Patterns of fluctuating asymmetry in developing primary feathers: a test of the compensational growth hypothesis

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The study of asymmetry ontogeny may reveal the mechanisms controlling the development of bilaterally symmetrical characters and the causes of asymmetry. In birds, flight feather asymmetries appear to increase at the beginning of growth and decrease at the end of their development. It has been proposed that such a pattern could be proximately caused by a developmental mechanism of compensational growth between the left and right wings, which should act to restore trait symmetry at the end of growth. In this study, I tested the hypothesis of the existence of a mechanism of compensational growth by performing an experiment, which consisted of provoking small asymmetries in the seventh primary feathers of house sparrows (*Passer domesticus*) by inducing the two feathers (one each side) to moult two days apart. On each side, the feathers grew in a similar way, independently of the growth of the other side. Feather length asymmetries were shortened with the advance of growth. However, the differences in time of growth persisted throughout development. These results do not support the existence of a mechanism of compensational growth. Primary feathers' asymmetries could decrease at the end of growth because the growth of the two feathers follows a programmed trajectory, which tends towards a certain maximum potential size.

Keywords: developmental stability; feather growth; feather length asymmetry; ontogeny;
Passer domesticus; regulatory mechanisms of asymmetry

1. INTRODUCTION

Fluctuating asymmetry (FA) is defined as small and random deviations from symmetry in otherwise bilaterally symmetrical characters (Van Valen 1962). Since the development of the two sides of the body is presumably under the control of identical genome and environment, it is assumed that FA represents a measure of ability to control development (Waddington 1957). Thus, some authors have postulated that the degree of FA is a measure of individual quality (review in Møller & Swaddle 1997), which may be used by females to assess male quality (e.g. Møller 1992, 1993; Thornhill 1992). Furthermore, several evolutionary theories have proposed that the patterns of FA reveal the mode of selection, either natural or sexual, of any character (Møller & Pomiankowski 1993; Balmford *et al.* 1993), and the honesty of secondary sexual traits (Møller 1990). It is known that high levels of either environmental or genetic stress may cause an increase of FA (reviews in Palmer & Strobeck 1986; Parsons 1990), but the mechanisms by which FA is developed are unknown.

FA appears to result from developmental processes. Thus, the studies on asymmetry ontogeny are of interest because they may yield insights into both the causes of asymmetries and the mechanisms controlling the development of bilaterally symmetrical characters. A few empirical studies have addressed the ontogeny of

asymmetry on several characters and species (e.g. Chipindale & Palmer 1993; Hallgrímsson 1993; Møller 1996; Teather 1996; Collin 1997; Swaddle & Witter 1997). The patterns found differed depending on the type of organism (see the review in Møller & Swaddle (1997)). Most of those studies were conducted on avian flight feathers, which found that the mean absolute asymmetry normally increased at the beginning of growth, peaked in the middle stages, and decreased as long as the traits reached their final length. Swaddle & Witter (1997) suggested that such patterns could respond to a change in the functional significance of symmetry during trait development. With reference to flight feathers, the cost of asymmetry in terms of flight performance is low when feathers are small, but as feathers become larger, the cost of wing feather asymmetry increases. The parabolic trajectory of FA throughout growth period could be, therefore, an optimal pattern resulting from a trade-off between the benefits of fast growth and the costs of asymmetry (Swaddle & Witter 1994; Møller & Swaddle 1997). On the basis of such a pattern of asymmetry, Swaddle & Witter (1997) proposed that a developmental mechanism of compensational growth between the left and right wings acts to restore trait symmetry at the end of growth.

Although the parabolic variation of asymmetry with the progress of growth may agree with the existence of a mechanism of compensational growth, a better support would be necessary to demonstrate such a mechanism;

Figure 1. (a) Model of growth of both sides (bold and light lines) of a character with a mechanism of compensational growth. Differences in the time taken to grow to a certain trait size decrease as development goes on. Thus $\Delta t_1 > \Delta t_2$. (b) Model of growth of both sides (bold and light lines) of a character when there is no mechanism of compensational growth, so that the two sides follow a parallel growth trajectory. Differences in the time taken to grow to a certain trait size is constant throughout development ($\Delta t_1 = \Delta t_2$).

