Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*)

CECILIA KULLBERG[1], THORD FRANSSON[1,2] AND SVEN JAKOBSSON[1]

[1] *Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden*
[2] *Swedish Museum of Natural History, Bird Ringing Centre, Box 50 007, S-104 05 Stockholm, Sweden*

SUMMARY

When birds are attacked by predators, take-off ability is crucial for the chance of survival. Recently, theoretical studies have predicted that predation risk in terms of reduced flight performance increases with body mass. However, empirical data are scarce. Because migratory birds sometimes double their body mass, mass dependent predation risk may be especially important during migratory fattening. Here we present the first study of take-off ability in relation to migratory fat load. Alarmed take-off flights of caged blackcaps (*Sylvia atricapilla*) induced by a simulated predator attack were analysed in terms of velocity and angle of ascent. Fat loads (percentage of fat-free body mass) of the birds ranged from 1% to 59%. An increase in fat load was found to influence both velocity and angle of ascent. From our results we calculated that blackcaps carrying 60% fat loads would have 32% lower angle of ascent and 17% lower velocity than blackcaps carrying no fat load. Even though the effect of fat load on the blackcaps was less than indicated in previous experimental studies of other species, our results suggest that the large fat loads needed for migration probably place them at increased risk of predation.

1. INTRODUCTION

The ability to store fat is crucial for many different species of bird. Small wintering birds rely on fat reserves accumulated during the day to survive during the cold nights or when food is not available (Lehikoinen 1987; Haftorn 1989; McNamara & Houston 1990). McNamara & Houston (1990) suggest that the risk of starvation decreases approximately exponentially with increasing fat reserves. However, large fat loads have costs as well as benefits (for a review, see Witter & Cuthill 1993) and the survival value of fat reserves is governed by a trade-off between starvation and predation risks (see, for example, Lima 1986; McNamara & Houston 1990). The use of fat loads also enables migrating birds to travel long distances to their wintering grounds. These migratory fat loads increase the body mass considerably, and fat loads of 20–30% of fat-free body mass are common (c.f. Alerstam & Lindström 1990). When passerine birds are about to cross wide barriers, they can almost double their mass by means of fat storage (see, for example, Nisbet *et al.* 1963; Fry *et al.* 1970; Blem 1980).

Recently, theoretical studies have focused on the potential cost of fat load in terms of an increased predation risk in birds. It has been suggested that birds with a heavy fat load should be less adept at escaping from predator attacks than lighter birds because of a reduced flight performance, such as take-off ability, manoeuvrability and climb rates (see, for example, McNamara & Houston 1990; Hedenström 1992; Witter & Cuthill 1993). Hedenström & Alerstam

(1992) observed reduced climb rates for shorebirds with very large fat reserves suggesting that the birds face a trade-off between climb rates and fuel loads. When, for example, a reptile or a mammalian predator launches an attack on a perching bird, a quick take-off is of utmost importance. Most predatory birds rely on a surprise attack and the success rate is much reduced if the prey get fully airborne (for examples, see Rudebeck 1950; Kenward 1978; Newton 1986; Lindström 1989; Cresswell 1993). Thus, if for example a heavy fat load reduce the take-off ability of a bird during an initial strike by a predator, this will impose an increased risk of being caught. Manoeuvrability or agility is important when a bird is chased by a raptor but it appears as if the hunting success of birds of prey is low once the prey is fully airborne (Page & Whittacre 1975; Temeles 1985; Cresswell 1993). However, a high fat load may well be costly if it affects the prey birds capacity to out-manoeuvre a chasing raptor (Hedenström 1992; Witter & Cuthill 1993). There are some studies showing indirect evidence for a trade-off between predation risk and fat loads in birds. In England, a population of great tits (*Parus major*) became markedly heavier over a period of years when sparrowhawks (*Accipiter nisus*) were absent because of pesticide poisoning, and declined in mass when the hawks re-established (Gosler *et al.* 1995). Thus, great tits seems to adjust fat loads to the perceived predation risk. A more direct approach would be to investigate how flight performance of individual birds is affected by variation in fat load. Ideally, birds with varying fat load should be observed in the wild when attacked by predators. However, such an approach has almost insurmountable difficulties as predatory events are

e-mail: Cecilia.Kullberg@zoologi.su.se

extremely hard to observe and the use of trained predators poses ethical problems (Huntingford 1984). Furthermore, the behaviour of individual birds is likely to be affected by their fat load, for example, fat birds compensate by sticking closer to cover (Witter *et al.* 1994) and thus there is a risk that birds caught by a predator are not representative (McNamara & Houston 1987; Witter & Cuthill 1993).

