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Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load

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Abstract Recent studies have shown that large fuel loads in small birds impair flying ability. This is the first study to show how migratory fuel load affects flying ability, such as velocity and height gained at take-off in a predator escape situation, in a medium-distance migrant, and whether they adjust their take-off according to predator attack angle. First-year robins (*Erithacus rubecula*) were subjected to simulated attacks from a model merlin (*Falco columbarius*), and take-off velocity and angle were analysed. Robins with a wing load of 0.19 g cm^{-2} took off at a 39% lower angle than robins with a wing load of 0.13 g cm^{-2}, while velocity remained unaffected. The robins did not adjust their angle of ascent in accordance with the predator's angle of attack. Since many predators rely on surprise attacks, a difference in flight ability due to varying fuel loads found in migrating robins can be important for birds' chances of survival when actually attacked.

Key words *Erithacus rubecula* · Predation risk · Take-off ability · Wing load · Fuel load

Introduction

In certain situations during the year, birds become heavy because of energy storage (Alerstam 1990). Although there are many advantages to storing energy – for example it has been suggested that starvation probability decreases exponentially with increasing fat reserves (McNamara and Houston 1990) – being heavy entails costs. Fat storage is the most common reason for body mass changes, but bird bodies can change in many other reversible ways, by, for example, increasing or decreasing muscle mass and various internal organ structures (Piersma and Lindström 1997). A heavier body (e.g. fat, artificial weights on the back, prey in the beak) reduces flight ability in birds according to simple physical laws (Pennycuick 1989; Alerstam and Lindström 1990). Indications of the cost of an increased body mass come from various studies showing that birds actively regulate their fat storage at levels that are neither at physiological nor environmental maxima (Witter and Cuthill 1993). Both field studies and experimental studies indicate that birds may adjust body mass in response to an enlarged predation risk (Witter et al. 1994; Gosler et al. 1995; Fransson and Weber 1997; Lilliendahl 1997; Adriaensen et al. 1998).

Although several theoretical studies have discussed an increased predation risk due to increased body mass in birds, with respect to both migratory fuel load and daily fat storage in wintering birds (Howland 1974; Lima 1986; McNamara and Houston 1990; Hedenström 1992; Houston and McNamara 1993; Houston et al. 1993; Bednekoff and Houston 1994a, 1994b; McNamara et al. 1994; Bednekoff 1996), empirical studies of the direct effect of an increased body mass on flight performance are scarce. Witter et al. (1994) showed reduced flight performance in alarmed starlings (*Sturnus vulgaris*) carrying artificially added weights of about 10% of the birds' body mass. However, in studies of escape flights in willow tits (*Parus montanus*) (Kullberg 1998) and great tits (*P. major*) (Kullberg et al. 1998), no measurable effect of daily body mass increase (8%) on take-off ability could be shown, suggesting that the relatively small energy reserves accumulated during a day in wintering tits do not increase predation risk as a consequence of reduced take-off ability (see also Veasey et al. 1998). Compared to wintering tits, migratory birds store extensive amounts of fuel, sometimes exceeding 100% of lean body mass (Fry et al. 1970). In an empirical study on take-off ability in migratory blackcaps (*Sylvia atricapilla*), Kullberg et al. (1996) found that take-off ability

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was impaired by large fuel loads. Blackcaps carrying an energy reserve of 60% of lean body mass had a 32% lower angle of ascent and a 17% lower velocity than birds carrying no fuel load (Kullberg et al. 1996). This reduced flight skill may play an important role in an escape situation, where a heavily loaded bird might be at a disadvantage and fall victim more easily to a predator attack. The initial stage of take-off might also be very important since most predators on small birds rely on surprise attacks, where the survival of the bird might depend on very small differences in take-off ability (cf. Rudebeck 1950; Cresswell 1993, 1996).

When taking off maximally, a bird faces a trade-off between a steep take-off angle and a high horizontal speed since a low angle permits the most rapid acceleration (Witter and Cuthill 1993). There is reason to believe that the optimal strategy with respect to this trade-off depends on the attack strategy of the predator, proximity to cover and presence of conspecifics (Witter and Cuthill 1993). In a study of escape strategy in great tits, Kullberg et al. (1998) showed that great tits adjusted their take-off angle according to the predator's angle of attack, which emphasises the importance of flexibility in anti-predator behaviour. The aim if this study was to investigate how the take-off ability of migrating robins (*Erithacus rubecula*) in response to a simulated attack is affected by different fuel loads, and if the predator's attack angle affects the take-off strategy.