there may be alternative hypotheses, which can explain the reduction of asymmetry at the end of development. In order to test the compensational growth hypothesis, I performed an experiment on house sparrows (*Passer domesticus*) which consisted of removing both of the seventh primary feathers two days apart, so as to provoke small asymmetries at the beginning of development. According to the compensational growth hypothesis, I expected that the feather which was removed later should grow faster than the one which was removed earlier, to compensate for feather size asymmetries. Hence, the difference in time at which both sides of a trait reach a certain size should decrease with the advance of growth stage (figure 1a). On the contrary, if there is no mechanism of compensational growth, both sides of a trait should grow independently of current asymmetry, and their development should follow parallel trajectories. Thus, growth rates of left and right traits should be indistinguishable, and on average, the difference in time taken to grow to a certain size should be constant throughout development (figure 1b).

2. METHODS

I carried out the experiment with 42 wild house sparrows (*Passer domesticus*), which were caught in January 1998, in a farm near Garcinarro, Cuenca, Spain (40°8' N, 2°45' W), and housed individually in 25 cm × 25 cm × 50 cm cages. During the experiment, birds were held under a natural photoperiod (light ranged from 10–12 h), and temperature ranging from 16–22 °C. Food and water were provided *ad libitum*. Food consisted of a mixture of canary seeds (Ornyzoo S. L., Spain) containing 16.5% protein and 13.7% fat, and supplemented with vitamins. Every week, each bird was provided with water for a bath for a

half-hour period. Birds were randomly assigned to three treatments, a control group and two experimental ones. After two weeks in captivity, the seventh primary feathers were removed to induce the growth of new feathers. In the control treatment, both feathers were plucked at the same time, while in the experimental treatments one feather was plucked two days later than the other. Experimental treatments are called either 'left treatment' if the left feather was removed first, or 'right treatment' if the right feather was removed first. Birds' wings were checked daily, from five days after plucking until the new feathers emerged. Each seventh primary feather was measured every two to three days throughout feather growth. The tips of feathers were checked carefully at all times to ensure that damaged feathers were not included in the analyses. Nine birds were excluded because their seventh primary feathers showed sign of abrasion or breakage. Besides, four birds died by unknown causes during the experiment. Therefore, analyses were performed using 29 individuals. The probability of an individual being excluded due to feather damage, as well as the probability of dying, were independent of treatment (logistical regression: $\chi^2 = 0.86$, d.f. = 2, $p = 0.65$; and $\chi^2 = 0.55$, d.f. = 2, $p = 0.77$, respectively).

To reduce measurement errors, I recorded four separate length measurements for each side at each session, interchanging right and left sides. The averages of the four measurements were taken as feather length measures. This procedure was repeated twice on several individuals in order to get two independent averages, and to test the repeatability of asymmetry measures. The repeatability of measures, as well as the statistical analyses of FA, were assessed on nine control individuals at three different stages of growth (at approximately 25%, 50%, and 75% development), and on all full-grown individuals before the experiment. Primary asymmetry was highly repeatable in all stages of growth (in all cases $F_{8,9} > 99$; $p < 0.0001$), as well as in full-grown individuals ($F_{41,42} = 11.3$; $p < 0.0001$). Furthermore, the signed asymmetry (L–R) exhibits the properties of FA, since the mean value, as well as kurtosis and skewness, did not differ from zero (*t*-test: in all cases $p > 0.1$).

Primary lengths were analysed using the statistical package for the Social Sciences' nonlinear least-squares curve-fitting procedure. The logistic growth model was used to fit curves to growth data for each feather, and so three basic parameters of growth were calculated: the growth rate constant (K), the constant indicating time at which inflection point occurs (b), and the asymptote (A). For each feather, time zero was the time at which the feather was plucked. To estimate the time taken to reach a certain size, I assumed that growth rates between two successive measurements (at intervals of two to three days) were constant.

3. RESULTS

In the control sparrows, mean absolute asymmetry of the seventh primary feather increased from the beginning of growth, peaked at mid-growth, and decreased with increasing time in the last stages of development. This pattern was significantly fitted to a quadratic function (figure 2a), but not to a linear one ($r = 0.04$; $F_{1,8} = 0.01$; $p = 0.92$). In both experimental treatments, the growth process of one side was delayed with respect to the other one, since the feathers were plucked at an interval of two days. In these treatments, the differences in feather length were also reduced as the growth process progressed (figure 2a).

