Effects of predation risk on diurnal mass dynamics and foraging routines of yellowhammers (Emberiza citrinella)

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Theoretical models predict that when having fat reserves is costly in terms of predation risk, birds should decrease their levels of fat reserves in response to increased predation risk. I performed an experiment in which yellowhammers were exposed to a control treatment, where a curtain was moved several times a day, 5 days in a row, and then to a predator treatment, where a perched, stuffed sparrowhawk appeared when the curtain was moved, 5 days in a row. Between the two treatments were 2 days without any experimental treatment. The birds were expected to decrease in mass, and/or to change the daily trajectory of mass increase in response to increased predation risk. Yellowhammers decreased in morning mass and evening mass in response to both the moving curtain and the sparrowhawk compared to an untreated day before the start of the experiment. However, the response to both treatments was not the same; in the sparrowhawk treatment the birds waited longer before resuming feeding and lost more weight after each exposure as compared to the curtain treatment. This loss was regained, and yellowhammers increased their intake rate. Due to that, they reduced, although not significantly, the time spent feeding under predation risk. A reduction in the time spent feeding under predation risk reduces the time exposed to predators. However, if an increase in intake rate also incurs a decrease in vigilance, this might increase predation risk. The results of this study, together with other studies, indicate that for yellowhammers a reduction in time exposed to predators might be more important for survival than a reduction in body mass. Key words: body mass, daily routines, Emberiza citrinella, exposure time, intake rate, starvation–predation trade-off, yellowhammers. [Behav Ecol 10:545–551 (1999)]

Winter in northern areas can be harsh for small passerines. Due to their high surface-to-volume ratio, they lose heat quickly, and every day they need to accumulate energy reserves to avoid starvation during the long and cold nights. Many bird species store reserves in the form of subcutaneous fat (Blem, 1990), and therefore undergo seasonal and daily mass changes (Baldwin and Kendeigh, 1938; Nice, 1938). The disadvantage of storing reserves in the form of body fat is that it has to be carried around (Witter and Cuthill, 1993). Recent research suggests that both the acquisition and maintenance of fat reserves can be costly in terms of predation risk. The acquisition cost is suggested to be higher exposure to predators due to increased foraging time and decreased vigilance while foraging (Ekman, 1987; Krause and Godin, 1996). The cost of maintaining fat reserves is suggested to be a lower escape ability from predator attacks when fat reserves are larger (Kullberg et al., 1996; McNaama and Ure, 1995; Witter et al., 1994; but see Kullberg, 1998, Veasey et al., 1998).

Recent theoretical investigations predict that when fat reserves are costly in terms of predation, birds should decrease fat reserves, and thus increase starvation risk, in situations of high predation risk (McNamara and Houston, 1990). Birds are expected to lower their morning mass and/or evening mass in response to increased predation risk, for which some evidence is found in experimental studies (Lilliendahl, 1997; Witter et al., 1994; but see Pravosudov and Grubb, 1998) and in a correlative study (Gosler et al., 1995). Besides mass decrease, there are many other behavioral responses through which individuals can reduce their predation risk—for example, decrease of exposure time, change of habitat, and change of food type (reviewed in Lima and Dill, 1990).

If decreasing body mass incurs too high a starvation risk, a bird can use a more fine-scaled adjustment to increased predation risk by altering the daily trajectory of mass gain. McNamara et al. (1994) modeled daily patterns of feeding in relation to predation risk. They predicted that birds subjected to predation risk with abundant and predictable food should postpone feeding until the end of the day in order to minimize the maintenance costs of fat reserves during the day. With this feeding routine birds experience low body mass during the day and a fast increase in body mass at the end of the day. However, when the food source is unpredictable, birds are expected to feed in the morning in order to avoid starvation, but to avoid predation birds should wait and do some feeding at the end of the day. This results in the typically found bimodal feeding pattern, with fast body mass gain in the morning and in the evening and slow increase of body mass in the middle of the day (Aschoff, 1966; Beer, 1961; Gibb, 1956; Lees, 1948; Morton, 1967).

