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Migratory fuelling in blackcaps (*Sylvia atricapilla*) under perceived risk of predation

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Abstract It has been argued that the body mass levels achieved by birds are determined by the trade-off between risks of starvation and predation. Birds have also been found to reduce body mass in response to an increased predation risk. During migration, the need of extra fuel for flights is obvious and crucial. In this study, migratory blackcaps (*Sylvia atricapilla*) were subject to an experimental stopover situation where the predation risk was manipulated by exposure to a stuffed predator. Blackcaps that perceived an imminent risk of predation increased their food intake and fuel deposition rate during the first period of stopover compared with a control group. The pattern of night activity indicates that birds that were exposed to the predator also chose to leave earlier than birds in the control group. Since there was no cover present at the stopover site, birds might have perceived the risk of predation as higher regardless of whether they were foraging or not. Under such circumstances it has been predicted that birds should increase their foraging activity. The findings in this study clearly indicate that birds are able to adjust their stopover behaviour to perceived predation risk.

Key words Predation risk · Fuel load · Migration · Blackcap · *Sylvia atricapilla*

Introduction

Birds normally are not able to forage whenever they want, and therefore energy often has to be stored and carried for future needs. Over night fasting and migratory flights are settings in which there is no energy gain. The body mass maintained and the rates of mass gain by birds have been viewed as the result of a trade-off between the risks of starvation and predation (see, for example, Lima 1986; Houston and McNamara 1993; Houston et al. 1993; Bednekoff and Houston 1994; McNamara et al. 1994; Weber et al., in press). The fact that birds are usually found to have body masses below their physiological capacity has been used to support the argument that an increased body mass entails costs (see, for example, Witter and Cuthill 1993). In theoretical calculations, mass-dependent effects on flight performance are obvious (Pennycuik 1985; Hedenström 1992), which predict that heavier birds should be less adept at escaping from predators. Recent experimental evidence demonstrates that individual birds' flight performance is impaired by mass loads (Witter et al. 1994; Metcalfe and Ure 1995; Kullberg et al. 1996). The predation risk due to an increased body mass may be an effect not only of impaired flight performance but also of increased exposure to predation during more intense foraging (for a review, see Witter and Cuthill 1993). Circumstantial evidence suggested that British great tits *Parus major* adjusted their mass to predation risk in the wild. The great tits were heavier during periods when sparrowhawks *Accipiter nisus* were absent due to pesticide poisoning (Gosler et al. 1995). It has also been shown in experiments that greenfinches *Carduelis chloris* adjust their body mass to a lower level in response to perceived predation risk (Lilliendahl 1997).

Seasonal migration between breeding and non-breeding areas is common in all groups of birds (e.g. Alerstam 1990). During these migratory flights, the supply of extra energy is crucial to the birds for making a successful migration (see, for example, Blem 1980).

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Subcutaneous fat deposits are used as fuel for flight, and these deposits normally have to be replenished at intermediate stopover sites. The conditions at stopover sites are probably in most cases unknown to the individual bird when it arrives and may vary in several unpredictable respects, for example food availability, competition and predation risk. Several studies show that birds are able to change behaviour in response to the situation of high energy demand during migration. These responses, when changing from a non-migratory to a migratory disposition, involve changing priorities between foraging and vigilance, switching from risk-averse to risk-prone foraging and resuming foraging sooner and handling food items much more quickly after seeing a predator (Metcalf and Furness 1984; Moore and Simm 1986; Moore 1995). Using an optimality approach, Alerstam and Lindström (1990) distinguished between time, energy and mortality minimisation as three different selective forces acting on migratory birds. They predicted that a bird maximising safety during migration should depart with a relatively small fuel load and that it should choose protective stopover sites with a lower deposition rate rather than sites with a high deposition rate but with a higher predation risk. It has been shown that migratory bramblings *Fringilla montifringilla* in southern Sweden choose feeding fields surrounded with protective cover (Lindström and Alerstam 1986) and when beech *Fagus sylvatica* set mast many bramblings appear to choose these more protective sites with a lower energy intake per unit time (Lindström 1990). Hence, migratory birds seem to respond adaptively to a variety of different situations during stopover. Weber et al. (in press) use a dynamic state-dependent model to analyse the effects of foraging intensity- and mass-dependent predation and time-dependent fitness effects on the rates of mass gain and departure loads of migrating birds that use discrete stopover sites. This model demonstrates that the response of migrating birds to predation risk can be expected to vary depending on how it acts on the individual bird during foraging and non-foraging episodes.

