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### High Migratory Fuel Loads Impair Predator Evasion in Sedge Warblers

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During migration, many species of birds rely on stored fat for fuel. The extra mass taken on for migration entails costs (Witter and Cuthill 1993). Time and energy must be devoted to foraging to build up fat loads, and increased feeding may increase the risk of being attacked by predators. An additional cost of increased fuel loads may be higher predation risk owing to reduced ability to take off, maneuver, and climb. Mass-dependent predation risk has been the focus of several recent theoretical studies (McNamara and Houston 1990, Hedenström 1992, Witter and Cuthill 1993, Brodin 2000). In species that depend on flight to escape from predators, takeoff ability is crucial because once the prey are airborne, the success rate of predators diminishes (e.g. Rudebeck 1950, Kenward 1978, Lindström 1989, Cresswell 1993).

Within the natural range of body mass of nonmigratory birds (ca. 10% diurnal increase in mass), mass seems to have no measurable effect on takeoff ability (Kullberg 1998, Kullberg et al. 1998, Veasey et al. 1998, van der Veen and Lindström 2000). In migratory birds, fuel loads of 20 to 30% of lean mass are common (Alerstam and Lindström 1990), and fuel loads may exceed 100% of lean mass when passerines are about to cross wide barriers (e.g. Fry et al. 1970, Finlayson 1981). Although fat storage is the most common explanation for mass changes in birds, mass may change because of other reversible processes, e.g. by increases or decreases in muscle mass and in various internal organs (Piersma and Lindström 1997).

To date, only two species of migrants have been studied with respect to takeoff ability in a predator-escape situation. Kullberg et al. (1996) calculated that Blackcaps (*Sylvia atricapilla*) carrying 60% of lean body mass as fuel would have an angle of ascent that was 32% lower and a velocity that was 17% lower

than Blackcaps that were carrying no fuel load. European Robins (*Erithacus rubecula*) carrying a fuel load off 27% took off at an angle that was 17% lower than robins carrying no fuel load, whereas velocity remained unaffected (Lind et al. 1999). The main aim of the study we report was to investigate how takeoff ability in Sedge Warblers (*Acrocephalus schoenobaenus*) is affected by large migratory fuel loads. In contrast to earlier studies, we studied wild Sedge Warblers just prior to a trans-Saharan crossing, thereby studying natural fuel loads versus fuel loads achieved in captivity.

*Methods.*—This study was conducted in October 1997 on the Island of Lesbos (39°01'N, 26°33'E) in the eastern part of the Greece archipelago. Sedge Warblers that breed in Europe winter in tropical Africa (Moreau 1972). In western Europe, Sedge Warblers feed heavily on reed aphids (*Hyalopterus pruni*) during autumn migration, accumulating very large fuel loads in preparation for trans-Saharan passage (Bibby et al. 1976, Bibby and Green 1981).

We trapped migrant first-year Sedge Warblers in mist nets between 0600 and 1200. Nets were checked every 20 min. After capture, birds were banded, weighed, and various morphometric measures collected. Visual fat scores were estimated following a scale modified from that of Pettersson and Hasselquist (1985), which ranged from zero (no visible fat) to six (whole belly covered with fat). Because many of the birds we trapped also had stored fat covering their breast muscles, we extended our scale to include three more stages. A bird with a fat score of nine had the whole abdomen (including belly and breast muscles) covered with fat. In total, we used 30 Sedge Warblers in the experiments. Birds were kept singly in small textile bags for 30 to 60 min before being released into the experimental cage. Each bird was only used once in the experiments, and all birds were successfully released back into the wild directly after each trial.

The experimental setup was similar to that of Kullberg et al. (1996) and Lind et al. (1999). However, because we conducted experiments under field condi-

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tions, we constructed a cage that could be easily transported. The experimental cage was a cubic tent-like construction (1.35 m long  $\times$  0.7 m wide  $\times$  1.35 m high), with three sides and the floor covered by thick unbleached cotton and the roof covered by thin white cotton to provide good light inside the cage. Aluminum pipes attached to the outside supported the cage, thereby avoiding any structures inside the cage. The only side that was covered by netting faced an additional tent that was attached to the experimental cage to provide protection from visual disturbance and wind. In the far upper end of this additional tent, a cardboard model of a Merlin (*Falco columbarius*) was hidden in a box. The model was three-dimensional and painted so that it closely resembled a gliding Merlin.