I subjected yellowhammers to experimentally elevated levels of perceived predation risk to test if they alter their diurnal trajectory of mass increase and foraging behavior in response to predation risk. Yellowhammers spend the winter in flocks in open fields, where they feed on seeds. As an open-field species, they do not use cover to escape predators, but depend on speed and climbing ability (Lima, 1993). I therefore expected yellowhammers to reduce body mass and/or to adjust the daily trajectory of mass gain in response to increased predation risk.

METHODS
This experiment was conducted on two groups of birds (group X and group Y), separated in time, due to a limited
Figure 1
Time schedule of group X and Y. Out: birds were kept in pairs in outdoor cages; In: birds were kept per group in large indoor cages; A: acclimatization in experiment room; C: curtain (control) treatment; S: sparrowhawk (experimental) treatment. Hatched boxes indicate time in experiment room.

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I captured 20 adult male yellowhammers between April 1994 and April 1995 in an area close to Uppsala, Sweden (59°50' N, 17°30' E). To avoid sex differences, and because males are easier to catch, I used only males in the experiment. The birds were blocked in pairs for tarsus length, after which each member of a pair was randomly assigned to one of two experimental groups, X or Y. This procedure ensured a comparable size distribution between the two groups. The birds were kept in random pairs in outdoor cages until 10 October 1995, when each group (X and Y) was moved to a large (2 × 1.5 × 2.5 m) indoor cage and kept under a fixed winter day–night rhythm (8:16 h light:dark, lights on at 0800 h). In these indoor cages temperatures ranged between 0 and 10°C, depending on outdoor temperature.

After at least 4 weeks in the indoor cages, I transferred the birds of group X into individual cages in the experiment room with a constant temperature of −5°C to simulate winter conditions. The birds were kept individually in cages to remove confounding effects of dominance on fat reserves (Ekman and Lilliehöld, 1993). The cages (50 × 50 × 50 cm) had board walls, except for the front, which was covered with chicken wire. They were placed in two rows on top of each other, so that the birds could not see each other. The birds were randomly assigned to the cages. The light regime in the experiment room was the same as in the indoor cages.

After an acclimatization period of 3 weeks, the birds were subjected to a control treatment (see below) for 5 consecutive days, followed by 2 days without any experimental treatment, and 5 days with experimental treatment (see below). The 2 days in between the treatments were needed to study how the birds behaved after the treatment, when they still perceived the environment as risky, but were not interrupted by the moving curtain. After the first run of experiments in December, in which the birds of group X were tested, group Y was submitted to the same sequence of tests (Figure 1). Although the indoor period was longer for group Y than for group X, this should not have influenced the results of the experiments because both groups had first been kept under room conditions for at least 4 weeks, which is longer than the time needed to recover body mass after moving from outdoors to indoors (Ekman and Hake, 1990). Furthermore, the acclimatization period in the experimental room was kept constant (3 weeks) for both experimental groups. In the acclimatization period of group Y, body mass was constant after an initial week of decline (van der Veen, unpublished data).

The birds were kept at a predictable ad libitum food source for a long time; therefore, they might have reduced their body mass (Ekman and Hake, 1990). However, birds were not at their minimum mass during this experiment. In April 1994, daily average body mass of adult male yellowhammers in the Uppsala population was about 27.5 g (Allander and Sundberg, 1997), as compared to 28.5 g at the start of this experiment.

The experimental treatment (sparrowhawk) consisted of showing a perched, stuffed sparrowhawk right in front of the cages, about 1.5 m away, four times a day, at 0900, 1100, 1300, and 1500 hr. This was done by lowering a curtain that was hanging in front of the sparrowhawk, and by moving the head of the sparrowhawk by means of radio control. After 2 min the curtain was raised again, so that the sparrowhawk disappeared. In the control treatment I also lowered the curtain and raised it again after 2 min, but the sparrowhawk was absent. This treatment was meant to control for the effect of a sudden movement of the curtain. Both groups (X and Y) were subjected to the curtain and sparrowhawk treatments in the same order on 5 consecutive days, so that the birds were used to the moving curtain when they were exposed to the sparrowhawk treatment for the first time. In this way the observed effects in the sparrowhawk treatment were due to the novel sparrowhawk, and no longer due to the moving curtain.