The only experiments done to investigate predation risk in relation to mass-dependent flight ability are two studies on starlings (*Sturnus vulgaris*) (Witter *et al.* 1994; Lee *et al.* 1996) and a study on zebra finches (*Taeniophygia guttata*) (Metcalfe & Ure 1995). Witter *et al.* (1994) manipulated body mass of starlings by adding weights on the birds. Starlings with manipulated higher body mass were less manoeuvrable, had lower rate of ascent but flew at the same velocity as non-experimental birds. As pointed out by Metcalfe & Ure (1995) there are several problems arising when adding weights on birds. It may, for example, be difficult to control for a shift in the centre of gravity because of the unnatural distribution of the added mass. Furthermore, by adding fixed weights, information is lost on the natural relation between mass and flight performance. The study by Metcalfe & Ure (1995) is the first study on the correlation between intra-individual diurnal oscillation in body mass and flight performance. They used a group of eight caged zebra finches and video recorded their take-off during different times of the day. On average the birds increased in weight by 6.8% over the day. Individual zebra finches were much faster and manoeuvred around obstacles more quickly in dawn than in dusk. The authors suggest that until now theoretical estimated values of mass dependent predation risk have underestimated the effect of increased mass on flight performance. Here we present the first study of flight ability in relation to a migratory fat load. Individually caged blackcaps (*Sylvia atricapilla*), with fat loads ranging between 1% and 59% of fat-free body mass, were subject to a simulated predator attack, and the alarmed take-off flight was analysed in terms of velocity and angle of ascent.

2. MATERIALS AND METHODS

Migrant juvenile male blackcaps (*Sylvia atricapilla*) were trapped by mist nets during September and October 1995 at Tovetorp Zoological Research Station, in south-east Sweden (58°56′N 17°08′E). We played blackcap song at night to entice migrating birds to the net area. Trapping started just before sun rise and lasted for about 4 h. To avoid effects of age and sex only juvenile males were used in the study. Furthermore, we only used birds that had completed their post-juvenile moult. The birds were housed in separate indoor cages (90 cm × 60 cm × 95 cm high). The cages were equipped with a perch in one upper corner and a perch at the feeding tray on the floor at the other side of the cage. The birds were fed with mealworms (*Tenebrio molitor*) and water *ad libitum*. Body mass of the birds were recorded on a Precisa 200A scale with an accuracy of 0.01 g. Birds were weighed every second or third day to check their body mass. All of the blackcaps started to gain body mass soon after they were caged. To get information from a wide range of different fat loads, birds were tested at different stages of the fat
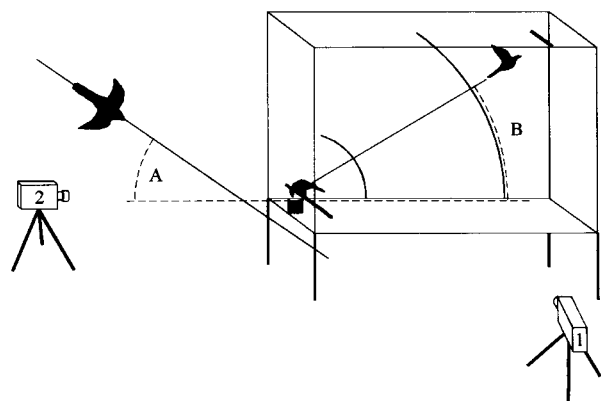

Figure 1. Experimental set-up. The merlin came gliding in at an angle of 34 degrees (A). The take-off was recorded by two video cameras (1 and 2). Two measurements of the take-off were taken: angle of ascent (B) and velocity. To calculate velocity the distance (45 cm) between two curved lines was used.