We regard the model as a very good general predator stimulus, and it has proven to elicit strong and immediate escape behaviors in Sedge Warblers and other species we have investigated. The fact that many birds elicited alarm calls after takeoff strongly suggests that they interpreted the model as a raptor. We placed a bent twig on the floor of the experimental cage to attract the bird to perch in a position where it sat facing the opposite side from where the Merlin would "attack." After release into the experimental cage, birds flew around for a few minutes before landing on the floor or on the twig. When a bird sat at the top of the bent twig and in the correct position, the falcon model was released in a standardized way and came gliding in an angle of 35° and at an average speed of 7 km per h. It took 1 s ( $\pm$  SE of 0.02 s) for the model to travel from the starting point inside the box until it stopped just in front of the netting.

We recorded takeoffs with two Hi-8 video cameras. One camera was placed perpendicular to the line of takeoff outside the tent. Because the video camera had to be about 30 cm from the tent wall to cover a sufficient area, we covered the area between the tent and the camera lens with cotton. The opening in the tent wall (40  $\times$  50 cm) was furthermore covered by transparent fiberglass. To record any side movements of the birds, a second camera was placed along the line of takeoff just outside the far end of the tent (a small hole in the cotton permitting video recording from outside). Side movements in takeoffs deviating from the center trajectory would give errors in the analysis owing to incorrect perspective given by the lens of the perpendicular camera. However, none of the takeoffs deviated more than 5 cm from the center trajectory when analyzing the video from the second camera, so no corrections had to be made in the analyses.

By analyzing the videos from the perpendicular camera, we measured velocity, acceleration, and angle of ascent of each bird in the same way as has been done previously (Lind et al. 1999). Analysis of the angle of ascent and velocity at 60 cm from the start was

made possible by videotaping an arc (at 60 cm distance) and every 5th angle from the horizontal plane drawn on a screen, which afterwards were redrawn from videotapes and used on the TV screen during analysis (see Lind et al. 1999). We measured velocity at the very start of the takeoff between the two first video frames when the bird was in the air. Because one video frame covered 0.02 s, the velocity (m per s) between two frames was calculated as the distance between two frames divided by 0.02. Acceleration (m per s<sup>2</sup>) between the first measured velocity ( $V_1$ ) and at 60 cm from the perch ( $V_2$ ) was calculated  $V_1 - V_2$  divided by the time in seconds between the two measured velocities. We recorded angle of ascent of each bird by measuring the angle from the perch to the point where the bird passed the 60cm distance from the perch.

A useful estimate of flight capacity in birds is wing loading. Pennycuik (1989) used N per m<sup>2</sup> for wing loading, but we use g per cm<sup>2</sup> because we find it more informative. This measurement takes into account each individual's wing area and body mass. We measured each experimental bird's body mass ( $\pm$  0.1 g), wing length ( $\pm$  1 mm), and wing span ( $\pm$  1 mm) and traced the outstretched left wing on a piece of paper. Wing area was later measured using Leica Q500IW image analysis equipment linked to a Hamamatsu C5810-10 ccd camera. These measurements enabled us to calculate wing loading according to the method used by Pennycuik (1989). Furthermore, to estimate fuel load of each bird, we used data on size-specific fat-free body mass related to wing length for 73 Sedge Warblers with no visual subcutaneous fat caught in southern Sweden from 1991 to 1994 (lean body mass [g] =  $-0.593 + 0.169 \times$  wing length [mm]; B. Peterson unpubl. data). Wing lengths of our birds varied from 63 to 69 mm, and estimated lean body mass ranged from 10.1 to 11.1 g. We estimated fuel load as a percentage of lean body mass by subtracting size-specific lean body mass from total body mass, dividing this by size-specific lean body mass, and multiplying by 100. We use the term "fuel load" as the increase in body mass that results from migratory fat and the eventual change in muscle mass and various internal organs that cannot be distinguished here (Piersma and Lindström 1997).

