass between birds on the left and right side of the corridor (side: $F_{1,4}$=0.60, P=0.48), nor were there any overall significant differences between the groups of cages (group: $F_{2,4}$=0.34, P=0.73).

Foraging delay

Birds that saw the sparrowhawk had more information about predation risk than the birds that only heard alarm calls. If incomplete information about predators leads to

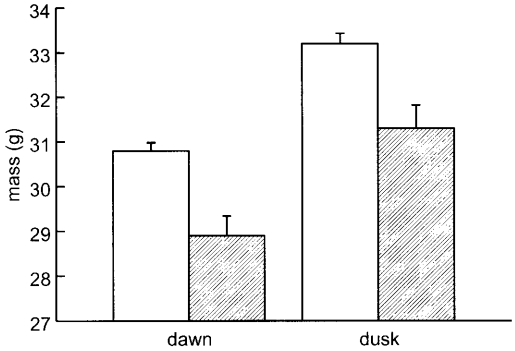

Fig. 2 Dawn and dusk mass (+SE) of sub-dominant (*open bars*) and dominant (*hatched bars*) yellowhammers (n=8)

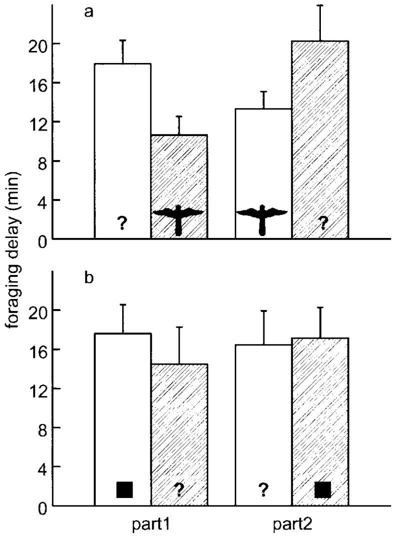

Fig. 3 Foraging delay (+SE) when yellowhammers saw a sparrowhawk model (**a** *sparrowhawk silhouette*) or a control (**b** *square*), or when they heard calls from birds that saw a sparrowhawk model (**a** *question mark*) or a control (**b** *question mark*) in the first and the second segment of the experiment. *Open bars* indicate the birds on the left side of the corridor (n=10), and *hatched bars* the ones on the right (n=6)

a higher estimation of the risk, the birds with more information are expected to start foraging sooner than the birds with incomplete information. In accordance with this expectation, there was a difference in foraging delay between the treatments (Table 1, treatment). When the birds saw the sparrowhawk, they resumed foraging fastest, and when they heard alarm calls they resumed foraging slowest (contrast analyses, P<0.05, Fig. 3a). This effect was independent of what side the birds were on; in the first segment of the experiment the birds on the left side heard alarm calls and resumed foraging slowest. In the second segment of the experiment the birds on the right side heard the alarm calls and resumed foraging slowest (Fig. 3a). No such effect was apparent in the control treatment, where half of the birds saw the control treatment (piece of wood), while the other half heard control (flight) calls (Fig. 3b).

Table 1 Results from a multivariate repeated measures ANOVA on foraging delays of dominant and sub-dominant yellowhammers after seeing a sparrowhawk model (*SS*), hearing alarm calls of birds that saw the sparrowhawk model (*HS*), seeing a control (*SC*), or hearing calls of birds that saw a control (*HS*). See Materials and methods for a description of the blocking factors side and group

Factor	λ	*F*	*df*	*P*
Dominance	0.68	1.84	1,4	0.25
Dominance × side	0.94	0.26	1,4	0.64
Dominance × group	0.66	1.05	2,4	0.43
Treatment	0.02	28.50	3,2	<0.05
Treatment × side	0.20	2.61	3,2	0.29
Treatment × group	0.10	1.46	6,4	0.37
Dominance × treatment	0.44	0.86	3,2	0.58
Dominance × treatment × side	0.42	0.91	3,2	0.56
Dominance × treatment × group	0.84	0.06	6,4	1.00
Side		0.14	1,4	0.73
Group		0.05	2,4	0.95

Table 2 Results of two-tailed sign tests for within subject differences in percentage alert perching time between the 6-min period before an exposure and 1–6 min, and 13–18 min after exposure to seeing a sparrowhawk model (*SS*), hearing alarm calls from birds that saw a sparrowhawk model (*HS*), seeing a control (*SC*), or hearing calls from birds that saw a control (*HC*). Sample sizes are 18 in all tests; however, n values in the tests can be lower due to ties, and k indicates the number of positive changes. α Levels are given for a sequential Bonferroni adjustment

