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Wingtip shape and flight performance in the European Starling *Sturnus vulgaris*

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Although wingform is known to differ among individuals of the same species it is not known how intraspecific variation in wingtip shape is associated with flight performance. In this study, we have examined both among- and within-individual variation in wingtip shape in relation to changes in flight performance in the European Starling *Sturnus vulgaris*. We found that level flapping-flight speed and the ability to negotiate an aerial obstacle course were unrelated to wingtip shape. However, take-off parameters did vary with wingtip shape; birds with more rounded wingtips tended to take off from the ground at a steeper angle of ascent than those with relatively more pointed wingtips. The same relationships between wingtip morphology and flight were present in both the inter- and intra-individual experimental analyses. The evolutionary importance of this variation in take-off ability is discussed in terms of predator avoidance and enhancement of individual survival.

Intraspecific studies of avian wing morphology have identified adaptations to a number of different selection pressures. For example, it has been reported that factors such as migration (reviews in Mulvihill & Chandler 1990, Lockwood *et al.* 1998), age-class (Alatalo *et al.* 1984, Tiainen & Hanski 1985), sexual selection (Madan Mohan *et al.* 1982, Tiainen 1982, Borras *et al.* 1993) and habitat (e.g. Hamilton 1961) may influence wing design and wingtip shape. However, we are not aware of any detailed intraspecific studies examining the relationships between wingtip shape and flight performance.

Aerodynamic theory has produced several predictions regarding the relationship between flight costs and wing design for different modes of flight (e.g. Saville 1957, Epting & Casey 1973, Tucker 1973, Pennycuick 1975, 1989, Rayner 1979, 1988, Anderson & Norberg 1981, Norberg & Rayner 1987, Norberg 1987, 1990, 1995). It is generally believed that wings of high aspect ratio (i.e. wings that have large span compared with their area) minimize flight costs (Rayner 1988, 1990, Norberg 1990) and are therefore expected to occur in species that rely on long-distance flight, such as migrants (Saville 1957, Lockwood *et al.* 1998, Voelke 2001). Broad wings with low wing loading may favour low-power flight (Norberg & Norberg 1971, Rayner 1988). Therefore, as manoeuvrability often requires slow flight and small turning radii, increased manoeuvrability in cluttered habitats may require short rounded wings with large second moments of area (cf. Saville 1957). There are relatively few predictions concerning the costs of flight for wings that differ in wingtip shape, although recent analyses have indicated that the shape of the wingtip (as opposed to the rest of the wing) commonly dominates aerodynamic performance, especially in flapping flight (Combes & Daniel 2001). It is expected that wings with pointed tapering wingtips generate little lift at the tips due to weak tip vortices and, hence, minimize induced drag during sustained flight. Rounded wings generate greater lift at the tip, shed larger vortices, and so create greater induced drag. Flow visualization studies of owls in flight, however, indicate that rounded wings can perform much more efficiently than previously thought. This discrepancy may be due to the relatively large spread of primaries in owls, which displace feather tips in both horizontal and vertical planes (Rayner 1995). The effective partitioning of vortices across separated feather tips helps to minimize induced drag. In addition, vortices are shed more quickly and tightly from pointed wingtips, which may also create greater induced drag than

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initially expected due to greater downwash in more pointed wings compared with rounded wings (Birch & Dickinson 2001). Aerodynamic theory also suggests that a wing with a rounded tip may maximize the thrust generated by flapping, while a pointed wingtip appears to minimize wing inertia and weight (Rayner 1986, 1993). Similarly, it has been proposed that a more convex wingtip may aid thrust production, whereas a concave wingtip may act to reduce wing weight and inertia (Lockwood *et al.* 1998).