Methods

This study was carried out at Tovetorp Zoological Research Station, in the south-east of Sweden (58°56′ N 17°08′ E). First-year robins were trapped by mistnets during their period of fall migration (September to October) in 1997. Swedish robins start the fall migration in September and it lasts until the beginning of November, with the main passage taking place during October. Their main wintering areas are Iberia, France and Italy, but they are found almost all around the Mediterranean Sea, from the north of Africa to the Caspian Sea (Pettersson and Hasselquist 1985). During migration, when passing the south of Sweden, fuel loads exceeding 30% are not unusual (Å. Lindström, personal communication). Individuals that had not completed their post-juvenile moult were not used in the experiment. To avoid effects of age, only first-year robins were used, but sex effects could not be avoided because first-year robins cannot be sexed. Robins were aged according to plumage differences between first-year and adult individuals (Svensson 1992). The birds were kept indoors in individual cages (90 × 60 × 95 cm) with two perches in each cage for the birds to rest and roost on. In each of the four rooms, three cages were separated with wooden screens to visually separate the birds. The robins had access to food (mealworms, *Tenebrio molitor*) and water ad libitum. To test birds with different amounts of stored fat, the birds were kept in captivity between 1 and 7 days.

The experiments were conducted in a neighbouring room with a larger cage with solid wooden walls (Fig. 1). The experimental cage (2 × 0.7 × 2 m) had an elevated floor at the feeding tray, which was at a height of 50 cm above the floor inside the cage, and the perch at this elevated floor was 10 cm high. Right in front of the perch, on the short side facing camera 2 (see below), was the feeding tray. The perch at the feeding tray was the only perch present in the experimental cage. To study the effect of fuel load with respect to flying ability, we investigated only alarmed flights caused by a predator model, a cardboard merlin (*Falco columbarius*), which could be sent down along a fishing line in two different angles towards the feeding tray. The merlin approached the feeding tray (and therefore the bird) and "attacked" with a velocity of 13 km h^{-1} independently of attack angle. This was made possible by the experiment set-up, where the predator model was pulled forward by a weight which was released from approximately 2.5 m aboveground (Fig. 1). When not in use, the merlin was positioned behind a blind, in which there was a hole through which the merlin appeared during the start of the attack. Since the merlin rested behind a blind during the experiments, it was not visible for the birds until it "attacked" through the hole.

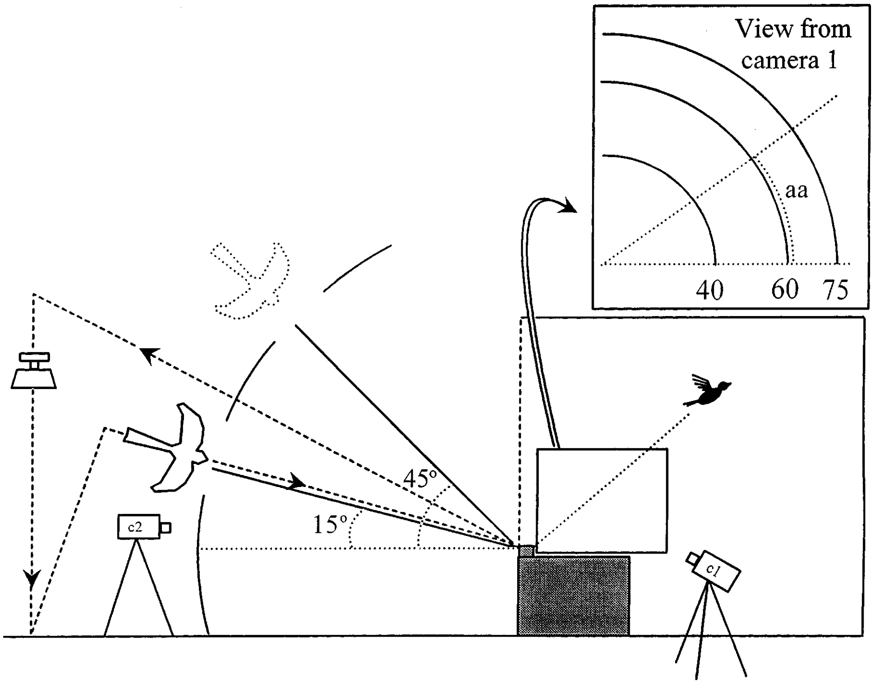

Fig. 1 The experimental set-up. The *inset* shows the screen which was recorded to analyse the take-offs. Angle of ascent (*aa*) was noted and velocity was calculated at each curved line (at 40, 60, 75 cm from point of take-off). The model merlin was pulled forward by the weight as indicated by the *arrows* and the videocameras (*c1* and *c2*) recorded the take-offs

This ensured that the robins did not react to anything else but the visual stimulus of a flying predator.