Detailed information on how small passerine birds behave, in terms of body mass increase and departure fuel load, at a stopover site with high predation risk are still lacking. Here we investigate the effect of perceived predation risk on the behaviour of blackcaps *Sylvia atricapilla* during a simulated stopover period in the laboratory.

Methods

The experiment was carried out at Tovetorp Zoological Research Station (58°56'N 17°08'E) about 90 km SW of Stockholm. Blackcaps were wild caught close to the station using song play back during night and early morning. At dawn mist nets were erected to trap birds attracted to the area. Only birds that fulfilled the following three criteria were used in the experiment; (1) 1st-year males, (2) completed post-juvenile moult, and (3) no or only small

visible fat stores on capture. Such individuals were quickly transferred to the laboratory where six birds were housed in three different standard laboratory rooms, situated in the same corridor. The birds were kept in individual cages (45 × 45 × 70 cm) arranged in a circle within the rooms, and separated from each other with a low wall giving no opportunity for the experimental birds to see each other (Fig. 1).

In two of the rooms a rotor with two arms was suspended from the ceiling, while the third room had no such construction and acted as a control. The movement of the arms over the cages was controlled from outside the room. The arms passed over each cage in an almost identical manner. In one room the arms were fitted with two plastic bottles (this treatment is called disturbance) while in the other, one of the plastic bottles was replaced with a stuffed sparrowhawk in flight position (Fig. 1). The rotating arms were moved one full circle at six randomly drawn occasions every day (between 0600 and 1600 hours), starting on the 1st day (the day of trapping). It took about 4 s for the arms to complete one full circle. While the arms were not moving, one of the plastic bottles in one of the rooms and the sparrowhawk in the other were hidden within a cardboard box. All cages were equipped with activity registration that counted when the birds were flying to and from the sitting perches. Technical problems gave missing values for some cages on a few occasions.

All birds were given 30 g of mealworms *Tenebrio molitor* daily and water ad libitum. The light regime in the experimental rooms followed the normal outdoor regime situation. Individual body masses were recorded between 1630 and 1700 hours every day by taking each bird out of the cage. Simultaneously the mealworm bowls were changed and the amount of food eaten measured. All weightings were made on a Precisa 200A balance with an accuracy of 0.01 g. The experiment was carried out during 8 days and included a total of 36 individuals, 12 in each treatment. It was divided into two sessions – the first group of birds was trapped between 4 September and 7 September 1995 while the other group was trapped between 19 September and 25 September 1995. The main interest of this experiment was to focus on the behaviour of individual birds during the first part of the stopover situation. Within the different treatments no difference was observed between the two experimental occasions during the first 4 days in body mass increase, amount of food eaten, day activity or night activity (*t*-tests, *df* = 10, *P* > 0.10 in all cases). Data from the two sessions

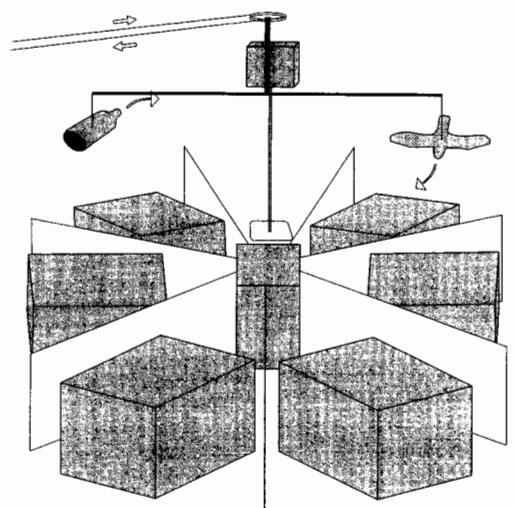


Fig. 1 The experimental setup with the arrangement of the six cages separated from each other with a wall. Shown is also the rotor with two arms suspended from the ceiling, used in two of the rooms. The movement was controlled from outside the room, and between the rotations one plastic bottle in one of the rooms and the sparrowhawk in the other were hidden in the cardboard box in the background

have therefore been pooled in the following analyses. The different treatments show inhomogeneous variances in several of the variables included (Cochran's test; Dixon and Massey 1969) and comparisons between the three treatments have consequently been performed with the Kruskal-Wallis ANOVA by ranks.