Lockwood *et al.* (1998) developed two size-independent indices of wingtip shape that appear to describe wingtip morphological adaptations to flight demands (in their case migration) more comprehensively than other published indices. The indices of wingtip roundedness and convexity that Lockwood *et al.* (1998) introduced were derived from primary feather length measurements from a broad range of avian taxa capable of flight, but have yet to be applied to an intraspecific study of flight. They define wingtip pointedness vs. roundedness as a shift of the wingtip towards the leading edge of the wing in a pointed wing, but away from the leading edge in a more rounded wing (Fig. 1a,b). Wingtip convexity is defined as a decrease in the acuteness of the wingtip which results from more rapid lengthening (from proximal to distal) of primary feathers close to the wingtip compared with more proximal feathers (Fig. 1c,d). Convexity particularly influences the outline of proximal areas of the handwing (refer to Lockwood *et al.* 1998 for a more detailed description and discussion of these shape differences).

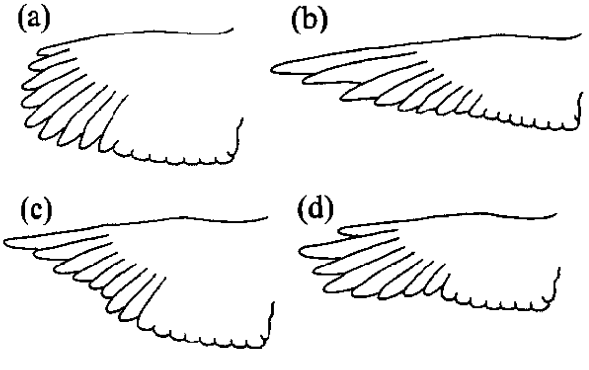

Figure 1. Stylized extreme representations of (a) rounded, (b) pointed, (c) concave and (d) convex wingtips. *C2* measures wingtip roundedness. *C3* measures wingtip convexity. Refer to Lockwood *et al.* (1998) for further details of these parameters. The Starlings in this study showed much less variation in *C2* and *C3* than depicted in these wing outlines.

Here, we apply these indices of roundedness and convexity to intraspecific differences in flight performance and wingtip morphology in the European Starling *Sturnus vulgaris*. We quantified three modes of flight (escape take-off, performance in an aerial manoeuvrability course, and level flapping-flight speed) in captive Starlings and compared measures of flight performance with among-individual differences in wingtip roundedness and convexity and within-individual changes in wingtip shape due to moult.

As Starlings have wings of average length compared with other avian taxa, they may be relatively unaffected by constraints acting upon wing weight or inertia. Therefore, we predict that wingtip roundedness (vs. pointedness) may have relatively more influence on flight performance than convexity (vs. concavity), although increased wingtip convexity may provide greater thrust. The influence of wing inertia may be more important at low flight speeds, for example during take-off and when performing aerial manoeuvres. In general, we predict that increasing wingtip roundedness (and to a lesser extent convexity) will generate greater thrust at low flight speeds, and is therefore expected to have greatest influence on take-off flight. As a more pointed wingtip may reduce vortex shedding, the power required for flight may be lower and hence the minimum power speed (V_{mp}) may be lower during level flapping-flight in these individuals, although any influence of subtle variation in wingtip shape on level flight is expected to be much smaller than on take-off or manoeuvrability.

METHODS

Experiment 1: wingtip shape, take-off and manoeuvrability

We used 43 adult European Starlings (14 males, 29 females) with undamaged flight plumage in this experiment. Birds were housed in a large outdoor aviary (approximately 2 × 5 × 2 m) in accordance with UK Home Office guidelines and provided with *ad libitum* food and water whilst not in the experimental arena. The length of each primary feather (on the left wing) was measured with Vernier callipers (to 0.01 cm accuracy) and used to derive measures of wingtip roundedness and convexity using the formulae developed by Lockwood *et al.* (1998). We assessed two forms of flight in these birds: escape take-off, and performance through an aerial obstacle course (defined as manoeuvrability for this study).