The birds were picked randomly with respect to number of days in captivity, each individual bird was used only once in the experiment, and they were taken one by one from the holding cage to the experimental room. A total of 31 birds were exposed to a low angle of attack (15°), and 15 birds were exposed to a high angle of attack (45°). After each experiment, the tested bird was released in proximity to the trapping site. The attack was made in a standardised manner. When the bird reached down to the feeding tray for food, the merlin was released. Two video cameras recorded the take-offs. Along the line of the take-off, a standard video 8 camera (camera 2) was used to analyse how much the bird's take-off deviated from the centre trajectory, and perpendicular to the take-off, a Super-VHS camera (camera 1) was used to calculate the take-off velocity and estimate its angle of ascent.

Analysis of the angle of ascent and velocity was made possible by videotaping arcs drawn on a screen (Fig. 1), which were afterwards redrawn from the videotapes and used on the TV screen during analysis. The arcs were drawn at 40, 60 and 75 cm from the point of take-off, and the angles were also marked on each arc, from 0 to 90°. Since the take-offs could deviate from the centre trajectory, the deviation was categorised in five groups, because different trajectories appear differently from the perpendicular view of the Super-VHS. Each category was analysed according to the screen videotaped at each specific standard trajectory; one category for those that flew straight away from the predator model, and two wide categories to the left and to the right. Birds that flew wider than the widest categories (>10 cm from the straight trajectory at the 60-cm arc) were excluded from the experiment. By using these categories, every bird covered the same distances to the arcs, avoiding the errors that would otherwise be made due to incorrect perspective given by the lens of the video camera.

Flights were analysed using the videotaped standard trajectories, the measurements for which were corrected so that the five categories became comparable. Velocity was calculated by measuring the distance travelled between two adjacent video frames when the 40-, 60- and 75-cm distances were crossed. As one frame covered 0.02 s, the velocity (m s^{-1}) = distance between two frames (m)/0.02 (s).

Body mass was measured directly after each experiment on a Precisa 200A electronic balance, with an accuracy of 0.01 g. To control for body size variation between the birds, percent fuel load of lean body mass was used. To assess fuel load, one can estimate the lean body mass from the body size (Ellegren 1989). The lean body mass of each bird was based on the relationship between wing length and body mass from 85 robins without visual fat, caught at Tovetorp (linear regression, $y = 4.13 + 0.15 \times \text{wing length}$, $R^2 = 0.18$, $P < 0.001$, $n = 85$). The fuel load of these robins was estimated visually using a standardised scale (Pettersson and Hasselquist 1985). The percentage fat of lean body mass (fuel load) was then estimated as: 100 × (total body mass–size-specific lean body mass)/size-specific lean body mass.

A more relevant measurement for estimating flight capacity is wing load, which is based on each individual's wing area and body mass. We calculated wing load according to Pennycuick (1989). To estimate each individual's wing load, the left wing of each bird was drawn directly after each experiment, and the wing areas were then measured using Leica Q500IW image analysis equipment linked to a Hamamatsu C5810-10 ccd camera. All statistical analyses were made using STATISTICA for Windows 5.1 (Statsoft).

Results

All robins reacted to the approaching predator model by taking off towards the opposite side of the cage. When reaching the opposite wall, the majority of the birds hovered against it for a short while until they flew down to the floor and remained motionless. No birds emitted any calls. The take-offs were analysed at three different distances from take-off: 40, 60 and 75 cm from the perch at the feeding tray. After take-off, the acceleration decreased quickly and the speed was already stable after approximately 60 cm of flight (Wilcoxons test for matched pairs: velocity at 40 and 60 cm, $T = 17.0$, $Z = 5.51$, $P < 0.0001$, $n = 46$; velocity at 60 and 75 cm, $T = 30.0$, $Z = 1.26$, $P = 0.21$, $n = 45$). Hence, statistical analysis will only be presented for the distance 60 cm from the perch. The average velocity of the birds was 2.7 ± 0.06 ms^{-1} at 60 cm and birds took slightly less than 0.3 s to fly 60 cm (see also Table 1).

We analysed the take-offs using a one-way ANCOVA to control for the fact that measures such as velocity and angle of ascent are not independent. Velocity decreased with higher angles of ascent (Tables 2, 3). This confirms that the birds are facing a trade-off between angle of ascent and velocity, since a low angle of ascent permits the highest acceleration (Witter and Cuthill 1993). Kullberg et al. (1998) found no such relationship during spontaneous take-offs.

