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Within-individual changes in developmental stability affect flight performance

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Developmental stability, as measured by fluctuating asymmetry, has been purported to be an indicator of individual quality, and low asymmetry can be selected for by sexual selection processes. However, low asymmetry can also arise due to biomechanical constraints operating on trait design, as it is predicted that asymmetry will decrease mechanical efficiency. Specifically, it has been predicted that wing length asymmetry will be negatively related to avian flight performance. To date, empirical investigations have only studied the influence of increasing asymmetry beyond naturally occurring average values. I examined the influence of within-individual changes in primary feather developmental stability on flight performance in European starlings by studying asymmetry and flight before and after wing molt. Individuals that exhibited a decrease in wing asymmetry through molt experienced increased aerodynamic performance in terms of both angle of takeoff and level flapping-flight speed. Birds that increased wing asymmetry suffered a decrease in flight performance. Takeoff speed and the ability to negotiate an aerial obstacle course were unaffected by asymmetry. My data provide empirical support for the predicted influence of wing asymmetry on flight, even though the changes in asymmetry were very small (mean = 0.47% of trait size) and further indicate the importance of biomechanical considerations in any study of developmental stability. *Key words:* developmental stability, flight, fluctuating asymmetry, molt, starling. *[Behav Ecol 8:601–604 (1997)]*

Developmental stability can be accurately estimated by measuring the asymmetry between left and right components of bilaterally symmetric traits (Beardmore, 1960; Ludwig, 1932; Waddington, 1960), i.e., by measuring fluctuating asymmetry (Ludwig, 1932). These minor deviations from symmetry can result from both genetic and environmental factors that disturb developmental processes (reviews in Clarke, 1993; Leary and Allendorf, 1989; Møller and Swaddle, in press; Watson and Thornhill, 1994). Recently there has been much interest in the role of fluctuating asymmetry in evolutionary biology, as low asymmetry can be related to high individual fitness (Møller and Swaddle, in press; Watson and Thornhill, 1994). Additionally, low asymmetry can be selected for through sexual selection processes (e.g., Allen and Simmons, 1996; Bennett et al., 1996; Møller, 1992, 1993; Swaddle and Cuthill, 1994a,b), resulting in symmetric individuals attaining increased reproductive success (Møller, 1992, 1993; Swaddle, 1996). However, low asymmetry is also predicted to occur for functional reasons, as asymmetry should often reduce biomechanical performance (Balmford et al., 1993; Evans and Hatchwell, 1993; Thomas, 1993). Experimental manipulations of morphological asymmetry have resulted in a loss of performance (Evans et al., 1994; Møller, 1991; Swaddle et al., 1996), although these manipulations have generally resulted in asymmetries substantially larger than those most often observed in nature. Additionally, all of these investigations have manipulated traits in order to increase asymmetry and decrease mechanical performance. A more convincing and conservative test of the purported relationship between asymmetry and performance is to increase mechanical efficiency through a decrease in asymmetry.

In this study, I examined the relations between developmental stability and performance by studying the within-individual changes in primary feather asymmetry between subsequent molts in European starlings (*Sturnus vulgaris*) and the associated changes in flight performance. It was predicted that birds that increased in wing asymmetry would suffer reductions in flight performance, whereas those that decreased wing asymmetry through molt would experience a relative increase in flight performance (cf. Thomas, 1993).

METHODS

I used 18 wild-caught adult starlings in this experiment. All birds were provided with food (turkey starter crumbs), drinking water, and bathing water ad libitum throughout the entire experiment. The birds had previously molted in captivity in large outdoor aviaries (approximately 2×5×2m) and were subsequently transferred to an indoor aviary (approximately 1.5×5×2m) and exposed to a 8 h:16 h light:dark photoperiod for 8 months to ensure that they became photosensitive (Burger, 1947; Farner et al., 1983). In July 1996, I transferred the birds to six outdoor experimental aviaries (approximately 3×3×2.5m) in groups of three. As the experimental aviaries were outdoors, all birds were exposed to natural photoperiodic cues to induce photorefractoriness and molt (Dawson et al., 1985). I assessed the asymmetry of all primary feathers and flight performance of all birds both before and after molt. One individual suffered significant wing abrasion and was excluded from the analyses, reducing the sample size to 17.

