

## SHIFTS IN BILATERAL ASYMMETRY WITHIN A DISTRIBUTION RANGE: THE CASE OF THE CHUKAR PARTRIDGE

SALIT KARK

Department of Biological Sciences, 371 Serra Mall, Stanford University, Stanford, California 94305-5020  
E-mail: salit@stanford.edu

**Abstract.**—Three major types of bilateral asymmetry (fluctuating asymmetry, directional asymmetry, and antisymmetry) have long been recognized in the literature. Little, however, is known about transitions between asymmetry types, especially in natural populations. It is often assumed that directional asymmetry and antisymmetry have a larger genetic basis than fluctuating asymmetry. This leads many scientists to exclude traits or populations showing either directional asymmetry or antisymmetry from developmental instability studies, focusing attention on fluctuating asymmetry alone. This procedure may bias the findings and thus our understanding of patterns of bilateral asymmetry and the factors influencing it. To examine changes in bilateral asymmetry across the distribution range of a species, I studied the length of the third toe in 11 chukar partridge (*Alectoris chukar*) populations across a steep environmental gradient of 320 km within the species' range in Israel. This trait was selected due to its adaptive value in the chukar, a species that spends much of its activity walking, and due to its high measurement repeatability. Moving from the core toward the very extreme periphery of the range, the following four trends are detected: (1) the expression of the directional asymmetry component significantly increases; (2) the frequency of symmetrical individuals in the population significantly decreases, with a sharp decline at the steepest part of the climatic and environmental gradient studied, within the Mediterranean-desert ecotone; (3) mean asymmetry levels, as estimated using the unsigned difference between the right and left toe, significantly increases; and (4) the range of asymmetry increases such that the most asymmetrical individuals originate from the very edge of the range. These findings provide primary evidence that substantial shifts in asymmetry may occur across short geographical distances within a species' distribution range. They show a continuum between asymmetry types and support the notion that all three types of asymmetry can reflect developmental instability. Further studies of developmental instability should be designed so that they enable detection of transitions between asymmetry types across natural populations. Such a procedure may partly resolve some of the contradictions seen in the literature regarding the relationship between bilateral asymmetry and environmental stress.

**Key words.**—*Alectoris chukar*, core-periphery, developmental instability, directional asymmetry, distribution range, ecotone, fluctuating asymmetry.

Received March 27, 2001. Accepted June 18, 2001.

The study of populations across the distribution range of a species, and especially the study of peripheral populations, has largely focused on understanding patterns of extinction, population dynamics, abundance, and morphological and genetic diversity (e.g., Andrewartha and Birch 1954; Lawton 1993; Hoffmann and Blows 1994). A more recent focus has been toward the conservation implications of these patterns and the processes underlying them (e.g., Safriel et al. 1994; Channell and Lomolino 2000). In this context, a central goal has been to reveal whether the levels of stress, as experienced by individuals, change across a species' distribution range. It is difficult, however, to assess the response of individuals to environmental changes in long-term field studies of population dynamics, physiology, and fitness that span the geographic range of a species. An approach that will enable us to study such spatial and temporal changes within natural populations across the distribution range, from core to periphery, would be useful. Substantial theoretical, experimental, and observational work suggests that the estimation of developmental instability using bilateral asymmetry may serve as a tool for assessing the degree to which individuals were able to buffer their development in the face of stress (e.g., McKenzie and Clarke 1988; Leary and Allendorf 1989; Clarke 1992; Møller 1998; Lens et al. 1999; reviewed in Lens et al. 2002), although this conception has recently been debated in relation to sexual selection (e.g., Bjorksten et al. 2000a,b).

Three principal types of bilateral asymmetries in morpho-

logical traits (i.e., deviation from perfect symmetry between the right and the left sides of an organism's body) have been described. These include fluctuating asymmetry (FA), directional asymmetry (DA), and antisymmetry (Van Valen 1962; Palmer and Strobeck 1986). The three differ in the distribution of the signed difference between the right and the left (R-L) sides of a trait in a population. Fluctuating asymmetry is defined (based on Ludwig 1932) as the small, random, nondirectional deviations from perfect bilateral symmetry in morphological traits in which symmetry is the normal state. In traits exhibiting FA, signed R-L values in the population are predicted to be normally distributed around a mean of zero. In traits showing DA, there is a consistent bias toward overdevelopment of one specific side relative to the other, and the R-L distribution shows a nonzero mean (Van Valen 1962; Palmer and Strobeck 1986; Møller and Swaddle 1997). Antisymmetry (handedness) is similar to DA in the sense that one side is usually larger than the other, yet the population shows a broad-peaked (platykurtic) or a bimodal distribution of signed R-L around a mean of zero (Palmer and Strobeck 1986).

Fluctuating asymmetry is often considered an indicator of developmental instability (Clarke and McKenzie 1987; Markow 1995), reflecting the ability of individuals to buffer themselves during development in the face of stress (Leary and Allendorf 1989; Swaddle et al. 1994). Unlike FA, the two other forms of asymmetry, DA and antisymmetry, due to their unknown heritable component, have not been con-

sidered as reliable indicators of developmental instability (e.g., Van Valen 1962; Palmer and Strobeck 1986). Although the discussion regarding the assumption that the heritability of FA is lower than that of the two other asymmetry types has not been entirely resolved (Markow and Clarke 1997), it has led to the recommendation that traits not showing FA (i.e., a normal distribution of signed R-L about a mean of zero) should be excluded from the analysis in studies of developmental instability in favor of traits showing pure FA only (e.g., Palmer and Strobeck 1992; see guidelines in Palmer 1994). Such a procedure does not allow potential shifts between asymmetry types to be identified, if they occur. In addition, this approach ignores cases where mixtures of more than one asymmetry type occur within a single population (Lens and Van Dongen 1999; Van Dongen et al. 1999a; Lens et al. 2002).

Graham et al. (1993a, 1998) challenged this conventional thinking and its practical implications for studies of developmental instability. Using a modified reaction-diffusion model, they suggested that DA and antisymmetry may often reflect developmental instability and predicted a continuum between the three asymmetry types. Indeed, several experimental studies involving human-induced stresses (e.g., insecticides) have shown that transitions between asymmetry types can occur even within a single population (Leary and Allendorf 1989; Graham et al. 1993b; Henshel et al. 1993). If asymmetry types can exhibit such shifts, findings of work focusing on a single population may largely depend on which populations were selected for study within the species' range. To test whether the level and form of asymmetry shift across a species' distribution range, I examined bilateral asymmetry patterns along a steep gradient within the native distribution range of the chukar partridge (*Alectoris chukar*) in Israel, from core to periphery.