The merlin's angle of attack had no effect on the take-off strategy of the robins (Table 1; one-way ANCOVA:

Table 2 Within-cell regression of the one-way ANCOVA revealing the effect of wing load on angle of ascent at alarmed take-offs (angle of attack as independent factor, angle of ascent as dependent variable and velocity and wing load as covariates)

Variable	*df* effect	*df* error	Beta	*t* (42)	*P*
Velocity	2	42	−0.45	−4.20	0.0001
Wing load	2	42	−0.51	−4.72	0.00003

Table 3 Within cell regression of the one-way ANCOVA showing the effect of wing load on velocity at alarmed take-offs (angle of attack as independent factor, velocity as dependent variable and angle of ascent and wing load as covariates)

Variable	*df* effect	*df* error	Beta	*t* (42)	*P*
Angle of ascent	2	42	−0.65	−4.20	0.0001
Wing load	2	42	−0.25	−1.58	0.12

Table 1 Angle of ascent and velocity when robins were exposed to high and low angles of attack at 60 cm after take-off. Also shown are the average wing length and body mass of the birds in these groups. Values are the mean ± SE

	Angle of ascent (°)	Velocity (m s^{-1})	Wing length (mm)	Weight (g)	*n*
Low angle of attack (15°)	50.8 ± 1.71	2.78 ± 0.07	73.7 ± 0.31	6.27 ± 0.26	31
High angle of attack (45°)	50.3 ± 2.29	2.67 ± 0.10	73.6 ± 0.52	6.36 ± 0.24	15

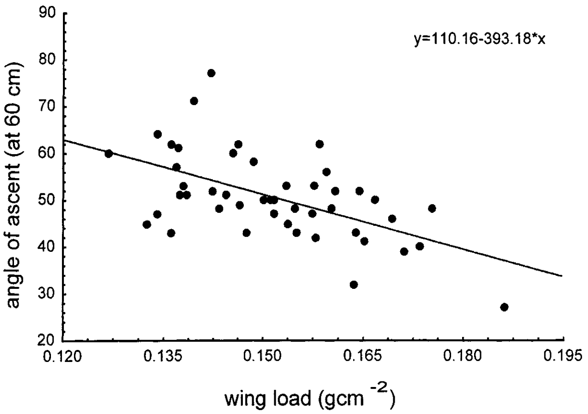

Fig. 2 Relationship between wing load and angle of ascent at 60 cm after take-off ($R^2 = 0.32$, $P = 0.00004$)

angle of ascent, $F_{1,42} = 0.41$, $P = 0.53$; velocity, $F_{1,42} = 1.28$, $P = 0.26$). Angle of ascent decreased with increasing wing loads, whereas velocity was not affected by wing load (Tables 2, 3). The wing load of the birds varied between 0.13 and 0.19 g cm^{-2} (mean 0.15 ± 0.002 SE). Thus robins with a wing load of 0.19 g cm^{-2} took off at a 39% lower angle than those with a wing load of 0.13 g cm^{-2} according to the relationship found (Fig. 2). The heaviest robin had a calculated fuel load of 27%, and according to the relationship between fuel load and angle of ascent ($y = 52.73–0.33x$, $R^2 = 0.08$, $P = 0.05$, $n = 46$), a robin carrying a fuel load of 27% took off at a 17% lower angle than one carrying no fuel load.

Discussion

Robins with a wing load of 0.19 g cm^{-2} took off at a 39% lower angle than robins with a wing load of 0.13 g cm^{-2}, implying a significant effect of migratory fuel load on flight capacity in robins. However, the velocity remained unaffected. Wing load is strongly dependent on the body mass of a bird, and hence also on fuel load, and we found that robins carrying a 27% fuel load took off at a 17% lower angle than birds carrying no fuel load. Since wing load, a direct measurement, includes the variation between individuals in both body size and mass, we suggest that wing load should be a preferred estimate of the load carried by a bird in empirical studies on bird flight capacity, as opposed to percent fuel load of lean body mass.