Escape take-off was assessed in a long, narrow flight aviary (approximately 3.5 × 1.2 × 2 m). One end of this experimental aviary contained perching sites, food, drinking water and bathing water. The opposite end of the aviary was empty except for a single perch positioned 5 cm above the floor, from which birds were released. Birds were placed by hand on the perch at the empty end of the aviary and released with the simultaneous sounding of a loud, vocal startle stimulus. All birds ascended immediately from the perch and flew to the end of the aviary containing perching sites. The take-offs were recorded on a Hi-8 video camera (Sony CCD-FX700E) at a shutter speed of 1/4000 s, the camera being placed perpendicular to the line of flight. We did not measure three-dimensional movement of the bird. However, all birds tended to fly directly away from the perch, so minimizing *z*-axis movement that was not captured on the video. The camera was focused so that the birds did not enter the periphery of the field of view (where the camera lens is curved to the greatest degree), hence minimizing parallax. The video tapes were subsequently analysed (using frame-by-frame playback on a Sony EV-2000E) and digitized (on a Macintosh 7500AV computer using the public domain NIH Image program) to derive measures of trajectory and speed. The first frame of take-off was taken to be the first frame when a bird's feet had left the perch. For each bird, the bill tip was digitized on the following five frames (i.e. 0.2 s of flight). Movements of the birds were analysed using software (MOVE program; see Rayner & Aldridge 1985 for algorithms) written by Jeremy Rayner (University of Bristol, UK) to obtain values of take-off angle and flight speed. Within a single flight, angle and speed data were averaged between digitized frames of the video. Before each trial, birds were weighed on an electronic balance to 0.1 g accuracy.

Performance through an aerial manoeuvrability course was assessed in the same flight aviary used for the take-off analysis. Wooden poles, covered in waterproof parcel tape, were suspended from the aviary ceiling in ordered rows. There were five parallel rows of poles, which alternated from having three to four poles per row, in a staggered arrangement (cf. Swaddle *et al.* 1996). Within rows, poles were 0.3 m or 0.25 m apart. Rows were 0.25 m apart. For each bird, the tips of the distal-most primaries from both wings were dipped in a small, standardized volume of water-soluble black ink. Birds were released from a perch approximately 1.5 m above the floor at the open end of the course and simultaneously exposed to a loud vocal startle stimulus. All individuals flew directly through the course to the opposite side of the aviary. We recorded the number of rows that each individual touched. This methodology has revealed relations between manoeuvrability and morphological parameters such as body mass and wing fluctuating asymmetry in previous studies (Witter *et al.* 1994, Swaddle *et al.* 1996, Swaddle & Witter 1998). As for the take-off analysis, body mass was recorded (to 0.1 g accuracy) on an electronic balance before each trial. After manoeuvrability trials, all birds were supplied with fresh bathing water.

Experiment 2: wingtip shape and level flight-speed

We used 17 wild-caught adult female European Starlings with undamaged flight plumage in this experiment. They were housed in identical conditions as described above. The same morphological measurements were taken as described in the first experiment. Here, we assessed level flapping flight speed by allowing birds to fly freely along a long flight corridor (approximately 14 × 1.5 × 2.5 m) between perches placed at either end that were 1.5 m above the floor. A video camera (as described above) was placed perpendicular to the line of flight and was focused at the central 2-m section of the corridor. We subsequently analysed three consecutive frames (0.12 s) of the video of each bird to measure level flight speed, using the same software and hardware as described for take-off. We ignored all flights made by birds in which they were seen to ascend, descend or turn while flying across the field of view. Turning flight was identified by the posture of the birds in flight on the video recordings and by our direct observations during flight trials. Ascent and descent were defined as changes in the vertical location of the birds by more than 10 cm during the flight across the field of view. Thus, we only recorded speed from straight level flights. We took the mean value of speed from the first four separate flights that satisfied our criteria for straight level flight for each bird. Body masses were also recorded immediately before each flight session, as described above.