*Results.*—We subjected 30 Sedge Warblers to a simulated predator attack by the model Merlin. Half of them tried to escape by taking off in a straight line away from the "attacking" Merlin, whereas 13 others darted sideways at an angle of almost 90° from the model. These two groups of birds did not differ significantly in wing length ( $t = -1.15$ ,  $P = 0.25$ ), body mass ( $t = 0.79$ ,  $P = 0.43$ ), or fuel load ( $t = 1.11$ ,  $P = 0.27$ ; all  $df = 26$ ). The two remaining birds did not fly at all. These two birds and the 13 that flew away in a trajectory that deviated more than 5 cm from a straight line were excluded from further analysis because estimations of flight speed and angle of ascent

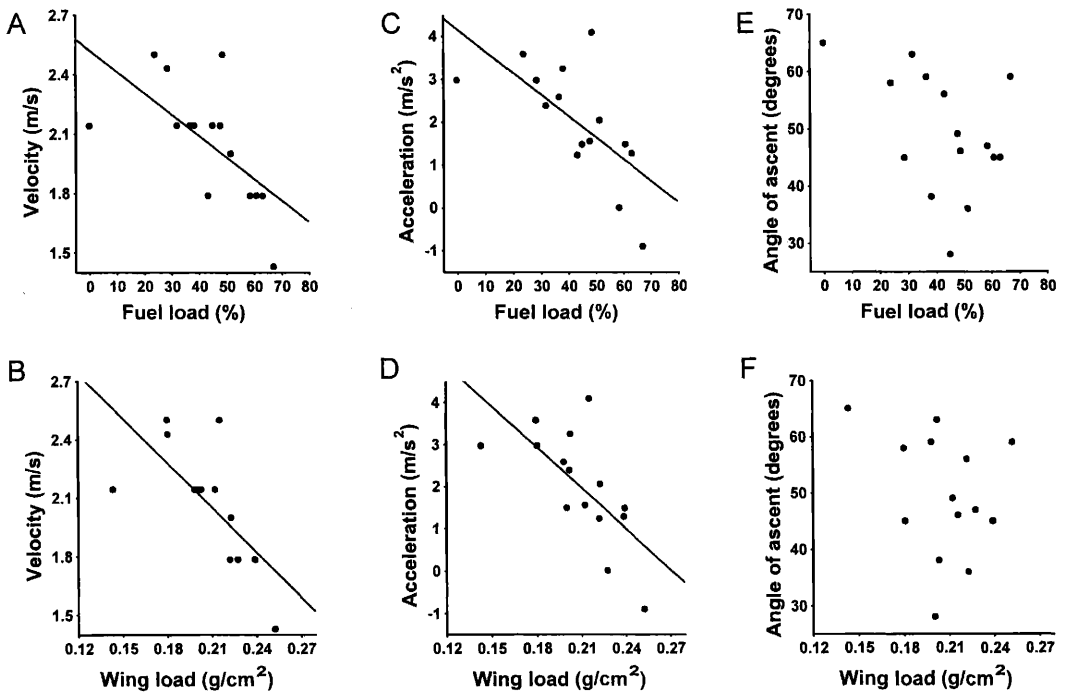


FIG. 1. Velocity (m per s) at 60 cm from the start, acceleration (m per s<sup>2</sup>) from the first measurable velocity to 60 cm from the start, and angle of ascent (degrees) at 60 cm from the start in relation to fuel (A, C, E) and wing loading (B, D, F) of experimental Sedge Warblers.

were impossible. Most Sedge Warblers emitted alarm calls when attacked.