## MATERIALS AND METHODS

### Study Area

A steep environmental gradient from Mediterranean to arid climatic regions is found in Israel and the region across short distances from areas in the northern Golan Heights, where mean annual rainfall is greater than 900 mm, to areas in the southern Negev Desert, where rainfall decreases to less than 50 mm (data from The Israel Meteorological Service, The Hebrew University of Jerusalem Geographical Information Systems Center, and from Bitan and Rubín 1991; for details and maps, see Kark 1999). An especially steep portion of this environmental gradient is along the northern Negev Mediterranean-desert ecotone (Fig. 1), where within a belt of several dozen kilometers mean annual rainfall decreases from over 450 to less than 150 mm and both temporal and spatial variability in rainfall increase (Bitan and Rubín 1991). This cline is associated with a change in a phytogeographical gradient from largely Mediterranean to largely Saharo-Arabian vegetation, with a combination of both at the ecotone region (Danin and Plitman 1987; Kark 1999). This gradient coincides with both northern and southern range peripheries of numerous species (Safriél et al. 1994; Frankenberg 1999).

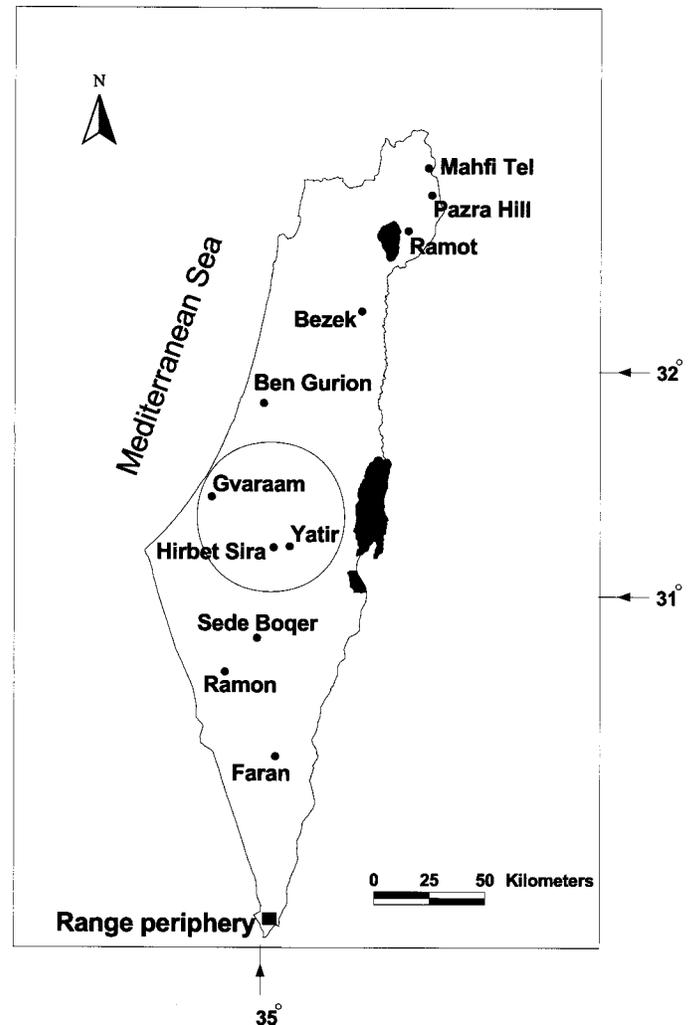


FIG. 1. Map of study area, population sampling locations, and range periphery. The Mediterranean-arid ecotone region is marked with a circle. Sample sizes appear in Table 1.

### The Chukar Partridge

The chukar is continuously distributed and has high population densities in the Mediterranean areas in the north and center of Israel (Shirihai 1996). The species reaches the edge of its continuous distribution in the northern Negev ecotone (Shirihai 1996). Chukar distribution becomes patchy and populations become smaller and more isolated toward the central and southern Negev Desert, a region that marks the global periphery of the species' distribution range (Fig. 1; Shirihai 1996). As far as is known, chukars in the study area are sedentary and do not exhibit latitudinal or altitudinal migrations (Shirihai 1996).

### Sampling and Measurement

Adult birds were collected by the Israel Nature and National Parks Authority rangers and authorized hunters, following Kark et al. (1999). Sampling took place during the nonbreeding season of 1995–1996 (August to February). Birds were measured in the field, except for those from Ben-

TABLE 1. Chukar partridge populations studied in Israel, population acronyms for Figures 2 and 3, distribution area, distance (km) from range periphery (see Fig. 1), sample size, and mean unsigned value of right minus left length of third toe (R-L) in the population (cm).

Population	Acronym	Distribution area	Distance from periphery (km)	Sample size	Mean  R-L  (cm)
Mahfi Tel	MT	Mediterranean core	408	23	0.013
Pazra Hill	PH	Mediterranean core	395	16	0.038
Ramot	LR	Mediterranean core	372	22	0.000
Bezek	BR	Mediterranean core	316	19	0.032
Ben-Gurion Airport	BG	Mediterranean core	264	21	0.033
Gvaraam	GV	ecotone	218	24	0.040
Yatir	HY	ecotone	199	19	0.026
Hirbet Sira	HS	ecotone	196	30	0.070
Sede Boqer	SN	arid periphery	148	27	0.100
Ramon	RM	arid periphery	129	28	0.111
Faran	FR	arid periphery	86	23	0.094

Gurion Airport, Bezek and Nevatim, which were measured in the laboratory. All measurements were taken by the author, using a metal ruler to an accuracy of 0.1 cm. Locations were sampled in a random order relative to the range periphery to avoid a potentially confounding bias stemming from the increasing experience of the measurer over the course of the study.