Experiment 3: within-individual changes in wingtip shape and flight performance

Twelve wild-caught adult female Starlings with undamaged flight plumage were used in this experiment. All birds were housed in identical conditions to those described above, except as follows. The birds had previously moulted in captivity in large outdoor aviaries (approximately 2 × 5 × 2 m) and were subsequently transferred to an indoor aviary (approximately 1.5 × 5 × 2 m) and exposed to an 8 : 16 h L : D photoperiod for 8 months to ensure that they became photosensitive (Burger 1947, Farner *et al.* 1983). In July, the birds were transferred to four outdoor experimental aviaries (approximately 3 × 3 × 2.5 m), with three birds in each. As the experimental aviaries were outdoors, all birds were exposed to natural photoperiodic cues to induce photorefractoriness and moult (Dawson *et al.* 1985). Wingtip shape and four measures of flight performance were assessed before moult commenced and after moult had been completed, so that within-individual changes in wingtip shape between moults could be compared with the associated within-individual changes in flight performance. (i) Angle of trajectory of take-off and (ii) speed of take-off were assessed in a long flight aviary (approximately 8 × 2 × 2.5 m) that was constructed in a similar fashion to that used in experiment 1. (iii) Performance through an aerial obstacle course (identical to experiment 1) was assessed in the same flight aviary as for take-off. (iv) Level flapping-flight speed was assessed in a long, narrow flight aviary (approximately 16 × 2 × 2.5 m). Protocols employed for flight analyses were identical to those used in the first two experiments. Birds were also weighed immediately before each flight session, as described above. In addition to measuring wingtip roundedness and convexity, we also recorded overall wing size (C*1*, first principal component from Lockwood *et al.*'s (1998) size-constrained component analysis), wing length (from folded wings) and Kipp's index ($I_k = 100 \cdot \Delta S1/W$, where $\Delta S1$ represents the distance from the tip of the first (outermost) secondary to the wingtip when the wing is folded and W represents wing length of a folded wing), which is a good surrogate for aspect ratio (Kipp 1959, Lockwood *et al.* 1998) for all birds, before and after moult.

Statistical analysis

The relationships between flight and wingtip shape were examined by linear regression analyses between wingtip shape and the residuals of the regression of body mass with flight performance. Hence, body mass was controlled for in all analyses. Experiments 1 and 2 examined the relationships between among-individual differences in wingtip shape and flight performance, whereas experiment 3 investigated the influence of within-individual changes in wingtip shape on aspects of flight. Within-individual changes in wingtip shape, flight performance and body mass were calculated by subtracting values 'before' moult from those obtained 'after' moult. All analyses were performed on Minitab for Windows (Minitab Inc. 1994) using two-tailed tests of significance.

RESULTS

Experiment 1

There were no sex differences in either measure of wingtip shape (roundedness: $F_{1,41} = 0.50$, $P = 0.486$; convexity: $F_{1,41} = 0.160$, $P = 0.160$). Therefore, sexes were pooled for all subsequent analyses.

Linear regression analysis of wingtip shape with the residual angle of take-off (controlling for body mass) revealed that wingtip roundedness was positively associated with angle of take-off ($r^2 = 0.12$, $F_{1,41} = 5.82$, $P = 0.020$; Fig. 2). There was also a non-significant positive association between wingtip

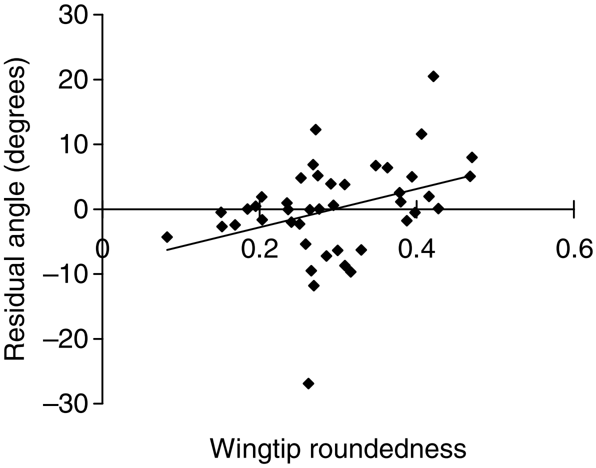

Figure 2. Residual angle of take-off, controlling for body mass, vs. wingtip roundedness. There was a significant positive relationship: residual angle = −8.75 + 29.7*roundedness; $r^2 = 0.12$, $F_{1,41} = 5.82$, $P = 0.020$. The linear regression line is indicated on the graph.