Treatment	Test	*n*	*k*	*P*	α
See sparrowhawk	Before vs 1–6 min	16	11	0.21	
	1–6 min vs 13–18 min	12	4	0.39	
Hear alarm calls	Before vs. 1–6 min	13	12	<0.005	0.007
	1–6 min vs 13–18 min	12	0	<0.001	0.006
See control	Before vs 1–6 min	12	10	<0.05	0.008
	1–6 min vs 13–18 min	11	3	0.15	
Hear control calls	Before vs. 1–6 min	15	11	0.12	
	1–6 min vs. 13–18 min	14	5	0.42	

The risk a bird is willing to take may depend on its state, and therefore differences in risk-taking and, thus, in foraging delay between dominant and sub-dominant birds may be expected. However, this was not the case (Table 1, dominance). There were no differences in foraging delay between birds on the left or right side of the corridor, nor between the groups of birds that were measured on the same day (Table 1, side, group)

Alert perching time

One could expect birds with less information about predators to become more alert immediately upon exposure. When the birds heard alarm calls, alert perching time increased significantly from before the exposure to the first 6 min after, and decreased again at 13–18 min after the exposure (Fig. 4a, Table 2). When the birds saw the control treatment, there was a non-significant tendency for an increase in alert perching time compared to before

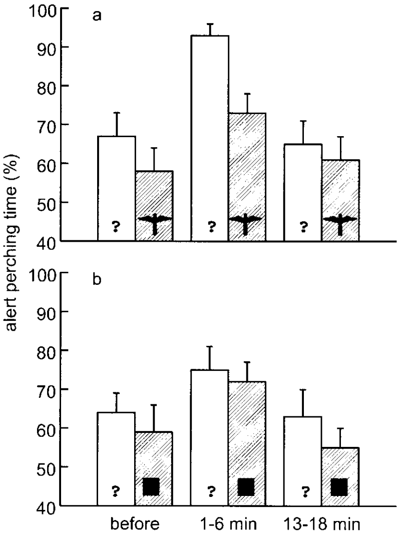

Fig. 4 Percentage of alert perching time (+SE) in a 6-min period before, 1–6 min after and 13–18 min after by yellowhammers exposed to a sparrowhawk model (**a** *sparrowhawk silhouette*) or a control (**b** *square*) for birds that saw the exposure (*hatched bars*) and birds that heard calls from the birds that saw the exposure (*open bars*, *question mark*). The first and second segments of the experiment were lumped in the figure (n=18)

the exposure (Fig. 4b, Table 2). When birds saw the sparrowhawk, or when they heard control (flight) calls, they showed a similar pattern; however this was not significant (Fig. 4a, Table 2).

Comparing the behavior of all four groups immediately upon exposure (Fig. 4a, b: 1–6 min), we can see that when yellowhammers heard alarm calls, they spent more time perched the first 6 min after the exposure than when they also saw the sparrowhawk [Fig. 4a, sign test: n=11, k=1, P<0.025 (α=0.025)]. This was not the case in the control treatment (Fig. 4b, n=10, k=4, P=0.38). Birds could be expected to be more alert when they heard alarm calls than when they heard flight calls. In accordance with this expectation, birds spent more time perched the first 6 min after an exposure when they heard alarm calls than when they heard control (flight) calls [Fig. 4a, b, sign test: n=9, k=1, P<0.025 (α=0.025)]. However, when birds saw the sparrowhawk, they did not spend more time perched than when they saw the control (Fig. 4a, b, sign test: n=13, k=6, P=0.50).

Discussion

Yellowhammers in this experiment, like many other animals (Sherman 1977), gave alarm calls when they saw a sparrowhawk model flying over, and hearing these alarm calls greatly affected the behavior of other birds. The birds that saw the predator model had information about where the predator was, how it behaved, if it was still around or in what direction it disappeared. Although I am not exactly sure what kind of information the alarm calls contained, I assume the birds that only heard the calls had less information about the predator and its behavior.

