Behav Ecol Sociobiol (1998) 42: 281–287

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Cluttered habitats reduce wing asymmetry and increase flight performance in European starlings

Received: 16 June 1997 / Accepted after revision: 28 December 1997

Abstract Fluctuating asymmetry is a measure of developmental instability and results from both genomic and environmental influences. Levels of asymmetry are (in part) influenced by mechanical constraints, as asymmetry is believed to reduce efficiency. Here we have investigated the influence of habitat structure ("open" and "cluttered" environments) on primary flight feather asymmetry and flight performance in European starlings. Our findings indicate that the increased flight demands of cluttered habitats act to reduce primary asymmetry and increase flight performance. These data are discussed in terms of the influence of asymmetry on flight performance and the mechanisms that give rise to asymmetry. This study also presents a novel method, i.e., examining within-individual changes in asymmetry, by which the detrimental and positive influence of the environment could be studied in subsequent field and laboratory studies without confounding environmental effects with genomic influences.

Key words Fluctuating asymmetry · Stress · Structural complexity · Starling

Introduction

Developmental stability can be accurately estimated by measuring the asymmetry between left and right components of bilaterally symmetric traits (Ludwig 1932; Beardmore 1960; Waddington 1960), i.e. fluctuating asymmetry (Ludwig 1932). These minor deviations from symmetry can result from both genetic and environmental factors that disturb developmental processes (reviews in Leary and Allendorf 1989; Clarke 1993; Watson and Thornhill 1994; Møller and Swaddle 1997). There has been much recent interest in the role of fluctuating asymmetry in evolutionary biology as low asymmetry can be related to high individual fitness (Watson and Thornhill 1994; Møller and Swaddle 1997). Additionally, low asymmetry can be selected for through sexual selection processes (Møller 1992, 1993; Swaddle and Cuthill 1994a,b; Allen and Simmons 1996) 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 (Evans and Hatchwell 1993; Balmford et al. 1993; Thomas 1993; Swaddle 1997). Experimental manipulations of asymmetry of functional traits have resulted in a loss of performance (Møller 1991; Evans et al. 1994; 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 decrease mechanical performance. A more convincing and thorough test of the purported relationship between asymmetry and performance is to increase mechanical efficiency through a decrease in asymmetry (Swaddle 1997).

In this study, we have manipulated the habitat of European starlings (*Sturnus vulgaris*) during their molt to increase flight demands by housing birds in either cluttered or open habitats. As developmental stability is, in part, influenced by environmental factors, the environmental manipulations were hypothesized to alter the developmental stress acting on each bird and hence alter levels of individual asymmetry. Although the ontogeny of asymmetry has received relatively little attention (see Swaddle and Witter 1997), fluctuating asymmetry could be viewed as resulting from a suite of interacting costs and benefits. Our environmental manipulations alter the

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costs of asymmetry, as flight demands are presumably greater in the cluttered compared with the open treatment. Therefore, birds that occupy the more demanding environment may act to decrease their primary flight feather asymmetry to lessen flight costs. By examining within-individual changes in asymmetry and flight performance ("before" compared with "after" molt) of birds in the two habitats, we have examined whether decreased fluctuating asymmetry is related to increased biomechanical performance. These data will also give insights into the mechanism of asymmetry production, as we manipulated the costs of asymmetry during feather growth.

Methods

We used 36 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 (approx. $2 \times 5 \times 2$ m) and were subsequently transferred to an indoor aviary (approx. $1.5 \times 5 \times 2$ m) and exposed to a 8:16 h L:D photoperiod for a period of 8 months to ensure that they became photosensitive (Burger 1947; Farner et al. 1983). In July 1996, the birds were randomly divided into groups of three and transferred to 12 outdoor experimental aviaries (approx. $3 \times 3 \times 2.5$ m). The aviaries were alternately allocated to one of two treatment groups, so that there were six aviaries (each containing three individuals) in each treatment group. The treatment groups were as follows: (1) open: 16 2-m bamboo canes were suspended vertically from the ceiling and placed around the internal perimeter of each aviary; (2) cluttered: 16 identical canes were suspended from the ceiling in a dispersed pattern throughout each aviary (Fig. 1). All aviaries were arranged so that perching sites were situated at the far end of each aviary, whereas food, drinking and bathing water were at the near end. This encouraged birds to make regular trips across the length of each aviary and hence fly past the poles. Observations made during the experiment confirmed that all birds flew regularly between the perching and food sites. As the experimental aviaries were outdoors, all birds were exposed to natural photoperiodic cues to induce photorefractoriness and molt (Dawson et al. 1985). Molt commenced approximately 4 weeks after introducing birds into the outdoor aviaries and took 15 weeks to complete. We measured the asymmetry of all primary feathers and flight performance of all birds on two occasions: (1) 9 days after birds were introduced into the outdoor aviaries but before molt commenced; and (2) within 1 week of completion of molt in the outdoor aviaries.