Individual fuel loads were normalised by scaling lean body masses by size, as estimated for blackcaps by Ellegren and Fransson (1992).

Results

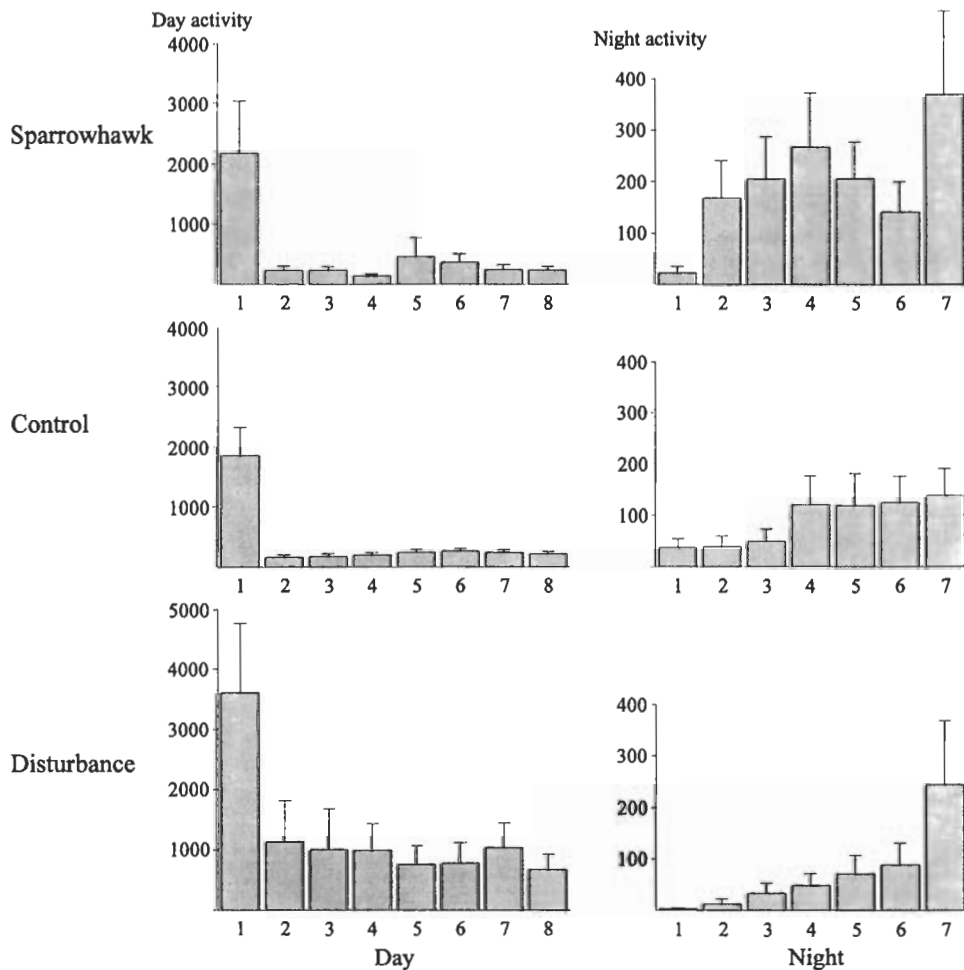
All birds quickly became acclimatised to the experimental situation and the daily activity pattern decreased rapidly to a significantly lower level in all groups after the first day (Fig. 2). The average amount of activity during the first day varied, but still no significant difference between the treatments was found ($H = 1.69$, $n = 34$, $P = 0.43$). The total activity throughout the entire period was, however, significantly higher in the disturbance group ($H = 6.54$, $n = 33$, $P = 0.04$). The overall activity level in the sparrowhawk group was more like the activity pattern in the control group (Fig. 2). The response of the birds depended on which stimulus they were exposed to. Birds experiencing the

moving sparrowhawk became motionless ("freezing") whereas birds exposed to moving bottles were very agitated. This could partly explain the differences in the recorded activity patterns (see Fig. 2). During the experiment the birds were most often silent and alarm/contact calls were heard only rarely.