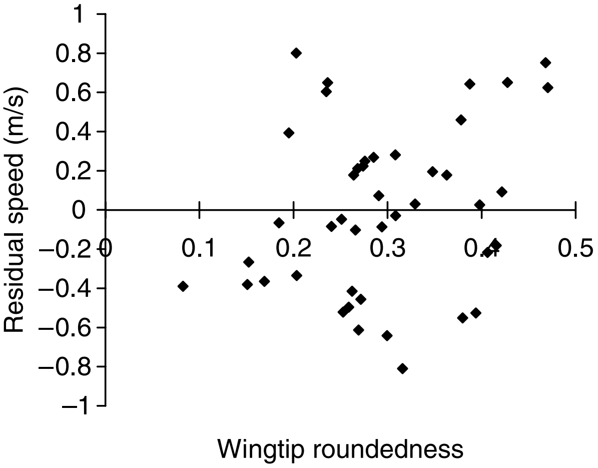

Figure 3. Residual speed of take-off, controlling for body mass, vs. wingtip roundedness. There was no discernible relationship.

roundedness and speed of take-off flight ($r^2 = 0.08$, $F_{1,41} = 3.32$, $P = 0.076$; Fig. 3). Wingtip convexity did not appear to be related to either take-off parameter (take-off angle: $F_{1,41} = 1.07$, $P = 0.308$; take-off speed: $F_{1,41} = 0.37$, $P = 0.548$). Performance through the manoeuvrability course, as assessed by the number of rows of poles that birds touched, was not related to either wingtip roundedness ($F_{1,41} = 1.16$, $P = 0.288$) or wingtip convexity ($F_{1,41} = 0.82$, $P = 0.370$), when body mass was controlled for.

Experiment 2

Level flapping-flight speed was not significantly related to wingtip roundedness ($F_{1,15} = 0.74$, $P = 0.403$) or wingtip convexity ($F_{1,15} = 0.46$, $P = 0.507$), when body mass was controlled for. Mean (± se) level flapping flight speed for these birds was 13.42 (± 0.24) m/s.

Experiment 3

We found no relationship between within-individual changes in wingtip roundedness ($F_{1,10} = 0.17$, $P = 0.69$) or convexity ($F_{1,15} = 0.20$, $P = 0.67$) and within-individual changes in take-off speed. However, within-individual changes in wingtip roundedness were significantly and positively related to within-individual changes in the angle of take-off trajectory ($r^2 = 0.50$, $F_{1,10} = 10.04$, $P = 0.010$; Fig. 4). There was no relationship between wingtip convexity and take-off angle ($F_{1,10} = 1.18$, $P = 0.30$).

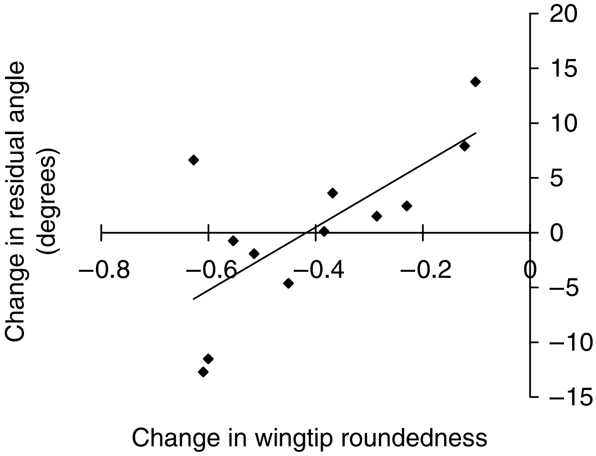

Figure 4. Residual change in take-off angle, controlling for body mass, vs. change in wingtip roundedness ('after' minus 'before' moult). There was a significant positive relationship: residual change in angle = 12.0 + 28.8*change in roundedness; $r^2 = 0.50$, $F_{1,10} = 10.04$, $P = 0.010$. The linear regression line is indicated on the graph. All birds in this experiment experienced a decrease in wingtip roundedness. This could be related to wingtip abrasion before moult, but we tried to ensure that birds used for this experiment did not have obviously abraded feathers.

To explore further the relationships between changes in take-off angle and flight morphology, we also compared within-individual changes in overall wing size (which is a good proxy for wing area), wing length and Kipp's index with changes in residual take-off angle (controlling for body mass). There were no associations between changes in overall wing size ($F_{1,10} = 2.41$, $P = 0.152$), wing length ($F_{1,10} = 1.73$, $P = 0.218$) or Kipp's index ($F_{1,10} = 1.79$, $P = 0.211$) with changes in residual take-off angle (controlling for body mass).