I also took measurements during the acclimatization period in the experiment room and on the untreated days between the curtain and sparrowhawk treatment. This was done to control for seasonal changes in body mass throughout the experiment. However, due to technical problems, some data are missing. Morning mass on the first day of treatment could be compared for both groups in both treatments by comparing day 1 with day 2. On day 1 morning mass was measured before the first exposure, and therefore it can serve as an untreated measurement. Evening mass on the first day of curtain treatment could not be compared in group X, whereas in group Y it could be compared with 3 days before start of the treatment. For both groups evening mass on the first day of sparrowhawk treatment was compared with the day before the sparrowhawk treatment.

Throughout the time in the experiment room, a balance was placed under the feeding tray of 8 of the 10 birds in each group. In group Y one balance was shifted to another bird after the acclimatization period, because the first bird did not sit on the balance while feeding. Weights were registered automatically every 15 s by a computer. Every time a bird started feeding, its mass could be calculated by subtracting the mass of the food available before the feeding attempt. Because mass was registered when the birds started feeding, the measurement at the next feeding attempt included the food eaten at the previous attempt. Due to spilling of food, it was not possible to get reliable mass measurements when the bird left the balance.

Mass registrations were accompanied by visual observations of behavior through a one-way mirror. Once per minute for half an hour before and half an hour after the exposures I observed if the birds were foraging.

### Analyses
Because all birds in this experiment served as their own controls, all analyses were done with repeated-measures MANOVA (Proc GLM; SAS Institute, 1990). Univariate repeated-measures models assume that all variances of the repeated measurements are equal and that all correlations between the pairs of repeated measurements are equal. This is usually not met in biological data, and violating this assumption increases the chance of type I errors (O’Brien and Kaiser, 1985). To avoid this, I used multivariate repeated-measures models.

In this experiment, “treatment” (curtain and sparrowhawk), a within-subject factor, is the factor of interest because...
it indicates the effect of increased predation risk on the test variable. All 5 test days are incorporated in the MANOVA models, and the factor “day” is a within-subject factor. Because the response was strongest on the first day of exposure, only this day is shown in the figures. The factor “group” (X and Y) is a between-subject factor.

I compared the untreated day before the first day of exposure and the first day of exposure where available using paired t tests, corrected with sequential Bonferroni. The corrected levels of significance (α) are given between brackets after the p values.

In the Results section, only the factors of interest described above are mentioned in the text. When there was no significant interaction between the factors “treatment” and “group” in the repeated MANOVA analyses, groups were pooled in the figures and in the paired t tests.

Variables tested were morning mass, measured at the first foraging event after the lights went on at 0800 h; evening mass, measured at the last feeding event before the lights went out at 1600 h; mass change after the exposures, the daily average mass the birds lost or gained between pre- and postexposure measurements; waiting time, the daily average time a bird waited before resuming feeding on the balance after each exposure; rate of mass change, daily average mass change per time past between the pre- and postexposure measurements; diurnal trajectory of mass gain (see below); feeding time, daily average time spent feeding, measured in eight pre- and postexposure periods of 30 min; intake rate, mass increase (evening mass−morning mass + mass loss) per feeding minute per day (extrapolated from feeding time).

I analyzed diurnal trajectories of mass gain by measuring rate of mass increase between 10 fixed occasions during the day: morning mass, a pre- and postexposure measurement at each of the four exposures, and evening mass, resulting in rates of mass increase in five periods per day; from morning mass to the first preexposure measurement (0800–0900 h), from each postexposure measurement to the next preexposure measurement (0900–1100, 1100–1300, 1300–1500 h), and from the last postexposure measurement to evening mass (1500–1600 h). Although in all other MANOVA models all 5 days of exposure were used, in this analysis only day 1 could be used due to missing values. The factors of interest in this analysis are “treatment” (curtain, sparrowhawk), indicating an effect of predation risk; “time” (the five periods per day described above), indicating a certain daily trajectory of mass increase; and the interaction between “time” and “treatment,” indicating an alteration of the daily trajectory of mass gain in response to predation risk. Both “treatment” and “time” are within-subject factors, and “group” (X and Y) is a between-subject factor.