A total of 138 males and 114 females in 11 populations were measured (Table 1, Fig. 1). In addition to population-based comparisons, to enlarge sample sizes populations were pooled into three predetermined ecogeographical distribution regions (Mediterranean core, ecotone, and arid periphery; see Table 1) and analyses were performed across the three regions. Two measures of third toe length (from joint to claw), including and excluding the claw (long and short measurement, respectively), were obtained for each bird, except for individuals from Pazra Hill and Ramon, for which only the long measurement was taken. The asymmetry pattern across the range was analyzed to test the following hypothesis: If birds tend to dig (e.g., for food) more with one leg, digging may have a different effect in dry versus mesic areas or in different soil types. Therefore, shifts between asymmetry types could potentially be caused by quicker and uneven erosion of the claws on the two sides of the body in different habitats (P. Taylor, pers. comm.). In such a case, I would predict that the pattern found for the long measure of asymmetry would not be repeated in the short measure, where the claw was excluded. However, this idea was not supported by the results. Similar trends were found for both the short and long measures across the study gradient. The correlation between mean unsigned R-L for the two measures across all populations was 0.91 ( $P < 0.0007$ ). Due to this congruence and given the larger sample size, results are presented here for the long measure.

The length of the third toe was selected for the following reasons: This trait is related with locomotion, highly important for this phasianid species that spends much of its daily foraging activity walking rather than flying (Alkon 1974). Thus, it seems reasonable to suggest that this trait will have adaptive value and would reflect selection pressures (Boag and Van Noordwijk 1987). In addition, this trait had by far the highest repeatability among a selection of traits that were premeasured on a subsample of birds at the onset of the study. These traits (including tarsus and wing length) are used in

many asymmetry studies due to their adaptive value in birds (Boag and Van Noordwijk 1987; Smith et al. 1997), being related with flight, locomotion, feeding ecology, and fitness (Nissani 1974; Smith 1993; Smith et al. 1997). Working with traits that have both potentially high adaptive value and that can be measured with high repeatability (low measurement error) is crucial when studying patterns in bilateral asymmetry and shifts between asymmetry types across a species range.

Measurement repeatability was estimated by measuring 10 individuals on both body sides, and then remeasuring the same set of individuals (giving a total of 40 measurements). The repeatability  $r$ -value represents the intraclass correlation coefficient (Lessells and Boag 1987; see also Siikämäki and Lammi 1998). These measurements were further analyzed using a mixed-model analysis of variance (ANOVA) with individual (I), side (S), and replicate (R) factors following Swaddle et al. (1994). In this model, the ratio between MS ( $I \times S$ ) and the combined MS ( $I \times S \times R$ ) and MS ( $I \times R$ ) provides an  $F$ -test for evaluating whether between-individual variation in estimated asymmetry is significantly greater than can be accounted for by measurement error taking into account session bias (Swaddle and Cuthill 1994; David et al. 1999).

Range periphery was taken as the center of the first grid in which chukar density reduces to zero based on the distribution grid system described in Shirihai (1996). Beyond this area, towards the desert, chukars are not currently known to live, except for an isolated postglacial relict population located in the southern Sinai Mountain region (Kark et al. 1999). Distance from the range periphery was taken from the center of the area of the population sampling (approximately 10 km<sup>2</sup> in all regions).

#### Estimation of Asymmetry

Distribution of signed R-L values over all individuals ( $n = 252$ ) was drawn and normality of the distribution was tested using the Shapiro-Wilk  $W$ -test (Shapiro et al. 1968) using JMP version 3.1.5 (SAS Institute 1995) statistical software. Asymmetry was calculated in several ways. First, asymmetry was estimated in each of the populations using the mean of the unsigned R-L value (FA1 of Palmer 1994). Then, the proportion of symmetrical individuals in each pop-

ulation was calculated and a regression between distance from range periphery and this proportion was examined. Both a linear and an arctangent regression (as described in more detail in the Results) were performed. An individual was considered symmetrical if the value of R-L was zero. This measure does not reflect the size of asymmetry but rather its proportion in a population, and although it may potentially be affected by measurement accuracy, it is useful as a relative measure for comparison among populations. Comparisons were further done among the three predetermined areas, to obtain larger sample sizes.

To test for normality of the distributions, the skewness and kurtosis of the signed R-L were calculated and the distribution was inspected across the three areas, following Palmer (1994). To test for shifts between asymmetry types across the distribution range, I used the following tests. Directionality in asymmetry was tested in each of the three areas using a Wilcoxon signed-rank test for deviation of the median from zero (Zar 1999). This aimed to test whether the median of R-L and the symmetry of the distribution change across the species' range. The statistical significance was estimated following a sequential Bonferroni correction (Rice 1989; Palmer 1994). Antisymmetry is predicted to show a distribution of unsigned R-L ranging from platykurtic to bimodal. When combined with DA, the populations will show a skewed bimodal distribution (see fig. 3c in Palmer and Strobeck 1992). It is often difficult to assess antisymmetry and to separate it from FA and DA, especially when mixed with other forms of asymmetry. Negative kurtosis has been suggested as an indicator of antisymmetry. To test for the antisymmetrical component I examined changes in the patterns of kurtosis across the range. To enlarge sample sizes, I used the three predetermined areas (Mediterranean-core, ecotone, and arid-periphery).

## RESULTS

### *Trends in Asymmetry across the Chukar Range in Israel*

Repeatability for the long measurement of the third toe was high ( $r = 0.99$ ,  $F = 76.6$ ,  $p < 0.0001$  for third toe measurement and  $r = 0.91$ ,  $F = 9.9$ ,  $p < 0.0007$  for asymmetry estimation of the difference between the right and the left sides). Between-individual variation in estimated asymmetry was significantly greater than can be accounted for by measurement error (mixed-model ANOVA  $F_{9,18} = 8.056$ ,  $P < 0.0001$ ). The proportion of symmetrical individuals in the population was significantly related to the distance of the population from the species' range periphery (Fig. 2), as seen in the regression analysis. In the linear regression, 74% of the variance in the percentage of symmetrical individuals in a population was attributable to the location of populations across the range ( $F_{1,9} = 25.2$ ,  $P = 0.0007$ ). The behavior of the percentage of symmetrical individuals against distance from the range periphery (see Fig. 2) showed a steplike shape caused by the rapid change in asymmetry levels in the ecotone area. For this reason, we modeled the behavior using the arctangent family of functions, whose members all have a steplike shape. The data model that we used for the regression was therefore  $Y_i = \alpha + \{\beta \arctan [(x - \gamma)/\delta]\} + \epsilon_i$ . Following, as described by Zar (1999) and using MATLAB, we

searched in the arctangent family of functions for the function with the best fit to the data (i.e., the least mean squares residual), and calculated the coefficient of determination,  $r^2$ . The best fitting parameters were:  $\alpha = 45.02$ ,  $\beta = 28.65$ ,  $\gamma = 185.78$ , and  $\delta = 48.37$ . This model explained 82% of the variance.

