

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

JOHN P. SWADDLE^{1*} & ROWAN LOCKWOOD²

¹Institute of Zoology, University of Oxford, Oxford, UK; ²Department of Zoology, University of Cambridge, Cambridge, UK; *Correspondence: j.p.swaddle@zoo.ox.ac.uk

Although wingform is known to differ among individuals of the same species it is not known

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 $3.5 \times 1.2 \times 2$ 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 y -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 $14 \times 1.5 \times 2.5$ 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 $2 \times 5 \times 2$ m) and were subsequently transferred to an indoor aviary (approximately $1.5 \times 5 \times 2$ 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 $3 \times 3 \times 2.5$ 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.*

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 ass-

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 roundness 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

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