Data were analyzed as recorded except for diurnal trajectories of mass gain and intake rate, which were ln transformed because of non-normality. Foraging activity, which is a proportion, was arcsine square-root transformed.

RESULTS

Daily pattern

Yellowhammer responded to the sparrowhawk treatment by either hiding in the back of the cage or by flying around intensively in the front of the cage, while alarm calling. The response to the curtain treatment was never hiding, but usually flying or sitting vigilant in the front of the cage.

If carrying fat reserves is costly for yellowhammers in terms of predation risk, the birds should alter their daily trajectory of mass gain in response to increased predation risk. This could be done by postponing mass gain or by losing mass. In this experiment birds lost body mass immediately after each exposure to a sparrowhawk or a curtain (Figure 2). Mass change after the exposure includes food eaten at the last feeding attempt before the exposure and mass loss in the inter-feeding interval. Average mass change after the exposure was significantly lower on the first day of both treatments compared to mass change at the moment at which an exposure would have occurred on the untreated day before the test. However, this effect was stronger in the sparrowhawk treatment (Figure 3a; paired t test: sparrowhawk: t<sub>15</sub> = −5.83, p = .0001, α = 0.025; curtain: t<sub>5</sub> = −2.41, p = .05, α = 0.05).

The sparrowhawk treatment was more frightening for the birds; on treatment days 1–5, their change in body mass was significantly lower when exposed to a predator than to a moving curtain (Figure 3a; treatment: k<sub>visit</sub> = 0.35, F<sub>1,14</sub> = 26.38, p = .0002).

If the exposure to the sparrowhawk was more frightening than the exposure to the curtain, one could expect the birds to wait longer before resuming feeding after being exposed to a sparrowhawk. This expectation was confirmed in this experiment (Figure 3b; treatment: λ<sub>init</sub> = 0.37, F<sub>1,14</sub> = 23.51, p = .0003). The birds waited longer with resuming feeding on the first day of the sparrowhawk treatment compared to the moment when exposure would have occurred on an untreated day before the sparrowhawk treatment (Figure 3b; paired t test: t<sub>5</sub> = 5.10, p = .0001, α = 0.025). This was not the case in the curtain treatment (Figure 3b; paired t test: t<sub>5</sub> = 0.52, p = .62, α = 0.05).

Because the birds both waited longer before resuming feed-
ing and lost more mass when exposed to a sparrowhawk than to a curtain, the question remains if this mass loss was due to the longer waiting time or due to increased stress when exposed to a sparrowhawk. If the birds were more stressed when exposed to a sparrowhawk, they would have lost mass faster while they were waiting to resume feeding (i.e., their rate of mass change would be lower or more negative). This was confirmed in this experiment (Figure 3c; treatment: $\lambda_{\text{wilks}} = 0.67$, $F_{1,14} = 6.79$, $p = .0208$). The birds did not differ in rate of mass change after the exposures between the first day of the curtain treatment and the moment when the exposure would have occurred on the untreated day before the curtain treatment (Figure 3c; paired $t$ test: $t_4 = -1.41$, $p = .21$, $\alpha = 0.05$), but this difference was significant when exposed to a sparrowhawk (Figure 3c; paired $t$ test: $t_5 = -4.44$, $p = .0005$, $\alpha = 0.025$). These results indicate that under the assumption that the birds ate as much during the preexposure measurement, the higher mass loss in the sparrowhawk treatment is not only due to the longer waiting time, but also due to a higher rate of mass loss as a result of stress when exposed to a predator.

Compensatory gain rate

As stated before, if carrying fat reserves is costly, the birds could, in response to increased predation risk, alter their diurnal trajectory of mass gain. There was no support for this hypothesis; although the birds did not gain mass at an equal rate during all five periods of the day (Figure 2; time: $\lambda_{\text{wilks}} = 0.07$, $F_{4,4} = 13.06$, $p = .0145$, repeated-measures MANOVA on day 1 only), the birds did not alter their diurnal trajectory of mass gain, and they did not postpone feeding to the end of the day in response to the sparrowhawk treatment (treatment $\times$ time: $\lambda_{\text{wilks}} = 0.52$, $F_{4,4} = 0.92$, $p = .35$, ns). On the contrary, in the periods between the exposures, birds gained mass faster on the first day of sparrowhawk exposure compared to the curtain exposure (Figure 2; treatment: $\lambda_{\text{wilks}} = 0.40$, $F_{1,7} = 10.43$, $p = .0145$).