Consistent results were found for the correlation between distance from the range periphery and mean unsigned R-L for both sexes. Because males and females exhibited similar trends, the two sexes were pooled for further analysis to enlarge sample sizes, except when otherwise indicated. The two ecotonal populations, Yatir and Hirbet Sira, located only several kilometers away from each other (Fig. 1), but occurring within a very steep part of the environmental gradient (Yatir having over 50% higher rainfall than Hirbet Sira), showed a sharp change from a mean unsigned R-L of 0.026 cm to 0.070 cm and from 79% to 33% symmetric individuals, respectively (Fig. 2). If body size had increased along the distribution range, from core to periphery, this could potentially have caused an apparent trend of increasing asymmetry. In such a case, mean unsigned R-L may increase even when remaining similar relative to the mean trait size in the population (R-L/mean [R,L]) when an unweighted estimator, such as FA1 is used. If this had occurred, a weighted estimate of asymmetry, such as FA3 of Palmer (1994), should have been used instead. However, body size in the chukars did not increase toward the desert (Kark 1999), and therefore the spatial trends in asymmetry could not have been caused by the use of an unweighted estimator.

When comparing the three areas, from the Mediterranean core through the Mediterranean-desert ecotone toward the arid periphery, mean asymmetry increased significantly and was highest in the arid periphery. An analysis of variance of mean FA1 (sexes pooled) by area was significant ( $F = 45.2$ ,  $P < 0.0001$ ). Similar results were obtained when the two sexes were analyzed separately. A Tukey-Kramer multiple comparison test was significant for all area pairs ( $P < 0.01$ ). Furthermore, the maximum deviation from symmetry (the absolute value of the R-L difference) increased toward the periphery such that the most asymmetrical individuals occurred near the periphery of the range (Figs. 3, 4).

### *Shifts in Asymmetry*

The distribution of signed R-L values over all individuals ( $n = 252$ ) showed a unimodal pattern with a median and mode of zero yet was not normal. When analyzed for the 11 populations and the three areas, a shift in the distribution of asymmetry was observed across the range, from core to periphery. As the degree of asymmetry increased, a directional trend (toward negative R-L) appeared (as seen in Fig. 3 across populations and Fig. 4 across the three areas). Although the median of the signed R-L did not significantly deviate from zero in the core, deviation from zero, as tested using the Wilcoxon signed-rank test, was significant in both the ecotone and the arid periphery (Table 2). The skewness of the distribution was significant at the periphery of the range (Table 2). Thus, as asymmetry increases toward the range periphery, there is a greater expression of the DA component.

Along with the decline in the percentage of symmetrical

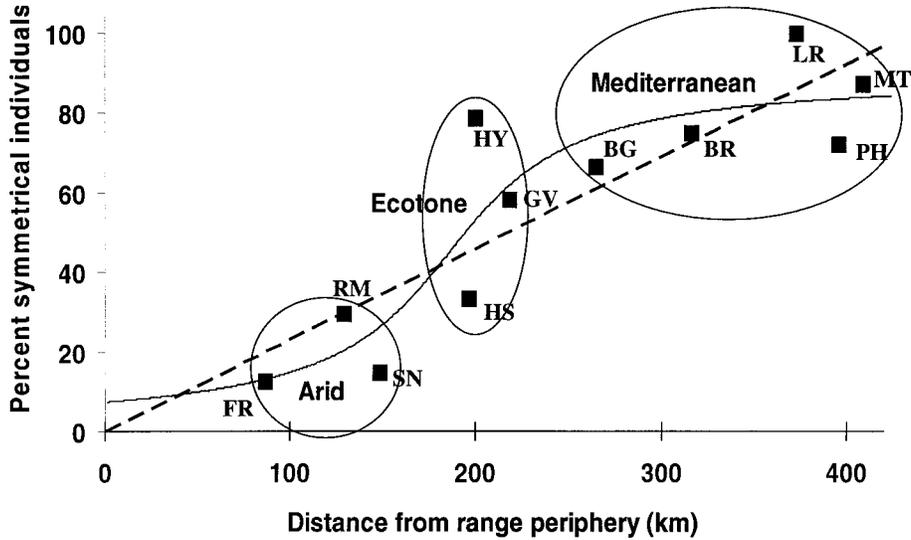


FIG. 2. Relationship between the distance of the population from the range periphery and the percentage of symmetrical individuals in the population, sexes pooled, with a linear (dashed line) and an arc tangent ( $tg^{-1}$ ) regression (solid line). Population acronyms and sample sizes appear in Table 1.

individuals in the population and the increasing expression of the DA component toward a larger left side (negative R-L), the proportion of individuals with positive R-L values increased from core to periphery (Figs. 3, 4). This occurred in both sexes, especially in the males (not shown). Distribution of R-L shifted from leptokurtic in the core to a mixed skewed distribution in the periphery. Significant positive leptokurtosis was found in the Mediterranean core region (Table 2). Leptokurtosis was lower in the ecotone, where it was negative, and in the periphery compared to the Mediterranean

core. Yet it was not negative in the periphery, probably due to the fact that antisymmetry was mixed with a strong left-toed DA component. Thus, it appears that there is a mixture of DA and antisymmetrical components in chukar populations located closer to the range periphery.

DISCUSSION

This study provides evidence for clear changes in the magnitude and patterns of bilateral asymmetry in the central