The 15 Sedge Warblers under study varied in body mass from 10.8 to 18.2 g, in fuel load from 0 to 67% of lean body mass, and in wing loading from 0.14 to 0.25 g per cm<sup>2</sup>. Some of them had large amounts of subcutaneous fat that almost totally covered their breast muscles. Accordingly, fat score was strongly correlated with body mass ( $R^2 = 0.76$ ,  $b = 0.7$ ,  $n = 30$ ,  $P < 0.001$ ), indicating that much of the variation in body mass resulted from fat storage.

Elevated body mass impaired takeoff ability of Sedge Warblers. Birds that carried a large fuel load, and thus had heavier wing loading, had a lower velocity at 60 cm from the perch than did lighter birds (fuel load,  $R^2 = 0.35$ ,  $b = -0.01$ ,  $n = 15$ ,  $P = 0.01$ ; wing loading,  $R^2 = 0.45$ ,  $b = -7.6$ ,  $n = 15$ ,  $P = 0.004$ ; Figs. 1A and 1B). The same pattern also occurred for acceleration (fuel load,  $R^2 = 0.38$ ,  $b = -0.05$ ,  $n = 15$ ,  $P = 0.007$ ; wing loading,  $R^2 = 0.40$ ,  $b = -32.5$ ,  $n = 15$ ,  $P = 0.006$ ; Figs. 1C and 1D), whereas fuel load had no significant effect on takeoff angle (fuel load,  $P = 0.10$ ; wing loading,  $P = 0.30$ ; Figs. 1E and 1F).

According to the relationship we found, increasing fuel load from 0 to 60% reduced flight velocity by 26%, and increasing wing loading from 0.14 to 0.25 g per cm<sup>2</sup> reduced flight velocity by 32%. When they crossed the line 60 cm from the perch, the fastest bird

had attained a velocity of 2.5 m per s, and the slowest bird was flying at 1.4 m per s.

*Discussion.*—Sedge Warblers often carry very large fuel loads for their migration between Europe and Africa. This is evident during both legs of migration: Sedge Warblers have been recorded with body masses up to 21.7 g during autumn in Britain (Gladwin 1963) and with masses up to 20 g in spring at Lake Chad in Africa (Fry et al. 1970). This indicates that Sedge Warblers regularly need to handle an increased predation risk owing to large fuel loads. Sedge Warblers with large body masses are caught less often at banding sites (Bibby et al. 1976), indicating that they behave in a more secretive way and probably are more reluctant to fly when they are heavier. Judging from prey remains at a colony of Eleonora's Falcons (*Falco eleonorae*) off Crete, Sedge Warblers are the most common prey species among the *Acrocephalus* warblers that migrate through the area (Ristow et al. 1986 in Handrinos and Akriotis 1997). However, Eurasian Reed-Warblers (*A. scirpaceus*) are much more commonly observed during autumn migration in Greece, indicating that Sedge Warblers are more susceptible to predation, maybe because of a different migratory strategy (Handrinos and Akriotis 1997).

Our results provide strong support for an increase in predation risk with increasing fuel loads in mi-

gratory Sedge Warblers. We found that increasing fuel load from 0 to 60% reduced flight velocity by 26% in Sedge Warblers. In a similar study on takeoff ability in Blackcaps, the same increase in fuel load reduced flight velocity by 17% (Kullberg et al. 1996). Interestingly, we were unable to demonstrate an effect of fuel load on angle of ascent in Sedge Warblers, whereas angle of ascent in heavy Blackcaps was affected to a larger extent than flight speed. Studies of European Starlings (*Sturnus vulgaris*) with artificially increased body mass and on gravid females indicate that heavier birds have a lower angle of ascent while maintaining the same velocity (Witter et al. 1994, Lee et al. 1996). A similar effect occurred in European Robins, where a 27% increase in fuel load lowered the angle of ascent by 17%, but takeoff velocity was unaffected (Lind et al. 1999). These results could indicate that takeoff decisions differ between species because a tradeoff occurs between angle of ascent and takeoff speed (Witter and Cuthill 1993, Kullberg et al. 1998).