Besides lowering its fat reserves under predation risk, a bird can decrease predation risk by decreasing the time spent feeding and increasing intake rate. This is important because birds are under higher predation risk while feeding compared to while resting. The birds spent slightly less time feeding in the sparrowhawk treatment, but this was not statistically different (treatment: $\lambda_{\text{wilks}} = 0.76$, $F_{1,14} = 4.35$, $p = .0558$). However, because the birds gained mass faster in the sparrowhawk treatment and spent slightly less time feeding, intake rate (gram mass increase per foraging minute) was significantly higher in the sparrowhawk treatment (curtain: mean = 0.043, SE = 0.005; sparrowhawk: mean = 0.068, SE = 0.011; treatment: $\lambda_{\text{wilks}} = 0.51$, $F_{1,14} = 13.54$, $p = .0025$).

Morning mass and evening mass

Besides altering the diurnal trajectory of mass gain to avoid the cost of carrying fat reserves, birds can also simply lower morning mass, evening mass, or a combination of these. In this experiment such a response was not confirmed (Figure 4), and the experiment suggests that the birds mainly responded to a disturbance, not so much to the predator. Evening mass was significantly lower on the first day of exposure to both treatments compared to an untreated day before the treatments (Figure 4, Table 1). Morning mass did not differ significantly between the untreated day and the first treatment day, except for a decrease in mass in group X in response to the sparrowhawk (Figure 4, Table 1). Morning and evening mass on days 1–5 did not differ between the sparrowhawk and curtain treatments (treatment: morning: $\lambda_{\text{wilks}} = \ldots$).
DISCUSSION

If fat reserves are costly in terms of predation risk (McNamara and Houston, 1990), one would expect a stronger and longer lasting decrease in mass in the sparrowhawk treatment than in the moving curtain treatment. This was, however, not the case in this study; yellowhammers changed their body mass in response to both a moving curtain and a stuffed sparrowhawk, and the change in morning mass and evening mass did not differ between the two treatments. However, the birds’ response to the two treatments was not the same. First, the birds were habituated to the moving curtain before exposure to the sparrowhawk. Furthermore, the birds waited much longer, up to 25 min, before resuming feeding when exposed to the sparrowhawk, and they lost mass at a higher rate after each exposure to a sparrowhawk than after exposure to the moving curtain. This indicates that, although the birds did not alter their mass gain, the treatments were not perceived as equally frightening.

The response to the sparrowhawk might just have been a response to a novel object, suddenly appearing behind the curtain. Ideally, the curtain treatment should have had a similar object present. However, if the birds perceived the novel object as a danger (which they apparently did), they should respond to it as being a risk, no matter what kind of risk. Furthermore, there is a possibility that the birds might have become dehabituated during the 2 days in between the treatments. It seems more likely that the birds were still habituated to the curtain and that the effect found in the sparrowhawk treatment is due to an enhanced risk.

Because all birds were tested in the same order, time and treatment are confounded. Although time within each treatment (i.e., habituation) was taken into account, there could have been a general time effect over the whole experiment. This possibility would have been avoided if I had presented the treatments in alternating orders. However, during the acclimatization period of group Y, body mass was constant after an initial week of decline (van der Veen, unpublished data). Therefore, a general time effect on body mass seems unlikely.

Furthermore, morning and evening mass decreased significantly from the day before the sparrowhawk treatment to the first day of sparrowhawk treatment. This also indicates that the mass changes are probably due to the treatment and not to time per se.

Yellowhammers exposed to a sparrowhawk lost more mass after the exposures compared to those exposed to a moving curtain, but they also increased in mass faster between the exposures, and as a result they did not end up with a lower evening mass.