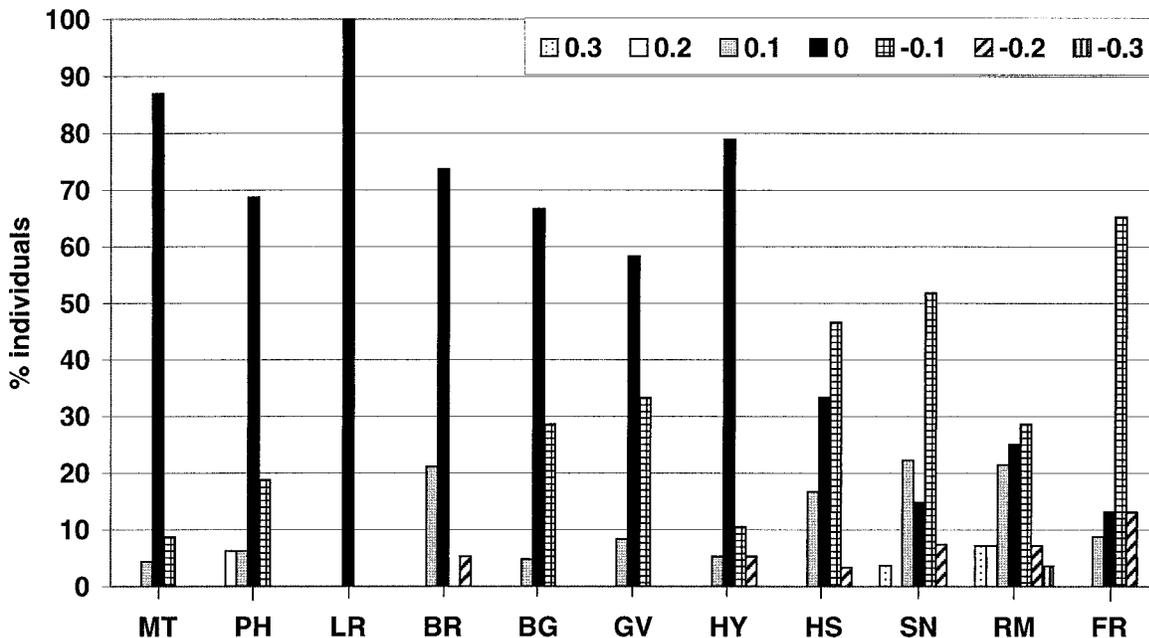


FIG. 3. Distribution of percentage of signed right minus left values of third toe length in 11 chukar populations shown from core (north) to periphery (south), sexes pooled. Population acronyms and sample sizes appear in Table 1. Perfect symmetry column (black) is marked for each population. Note the shift between asymmetry types in the ecotone, as apparent when Yatir (HY) and Hirbet Sira (HS) are compared, with 79% and 33% symmetrical individuals, respectively.

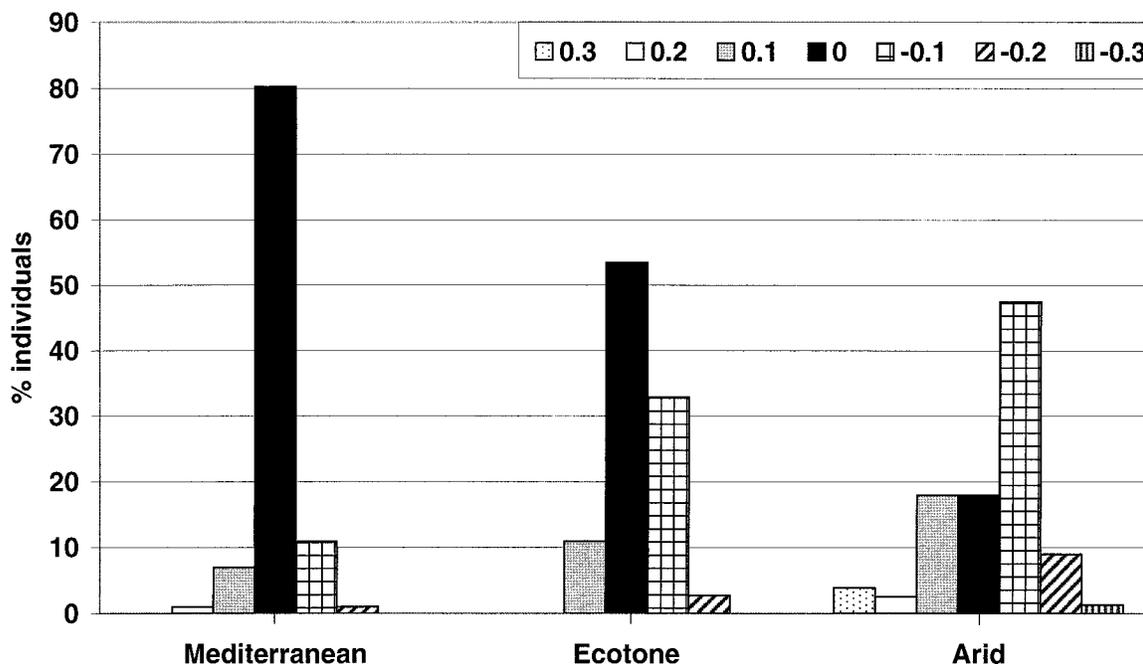


FIG. 4. Distribution of percentage of signed right minus left values of third toe length in each of three predetermined regions (Mediterranean core, ecotone, and arid periphery), sexes pooled. Sample sizes appear in Table 1.

(third) toe across short geographical distances within the chukar range in Israel, from core to periphery. Mean unsigned R-L significantly increased from 0.00–0.04 cm in core populations to 0.09–0.11 cm in the periphery. The frequency of symmetrical individuals in the population decreased across the core-periphery gradient. The range of individual asymmetry increased so that the least symmetrical individuals originated from the arid periphery of the range.

The development of a bilateral trait on both sides of an individual is presumably under the influence of the same gene or gene complex (Clarke 1993). Therefore, it has been suggested that deviation from symmetry toward the right or the left sides does not have a significant genetic basis and represents variation of environmental origin (e.g., Palmer and Strobeck 1992), although the tendency to develop in a stable path and to exhibit asymmetry may have a genetic component (Palmer and Strobeck 1986; Møller and Swaddle 1997). However, DA and antisymmetry in a trait have been thought to have a genetic basis (e.g., Van Valen 1962). Yet, recent work suggests that the additive genetic component of DA and antisymmetry is often small, comparable to that of FA, and in

many cases is actually too small to detect (Graham et al. 1998). The underlying assumption in many studies of asymmetry is that shifts between asymmetry types do not occur within a single trait, and if they do occur, they are rare. Thus, traits are often referred to as having a single fixed type of asymmetry. Based on simulation models and empirical evidence, Graham et al. (1998) suggested that the three types of asymmetry are dynamically interrelated and are part of a continuum rather than separate phenomena, with shifts between the different forms of asymmetry. Transition from FA to antisymmetry and to DA can reflect severe developmental instability (Graham et al. 1993a). Indeed, several studies have shown shifts from one type of asymmetry to another under experimental human-induced environmental stress. For example, McKenzie and Clarke (1988) found that during the development of resistance to Diazinon, an Australian blowfly (*Lucilia cuprina*) population shifted from FA to antisymmetry. After developing resistance the population shifted back to FA. Antisymmetry was generated in rainbow trout mandibular pores under stress (Leary and Allendorf 1989). Graham et al. (1993b) demonstrated that under stressful con-

TABLE 2. Statistics of the distribution of right minus left side measurements (cm) of third toe in chukars across three predetermined study regions.

