Evidence for organism-wide asymmetry in five bird species of a fragmented afroropical forest

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Empirical evidence for between-trait correlation in fluctuating asymmetry (FA) at the individual level is generally lacking or contradictory. Yet the assumption of organism-wide asymmetry, estimated by the asymmetry of any given trait, is inherent to most studies that use FA as a measure of developmental stability (DS). A commonly assumed reason for this weak between-trait correlation is the low repeatability of individual, single-trait asymmetry. In this paper we describe high repeatability and significant between-trait correlation in population- and individual-level FA in five afroropical bird species inhabiting a fragmented cloud forest. Absence of anti-symmetry and of between-trait correlation in signed FA levels permits us to translate the observed patterns into the presumed underlying DS, using the concept of hypothetical repeatability. This correction, which has not been applied before in this context, proved adequate as it yielded correlations comparable to those found at the population level.

Keywords: fluctuating asymmetry; developmental stability; organism-wide asymmetry; individual asymmetry parameter; hypothetical repeatability; habitat fragmentation

1. INTRODUCTION

Fluctuating asymmetry (FA), i.e. random deviations from perfect symmetry in bilaterally paired traits (Van Valen 1962), has been shown to increase with environmental and/or genetic stress (Palmer & Strobeck 1986; but see e.g. Fowler & Whitlock 1994) and may be related to individual fitness and quality (Møller 1990; Thornhill 1992; but see Clarke 1998a). For single-trait FA to be a useful measure of stress or quality, however, individual- and population-level FA should be correlated between different traits. The existence of a population asymmetry parameter has been supported by several studies (see Clarke (1998b) and references therein) although patterns remain equivocal. In contrast, between-trait concordance of FA at the individual level (providing a measure of organism-wide asymmetry; Evans *et al.* 1995) is generally weak or absent, even for traits that are correlated developmentally (Clarke *et al.* 1992; Leamy 1993; Clarke 1998b). Nevertheless, the presence of an individual asymmetry parameter is generally assumed in evolutionary models of FA (e.g. Dufour & Weatherhead 1996).

The overall failure to detect between-trait correlations in individual-level FA may be due to trait-specific timing during ontogeny when environmental perturbations can cause aberrant phenotypes (Clarke 1995). If so, developmental noise acting randomly on individual traits cannot be expected to cause concordance at the individual level, independently of whether the genetic basis of stability is genome wide or character dependent (Clarke 1998b).

Alternatively, detection failure may be mainly a consequence of low repeatability of FA at the individual level (as opposed to population-level FA), resulting from high sampling variability in estimating individual FA (Whitlock 1996) or proportionally large measurement error (Van Dongen 1998a). Low repeatability results in poor estimates of the presumed underlying developmental stability (DS) and, thus, in a downward bias of between-trait correlations (Whitlock 1996). However, it is possible to correct for this bias by applying hypothetical repeatability, defined as the ratio of the between-individual component of variation in the unsigned FA divided by the total variance (Whitlock 1996; Van Dongen 1998a). Such a correction is needed when examining whether FA and/or DS of different traits are expected to correlate, i.e. whether single-trait FA may reflect overall quality at the individual level.

We applied the concept of hypothetical repeatability to translate patterns of between-trait correlation in FA into patterns of DS in five bird species inhabiting a severely fragmented cloud forest in south-east Kenya. Elsewhere we have shown that population-level FA in tarsus length sharply increased with decreasing forest fragment quality for a suite of forest-restricted bird species (L. Lens, S. van Dongen, C. M. Wilder, T. M. Brooks and E. Matthysen, unpublished data). We concluded that the efficiency of DS mechanisms had been reduced in relation to exposure to systemic stress and that repeated measurement of accurately measurable traits could provide an early warning system for monitoring stress effects (see also Manning & Chamberlain 1994; Badyaev 1998). In this paper we measure a series of additional feather traits and analyse patterns of

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between-trait correlation in signed and unsigned FA at the population and individual levels.