Figure 2. (a) Variations of seventh primary-feather length asymmetry (mean left-right $\pm$ s.d.) in relation to percentage growth. Curves are the result of fitting quadratic functions to mean asymmetry by using least-squares regression (for control treatment: $y = 0.11$ (s.e. 0.08) + 0.044 (0.003) x - 0.000401 (0.000032) x^2 , $r^2 = 0.96$, $F_{2,7} = 79$, $p < 0.0001$; for experimental treatments: $y = 5.66$ (0.18) + 0.087 (0.008) x - 0.001379 (0.00007) x^2 , $r^2 = 0.99$, $F_{2,7} = 940$, $p < 0.0001$). (b) Mean ($\pm$ s.d.) difference, between the two seventh primary feathers, in the time taken to reach a certain degree of development (time asymmetry) in relation to the percentage of growth. Open and filled squares represent control and experimental treatments, respectively.

In order to test the existence of a mechanism of compensational growth, I analysed the variation of the differences in time taken for the feathers to grow to a certain size throughout development. In the two

experimental treatments one feather was removed two days later than the other. Such differences in time persisted during the feather growth period, since any given size was reached two days earlier by the first-plucked feather than the second-plucked one (repeated-measures ANOVA comparing growth stages: $F_{4,72} = 0.68$, $p = 0.61$; statistical power = 0.21; figure 2b). In the control group, the two seventh primary feathers were removed at the same time. As expected, the difference in time taken by both left and right feathers to reach a certain growth stage did not vary throughout development (repeated-measures ANOVA: $F_{4,32} = 0.79$, $p = 0.54$; statistical power = 0.23; figure 2b). Furthermore, after fitting logistic growth models to growth data for each feather, I compared the growth parameters of both of the seventh primary feathers of birds undergoing the three treatments (control, left treatment and right treatment). Neither growth rate, nor asymptotic size, nor the constant related to inflection point differed significantly between both sides within any treatment (table 1). Moreover, between treatments, there was no significant difference in any relative (left minus right) parameter of growth (MANOVA: Wilks' $\lambda = 0.84$, $F_{6,48} = 0.74$, $p = 0.6$). Therefore, the results indicate that the two seventh primary feathers grew in parallel, and there was no solid evidence of compensational growth.

4. DISCUSSION

Swaddle & Witter (1997) suggested that the functional importance of traits should influence the mechanism by which the asymmetries develop. Hence, they hypothesized about the existence of a mechanism of compensational growth between left and right sides of characters such as flight feathers, where the cost of asymmetry is higher as the feathers increase their length (see Balmford *et al.* 1993). This mechanism of compensational growth should restore trait symmetry as feathers reach their final growth stages. In support of this hypothesis, they found that primary-feather asymmetry of European starlings (*Sturnus vulgaris*) decreases after the midpoint of growth in feather development. In this study, I found a similar pattern of asymmetry during the growth of the seventh primary feathers of house sparrows (figure 2a). However, it is not enough to support that hypothesis. In fact, an experimental test manipulating initial asymmetries did not show any evidence in support of the existence of a compensational growth mechanism, because the two homologous feathers showed similar patterns of growth independently of which shows a more advanced development stage (table 1). Moreover, although the experimentally induced asymmetries in feather length decreased throughout development (figure 2a), the differences in the time of growth between both right and left feathers were not shortened (figure 2b). Therefore, these results suggest that the growth of each side of a trait follows a programmed trajectory, which is independent of the growth of the other side.

Apart from the compensational growth hypothesis, none of five hypotheses currently proposed in the literature on the ontogeny of developmental instability can explain why asymmetries of some characters decrease at the end of growth (see the review in Swaddle & Witter

Table 1. *Relative parameters of growth*

(Values are given as the mean difference, left–right values, $\pm$ s.d. Statistical results from paired *t*-tests are given between brackets.)