There were no significant relationships between within-individual changes in wingtip shape and manoeuvrability (roundedness: $F_{1,10} = 0.11$, $P = 0.75$; convexity: $F_{1,10} = 0.16$, $P = 0.69$). Similarly, there were no associations between changes in level flapping-flight speed and wingtip roundedness ($F_{1,10} = 0.58$, $P = 0.46$) or convexity ($F_{1,10} = 0.01$, $P = 0.97$).

DISCUSSION

Flight performance analyses of birds from experiment 1 indicate that there was a correlation between wingtip shape and angle (but not speed) of escape take-off among individuals. These among-individual differences appeared consistent with the data generated by experiment 3, in which we examined within-individual changes in wingtip shape and flight. In experiment 3, birds whose wingtip shape became more rounded after moult took off from the ground at a steeper angle than birds whose wingtip shape became relatively more pointed. The data from all three experiments consistently indicate a lack of association between wingtip shape and level flight speed or performance through an aerial manoeuvrability course. These data are compatible with our prediction that changes in wingtip shape are more likely to influence low-speed flight than flight at intermediate and higher speeds.

The positive association between wingtip roundedness and angle of take-off in both experiments 1 and 3 indicates that birds with relatively rounded wingtips take off from the ground at a steeper angle of trajectory. However, these data do not allow us to disentangle direct and indirect effects of wingtip shape on take-off performance. In experiment 1, there may have been among-individual correlates of wingtip shape (either physiological or behavioural) that could influence flight performance. In experiment 3, we controlled for among-individual differences by studying within-individual changes in wing form and flight associated with moult. Nevertheless, there could potentially be within-individual changes in physiological parameters associated with moult that are correlated with consistent changes in wingtip shape. All individuals in experiment 3 displayed a noticeable reduction in wingtip roundedness (Fig. 4), and hence birds that displayed the greatest changes in wingtip shape were also those that became more 'pointed'. It is possible that these individuals also experienced a change in some other (undetected) factor that influenced their flight performance so that they took off at a shallower angle of ascent. To examine this possibility, we used regression analysis to test for differences in body condition (defined here as within-individual changes in body mass, i.e. changes in mass controlling for body size) between birds that experienced large changes in wingtip shape and those that experienced small changes ($F_{1,10} = 0.15$, $P = 0.703$). There appeared to be no detectable change in the condition of birds due to within-individual changes in wingtip shape. It is also important to point out that changes in take-off angle could not be explained by the small variations in wing length or wing size that occurred between moults, and that take-off was not related to Kipp's index. It is probable that the only way truly to isolate and quantify any direct causal relationship between wingtip shape and flight is to perform an experimental manipulation of wingtip shape. We hope that our preliminary data will help to indicate the possible effects (or lack thereof) of wingtip shape on flight performance and generate further study in other species.

A more rounded wing will produce a greater proportion of its lift from the distal part of the handwing, where the wing is moving faster. Producing lift more distally will result in greater force generation, which should aid slow flight, in particular take-off from a standing start on the ground. In addition, it has been hypothesized that a more rounded wingtip will generate greater thrust during slow flight (Lockwood *et al.* 1998). These factors combined support, and perhaps explain, our finding that Starlings with more rounded wingtips take off from the ground at a steeper angle of ascent.

No matter how the relationship between wingtip shape and angle of take-off can best be explained, the enhanced ability of individuals with rounded wingtips to take off from the ground more steeply may have significant implications for individual survival and fitness. The ability to take off at a steep angle of ascent has been demonstrated to be an effective means of predator-avoidance, particularly in small passerines (reviews in Lima 1993, Witter *et al.* 1994). Hence, our findings could imply that individuals with relatively rounded wingtips may, with other ecological and morphological factors being equal, experience a lower level of predation risk due to their enhanced take-off performance. In light of this, it may be relevant that we have previously reported a significant negative relationship between relative predation risk and wingtip roundedness in small passerine species predated by Eurasian Sparrowhawks *Accipiter nisus*, i.e. species with relatively rounded wings experienced a lower predation risk (Swaddle & Lockwood 1998).