As noted by Hedenström (1992), turning radius increases with increased body mass. Thus, an alternative explanation for our results is that heavy birds chose a low flight speed to maintain maneuverability. However we believe that in the very initial phase of the escape, it is of utmost importance for the bird to get fully airborne before initiating other evasive strategies, such as trading speed for maneuverability. It is important to note that we measured only the initial phase of takeoff (60 cm), and the birds could fly as much as 1.8 m before having to maneuver (reaching the top of the tent). In fact, most birds did not maneuver but flew straight into the cotton ceiling.

Another interesting result is that a high proportion (43%) of Sedge Warblers took off almost perpendicular to the model's attack trajectory. Placed in the same experimental setup, only 1 out of 73 Blackcaps chose a similar strategy (C. Kullberg et al. unpubl. data). For Sedge Warblers, which live close to the ground in dense bushes or reeds, darting off at a sharp angle to a predator's line of attack may be adaptive because the probability of disappearing from the predator's view is high in dense vegetation. Blackcaps often live in a microhabitat that is more open and thus may be less prone to use this escape strategy. We expect to find an array of different escape tactics depending on a species' habitat, but at present, little is known about species-specific escape strategies (Pulliam and Mills 1977, Lima 1993).

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#### LITERATURE CITED

- ALERSTAM, T., AND Å. LINDSTRÖM. 1990. Optimal bird migration: The relative importance of time, energy, and safety. Pages 331–351 in *Bird migration: Physiology and ecophysiology* (E. Gwinner, Ed.). Springer-Verlag, Berlin.
- BIBBY, C. J., AND R. E. GREEN. 1981. Autumn migration strategies of Reed and Sedge warblers. *Ornis Scandinavica* 12:1–12.
- BIBBY, C. J., R. E. GREEN, G. R. M. PEPLER, AND P. A. PEPLER. 1976. Sedge Warbler migration and reed aphids. *British Birds* 69:384–399.
- BRODIN, A. 2000. Why do hoarding birds gain fat in winter in the wrong way? Suggestions from a dynamic model. *Behavioral Ecology* 11:27–39.
- CRESSWELL, W. 1993. Escape responses by Redshanks, *Tringa totanus*, on attack by avian predators. *Animal Behaviour* 46:609–611.
- FINLAYSON, J. C. 1981. Seasonal distribution, weights and fat of passerine migrants at Gibraltar. *Ibis* 123:88–95.
- FRY, C. H., J. S. ASH, AND I. J. FERGUSON-LEES. 1970. Spring weights of some Palaearctic migrants at Lake Chad. *Ibis* 112:58–82.
- GLADWIN, T. W. 1963. Increases in the weight of acrocephali. *Bird Migration* 2:319–324.
- HANDRINOS, G., AND T. AKRIOTIS. 1997. *The birds of Greece*. Christopher Helm, London.
- HEDENSTRÖM, A. 1992. Flight performance in relation to fuel load in birds. *Journal of Theoretical Biology* 158:535–537.
- KENWARD, R. E. 1978. Hawks and doves: Factors affecting success and selection in Goshawk attacks on Woodpigeons. *Journal of Animal Ecology* 47:449–460.
- KULLBERG, C. 1998. Does diurnal variation in body mass affect take-off ability in wintering Willow Tits? *Animal Behaviour* 56:227–233.
- KULLBERG, C., T. FRANSSON, AND S. JAKOBSSON. 1996. Impaired predator evasion in fat Blackcaps (*Sylvia atricapilla*). *Proceedings of the Royal Society of London Series B* 263:1671–1675.
- KULLBERG, C., S. JAKOBSSON, AND T. FRANSSON. 1998. Predator induced take-off strategy in Great Tits (*Parus major*). *Proceedings of the Royal Society of London Series B* 265:1659–1664.
- LEE, S. J., M. S. WITTER, I. C. CUTHILL, AND A. R. GOLDSMITH. 1996. Reduction in escape performance as a cost of reproduction in gravid Starlings, *Sturnus vulgaris*. *Proceedings of the Royal Society of London Series B* 263:619–624.
- LIMA, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attacks: A survey of North American birds. *Wilson Bulletin* 105:1–215.