accumulation. The birds were kept in captivity for an average of 5 d (ranging from 2 to 12 d) before the experiment. All experiments were made during the afternoon. Each bird was only used once in the experimental set up (*n* = 28) and fat loads of the individuals ranged between 1% and 59% of their fat-free body mass. The experiment was done in a special room with a one-way window along one wall to permit observation from outside. In the experimental room there was a cage identical to the holding cages placed on a low table. A cardboard model of a flying merlin (*Falco columbarius*) was sent down along a fishing line in an angle of 34 degrees towards the experimental cage. The model appeared from behind a blind in the upper corner of the room and disappeared under the cage (see figure 1). One blackcap at a time was taken from their holding cage for the experiment in the experimental room. The model merlin was released in a standardized way when the blackcap had just taken a mealworm from the feeding tray and was sitting on the perch facing the side of the room where the merlin would appear. The merlin was visible for about 1 s and 'attacked' with a velocity of 20 km h⁻¹. The take-off of the blackcap was recorded by two video cameras. A Super-VHS camera was placed perpendicular to the line of the take-off (camera 1 in figure 1) and a standard Video 8 camera was placed along the line of the take-off to record side movements by the bird (camera 2 in figure 1). By analysing the video from camera 1 we measured flying velocity and angle of ascent of each bird. Velocity of each bird was recorded between two lines drawn on the back of the cage. By using curved lines with constant distance to the perch at the feeding tray (15 cm and 60 cm respectively) the birds had covered the same distance (45 cm) when velocity was measured irrespective of their flight angle. Flying velocity was calculated by using the number of frames (estimated to the nearest 1/4 frame) on the video between the two lines. Because the flight trajectory may diverge from the distance of 45 cm between the two lines, depending on the birds movements perpendicular to the camera (this deviation is impossible to observe on the video from camera 1), we made corrections by analysing each bird's side movements on the video from camera 2. The trajectory was then corrected by adding 0% (no deviation), 1.2% (small deviation) or 6.2% (large deviation) to the 45 cm distance depending on how much each bird deviated from a straight line. As one frame covered 0.02 s, the velocity (m s⁻¹) was calculated as:

velocity = corrected distance/no. of frames × 0.02

Angle of ascent of each bird was recorded by measuring the angle from the perch at the feeding tray to the point where each bird crossed the second line at 60 cm distance (figure 1).

Body mass and wing length of the birds were measured directly after each experiment. To estimate fat load of each bird we used estimations on size-specific fat-free body mass related to wing length for blackcaps calculated by Ellegren & Fransson (1992). These estimations were based on relations between body mass and visual fat score for birds of different sizes, and the fat-free body mass was found to increase with 0.35 grammes per millimetre wing length. In our material, where wing length varied between 73 mm and 78 mm, the estimated fat-free body mass ranged between 14.9 g and 16.7 g. Fat load (%) was thus estimated according to:

fat load (% of fat-free body mass) = (total body mass
– size-specific fat-free body mass/size-specific fat-free
body mass) × 100

Statistical calculations were made using STATISTICA for Windows 4.2, Statsoft Inc.