Primary asymmetry

Before molt commenced, the length of all nine primary feathers on all individuals were measured on both left and right wings with Vernier callipers to 0.01 cm accuracy. All individual feather 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 ($F_{35,140} > 7.09$; $P < 0.0001$; in all cases) (Swaddle et al. 1994). All feathers displayed the statistical properties of fluctuating asymmetry, i.e. a normal distribution (Anderson-Darling $a^2 < 0.463$, $P > 0.243$, in all cases) around a mean of zero ($t < 1.52$, $P > 0.14$, in all cases) (Palmer 1994; Swaddle et al. 1994). Any abraded or damaged feathers were not included in asymmetry analyses (Cuthill et al. 1993; Swaddle et al. 1996). The same measurements were repeated on all individuals after molt had been completed in the experimental aviaries. Primary size [(L + R)/2] and absolute asymmetry were not related in any of the primary feathers (Spearman rank correlation coefficients: $-0.578 < r_s < 0.105$, $P > 0.131$); therefore, we did not correct asymmetry measures for a size-dependent relationship.

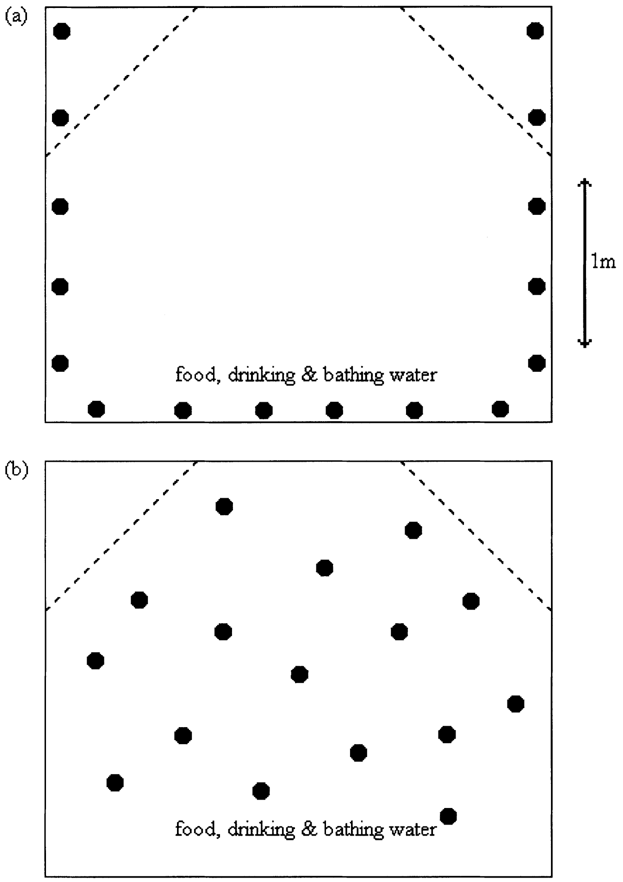

Fig. 1 Plan view of **a** open and **b** cluttered habitat aviaries. *Filled circles* represent bamboo canes suspended from the ceiling; *dashed lines* represent fixed perches

Flight performance

Both before and after molt, we recorded four measures of flight performance

1. Angle of trajectory of take-off and
2. speed of take-off were assessed in a long flight aviary (approx. $8 \times 2 \times 2.5$ m). Most of the aviary was open space, except for one end which 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 (cf. Witter et al. 1994). Take-offs were recorded on video tape (Sony CCD-FX700E), the camera being placed perpendicular to the line of flight. Each video frame of take-off was subsequently digitized using a Hi-8 video player (Sony EV-C2000E), a Power Macintosh 7500AV and the public domain 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 these co-ordinates, we calculated the speed of take-off and angle of trajectory using software written by Jeremy Rayner, University of Bristol. 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 maneu-

verability contains elements of both maneuverability and agility). The obstacle course measured 1 × 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 two poles in a staggered arrangement 0.3 m and 0.25 m apart. Rows were 0.25 m apart. Both wings of each bird were dipped in a small, standardized volume of water-soluble black ink. Birds were held by an 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 (approx. 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. We subsequently digitized the position of each bird over 0.12 s of flight, using the same procedure as in the take-off analysis, to derive a measure of level flapping-flight speed. We ignored all flights made by birds in which they were seen to ascend, descend (by more than 10 cm) or turn while flying across the field of view. We took the mean value of speed from the first three separate flights that satisfied our criteria for level flight for each bird. Body masses were also recorded immediately before each flight session, as described above.