Area	Sample size	Mean (SE)	Skewness (SE)	Kurtosis (SE)	Wilcoxon signed-rank statistic
Mediterranean core	101	-0.0040 (0.0051)	-0.0717 (0.2402)	4.7963 (0.4761)***	-19.0
Ecotone	73	-0.0274 (0.0081)	-0.0914 (0.2810)	-0.1272 (0.5552)	-165.5**
Arid periphery	78	-0.0346 (0.0138)	0.8344 (0.2722)**	0.6919 (0.5382)	-376.5**

\*\*  $P < 0.01$ , \*\*\*  $P < 0.001$  after a sequential Bonferroni procedure.

ditions of high benzene concentration *Drosophila melanogaster* showed DA in sternopleural bristles compared to unstressed flies, which exhibited FA for the trait. Lens and Van Dongen (2000) compared three populations of several passerine species in Taita Hills, Kenya, that have been exposed to different levels of forest fragmentation in recent decades. They showed that under high levels of this human-induced disturbance, asymmetry in the bird populations shifted from FA to DA. This shift was overlooked in a previous study by the same authors (Lens and Van Dongen 1999), and was revealed only when new analysis methods that enable the detection of shifts between asymmetry types were used (Van Dongen et al. 1999a; Lens and Van Dongen 2000). Thus, it seems that DA and antisymmetry can reflect extreme developmental and/or genetic instability in various cases (McKenzie and Clarke 1988; Graham et al. 1993a). This study of the chukar partridge provides evidence that shift between asymmetry types may occur in a single trait across a species' natural distribution range. This phenomenon may be much wider yet undetected because many bilateral asymmetry studies focus attention on FA alone and select only the subsample of the traits and populations that show significant FA, while disregarding other traits and populations.

Indeed, it has been shown that the distribution of the signed R-L in a population can be a mixture of different asymmetry components (Van Dongen et al. 1999a,b). The findings of this work demonstrate that different asymmetry types can occur across the distribution range in a single trait, supporting the notion that all three asymmetry types are interrelated rather than separate phenomena. Levels of asymmetry increase toward the range periphery with a notable addition of a directional component in the ecotone region. Mean R-L deviates from zero with a significant DA component (toward a larger left side) in both the ecotone and the arid periphery of the range. A mixture of DA and antisymmetry appears when approaching the periphery. The directional and antisymmetrical components may be strongly expressed under conditions where perturbations during development are the norm.

It is difficult to explain the findings based only on the genetic-basis approach to DA and antisymmetry. It is more likely that the changes in directionality and asymmetry expression in more peripheral populations reflect increasing environmental stress with a consequential increase in developmental instability. Population genetics studies have revealed genetic structuring among populations in the study area despite high levels of gene flow, suggesting that local selection pressures are acting (Kark et al. 1999). Dissimilar asymmetry patterns were found even among neighboring populations from very different environments, such as the two ecotonal populations from Yatir and Hirbet Sira (Table 1, Fig. 3). The population from Yatir was much more similar in its R-L distribution to populations located dozens of kilometers away in the Mediterranean core than to that of Hirbet Sira, sampled only several kilometers away, whereas the latter was more similar to the arid peripheral populations located dozens of kilometers away to the south. This suggests that local chukar populations experience different environmental pressures and stresses. It could be hypothesized that the increase in asymmetry across the chukar range results from a

decline in population size toward the periphery, and thus an increase in genetic stress due to low heterozygosity near the periphery. Yet, an analysis of genetic diversity looking at allozyme heterozygosity patterns of the same individuals shows no significant correlation between genetic diversity and asymmetry levels across the range or within single populations. Heterozygosity does not decline in a similar fashion toward the chukar range periphery (Kark et al. 2001).

In this study we used a single trait, a fact that limits our ability to discuss the generality of these patterns. Yet our approach suggests that searching for these shifts, rather than excluding traits that show nonclassical FA distributions, may potentially lead to important insights, and to a better understanding of the underlying factors of ecological and evolutionary patterns in bilateral asymmetry. Whereas ignoring these shifts causes a bias in our understanding of developmental instability patterns and processes, their study may help us solve some of the apparent contradictions seen in the asymmetry literature. Further studies are needed to test the generality of the patterns. A question that arises is whether the selected trait (i.e., central toe length) will reflect the patterns at the individual and population level of other traits, reflecting organismwide asymmetry. Empirical evidence for correlation between asymmetry levels of different traits of a single individual appears to be inconsistent (Clarke 1998a,b). Yet, at least part of this inconsistency and the failure to detect individual-level concordance in unsigned FA may result from methodological factors, such as low repeatability (Lens and Van Dongen 1999; Lens et al. 2002). Lens and Van Dongen (1999) have found positive correlation between unsigned FA values in five passerine species using a novel approach that corrects for the bias resulting from low repeatability at the individual level (termed hypothetical repeatability; and defined as the ratio of the between-individual component of variation in the unsigned FA divided by the total variance; Van Dongen 1998). At the population level, the focus of this study, increasing evidence suggests that FA levels are correlated among different traits (Clarke 1998a; Lens and Van Dongen 1999). Yet, we do not know whether patterns of shifts between asymmetry types are correlated between traits. It would be interesting to further compare differences and similarities in such shifts in different traits at the population level in future studies, working across species ranges.

As suggested in Materials and Methods, the selected trait potentially has high adaptive value and can be measured with high repeatability, factors that are crucial when studying patterns in bilateral asymmetry and shifts between asymmetry types across a species range. In light of this, the clear and significant patterns found across the chukar range, and especially the substantial differences in asymmetry between populations that are geographically very close to each other, are noteworthy. These populations are genetically similar and experience homogenizing gene flow, yet occur in regions with different environments (e.g., Yatir and Hirbet Sira). Revealing the underlying mechanisms following an experimental approach should be a central direction in future studies in this field.