Another consistent pattern across all three experiments was that wingtip convexity was unrelated to any of the flight parameters we quantified. This could be, in part, because the index of wingtip convexity discussed and developed by Lockwood *et al.* (1998) explains less variation in avian wingtip shape than does their roundedness index (14% of shape variation explained by convexity vs. 77% explained by roundedness, in an interspecific sample).

Relationships between among-species variation in wing shape and take-off parameters have been reported previously. For example, Raikow (1973) reported that diving duck species that take off from water by running across the surface and flapping their wings until sufficient speed and lift are attained have a more pointed wing than 'dabbling' duck species that can 'rocket' clear of the water surface during take-off, ascending almost vertically. Additionally, Pennycuick (1983) proposed that among-species variation in wing roundedness may influence take-off in three species of tropical bird. However, we are not aware of any intraspecific studies of wingtip shape and flight performance within any bird group.

This study indicates that wingtip shape can be related to flight performance in European Starlings. Birds with rounded wingtips take off from the ground at a steeper angle of trajectory. Although the mechanism by which wingtip shape influences take-off is as yet not clear, the increased take-off ability of individuals with rounded wingtips may have implications for individual survival, as take-off is an important antipredator behaviour.

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REFERENCES

Alatalo, R.V., Gustafsson, L. & Lundberg, A. 1984. Why do young passerine birds have shorter wings than older birds? *Ibis* **126**: 410–415.

Anderson, M. & Norberg, R.Å. 1981. Evolution of sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15**: 105–130.

Birch, J.M. & Dickinson, M.H. 2001. Spanwise flow and the attachment of the leading-edge vortex on insect wings. *Nature* **412**: 729–733.

Borras, A., Cabrera, J., Colome, X. & Senar, J.C. 1993. Sexing fledglings of cardueline finches by plumage color and morphometric variables. *J. Field Ornithol.* **64**: 199–204.

Burger, J.W. 1947. On the relation of day length to the phase of testicular involution and inactivity of the spermatogenic cycle of the Starling. *J. Exp. Zool.* **195**: 259–268.

Combes, S.A. & Daniel, T.L. 2001. Shape, flapping and flexion: wing and fin design for forward flight. *J. Exp. Biol.* **204**: 2073–2085.

Dawson, A., Goldsmith, A.R. & Nicholls, T.J. 1985. Thyroidectomy results in termination of photorefractoriness in Starlings (*Sturnus vulgaris*) kept in long day lengths. *J. Reprod. Fertil.* **74**: 527–533.

Epting, R.J. & Casey, T.M. 1973. Power output and wing disc loading in hovering hummingbirds. *Am. Nat.* **107**: 1–46.

Farner, D.S., Donhan, R.S., Matt, K.S., Mattocks, P.W., Moore, M.C. & Wingfield, J.C. 1983. The nature of photorefractoriness. In Mikami, S., Homma, K. & Wada, M. (eds) *Avian Endocrinology: Environmental and Ecological Perspectives*: 149–166. Tokyo: Japanese Science Society Press.

Kipp, F. 1959. Der Handflügel-Index als flugbiologische Maß. *Vogelwarte* **20**: 77–86.

Lima, S.L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *Wilson Bull.* **105**: 1–47.

Lockwood, R., Swaddle, J.P. & Rayner, J.M.V. 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *J. Avian Biol.* **29**: 273–292.

Madan Mohan, B., Vijaya, N. & Chari, N. 1982. Flight parameters and energetics of House Sparrow. *Comp. Physiol. Ecol.* **7**: 8–10.

Minitab Inc. 1994. *Minitab 10, User's Guide*. State College, PA: Minitab Inc.

Mulvihill, R.S. & Chandler, C.R. 1990. The relationship between wing shape and differential migration in the Dark-eyed Junco. *Auk* **107**: 490–499.

Norberg, U.M. 1987. Wing form and flight mode in bats. In Fenton, M.B., Racey, P. & Rayner, J.M.V. (eds) *Recent Advances in the Study of Bats*: 43–56. Cambridge: Cambridge University Press.