It has been shown in several studies that birds delay foraging after being exposed to a predator (reviewed in Lima 1998). In this study, birds that saw a predator model resumed foraging fastest, while birds that only heard alarm calls resumed foraging slowest. Thus, it seems that birds with less complete information perceive predation risk as being higher (as in Bouskila and Blumstein 1992; Sih 1992; Koops and Abrahams 1998). In the non-breeding season, when the fitness costs of a lost feeding opportunity may be relatively small, an animal may be expected to overestimate predation risk (Koops and Abrahams 1998). When overestimating, an animal loses a feeding opportunity; however, when underestimating it risks death by predation. Since yellowhammers are able to regain mass losses quickly after a predator exposure (van der Veen 1999; van der Veen and Sivars 2000), their costs of lost feeding opportunities may be relatively small compared to the cost of emerging too early. This may explain why yellowhammers with incomplete information are more cautious. Waiting longer before resuming foraging reduces the risk of making the error of resuming foraging while the predator is still around, which could incur large fitness costs. Although not significantly so, birds seemed to resume foraging faster when they saw the predator model than in the control treatment. A potential explanation for this seemingly short foraging delay when the birds saw the sparrowhawk model may be that avian predators tend to return to the same hunting area (Rijnsdorp et al. 1981). If so, the longer the birds wait after an encounter, the higher the chance will be that the predator will appear again.

When yellowhammers had less complete information about the sparrowhawk they increased their alert perching immediately after exposure to the model. When the birds saw the sparrowhawk, heard flight calls or saw the control, alert perching time also increased immediately after exposure; however, these effects were non-significant and less pronounced. A reduction of activity, and an increase in alert perching after a predator attack, has been shown for many species in a number of taxa (reviewed in Lima 1998).

Although many of the responses to the control treatment and the flight calls were not statistically significant, it is puzzling why the birds responded to it in a more or less similar way as to the predator model and alarm calls. It could be simply an effect of fear of a novel object (Greenberg 1983). It may also be that the piece of wood is perceived as a disturbance of feeding. Flight calls are normally used to signal the intention to move to another area and may be some intermediate form of an alarm call. Yellowhammers normally leave a feeding area after an encounter with a predator (van der Veen 2000). Although flight calls might not directly signal a predator's presence, it may signal that it is better to go somewhere else. The response to the flight calls may thus be an intermediate response to a disturbance of feeding. The fact that, in this experiment, the birds were not able to move to another area may have made the response to the control treatment and the flight calls more pronounced than it would have been in a natural situation.

It could be argued that not all birds in the ‘see sparrowhawk’ treatment actually saw the sparrowhawk. However, this would only make my tests more conservative, because it would decrease the differences between the treatments, and increase the within-group variance. Even so, one may have to be careful when drawing conclusions from this experiment, because individuals may have influenced each other’s behavior. However, I tried to take such dependencies into account in the statistical analyses and, furthermore, I observed the same effect twice. Therefore, I am inclined to think that this lack of independence did not influence my conclusions to a large extent.

To my knowledge, the only other study that aimed to investigate effects of completeness of information about predators is that by Sih (1992). He showed theoretically that prey should stay in refuge longer when they have less information about the risk. Although he showed empirically that hunger and predator threat influenced hiding time, he did not actually manipulate information about predation risk.

In this experiment dominant birds tended to maintain lower body mass than sub-dominant birds. Sub-dominant birds may need to maintain a higher body mass, since dominant birds can exclude them from food sources (Ekman and Lilliendahl 1993). The fitness costs of a lost feeding opportunity depend on the state of an animal (Abrams 1994). Therefore, the costs of a lost feeding opportunity may be higher for sub-dominant birds than for dominant birds, and thus, a shorter foraging delay in sub-dominant birds could be expected. Although such an effect has been shown in other studies (Zanette and Ratcliffe 1994; Koivula et al. 1995), the birds in this study did not differ in foraging delay with respect to dominance.

This study shows that the completeness of information about predators can affect the behavior of birds. Birds that had more information were able to start foraging sooner and were less alert after a predator encounter, and thus lost fewer foraging opportunities than birds with incomplete information. Completeness of information and its effect on decision-making may thus affect the fitness of an animal.

Acknowledgements I would like to thank Putte Sundberg for letting me use his birds, Hannu Rita for statistical advice, and Ingrid Ahnesjö, Jan Ekman, Henk van der Jeugd, Ben Sheldon, Lisa Shorey, Staffan Ulfstrand, and three anonymous referees for comments on earlier versions of this manuscript. This experiment was conducted with the approval of the ethical committee in Uppsala, license NR c253/94.

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