There were large individual variations in the activity pattern during night. The average activity in the sparrowhawk group increased however significantly between the 1st and the 2nd nights (Wilcoxon matched pairs test, $z = 2.44$, $P = 0.01$, Fig. 2). The activity patterns during this 2nd night were significantly different between the treatments ($H = 10.16$, $n = 36$, $P < 0.01$). In the other two treatments the average activity increased more slowly but significantly during the experiment (disturbance $r = 0.34$, $P < 0.01$, $n = 84$ and control $r = 0.27$, $P < 0.05$, $n = 84$; Fig. 2).

The average food intake during the first 2 days differed significantly between the treatments. The food intake was higher in the sparrowhawk group (Fig. 3). The average increase in body mass during the two first days differed accordingly between treatments ($H = 9.5$, $n = 36$, $P < 0.01$, Fig. 4.), while no significant difference was found during the following two days ($H = 4.96$, $n = 36$, $P = 0.08$). The highest propor-

Fig. 2 Average (+SE) day and night activity measurements in blackcaps subject to different treatments during the experiment. Each treatment included 12 individuals



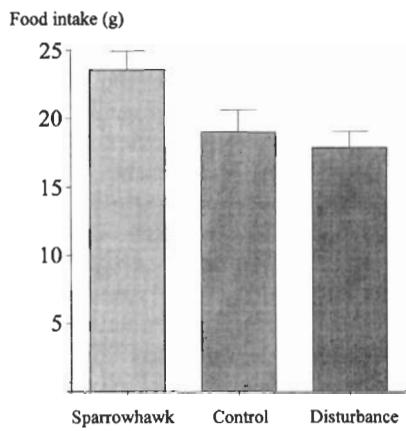
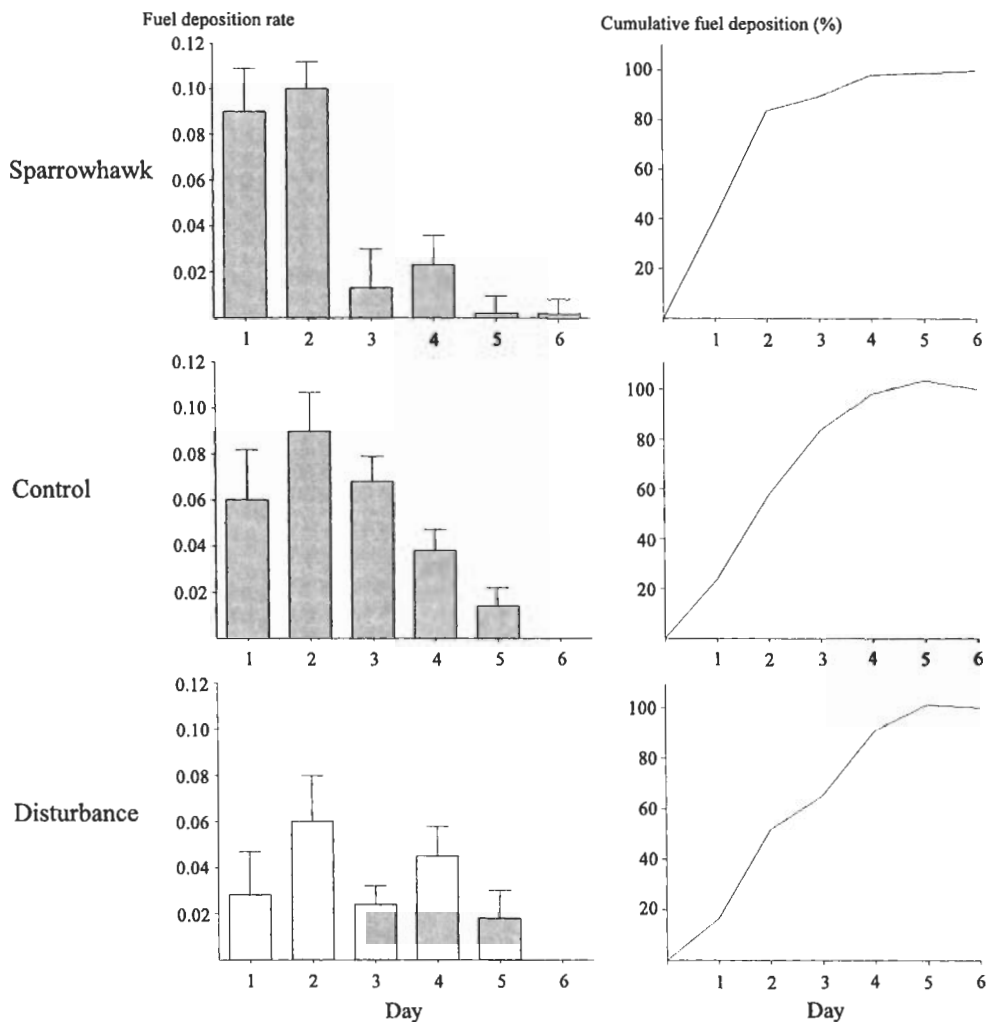