The yellowhammers in this experiment increased in mass mainly in the morning, little in the middle of the day, and again slightly at the end of the day, even in the control treatment. This is the expected trajectory under risk of predation with an unpredictable food source (McNamara et al., 1994). Yellowhammers in the field did not show such a pattern during midwinter; instead they were foraging at a constant level throughout the day (van der Veen, in press). Because the birds already showed a bimodal pattern in the curtain treatment, the pattern could only become more pronounced in response to increased predation risk. This might be too risky in terms of starvation risk and might therefore have been avoided by the birds. However, food was available ad libitum and was never removed from the cages; thus the risk of starvation by postponing feeding to the end of the day was probably extremely small. On the other hand, starvation risk might have increased due to the predator-induced feeding interruption at the end of the day, which made the risk of not gaining enough reserves at the end of the day larger.

It is difficult to translate results from this study to a natural predation situation. The birds in this study could not behave as they would normally under predation risk. Yellowhammers in the field always fly around for a short while when they are attacked. Then they usually fly to another feeding area, either immediately or after waiting in a nearby tree for a while (van der Veen, in press). This option was not possible for the yellowhammers in this study. Furthermore, if in the field the predator is as close as the predator was in this experiment, a bird would probably not be able to escape. However, performing such a study on captive birds is still worthwhile, because it gives detailed information on within-individual changes in body mass and behavior that is not possible to obtain in the field for a species like the yellowhammer.

In a study on greenfinches, where a flying sparrowhawk model was used to investigate the effect of predation risk on body mass, greenfinches waited on average 16 min before resuming feeding on the first day of exposure (Lilliendahl, "Predation risk and diurnal routines".

Table 1

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α indicates significance levels adjusted by sequential Bonferroni. * indicates significant difference.
In my experiment birds waited longer, maybe because the sparrowhawk did not fly away but just disappeared behind a curtain.

The question of how a bird perceives the cage can be interpreted in several ways. The bird might see it as a safe environment, because it is closed and no predator can get in. However, sparrowhawks can take birds from dense bushes by pulling them out by their talons (Newton, 1986), and the same could happen in a cage. Probably, the birds perceive the cage as a risky environment, without any protective cover and without the possibility to flee. Because the birds were forced to stay and the predator was so close, they might have interpreted this situation as much more risky than they normally perceive a predatory attack. But the birds did habituate to the predator. This is probably due to the fact that although the predator was nearby, it never attacked.

Other studies have shown a decrease in fat reserves in response to increased predation risk. For example, greenfinches (Carduelis chloris) decreased in body mass when exposed to a flying sparrowhawk model (Lillienhådl, 1997). Some studies have given indirect indications for the trade-off between starvation and predation. For example, Witter et al. (1994) showed that starlings (Sturnus vulgaris) carried higher fat reserves when able to feed closer to protective cover, which they interpret as lower predation risk. Gosler et al. (1995) showed a negative correlation between the body mass of great tits (Parus major) and the abundance of sparrowhawks, while Pravosudov and Grubb (1998) showed the opposite effect for tufted titmice (Baeolophus bicolor) in an experimental study. There is also another study on yellowhammers failing to show an adaptive decrease in body mass in response to increased predation risk (Lillienhådl, 1998).

Why then do yellowhammers respond differently to predation risk than greenfinches, starlings, and great tits? The experimental design, statistical power, and the artificial environment during the experiment might be the reason for the discrepancy between theoretical predictions and the observations. However, Rogers et al. (1994) suggested three types of winter fatteners: responders, who fatten as a response to proximate cues; predictors, who respond to ultimate cues; and responder-predictors, who use a combination of both strategies. For all three strategies evidence has been found in nature, and the strategy a bird uses depends in part on between-season variability and predictability of the food source (Witter and Cuthill, 1993; Rogers et al., 1994). Great tits seem to be responders, who react fast to changes in temperature (Bednekoff and Krebs, 1995; Bednekoff et al., 1994; Lillienhådl et al., 1996). Evans (1969) showed that fat reserves of yellowhammers were not correlated with the temperature on the day of capture, but were highly correlated with the average temperature on that day over a period of 20 years, which indicates that yellowhammers are predictors. Thus, yellowhammers do not seem to react to short-term changes in their environment, but adjust their mass to ultimate cues instead. If the yellowhammer is a predictor, this might explain the lack of adaptive weight decrease in response to the stuffed sparrowhawk model in this experiment. However, it seems unlikely that as strong an evolutionary force as predation risk would be ignored as a proximate cue by yellowhammers. Another explanation for the lack of response in this study might possibly be another type of cost of having fat reserves in this species.