3. RESULTS

All blackcaps reacted to the 'attacking' merlin as soon as it came into sight by flying up towards the opposite upper side of the cage. All birds landed on the cage bars; none used the upper perch in the cage. Blackcaps showed strong behavioural responses after completing the escape flights. Some froze for several minutes whereas others raised their head feathers and emitted alarm calls. Fat load was the single most important factor affecting both take-off angle and velocity (multiple regression with take-off angle as dependent variable, independent variables are: fat load: $b = -0.25$, $p = 0.02$; wing length: $b = 1.85$, $p = 0.11$; number of days in captivity: $b = -0.19$, $p = 0.74$; multiple regression with velocity as dependent variable, independent variables are: fat load: $b = -0.01$, $p = 0.03$; wing length: $b = -0.03$, $p = 0.35$; number of days in captivity: $b = -0.02$, $p = 0.24$). Birds carrying a large fat reserve faced a reduced take-off ability compared with lighter birds (figures 2 and 3). The measured velocities of the take-off ranged from 1.8 m s^{-1} to 2.7 m s^{-1}, thus, the slowest bird covered the measured distance of 45 cm in 0.25 s whereas the fastest made it in 0.17 s. The angle of ascent varied
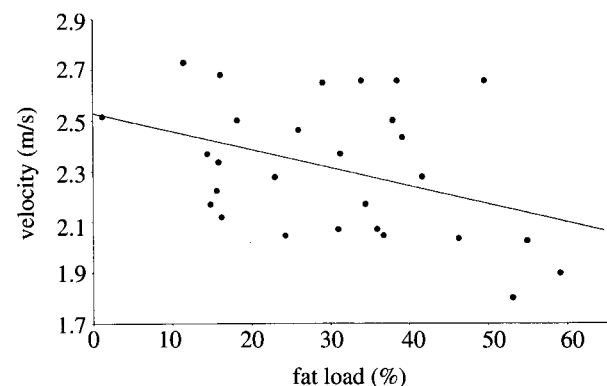
Figure 2. Take-off velocity (m s^{-1}) in relation to fat load (% of fat-free body mass); $r^2 = 0.16$, $b = -0.007$, $n = 28$, $p = 0.04$.
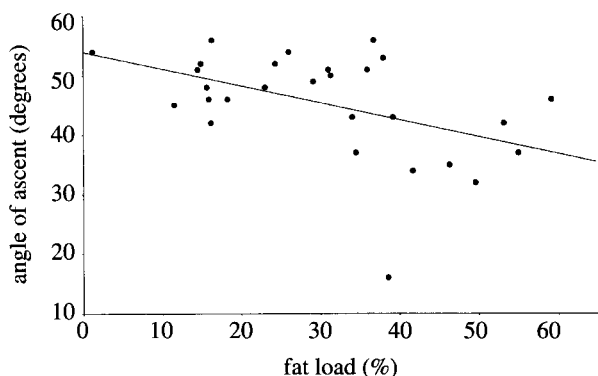
Figure 3. Angle of ascent (degrees) in relation to fat load (% of fat-free body mass); $r^2 = 0.22$, $b = -0.28$, $n = 28$, $p = 0.01$.
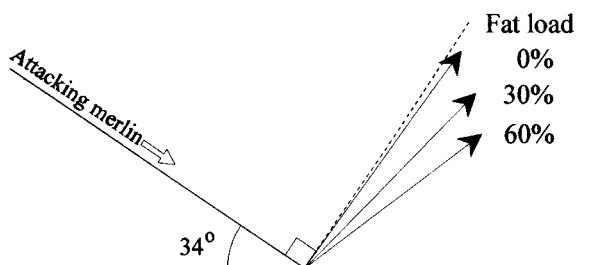
Figure 4. Angle of ascent for birds with 0%, 30% and 60% fat load according to the relation found. The length of the arrows represents the distance covered during a given time span according to the relation found between fat load and velocity. The broken line indicates an angle perpendicular to the predator's line of attack (i.e. ascent at 56 degrees).

from 16 degrees to 56 degrees, where 56 degrees represents a right angle to the merlin's attack line. According to the relations found (figures 2 and 3), increasing fat load from 0% to 60% will reduce the angle of ascent by 32% and the flight velocity by 17% in blackcaps (figure 4). When analysing the effect of fat load on flight ability, a nonlinear method of least square did not give a better fit than the linear model (velocity: $r^2 = 0.16$; angle of ascent: $r^2 = 0.22$).

4. DISCUSSION

Many theoretical papers have discussed the potential importance of mass-dependent predation risk because of reduced flight ability (Howland 1974; Lima 1986; McNamara & Houston 1990; Hedenström 1992; Houston & McNamara 1993; Houston *et al.* 1993; Witter & Cuthill 1993; Bednekoff & Houston 1994; McNamara *et al.* 1994), but empirical evidence of mass dependent effects has been scarce until recently. As migratory birds often carry large fat loads, a mass dependent effect on flight performance may be especially important for migratory birds. Our results show that migratory blackcaps with larger fat loads flew more slowly and at a lower angle of ascent when 'attacked' by a model predator.

Metcalfe & Ure (1995) studied the diurnal variation in body mass and its influence on flight performance in eight zebra finches. Zebra finches were on average 6.8% heavier at dusk than at dawn and flight velocity