Fig. 3 Average food intake (+SE) in blackcaps subject to different treatments during the first 2 days of experiment ($H = 8.90$, $n = 36$, $P = 0.01$)

tional increase of the average daily body mass, just above 10% of lean body mass in the sparrowhawk group, was in all groups observed on the second day. In the sparrowhawk group, the increase on the first 2 days

Fig. 4 Average (+SE) daily fuel deposition rate (in relation to lean body mass) and the average cumulative fuel deposition in relation to the total fuel deposition observed during the experiment in blackcaps subject to different treatments. Each treatment included 12 individuals



constituted 84% of the total body mass increase found during the experiment. Corresponding figures for the control and the disturbance groups were 58% and 51%, respectively (Fig. 4). In the sparrowhawk group the body mass increase levelled off significantly between the second and the third day (Wilcoxon matched pairs test, $z = 3.06$, $P = 0.002$), which coincide with the time when night activity increased in this group. The daily body mass increase in the disturbance group was more irregular during the experiment (Fig. 4). Despite these differences the average fuel load in relation to lean body mass at the end of the experiment (sparrowhawk $34.9\% \pm 0.03$ SE, control $34.7\% \pm 0.02$ SE and disturbance 28.7 ± 0.03 SE) did not differ significantly between the treatments ($H = 5.06$, $n = 36$, $P = 0.08$).

Discussion

The blackcaps initially increased their food intake and fuel deposition rate under a perceived risk of predation. Field data on great tits in Britain (Gosler et al. 1995) as

well as in an experimental study of greenfinches (Lilliendahl 1997) show that birds under a perceived predation risk adjust their body mass to a lower level, which suggests that an increased body mass entails costs in terms of an increased predation risk (cf. Witter and Cuthill 1993). The objective for birds acquiring fuel for migration is, however, quite different from stationary birds balancing their ordinary energy requirements. Migrants need to attain a certain amount of fuel before departing on a migratory flight.

We first address the question of departure loads. The birds under perceived risk of predation increased their night activity significantly after 2 days. It has previously been argued that migratory restlessness (*Zugunruhe*) is an indicator of the birds' flight activity (cf. Gwinner 1996). Based on these results we interpret their fuel load at that point in time as their departure load. In the control group the pattern is less clear, but a corresponding increase in night activity after 2 days was absent. Night activity increased more slowly over time. This indicates that the blackcaps under perceived risk of predation probably chose to depart earlier and with a slightly lower departure load than the control group. The average fuel load (in relation to lean mass) was 31.5% after 2 days in the sparrowhawk group compared to 37.4% in the control group when the increase levelled off after 5 days. The pattern of higher daytime activity and slowly increasing body mass observed in the group of blackcaps exposed only to plastic bottles indicates that they were disturbed and did not show a normal behaviour. Still, it is important to keep in mind that the difference between the two treatments was confined to the one plastic bottle was replaced by the stuffed sparrowhawk. It could be argued that they were reacting to a novel moving object rather than to a recognised predator, but the sustained and pronounced behavioural response (i.e. freezing, rather than agitation) suggests that they were not simply responding to a novel disturbance.