Norberg, U.M. 1990. *Vertebrate Flight*. Berlin: Springer-Verlag.

Norberg, U.M. 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Funct. Ecol.* **9**: 48–54.

Norberg, R.Å. & Norberg, U.M. 1971. Take-off, landing and flight speed during fishing flights. *Ornis Scand.* **2**: 55–67.

Norberg, U.M. & Rayner, J.M.V. 1987. Ecomorphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond. B* **316**: 335–427.

Pennycuick, C.J. 1975. Mechanics of flight. In Farner, D.S. & King, J.R. (eds) *Avian Biology*, Vol. 5: 1–75. New York: Academic Press.

Pennycuick, C.J. 1983. Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificens*, *Pelecanus occidentalis* and *Coragyps atratus*. *J. Exp. Biol.* **102**: 307–325.

Pennycuick, C.J. 1989. *Bird Flight Performance: a Practical Calculation Manual*. Oxford: Oxford University Press.

Raikow, R.J. 1973. Locomotor mechanisms in North American ducks. *Wilson Bull.* **85**: 295–307.

Rayner, J.M.V. 1979. A new approach to animal flight mechanics. *J. Exp. Biol.* **80**: 17–54.

Rayner, J.M.V. 1986. Vertebrate flapping flight mechanics and aerodynamics, and the evolution of flight in bats. In Nachtigall, W. (ed.) *Biona Report 5. Bat Flight – Fledermausflug*: 27–74. Stuttgart: Gustav Fischer.

Rayner, J.M.V. 1988. Form and function in avian flight. *Curr. Ornithol.* **5**: 1–66.

Rayner, J.M.V. 1990. The mechanics of flight and bird migration performance. In Gwinner, E. (ed.) *Bird Migration: the Physiology and Ecophysiology*: 283–299. Berlin: Springer-Verlag.

Rayner, J.M.V. 1993. On aerodynamics and the energetics of vertebrate flapping flight. In Cheer, A.Y. & van Dam, C.P. (eds) *Fluid Dynamics in Biology*: 351–400. Providence, RI: American Mathematics Society.

Rayner, J.M.V. 1995. Dynamics of the vortex wakes of swimming and flying vertebrates. *Symp. Soc. Exp. Biol.* **69**: 131–155.

Rayner, J.M.V. & Aldridge, H.D.J.N. 1985. Three-dimensional reconstruction of animal flight paths and the turning flight of microchiropteran bats. *J. Exp. Biol.* **118**: 247–265.

Saville, D.B.O. 1957. Adaptive evolution in the avian wing. *Evolution* **11**: 212–224.

Swaddle, J.P. & Lockwood, R. 1998. Morphological adaptations to predation risk in passerines. *J. Avian Biol.* **29**: 172–176.

Swaddle, J.P. & Witter, M.S. 1998. Cluttered habitats reduce wing asymmetry and increase flight performance in European Starlings. *Behav. Ecol. Sociobiol.* **42**: 281–287.

Swaddle, J.P., Witter, M.S., Cuthill, I.C., Budden, A. & McCowen, P. 1996. Plumage condition affects flight performance in Common Starlings: implications for developmental homeostasis, abrasion and moult. *J. Avian Biol.* **27**: 103–111.

Tiainen, J. 1982. Ecological significance of morphometric variation in three sympatric *Phylloscopus* warblers. *Annal. Zool. Fenn.* **19**: 285–295.

Tiainen, J. & Hanski, I.K. 1985. Wing shape variation of Finnish and Central European Willow Warblers *Phylloscopus trochilus* and Chiffchaffs *P. collybita*. *Ibis* **127**: 365–371.

Tucker, V.A. 1973. The energetics of bird flight. *Sci. Am.* **220**: 70–78.

Voelke, G. 2001. Morphological correlates of migratory distance and flight display in the avian genus *Anthus*. *Biol. J. Linn. Soc.* **73**: 425–435.

Witter, M.S., Cuthill, I.C. & Bonser, R.H.C. 1994. Experimental investigations of mass-dependent predation risk in the European Starling, *Sturnus vulgaris*. *Anim. Behav.* **48**: 201–222.

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