Many studies have discussed an increased predation risk due to impaired flying ability caused by heavy loads (e.g. fat, prey load, egg load) and most of these studies have been strictly theoretical (for example McNamara and Houston 1990; Bednekoff and Houston 1994a). A few experimental studies have been made more recently, and empirical evidence is beginning to accumulate (Table 4). The present study on robins is one of the first to demonstrate an effect of fuel load in a migratory species. In a study on migratory blackcaps, heavy individuals neither ascended as high nor as fast as individuals with lighter fuel loads (Kullberg et al. 1996). Witter et al. (1994) showed that starlings took off at lower angles and were less manoeuvrable when artificial weights were added, although the "heavy" starlings did not fly slower. Thus an effect on velocity has been found in blackcaps but not in robins or starlings. A combination of two reasons might explain this result. First, the robins' fuel loads were not as high as those of the blackcaps: only 12 birds had a fuel load greater than 10% (compared to the blackcap study where almost all examined birds had a fuel load larger than 10%). The starlings had, like the robins, rather small loads (7–14%), which could account for the similarities between the two studies. This also supports the idea from Witter et al. (1994) that the birds seem to defend the take-off velocity by decreasing the angle of ascent. Secondly, robins might handle the trade-off between angle of ascent and velocity differently than blackcaps, for example as a consequence of different ecological situations and differences in behavioural repertoires (cf. Lima 1993). Robins and blackcaps may

Table 4 Empirical studies on the effect of body mass on take-off ability in alarmed birds (* estimations using information in the paper, the effect is given as 0% when no statistically significant effect was found; – not measured, *n* number of birds used in each study)

Authors	Species	Variation in body mass	Increase in body mass (%)	Effect on velocity (% reduction)	Effect on angle of ascent (% reduction)	*n*
Witter et al. 1994	Starling (*Sturnus vulgaris*)	Artificially added weights	10*	0*	40–50*	24
Lee et al. 1996	Starling	Gravid females	7*	0*	29*	10
Veasey et al. 1998	Zebra finch (*Taenophygia guttata*)	Diurnal variation in body mass	~7*	0*	–	22
Kullberg 1998	Willow tit (*Parus montanus*)	Diurnal variation in body mass	8	0	0	18
Kullberg et al. 1998	Great tit (*Parus major*)	Diurnal variation in body mass	8	0	0	40
Kullberg et al. 1996	Blackcap (*Sylvia atricapilla*)	Migratory fuel load	60	17	32	28
This study	Robin (*Erithacus rubecula*)	Migratory fuel load	27	0	17	46

also handle the problems of migration differently. Robins are not forced to cross any extreme barriers, and they do not migrate as far. They may therefore travel with smaller fuel loads and thus be better able than, for example tropical migrants, to give priority to safety during migration. When the robins arrive at the wintering area, they do in fact choose territories mainly for protection, and not for good feeding opportunities (Cuadrado 1997).

As noted in the Introduction, birds may undergo various internal changes during their life history (Piersma and Lindström 1997). If the robins' flight muscles increase to compensate for increased wing load, the results from this study (see also Kullberg et al. 1996) suggest that muscle hypertrophy cannot compensate completely for the increased wing load caused by the migratory fuel load.

Kullberg et al. (1998) showed that great tits adjust their angle of ascent according to the predator's angle of attack, but the robins in our study did not. Anti-predator behaviour may depend on the environment of the species. A secretive robin that mostly forages on the ground close to cover (Cuadrado 1997) may have other predator responses than, for example, a great tit, which mainly forages aboveground. This result also implies that it is not a given fact that the best strategy to evade a predator is by maximising the distance between oneself and the predator. Differences in the physical environment, for example distance to protective cover, experienced by different species might be expressed in different response behaviours (Pulliam and Mills 1977). The presence or absence of protective cover in a species' natural environment may be one factor that is important in determining not only how a bird should respond to a predator, but also in what environment a bird can handle an attack (cf. Lima 1993). The behavioural complexity of escaping avian predators, such as sparrowhawks (*Accipiter nisus*) and peregrines (*F. peregrinus*), was shown in a study on escape responses in redshanks (*Tringa totanus*) (Cresswell 1993): a response that led to escape from one predatory species also led to more frequent capture by another predatory species.

Does the fact that robins with large fuel loads took off at lower angles of ascent make a real difference with respect to risk of predation, and if so what impact does this have on an individual bird's life? In the blackcap study (Kullberg et al. 1996), high fuel loads (>40%) had severe effects on take-off, and fuel loads of this magnitude are commonly observed in the wild. In fact, some species almost double their body mass before crossing wide ecological barriers (Fry et al. 1970). In the present study, an effect was found even though fuel loads did not exceed 30%. Important predatory species such as sparrowhawks and merlins rely to a large extent on surprise attacks when hunting (Rudebeck 1950; Cresswell 1996). Therefore, small changes in take-off ability can possibly make all the difference for a small bird between ending up as dinner (Bednekoff 1996; see also for example Dawkins 1982 for examples of the life/dinner principle) or continuing the migration with a possibility to reproduce the next breeding season. Hence, fitness gains due to survival, for example avoidance of predation, are very direct (Alerstam and Lindström 1990; Lima and Dill 1990), and the selective force of predation can thus play a major role in shaping fuel load strategies in birds.

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