Statistical analyses

As birds in the same aviary cannot be treated as independent data points (Hurlbert 1984), we derived a group mean asymmetry measure for each aviary; hence $n = 6$ for each treatment group. The group mean asymmetry measure was obtained by first calculating the mean absolute asymmetry across feathers for each individual, and then calculating the mean value for the three individual asymmetry estimates for each aviary. Mean flight performance for each aviary was calculated as the mean performance of each set of three individuals.

The within-group changes in mean asymmetry, comparing asymmetry before birds molt with asymmetry after molt in the treatment groups, were analyzed by Friedman non-parametric two-way analyses of variance. The initial difference in mean asymmetry between treatment groups before molt in the experimental aviaries was explored by Kruskal-Wallis non-parametric one-way analysis of variance. Changes in asymmetry due to molt in the treatment groups (asymmetry before molt subtracted from asymmetry after molt in the experimental aviaries) was also explored by a Kruskal-Wallis test. Flight analyses were performed using the MANOVA procedure with a within-subjects factor "time" (either before or after molt) and between-subjects factor "group" (treatment group) with body mass as a covariate. Statistical analyses were performed on Minitab for Windows (Minitab 1994) and SPSS for Windows (SPSS 1988) using two-tailed tests of significance.

Results

There was no difference in mean asymmetry between treatment groups before molt had commenced in the experimental aviaries ($H = 0.64$, $df = 1$, $P = 0.424$). "Open" birds did not differ in mean asymmetry comparing asymmetry before with after molt in the experimental aviaries ($S = 0.67$, $df = 1$, $P = 0.414$). In contrast, "cluttered" birds exhibited a significant decrease in asymmetry due to molt in the experimental treatments ($S = 6.00$, $df = 1$, $P = 0.014$). However, this within-group change in asymmetry for the cluttered birds is confounded with time, so it is important to examine the between-treatment difference in the within-group response to the treatments. This analysis revealed that, the birds in the cluttered treatment reduced their wing feather asymmetry relative to birds in the open treatment ($H = 4.33$, $df = 1$, $P = 0.038$; Fig. 2). As these data are within-group changes in asymmetry, the relative decrease in asymmetry of the cluttered groups is best explained through the environmental differences between the treatment groups.

In terms of flight performance, birds in the cluttered treatment exhibited a relative increase in take-off speed, compared with birds in the open treatment, after they had completed molt ($F_{1,9} = 5.17$, $P = 0.049$; Fig. 3a). However, there was no associated change in the angle of trajectory of take-off ($F_{1,9} = 0.59$, $P = 0.462$; Fig. 3b). Birds in the cluttered aviaries also displayed a relative improvement in aerial maneuverability compared with open birds ($F_{1,9} = 14.31$, $P = 0.004$; Fig. 4); but there was no difference in level flapping-flight speed ($F_{1,9} = 0.46$; $P = 0.516$; Fig. 5).

Discussion

These data clearly indicate that birds in the cluttered treatment had lower wing feather asymmetry and experienced a subsequent change in their flight performance, compared with birds in the open treatment. These

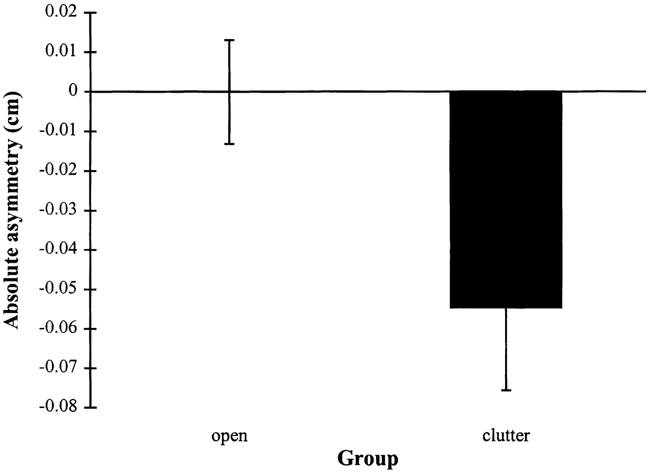

Fig. 2 Change in mean group absolute asymmetry (cm) from before to after molt versus treatment group. *Open* birds from open treatment, *clutter* birds from cluttered treatment. Mean group asymmetry was calculated from mean asymmetry across individuals within groups. Individual asymmetry was calculated from mean absolute asymmetry across all primary feathers within individuals