Primary asymmetry

I measured the length of all nine primary feathers on all individuals on both left and right wings with Vernier calipers to 0.01 cm accuracy. From these measures absolute asymmetry (|L − R|) was derived for each feather on each individual. All asymmetry measurements were repeated three times on each side to minimize measurement error (Palmer, 1994; Swaddle et al., 1994) and were shown to be highly repeatable ($F_{33,132} > 4.48$; $p < .0001$ in all cases). All feathers displayed the statistical properties of fluctuating asymmetry, i.e. signed asymmetries exhibited a normal distribution (Anderson-Darling *a2* < 0.278, $p > .602$ in all cases) around a mean of zero ($t < 1.21$, $p > .122$, in all cases) (Palmer, 1994; Swaddle et al.,

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1994). Any abraded or damaged feathers were not included in asymmetry analyses (Cuthill et al., 1993). I calculated mean absolute asymmetry across all primary feathers for each individual.

Flight performance

I assessed four measures of flight performance: (1) angle of trajectory of takeoff and (2) speed of takeoff were assessed in a long flight aviary (approximately 8 × 2 × 2.5 m). Most of the aviary was open space, except for one end that contained vegetation (protective cover). Birds were released in the open end of the aviary from a perch positioned 5 cm above the ground, simultaneously with the sounding of a loud vocal startle stimulus (see Witter et al., 1994). Takeoffs were recorded on videotape (Sony CCD-FX700E); the camera was placed perpendicular to the line of flight. Each video frame of takeoff was subsequently digitized using a Hi-8 video player (Sony EV-C2000E), a Power Macintosh 7500AV, and the public domain software NIH Image. Specifically, the position of the tip of each bird's bill was digitized from immediately after the bird had ascended from the perch and the subsequent 0.2 s of flight. From the coordinates of the bird in each frame, I calculated the speed of take-off and angle of trajectory using software written by Jeremy Rayner, University of Bristol (algorithms in Rayner and Aldridge, 1985). Before each trial, body mass was recorded on an electronic balance to 0.01 g accuracy.

(3) Performance through an aerial obstacle course was used to assess each bird's maneuverability (this definition of maneuverability contains elements of both maneuverability and agility). The obstacle course measured 1.5 × 2 × 4 m and comprised a series of rows of identical wooden poles covered in parcel tape, suspended from the course ceiling, which the birds had to negotiate (see Witter et al., 1994). There were five rows of poles, which alternated from having three or four poles in a staggered arrangement 0.3 m and 0.25 m apart. Rows were 0.25 m apart. Both wingtips of each bird were dipped in a small, standardized volume of water-soluble black ink. Birds were held by the experimenter on a perch approximately 1.5 m from the floor at the beginning of the course. They were then exposed to a short vocal startle stimulus and simultaneously released. Birds flew directly through the course, and the number of rows that each individual made contact with, displayed by black ink marks on the poles, was noted (cf. Møller, 1991). Body masses were also recorded immediately before each flight session, as described above. After maneuverability trials, all birds were supplied with fresh bathing water.

(4) Measurements of level flapping-flight speed were assessed in a long, narrow flight aviary (approximately 16 × 2 × 2.5 m) where birds were allowed to fly freely between perches placed at either end that were 1.5 m above the floor. A video camera (as above) was placed perpendicular to the line of flight and was focused at the central 2-m section of the corridor. I digitized the position of each bird over 0.12 s of flight, using the same procedure as in the takeoff analysis, to derive a measure of level flapping-flight speed. All flights in which birds ascended, descended (by more than 10 cm), or turned while flying across the field of view were ignored. The mean value of speed from the first three separate flights that satisfied the criteria for level flight for each bird was used in analyses. Body masses were also recorded immediately before each flight session, as described above.

Statistical analyses

I calculated within-individual changes in mean asymmetry and flight performance by subtracting values from before molt from those obtained after molt. Changes in mean asymmetry were then compared with changes in flight performance by performing Spearman rank correlations (Siegel and Castellan, 1988) between asymmetry and the residuals of regression analyses of each flight measure with body mass. Hence, body mass was controlled for in all flight analyses. All statistical analyses were performed on Minitab for Windows (Minitab Inc., 1994) using two-tailed probability tests. All values are given as means (±SE)..

RESULTS AND DISCUSSION

Overall asymmetry, across the whole population, did not differ between before and after molt (Wilcoxon matched-pairs signed-ranks test, $T = 74.0$, $N = 17$, $p = .93$), indicating that environmental conditions were similar during both molts. Additionally, overall flight performance did not differ across the whole population between molts ($t < 0.01$, $N = 17$, $p > .96$, for all flight measures), suggesting that overall flight behavior was not differentially influenced by either molt episode. As a population, birds exhibited similar wing asymmetries and flight behaviors both before and after molt.