Chukars are not well adapted to desert conditions, and in arid and hot environments they are distributed mainly in food- and water-rich patches (Degen et al. 1984). The differences

in asymmetry suggest that even within these apparently favorable arid-zone resource patches, individuals confront higher levels of stress compared to those from more mesic regions. The increasing levels of asymmetry in the examined trait across the range support recent work showing higher FA in peripheral populations (Møller 1995; Carbonell and Tellería 1998; Siikämäki and Lammi 1998; but see Auffray et al. 1999). Yet unlike previous studies that focused mostly on a core-periphery dichotomy, this study tested asymmetry trends across a more continuous distribution gradient, including the ecotone region, where the edge of the chukar's continuous distribution is found. This enabled me to test for shifts in asymmetry types and characteristics across the species' range. This work indicates that the ecotone is an area of transition between types and levels of third toe asymmetry. Beyond the ecotone, toward the extreme periphery of the range, asymmetry levels significantly increase and change. If only part of this range (e.g., the periphery alone) would have been sampled rather than the continuum from core to periphery, completely different conclusions as to the type and extent of asymmetry in this trait would have been drawn. The study suggests that asymmetry can greatly shift across the distribution range, even within short geographical distances and in a single trait. I recommend that future studies of asymmetry and of developmental instability do not ignore those traits not showing clear FA, but rather focus on transitions and interconnections between the various forms of asymmetry. This may lead to new insights in the field, in a test of the dynamic interface between asymmetry types.

## ACKNOWLEDGMENTS

Many thanks to T. Blackburn, S. Clegg, A. Genin, J. Graham, J. Kark, I. Lovette, L. Lens, U. Safrieli, T. Schaffer, E. Schmidt, S. Shafir, T. Smith, H. Soreq, S. Van Dongen, H. Lisle Gibbs, and two anonymous reviewers for their most helpful reviews of the manuscript; to P. Alkon, G. Clarke, S. Field, I. Noy-Meir, E. Randi, D. Russel, and P. Taylor for discussion; and to G. Clarke, O. Farber, G. Livshits, I. Milstein, S. Rosset, P. Siikämäki, and S. Van Dongen for statistical advice. I thank the Israel Nature and National Parks Authority for their help with fieldwork. This research was funded by grants from the Rothschild Foundation, the Inter-University Ecology Fund, the Rieger Foundation and the Pontremoli Fund founded by the JNF, and by the Blaustein International Center for Desert Studies, Ben Gurion University of the Negev. This paper is dedicated to A. Merkin, a friend and collaborator, without whom this study would not have been possible.

## LITERATURE CITED

- Alkon, P. U. 1974. Social behavior of a population of chukar partridge (*Alectoris chukar*) in Israel. Cornell Univ. Press, Ithaca, NY.
- Andrewartha, H. G., and L. C. Birch, 1954. The distribution and abundance of animals. Univ. of Chicago Press, Chicago, IL.
- Auffray, J.-C., S. Renaud, P. Alibert, and E. Nevo. 1999. Developmental stability and adaptive radiation in the *Spalax ehrenbergi* superspecies in the Near-East. *J. Evol. Biol.* 12:207–221.
- Bitan, A., and S. Rubin. 1991. Climatic atlas of Israel for physical and environmental planning and design. Ministry of Transport, Jerusalem.
- Bjorksten, T., P. David, A. Pomiankowski, and K. Fowler. 2000a. Fluctuating asymmetry of sexual and nonsexual traits in stalk-eyed flies: a poor indicator of developmental stress and genetic quality. *J. Evol. Biol.* 13:89–97.
- Bjorksten, T., K. Fowler, and A. Pomiankowski. 2000b. What does sexual trait FA tell us about stress? *Trends Ecol. Evol.* 15:163–166.
- Boag, P. T., and A. J. Van Noordwijk. 1987. Quantitative genetics. Pp. 45–78 in F. Cooke and P. A. Buckley, eds. *Avian genetics: a population and ecological approach*. Academic Press, London.
- Carbonell, R., and J. L. Tellería. 1998. Increased asymmetry of tarsus-length in three populations of blackcaps *Sylvia atricapilla* as related to proximity to range boundary. *Ibis* 140:331–333.
- Channell, R., and M. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. *Nature* 403:84–86.
- Clarke, G. M. 1992. Fluctuating asymmetry: a technique for measuring developmental stress of genetic and environmental origin. *Acta Zool. Fenn.* 191:31–35.
- . 1993. The genetic basis of developmental stability. I. Relationships between stability, heterozygosity and genomic coadaptation. *Genetica* 89:15–23.
- . 1998a. The genetic basis of developmental stability. IV. Individual and population asymmetry parameters. *Heredity* 80:553–561.
- . 1998b. The genetic basis of developmental stability. V. Inter- and intra-individual character variation. *Heredity* 80:562–567.
- Clarke, G. M., and J. A. McKenzie. 1987. Developmental stability of insecticide resistant phenotypes in blowfly: a result of canalizing natural selection. *Nature* 325:345–346.
- Danin, A., and U. Plitman. 1987. Revision of the plant geographical territories of Israel and Sinai. *Syst. Evol.* 156:43–53.
- David, P., A. Hingle, K. Fowler, and A. Pomiankowski. 1999. Measurement bias and fluctuating asymmetry estimates. *Anim. Behav.* 57:251–253.
- Degen, A. A., B. Pinshow, and P. J. Shaw. 1984. Must desert chukars (*Alectoris chukar sinaica*) drink water? Water influx and body mass changes in response to dietary water content. *Auk* 101:47–52.
- Frankenberg, E. 1999. Will the biogeographical bridge continue to exist? *Isr. J. Zool.* 45:65–74.
- Graham, J. H., D. C. Freeman, and J. M. Emlen. 1993a. Antisymmetry, directional asymmetry, and dynamic morphogenesis. *Genetica* 89:121–137.
- Graham, J. H., K. E. Roe, and T. B. West. 1993b. Effects of lead and benzene on the developmental stability of *Drosophila melanogaster*. *Ecotoxicology* 2:185–195.
- Graham, J. H., J. M. Emlen, D. C. Freeman, L. J. Leamy, and J. A. Kieser. 1998. Directional asymmetry and the measurement of developmental instability. *Biol. J. Linn. Soc.* 64:1–16.
- Henshel, D. S., K. M. Cheng, R. Norstrom, P. Whitehead, and J. D. Steeves. 1993. Morphometric and histologic changes in brains of great blue heron hatchlings exposed to PCDDs: preliminary analyses. Pp. 262–277 in W. G. Landis, J. S. Hughes and M. A. Lewis, eds. *Environmental toxicology and risk assessment*. Publication no. 1179, American Society for Testing and Materials, Philadelphia, PA.
- Hoffmann, A. A., and M. W. Blows. 1994. Species borders: ecological and evolutionary perspectives. *Trends Ecol. Evol.* 9:223–227.
- Kark, S. 1999. Within-population diversity in the distribution range: partridges as a research model. The Hebrew University of Jerusalem, Jerusalem. Available via <http://www.stanford.edu/group/Mooney/salit>.
- Kark, S., P. U. Alkon, U. N. Safrieli, and E. Randi. 1999. Conservation priorities for the chukar partridge in Israel based on genetic diversity across an ecological gradient. *Conserv. Biol.* 13:542–552.
- Kark, S., U. N. Safrieli, C. Tabarroni, and E. Randi. 2001. Relationship between heterozygosity and asymmetry: a test across the distribution range. *Heredity* 87:119–127.
- Lawton, J. H. 1993. Range, population abundance and conservation. *Trends Ecol. Evol.* 8:409–413.