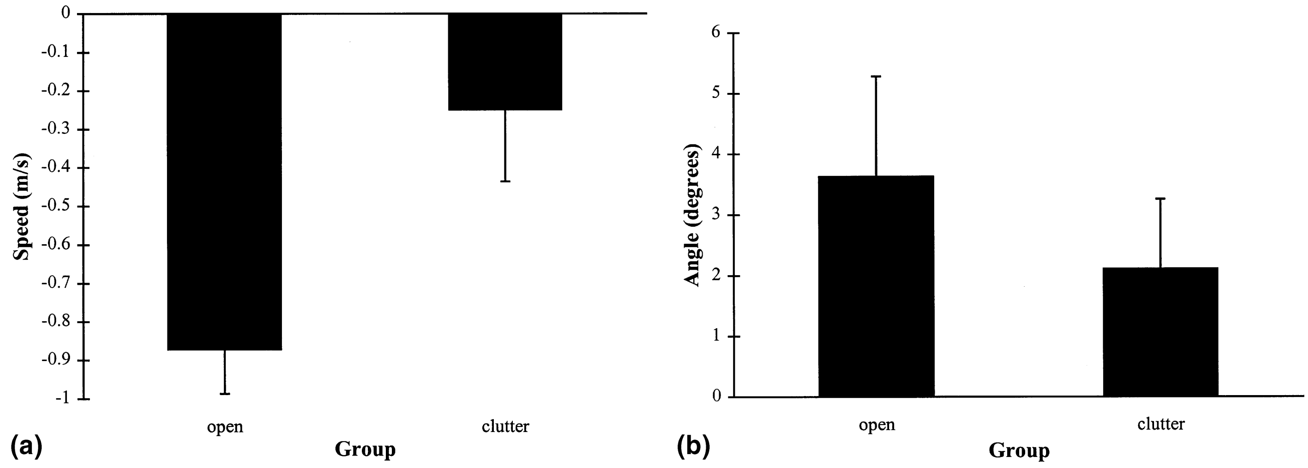

Fig. 3 Mean (± SE) change in **a** speed of take-off (m s^{-1}); **b** angle of take-off (°) from before to after molt versus treatment group. *Open* birds from open treatment, *clutter* birds from cluttered treatment

changes can be seen as enhancements of performance, as both an increased ability to perform aerial maneuvers and an increased speed of take-off are 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; Lindström 1989; Lazarus and Symonds 1992). The speed of such a take-off response has been suggested as an important determinant of predation risk (Page and Whitacre 1975; Kenward 1978; Cresswell 1993; Witter et al. 1994; Metcalfe and Ure 1995). Additionally, maneuverability and agility may be of primary importance in evading aerial predators (see Rudebeck 1950; Bijlsma 1990; Cresswell 1993). Increased maneuverability and agility are also likely to be highly positively related to the ability to negotiate crowded habitats (e.g., woodlands) without suffering wing damage and also the ability to catch aerial prey items. Hence, birds in the cluttered habitats reduced wing asymmetry through molt and increased their flight performance. It should be noted that the differences in flight performance between the treatment groups cannot be solely attributed to the differences in wing asymmetry, as there may be additional non-specific effects of developmental instability on biomechanical performance. The observed differences in flight performance may also, in part, be related to cluttered birds being "trained" to fly around obstacles during their molt; open birds did not receive this training. However, cluttered birds were exposed to their experimental treatment for 9 days before molt commenced, after which the first flight measures were recorded. This period may also have exposed cluttered birds to some elements of obstacle-avoidance flying and hence reduced any 'training' effects on the between molt change in flight performance in the cluttered treatment. Overall, as flight performance is highly related to wing morphology (reviews in Rayner 1988; Norberg 1990) and we have studied within-subject