Within-individual changes in asymmetry did not influence takeoff speed ($r_S = .189$, $N = 17$, $p = .438$). However, changes in mean wing asymmetry were negatively related to change in angle of takeoff ($r_S = -.542$, $N = 17$, $p = .0165$). Individuals that decreased their primary asymmetry between molts also increased the angle of their takeoff trajectory (Figure 1). This change in flight behavior can be seen as an enhancement of performance, as an increased angle of takeoff is likely to increase aspects of individual fitness (Lima, 1993; Witter et al., 1994). For example, many avian species rely on a short escape flight to cover to evade predation (e.g., Grubb and Greenwald, 1982; Lazarus and Symonds, 1992; Lindström, 1989). The trajectory of such a takeoff response has been suggested as an important determinant of predation risk (e.g., Cresswell, 1993; Kenward, 1978; Page and Whitacre, 1975; Witter et al., 1994).

Surprisingly, performance through the aerial maneuverability course was not influenced by changes in primary asymmetry ($r_S = .086$, $N = 17$, $p = .726$). Previous investigations of the effects of asymmetry on flight performance have indicated that asymmetry of both wings and tails decreases maneuverability and agility (Evans et al., 1994; Møller, 1991; Swaddle et al., 1996). It is possible that the method of quantifying maneuverability used here is not sufficiently sensitive to discriminate subtle changes in this flight parameter. Therefore, it is difficult to interpret this non-significant result. Detailed kinematic analyses of high-speed video footage of birds performing standardized maneuvers may be more revealing in this context.

Within-individual changes in primary asymmetry did influence level flapping-flight speed ($r_S = .463$, $N = 17$, $p = .046$). Birds that experienced a decrease in wing asymmetry between molts flew at a slower speed after molt, whereas those that experienced an increase in wing asymmetry between molts subsequently flew at a greater speed (Figure 2). Thomas (1993) predicted that, at a flight speed of approximately 9 m/s, a 0.5% wing length asymmetry would increase the power required for flight by approximately 1%. The changes in asymmetry recorded were approximately 0.47% (±0.08%) of trait size, although these asymmetries did not specifically measure wing length differences (see discussion in Swaddle et al., 1996), and the birds flew at a mean speed of 8.64 (±0.73) m/s before molt and 8.81 (±0.71) m/s after molt. As asymmetry is predicted to increase the power required for flight, it could also be predicted that asymmetry will increase both minimum power speed (V_{mp}) and maximum range speed

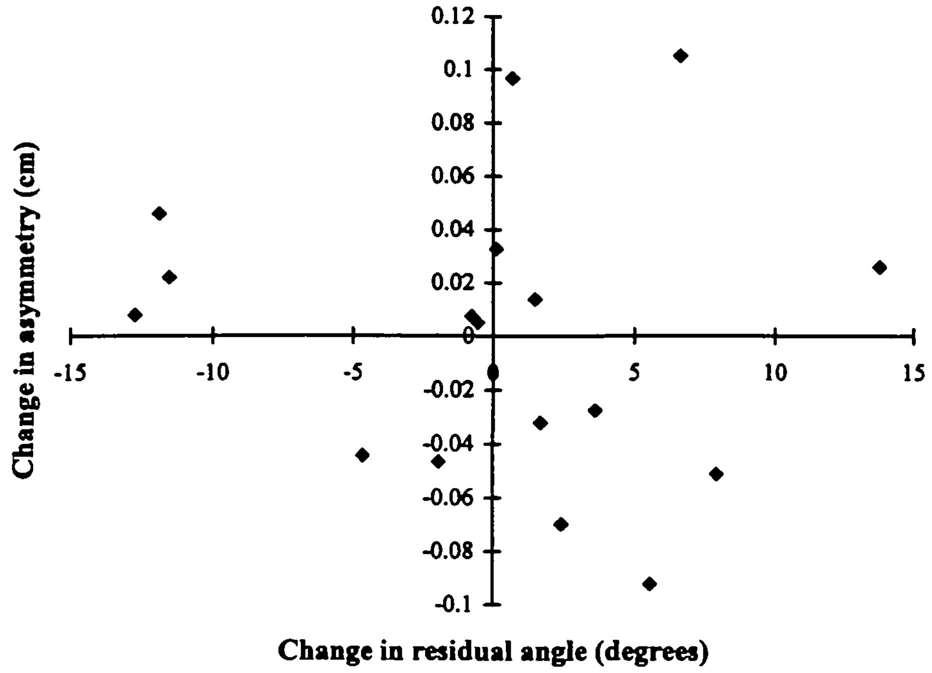

Figure 1
Within-individual change in residual angle of take-off (controlling for body mass) versus within-individual change in mean primary feather asymmetry. Each data point represents one individual. There is a significant negative relationship.