- LIND, J., T. FRANSSON, S. JAKOBSSON, AND C. KULLBERG. 1999. Reduced take-off ability in Robins (*Erithacus rubecula*) due to migratory fuel load. *Behavioral Ecology and Sociobiology* 46:65–70.
- LINDSTRÖM, Å. 1989. Finch flock size and risk of hawk predation at a migratory stopover site. *Auk* 106:225–232.
- MCMNAMARA, J. M., AND A. I. HOUSTON. 1990. The value of fat reserves and the trade-off between starvation and predation. *Acta Biotheoretica* 38:37–61.
- MOREAU, R. E. 1972. The Palaearctic-African bird migration systems. Academic Press, London.
- PENNYCUICK, C. J. 1989. Bird flight performance. A practical calculation manual. Oxford University Press, Oxford.
- PETTERSSON, J., AND D. HASSELQUIST. 1985. Fat deposition and migration capacity of Robins *Erithacus rubecula* and Goldcrests *Regulus regulus* at Ottenby, Sweden. *Ring and Migration* 6:66–76.
- PIERSMA, T., AND Å. LINDSTRÖM. 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends in Ecology and Evolution* 12:134–138.
- PULLIAM, H. R., AND G. S. MILLS. 1977. The use of space by wintering sparrows. *Ecology* 58:1393–1399.
- RUDEBECK, G. 1950. The choice of prey and modes of hunting of predatory birds with special references to their selective effect. *Oikos* 2:65–88.
- VAN DER VEEN, I. T., AND K. M. LINDSTRÖM. 2000. Escape flights of Yellowhammers and Greenfinches: More than just physics. *Animal Behaviour* 59:593–601.
- VEASEY, J. S., N. B. METCALFE, AND D. C. HOUSTON. 1998. A reassessment of the effect of body mass upon flight speed and predation risk in birds. *Animal Behaviour* 56:883–889.
- WITTER, M. S., AND I. C. CUTHILL. 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London Series B* 340:73–92.
- WITTER, M. S., I. C. CUTHILL, AND R. H. C. BONSER. 1994. Experimental investigation of mass-dependent predation risk in the European Starling, *Sturnus vulgaris*. *Animal Behaviour* 48:201–222.

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## Versatility from a Single Song: The Case of the Nightingale Wren

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Versatility in song production of birds has drawn considerable attention since its description by Hartshorne (1956), who suggested that birds vary their vocal output to avoid habituation in listeners, especially if singing is extensive. The best-known route to song versatility involves creating permutations and combinations of song elements learned from neighbors or relatives, combined with improvisations (Nowicki et al. 1999). Birds may learn whole songs or individual song elements, which then may be arranged in novel ways.

Versatility might be achieved in other ways besides acquiring numerous song types. For example, individuals could shift the tempo of their songs by altering internote or intersong intervals. Alternatively, birds might sing the same pattern of notes but shift their frequency range. Black-capped Chickadees

(*Poecile atricapilla*) shift the frequency of their whistled songs, which has been suggested to function as a repertoire-enlarging strategy (Horn et al. 1992). Without changing the order of song elements, shifts in tempo or frequency might change the perception of the song sufficiently to prevent habituation.

Here, we describe songs of three Nightingale Wrens (*Microcerculus philomela*), which are residents of tropical lowland forests from southern Mexico to central Costa Rica (AOU 1998). The song of this species has a peculiar quality that has struck some observers as being "random" because it is difficult to discern a clearly recurring pattern (Howell and Webb 1995). This distinctive song has been the primary justification for splitting *M. philomela* from *M. marginatus*, the Scaly-breasted Wren (Slud 1958; Stiles 1983, 1984).

*Methods.*—Recordings of Nightingale Wren songs were made by DWL at La Selva Biological Station, Costa Rica (10°26'N, 83°59'W), using a Sony TCM-

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