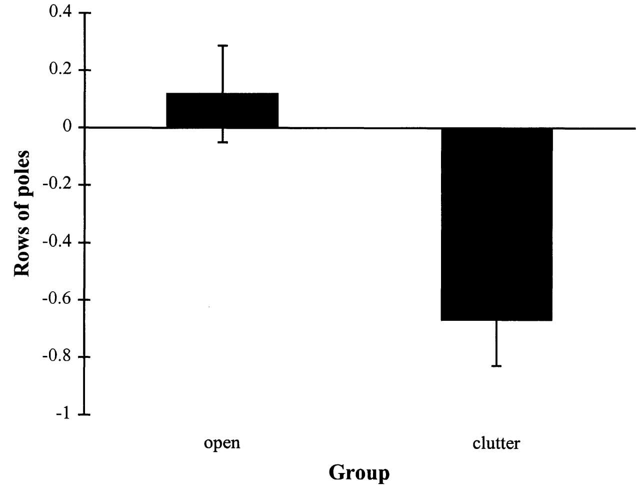

Fig. 4 Mean (± SE) change in number of rows of poles with which birds made contact with from before to after molt versus treatment group. *Open* birds from open treatment, *clutter* birds from cluttered treatment

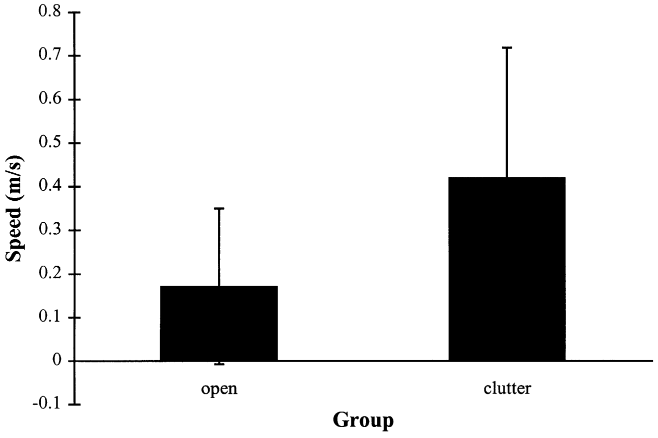

Fig. 5 Mean (± SE) change in level flight speed (m s^{-1}) from before to after molt versus treatment group. *Open* birds from open treatment, *clutter* birds from cluttered treatment

Table 1 Summary statistics for each primary feather before molt in the experimental aviaries. *Size* mean (±SE) primary length [(L + R)/2], *D. A.* mean (±SE) signed primary length asymmetry (L−R), *F. A.* mean (±SE) absolute length asymmetry (|L − R|). All morphometric measures are shown in cm. Body mass before molt in the experimental aviaries: mean (±SE) = 74.5 (±0.67) g

Statistic	Primary feather								
	1	2	3	4	5	6	7	8	9
Size	7.21 (0.03)	7.46 (0.03)	7.71 (0.03)	8.00 (0.06)	8.30 (0.03)	8.74 (0.03)	9.06 (0.05)	9.13 (0.06)	8.97 (0.04)
D. A.	0.04 (0.02)	0.01 (0.01)	−0.01 (0.01)	−0.01 (0.01)	0.02 (0.02)	0.03 (0.02)	−0.02 (0.02)	0.03 (0.01)	0.02 (0.02)
F. A.	0.08 (0.01)	0.05 (0.01)	0.04 (0.01)	0.05 (0.01)	0.07 (0.01)	0.10 (0.01)	0.08 (0.01)	0.06 (0.01)	0.08 (0.01)
Kurtosis	0.468	2.435	0.117	−0.008	2.211	−0.198	3.492	2.698	2.146
Skew	−0.380	0.679	−0.252	0.032	0.762	−0.512	−1.819	1.370	−0.551

changes in developmental stability and performance, the proposed direct relation between asymmetry and flight seems plausible although it is perhaps not the only explanation of the our results (Swaddle 1997).