(V_{mr}) (see Norberg, 1990). Therefore, the data fit the theoretical predictions; asymmetry increases level flight speed. Here, decreasing asymmetry can also been interpreted as increasing flight performance, as the costs of flight are apparently decreased in birds that reduced their primary feather asymmetry through molt.

Previous theoretical considerations of the influence of minor asymmetries on flight performance have predicted that many aspects of flight would be detrimentally affected by increasing asymmetry and, conversely, aerodynamic performance would be enhanced by decreased asymmetry (Thomas, 1993). However, empirical studies have generally used asymmetries much larger than those commonly observed in nature; all manipulations performed to date have increased rather than decreased asymmetry within the experimental designs (Evans et al., 1994; Møller, 1991; Swaddle et al., 1996). The present study is the first to implement a protocol in which the biomechanical consequences of a decrease in developmental stability have been observed and hence it provides a more conservative test of the flight predictions. Nevertheless, the data largely uphold Thomas's (1993) model; wing asymmetry is negatively related to flight performance. In terms of both takeoff angle and level flight speed, birds that experienced a reduction in primary feather asymmetry as a consequence of molt exhibited an increase in aerodynamic performance.

Because asymmetry was not manipulated independent of the underlying physiology, it is possible that the observed associations between wing asymmetry and flight parameters

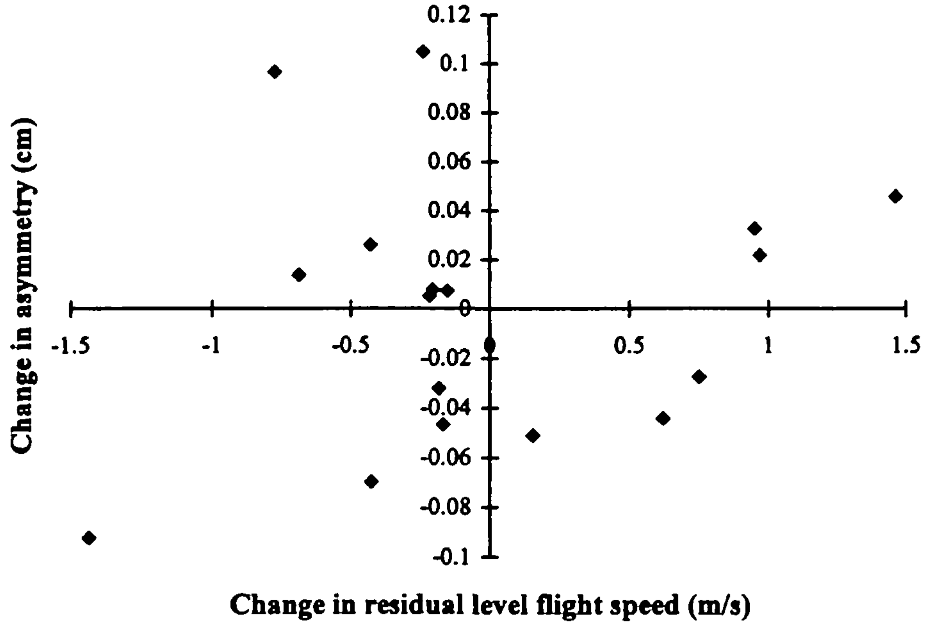

Figure 2
Within-individual change in residual level flapping-flight speed (controlling for body mass) versus within-individual change in mean primary feather asymmetry. Each data point represents one individual. There is a significant positive relationship.

could be mediated through an indirect effect of developmental stability. Even though within-individual changes were studied, this does not exclude the possibility that birds' condition was in some way correlated with their change in wing asymmetry and hence change in flight behavior. However, it has been hypothesized that a single genome is capable of producing a range of asymmetry values (see Whitlock, 1996), and flight feathers regrew, whereas the underlying tissues were not regenerated anew, so it could be postulated that the observed within-individual changes in aerodynamic performance were mediated by the changes in primary feather asymmetry. Whether flight was affected directly or indirectly by primary developmental stability, the conclusions do not alter; subtle within-individual decreases in wing asymmetry are associated with increased flight performance.

In summary, this study provides empirical support for the published hypotheses relating asymmetry with flight performance by indicating that reduced developmental instability is associated with increased flight performance. This further highlights the importance of biomechanical considerations in studies of developmental stability and supports the idea that developmental stability is a manifestation of a whole nexus of interacting costs and benefits.

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