of individual birds decreased from dawn to dusk with 30%. They concluded that the relation between body mass and flight ability might be considerably steeper than usually assumed. The same increase in fat load in blackcaps, according to our results, would reduce flight velocity with only 2% and angle of ascent with 4%. The results from the zebra finch study are, however, mainly based on normal take-off without disturbance and only a few measurements were made on alarmed take-off. It is reasonable to suggest that a bird performing a normal take-off will make a trade-off between flight speed and energy expenditure and thus fly slower when heavier, to reduce the energy costs (Pennycuick 1989). However, when attacked by a predator the bird should use all available energy to minimize the risk of being killed (c.f. Hedenström & Alerstam 1995). Thus, when estimating mass-dependent take-off ability it is important to make sure that the bird fly with maximum speed. The zebra finch study indicates that birds in normal take-off do not fly with maximum velocity (Metcalfe & Ure 1995). Another reason for the strong effect of fat load on flight velocity in the study by Metcalfe & Ure could be the fact that they forced the birds to fly up rather than allowing them to fly across, all take-offs with a lower angle than 45 degrees were excluded from analyses. If we had forced our blackcaps to fly in a steep angle the effect of fat load on velocity is likely to have been enhanced. Furthermore, the large differences in mass-dependent take-off ability between the two investigations may be explained by differences between the species in terms of wing shape and wing area, and thus wing load (body mass divided by wing area) causing different effects on flight ability. Natural selection may operate on different life-history traits in a migratory species compared with a non-migratory tropical species like the zebra finch. Perhaps, selection pressure has operated more heavily on migratory birds to cope with heavy body mass. It is possible that blackcaps, along with fat, also store some non-fat components (mainly muscle protein) which might improve flight ability. Such a muscle hypertrophy has been shown in waders during migration, but whether it also occurs among passerine migrants is not clear (for a review, see Lindström & Piersma 1993).

The diminishing return of an increased fat load on the potential flight range has been proposed as an important cue for how a migratory bird should adjust its fat load in different situations (Alerstam & Lindström 1990). When fat loads were moderate, flight ability of our blackcaps were affected surprisingly little. However, when fat load exceeded 40% of the fat-free body mass, take-off ability was affected heavily, suggesting that migratory birds, accumulating large fat loads, also may face a reduction in the ability to escape from a predator. This may contribute to the explanation that fat loads of migratory passerine birds exceeding 50% mainly are observed when birds are about to cross wide barriers like the Sahara desert (see, for example, Fry *et al.* 1970; Finlayson 1981; Bairlein 1991) and thus are forced to carry this heavy load. Even though the strongest effect of fat load on flight ability in our study seemed to be on the heaviest birds,

a nonlinear model did not give a better fit than the linear regression. However, to investigate if a threshold of the effect of fat load on take-off ability exists, further studies with larger samples of heavier birds should be done.

A small bird perched close to the ground can try to escape an attacking raptor either by flying at maximum horizontal speed or by out-climbing the predator. As a low angle of take-off allows the most rapid acceleration, birds face a trade-off between a steep climb and a high horizontal speed (Witter & Cuthill 1993). As Lima has pointed out (1993) the numerous anti-predator escape tactics in birds often reflects differences in the bird's physical environment. One possibility for a bird to keep predation risk low is to choose sites where protective cover is available and possible to reach in case of a predator attack (c.f. Lima 1993; Witter & Cutthill 1993). Thus, when a bird escapes a predator, the outcome of the trade-off between velocity and angle of ascent is probably dependent on the availability and location of cover. Furthermore, in one of the experiments of mass-dependent predation risk by Witter *et al.* (1994), starlings stored larger amounts of fat when protective cover was available than when it was absent, suggesting that the perceived predation risk influences the amount of stored fat. In their study of mass dependent flight ability in starlings, Witter *et al.* (1994) provided cover in one half of the aviary whereas in our experiment, cover was absent. Starlings with manipulated heavy weights (about 10% of the fat-free body mass of starlings) seemed to prefer high velocity at the expense of rate of ascent. However, in our study, where fat loads ranged up to 59% of fat-free body mass, both velocity and angle of ascent were affected by fat load. Thus, it is possible that very heavy body masses have to be investigated to be able to discern any effects of body mass on flight velocity.

Disregarding velocity, one way of maximizing the distance to the predator could be to take-off in a right angle to the predators attack flight. This was the case for the lightest birds in our experiment, whereas birds with heavier fat loads flew in larger angles to the predators attack trajectory (see figure 4). Whether this is a strategy by the lightest birds or mere coincident needs further study.

The results in this study support earlier theoretical studies suggesting that body mass in birds may affect predation risk because of reduced flight performance. However, we found that the effect of body mass on take-off ability was much less than previously documented for zebra finches (Metcalfe & Ure 1995). Our results, together with the result previously published on flight performance in relation to fat load in starlings (Witter *et al.* 1994), indicate that an increased fat load has a stronger effect on angle of ascent compared with flight velocity. We conclude that blackcaps appear to be well adapted to quick take-offs, but that large migratory fat deposits may incur an increased risk of predation.

REFERENCES