Fat reserves have several costs, and birds can adjust to increased predation risk in several ways. By reducing their body mass, birds reduce the maintenance costs of having lower escape performance with large reserves (Kullberg et al., 1996; Metcalfe and Ure, 1995; Witter et al., 1994). However, this cost could not be shown in all studies of daily mass changes of birds (Kullberg, 1998, Veasey et al., 1998), and also not for yellowhammers (van der Veen and Lindström, unpublished data).

Another possibly important cost of fat reserves is increased time exposed to high predation risk, due to increased feeding time (McNamara and Houston, 1990) and decreased vigilance while feeding (Krause and Godin, 1996). Although yellowhammers in this experiment did not adaptively decrease their body mass nor adjust their daily routines in response to a sparrowhawk, they did decrease the time spent feeding under predation risk. However, because the rate of mass gain was significantly higher in the sparrowhawk treatment, the birds must have been more efficient in the sparrowhawk treatment, either while feeding or in the periods between feeding. This has been shown in other studies as well; for example, oyster-catchers (Haematopus ostralegus) under time stress increased their intake rate (Swennen et al., 1989). Birds could also save energy in the periods between feeding to be able to reduce the time spent foraging and reduce the time exposed to higher predation risk (Krause and Godin, 1996). Birds under time stress have been shown to reduce their activity to save energy and thus to gain an equal amount of mass with less time spent feeding (Bednekoff and Krebs, 1995; Meijer et al., 1996; Pravosudov and Grubb, 1997).

The lack of effect of body mass on escape performance in this species (van der Veen and Lindström, unpublished data), together with the lack of response in body mass to increased predation risk in this study, indicate that, for yellowhammers, carrying fat reserves might not be the most important cost of having fat reserves. Reducing the time spent feeding, through which they reduce the time exposed to predation risk, might be of greater importance for survival (see Götmark et al., 1997). However, a potential disadvantage of increasing intake rate is a reduction in vigilance. In terms of predation risk, the benefits of an increase in intake rate should be higher than the costs of a decrease in vigilance.

In this experiment group X and group Y differed in several variables. This might be due to seasonal differences between the test periods of the two groups. The first group was measured before mid-winter and the second group after mid-winter. This scheme was chosen to keep the difference in the natural daylight periods between the groups as small as possible. Because the coldest day is usually later in season than the shortest day, the period from the shortest day to mid-winter might not be the turning point of the seasonal processes, and therefore the two groups might have differed in mass. Although the birds were kept under constant daylight conditions since October, their endogenous photoperiodic rhythm might still have influenced their fat reserves. Another possibly important factor is that although birds could not see each other, they were able to hear each other, and this can result in synchronization of behavior (van der Veen, personal observation), which could minimize variance within a group and could have enhanced differences between the groups.

In summary, yellowhammers decreased in morning mass and evening mass in response to both a moving curtain and a sparrowhawk. However, the birds waited longer before resuming feeding and lost more weight after each exposure to a sparrowhawk. Against the predictions of theoretical models, these losses were regained, and yellowhammers increased in mass faster between the exposures in the sparrowhawk treatment than in the curtain treatment. At the same time, yellowhammers increased their intake rate in the sparrowhawk treatment. In that way they reduced, although not significantly, the time spent feeding under predation risk. A reduction in the time spent feeding decreases the overall risk of being taken by a predator. However, a higher intake rate may also decrease the time spent vigilant while eating, and this might increase predation risk. If predation risk is decreased more by the ben-
effects of reducing exposure time than it is increased by the costs of reducing vigilance, a reduction in exposure time might be an important survival strategy.

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