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 (Thomas 1993). However, empirical studies have generally resulted in asymmetries much larger than those commonly observed in nature, as all manipulations performed to date have acted to increase (rather than decrease) asymmetry within the specified experimental designs (Møller 1991; Evans et al. 1994; Swaddle et al. 1996). This study implements a protocol in which asymmetry is decreased and hence provides a more rigorous test of the biomechanical predictions made (cf. Swaddle 1997). In agreement with the model of Thomas (1993), take-off, maneuverability and agility are enhanced by a reduction in wing asymmetry. However, there was no difference in level flapping-flight speed. It is possible that the birds had not reached an optimum flight speed within the flight tunnel [mean (±SE) flight speed = 8.76 (±0.71) m s^{-1}], and hence applying predictions concerning the relationship between level flight speed and asymmetry may be problematic. Alternatively, small changes in asymmetry (approximately 0.7% relative asymmetry change observed here) may make little difference to flight at faster speeds, i.e. level flight, whereas it may influence flight at slow speeds, i.e. take-off and maneuverability. However, Swaddle (1997) has demonstrated that changes in asymmetry of the same magnitude can influence both high and low-speed flight in starlings in similar flight trials.

As these data reveal within-aviary changes in asymmetry, we have successfully controlled for the genetic differences that may give rise to differences in developmental instability. Therefore, the relative decrease in asymmetry of the cluttered groups is best explained through the differences in habitat between the treatment groups. Previous estimates of the influence of environmental variables on developmental stability have consistently confounded among-group genomic differences with the effects of environmental stressors (review in Møller and Swaddle 1997). Therefore, this study also provides novel data on the effects of environmental influences on within-subject changes in developmental stability. This protocol, i.e. studying within-subject changes of developmental stability, could be applied to the assessment of environmental stressors in other laboratory and field situations. This may be particularly useful in captive and managed wildlife systems where properties of the environment are more readily controlled and manipulated than in the wild. Repeated assessment of developmental stability may allow the managers of captive populations to quantify aspects of the welfare value of existing housing conditions and the relative effects of any environmental alterations made as a part of management policies. Using organisms as a bioassay of developmental conditions may be more effective than traditional methods of environmental monitoring (e.g. assessing pollutant or chemical concentrations, see Lockie et al. 1969; Newton 1974) as the organisms themselves calibrate the detrimental effect of the environment. Studying changes in developmental stability over repeated growth stages of the same individuals in different habitats (or, alternatively, examining the asymmetry of genetically homogenous populations from different habitats) may be less invasive, cheaper and more straightforward than traditional eco-toxicology and environmental monitoring techniques.

It is not possible to precisely identify what elements of the cluttered habitat caused a relative decrease in developmental instability compared with the open habitat. Other than the positioning of the bamboo canes, there were no systematic differences between the two habitat types; hence it is likely that the asymmetry differences we observed result from the greater flight demands of the arrangements of the cluttered habitat. This conclusion is supported by the increased flight performance of birds in the cluttered treatment. However, there may also have been a stress-reducing effect of an apparent increased structural complexity of the cluttered habitat (e.g., Gvaryahu et al. 1994; Millam et al. 1995; Bubier 1996). We attempted to control for structural complexity by placing the same number of poles in each treatment group, however, the arrangement of these poles may have had some influence. Nevertheless, whichever explanation is most applicable, the overall findings and conclusions of the study are not altered. It is also important to point out that this study provides the first empirical evidence that organisms can reduce their asymmetry (i.e. reduce developmental instability) in response to environmental cues. The directionality of this response is an important distinction from other investigations as most studies of the environmental influences of asymmetry have only investigated increases in developmental instability (reviews in Leary and Allendorf 1989; Clarke 1993; Graham et al. 1993). As we have manipulated the costs of asymmetry, our data provide empirical support for the view that fluctuating asymmetry results from a trade-off of competing costs and benefits (discussion in Møller and Swaddle 1997).

In summary, this study provides empirical support for the published hypotheses relating asymmetry with flight performance by indicating that reduced asymmetry is associated with increased flight performance. Asymmetry appears to have been reduced by the relative increase of flight costs in the cluttered treatment. This further highlights the importance of biomechanical considerations in studies of fluctuating asymmetry, and that developmental stability is a manifestation of a whole nexus of interacting costs and benefits. This study has also introduced an important methodology by which the detrimental and positive influence of environmental factors can be monitored by within-individual changes in asymmetry.

Acknowledgements We thank the technical staff at the Brian Laboratory, Garscube, Glasgow for routine maintenance of the birds, and also Neil Metcalfe and Pat Monaghan for comments on earlier versions of the manuscript. J.P.S. was funded by a NERC postdoctoral fellowship and a Royal Society research grant; M.S.W. was funded by a NERC postdoctoral fellowship.

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Communicated by S. Pruett-Jones