- Leary, R. F., and F. W. Allendorf. 1989. Fluctuating asymmetry as an indicator of stress: implications for conservation biology. *Trends Ecol. Evol.* 4:214–217.
- Lens, L., and S. Van Dongen. 1999. Evidence for organism-wide asymmetry in five bird species of a fragmented afro-tropical forest. *Proc. R. Soc. Lond. B* 266:1055–1060.
- . 2000. Fluctuating and directional asymmetry in natural bird populations exposed to different levels of habitat disturbance, as revealed by mixture analysis. *Ecol. Lett.* 3:516–522.
- Lens, L., S. Van Dongen, C. Wilder, T. Brooks, and E. Matthysen. 1999. Fluctuating asymmetry increases with habitat disturbance in seven bird species of a fragmented afro-tropical forest. *Proc. R. Soc. Lond. B* 266:1241–1246.
- Lens, L., S. Van Dongen, S. Kark, and E. Matthysen. 2002. Fluctuating asymmetry as an indicator of fitness: Can we bridge the gap between studies? *Biol. Rev. In press.*
- Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104:116–121.
- Ludwig, W. 1932. *Das rechts-links problem im tierreich und beim menschen.* Springer, Berlin.
- Markow, T. A. 1995. Evolutionary ecology and developmental instability. *Annu. Rev. Entomol.* 40:105–120.
- Markow, T., and G. Clarke. 1997. Meta-analysis of the heritability of developmental stability: a giant step backwards. *J. Evol. Biol.* 10:31–37.
- McKenzie, J. A., and G. M. Clarke. 1988. Diazinon resistance, fluctuating asymmetry and fitness in the Australian sheep blowfly, *Lucilia cuprina*. *Genetics* 120:213–220.
- Møller, A. P. 1995. Patterns of fluctuating asymmetry in sexual ornaments of birds from marginal and central populations. *Am. Nat.* 145:316–327.
- . 1998. Developmental stability as a general measure of stress. Pp. 181–213 in A. P. Møller, M. Milinski, and P. J. B. Slater, eds. *Advances in the study of behavior.* Vol. 27. Academic Press, London.
- Møller, A. P., and J. P. Swaddle. 1997. *Asymmetry, developmental stability, and evolution.* Oxford Univ. Press, Oxford, U.K.
- Nissani, R. 1974. Geographic variability of the chukar *Alectoris chukar* (Gray) and Bergmann's rule. (In Hebrew, abstract in English). The Hebrew University, Jerusalem.
- Palmer, A. R. 1994. Fluctuating asymmetry analyses: a primer. Pp. 335–364 in T. A. Markow, ed. *Developmental instability: its origins and evolutionary implications.* Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Palmer, A. R., and C. Strobeck. 1986. Fluctuating asymmetry: measurement, analysis, patterns. *Annu. Rev. Ecol. Syst.* 17:391–421.
- . 1992. Fluctuating asymmetry as a measure of developmental stability: implications of non-normal distributions and power of statistical tests. *Acta Zool. Fenn.* 191:57–72.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Safriel, U. N., S. Volis, and S. Kark. 1994. Core and peripheral populations, and global climate change. *Isr. J. Plant Sci.* 42:331–345.
- SAS Institute. 1995. JMP. Ver. 3.1.5. SAS Institute, Inc., Cary, NC.
- Shapiro, S. S., M. B. Wilk, and H. J. Chen. 1968. A comparative study of various tests for normality. *J. Am. Stat. Assoc.* 63:1342–1372.
- Shirihai, H. 1996. *The birds of Israel.* Academic Press, London.
- Siikämäki, P., and A. Lammi. 1998. Fluctuating asymmetry in central and marginal populations of *Lychnis viscaria* in relation to genetic and environmental factors. *Evolution* 52:1285–1292.
- Smith, T. B. 1993. Disruptive selection and the genetic basis of bill size polymorphism in the African finch *Pyrenestes*. *Nature* 363:618–620.
- Smith, T. B., R. K. Wayne, D. J. Girman, and M. W. Bruford. 1997. A role for ecotones in generating rainforest biodiversity. *Science* 276:1855–1857.
- Swaddle, J. P., and I. C. Cuthill. 1994. Preference for symmetric males by female zebra finches. *Nature* 367:165–166.
- Swaddle, J. P., M. S. Witter, and I. C. Cuthill. 1994. The analysis of fluctuating asymmetry. *Anim. Behav.* 48:986–989.
- Van Dongen, S. 1998. How repeatable is the estimation of developmental stability by fluctuating asymmetry? *Proc. R. Soc. Lond. B Biol. Sci.* 265:1423–1427.
- Van Dongen, S., L. Lens, and G. Molenberghs. 1999a. Mixture analysis of asymmetry: modelling directional asymmetry, anti-symmetry and heterogeneity in fluctuating asymmetry. *Ecol. Lett.* 2:387–396.
- Van Dongen, S., G. Molenberghs, and E. Matthysen. 1999b. The statistical analysis of fluctuating asymmetry: REML estimation of a mixed regression model. *J. Evol. Biol.* 12:94–102.
- Van Valen, L. 1962. A study of fluctuating asymmetry. *Evolution* 16:125–142.
- Zar, J. H. 1999. *Biostatistical analysis.* Prentice-Hall, Upper Saddle River, NJ.

Corresponding Editor: H. L. Gibbs