Furthermore, there is the question of why the control group did not feed and deposit fuel at the maximum rate. It is reasonable to assume that the birds in this group – even though they experienced no actual predators – reflect an evolved behaviour where some predation risk is always expected. Thus, the pattern observed in the control group suggests that feeding at a high rate has some cost and that the birds adjust their feeding behaviour accordingly. Several theoretical studies have analysed the variables that could influence predation risk, such as foraging intensity and body mass, and the consequences for behaviour under changed circumstances (Houston et al. 1993; McNamara and Houston 1994). When interpreting the behaviour of the blackcaps in the experiment it is first of all important to identify the selective pressures under which they need to complete their migratory journeys. Alerstam and Lindström (1990) argue that time of arrival at the migratory destination is likely to be of major importance in shaping migratory strategies. Weber et al. (in press) demonstrate that if these benefits of early arrival only decrease slowly

with time and if foraging is very costly in terms of predation risk, then birds can be expected to forage below maximum intensity. It could well be the case that the benefits of early arrival change more slowly with time in autumn – the time when this experiment was carried out – than in spring. This could explain why the control birds fed at a rate below maximum.

How a bird on stopover responds to changes in perceived predation risk also depends on which aspect of predation risk that is affected. The behaviour of the birds is consistent with a formalisation of predation risk used by McNamara and Houston (1994) and Weber et al. (in press), who model predation risk m as a function of foraging effort u in the following way:

$$m = m_0 + ku^a, \quad a > 1,$$

where m_0 is a background mortality independent of behaviour and ku^a is the risk associated with increased time u invested in feeding rather than vigilance during foraging (Houston and McNamara 1993). Weber et al. (in press) show that if the constant k is increased, birds should decrease their foraging intensity: it is optimal to stay longer at a more dangerous site feeding with less effort and being more vigilant compared to feeding with higher intensity being less vigilant and incurring accelerating mortality costs. If, however, the background mortality m_0 is increased, birds should increase their foraging effort to leave a site earlier. In this experiment birds had no effective cover to hide in when not foraging. Therefore the birds might have interpreted the presence of predators as a high background mortality risk acting both during foraging and non-foraging periods. Under such circumstances there is nothing to be gained from refraining from foraging. The above conclusions were derived under the assumption that the birds need to achieve a fixed level of fuel reserves. The general patterns of changes in foraging activity will, however, be valid also if the birds have some scope to adjust their departure loads. It would be of interest to conduct a study where effective cover is present, because under such circumstances perceived predation risk might very well result in a quite different behavioural response.

Several studies have shown that birds arriving to a new stopover site often have a time delay before their body mass gain starts (e.g. Alerstam and Lindström 1990). Both behavioural and physiological mechanisms have been suggested to explain this settlement cost (cf. Rappole and Warner 1976; Klaassen and Biebach 1994). The lower average increase observed during the first day compared to the second day may give a hint to that this also affected the blackcaps in this experiment. The novel situation met by the birds in this experiment might very well correspond to the situation when birds arrive at a new and unknown stopover site. Another interesting fact is that the birds in the control group after the second day decrease their fuel deposition rate continuously during the stopover period. Weber et al. (in press) predict such a pattern, if mass-dependent predation acts in addition to intensity-dependent predation and both sources interact

n a multiplicative way. With such a combination of mortality factors it is not feasible to derive analytic results on how foraging effort should change with changes in parameters; but as long as mortality increases in an accelerating way with effort the conclusions derived above will be robust.

This study gives clear support to the idea that the time invested in foraging can have mortality costs and that birds are able to adjust stopover behaviour to perceived risks.

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