treatments	growth rate (K)	constant (b)	asymptote (A)	N
right	-0.000 ± 0.015 ($t=0.01, p=1$)	-19.78 ± 105.47 ($t=0.56, p=0.59$)	0.44 ± 1.34 ($t=0.98, p=0.36$)	9
control	0.003 ± 0.006 ($t=1.43, p=0.20$)	8.39 ± 50.70 ($t=1.22, p=0.26$)	-0.06 ± 0.51 ($t=0.36, p=0.73$)	9
left	-0.001 ± 0.012 ($t=0.30, p=0.77$)	5.78 ± 40.65 ($t=0.47, p=0.65$)	-0.36 ± 1.39 ($t=0.86, p=0.41$)	11
left+right ^a	-0.001 ± 0.013 ($t=0.20, p=0.85$)	12.08 ± 74.87 ($t=0.72, p=0.48$)	-0.40 ± 1.33 ($t=1.33, p=0.20$)	20

^aMean differences are given as (first plucked feather–second plucked feather).

Figure 3. Model of character asymmetry caused by differences in growth rate. The solid line represents the ideal growth trajectory that both sides of a bilateral trait attempt to follow. Either side, right (R) or left (L), may retard its growth due to developmental errors, so that these growth delays will cause character asymmetries. The degree of asymmetry depends on both the magnitude of growth retardation and the slope of the growth trajectory. Thus, individual 1 shows a lower degree of growth retardation than individual 2, but the first one presents a higher degree of character asymmetry than the second one.

(1997)). Nevertheless, some of these hypotheses make predictions about the effects of developmental instability at the microscopic level, while trait asymmetry is the macroscopic product of those developmental errors. The ontogeny patterns of variation of both microscopic and macroscopic developmental errors may be quite different. For example, the so-called 'coin toss' hypothesis suggests that morphogenesis is composed of independent developmental units randomly assigned, so that there will be a positive relationship between absolute differences between sides in developmental units and the number of developmental units. However, since trait length may depend nonlinearly on developmental units, the relationship between FA and trait length will not always be positive (Aparicio 1999). Hence, the hypotheses predicting microscopic developmental errors may be difficult to test.

At the macroscopic level, I suggest that the variations of FA throughout development can depend on the growth pattern. Trait asymmetry could be originated by small and random developmental perturbations, which may lightly retard development in either side of a trait growing on a programmed, ideal trajectory. Hence, trait

asymmetry value will depend on both the magnitude of time retardation of growth and the slope of the ideal growth trajectory at a particular point. For example, if the two sides of a trait are growing at a certain rate, and the growth of a side is delayed by one day, the level of asymmetry caused will be proportional to the growth rate at that moment (figure 3). Therefore, asymmetry will be greater as the slope becomes steeper. The development of characters with determinate growth usually follow sigmoidal trajectories that tend towards an asymptote (e.g. Bryant & Simpson 1984; Ricklefs 1983; Reiss 1989). The slopes of this type of function present a maximum value at the midpoint, and tend towards zero at the outermost points, i.e. at the beginning and at the end of growth. Therefore, the reduction of asymmetry at the end of development will occur even when developmental errors at the microscopic level are increasing, because growth rates tend towards zero as the trait reaches its maximum potential size. In agreement with this hypothesis, aside from feathers, the ontogeny of the FA of other characters with determinate growth (e.g. tarsus length) appears to adjust to a parabolic function (see Teather 1996; Aparicio 1999).

The hypothesis on the effects of the pattern of growth may also be applicable to animals with indeterminate growth, i.e. those which grow throughout life. In these cases, growth rates could be sustained above a certain level, so that asymmetry may increase with the advance of growth stages (e.g. Chippindale & Palmer 1993; Collin 1997). However, in order to predict a particular pattern of asymmetry ontogeny for characters with unlimited growth, it is necessary to know their particular pattern of growth.

The question arising under the hypothesis of limited growth, is why fluctuating asymmetries of full-grown traits do not always become zero? This may be because asymmetries of a character would always be zero in the unlikely case that all individuals grow both sides of the character up to the maximum potential size. Some experiments have shown that the final sizes reached by several characters with determinate growth may change depending on environmental conditions (e.g. Boag 1987; Johnston 1993; Nilsson 1994). It is likely that natural conditions are not normally sufficient to cause development to the maximum potential size. Moreover, since

variations of final trait size with respect to the maximum potential size may affect the degree of FA, the fact that the final sizes of some traits may be lower than their maximum potential sizes may be an interesting aspect. If each character shows a different degree of flexibility to reach its maximum potential size, these differences between characters could explain some patterns of FA (Aparicio 1999).

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