2. METHODS

(a) *Study site and species*

Fieldwork was conducted between July 1996 and July 1998 in the Taita Hills, south-east Kenya (03° 20' S, 38° 15' E and maximum altitude 2209 m). Forest fragmentation and degradation since the 1960s has been substantial, resulting in a conversion of the indigenous forest block to a scatter of 12 remnants, eight of which are smaller than 5 ha (details in Beentje 1987; Brooks *et al.* 1998). The three larger fragments differ considerably in quality (Wilder *et al.* 1999). The least disturbed fragment (Mbololo, 20 ha) has more biomass, higher stem densities, more tree species, higher diversity, higher equitability, greater canopy cover, more open shrub layer, higher leaf litter cover and less herbaceous cover than the intermediate (Ngangao, 92 ha) and most disturbed ones (Chawia, 50 ha).

We measured morphometrical traits on the following forest-restricted bird species that were captured by passive mist netting (no use of tape luring or artificial feeders): Taita thrush (*Turdus helleri*, $n=113$), Taita white eye (*Zosterops silvanus*, $n=142$), white-starred robin (*Pogonocichla stellata*, $n=312$), stripe-cheeked greenbul (*Andropadus milanensis*, $n=136$) and olive sunbird (*Nectarinia olivacea*, $n=309$).

(b) *FA measurement*

Four ringers made two repeated and independent measurements (sequence left–right–left–right or right–left–right–left) of either side of a series of bilaterally paired traits. Each processed birds in all fragments and was unaware of the hypotheses tested. Tarsus length (TL; fully-grown at fledging) was measured for every species, from the notch on the back of the intertarsal joint to the point obtained by bending the toes to an angle of 90° to the tarsus (Svensson 1992). Species-specific feather traits (fully-grown after first full moult) were chosen primarily on the basis of accuracy of measurement.

- (i) Taita thrush: length of the left and right outer rectrix (ORL), measured by placing a ruler under the tail between the tail feathers and the under-tail coverts and pushing it gently against the root of the central pair (Svensson 1992), and maximal width of left and right post-ocular patch (PPW).
- (ii) Taita white eye: maximal width (ERW) and height (ERH) of left and right eye ring.
- (iii) White-starred robin: maximal width (PSW) and height (PSH) of left and right pre-ocular spot.
- (iv) Stripe-cheeked greenbul: maximal width of left and right cheek patch (CPW).
- (v) Olive sunbird: maximal width of left and right pectoral tuft (PTW).

Rectrices were measured with a specially designed ruler to the nearest 1 mm and the other traits were measured with slide callipers to the nearest 0.1 mm. Whereas tarsus length was taken on each captured individual, feather traits were measured on a random subsample, since we tried to minimize stress to the birds by restricting their handling time and the ruffled plumage of a small number of individuals caused by extraction from the nets did not allow accurate measurements. As a result, sample sizes vary among analyses.

(c) *FA analysis*

We carried out mixed regression analysis with restricted maximum likelihood (REML) parameter estimation to separate real asymmetry (signed FA; left minus right trait length) from measurement error (ME) (Van Dongen *et al.* 1999). The significance of FA was obtained from a likelihood ratio test while directional asymmetry was tested by an F -test, adjusting the denominator degrees of freedom by Satterthwaite's procedure (Van Dongen *et al.* 1999). We inspected the distribution of the signed and unsigned FA (the magnitude of the signed FA) and calculated the hypothetical repeatability $R=1-(((V_{FA}+V_{ME})\times(\pi-2)/\pi)/V_{FA})$, whereby V_{FA} , V_{FAI} and V_{ME} are the variances of the signed and unsigned FA and measurement error (Van Dongen 1998a). High hypothetical repeatability indicates high between-individual heterogeneity in the underlying DS, causing a leptocurtic distribution of the signed FA. To translate correlations in unsigned FA into correlations in the presumed underlying DS, we divided each correlation coefficient by the square root of the product of the hypothetical repeatabilities of the corresponding traits (Whitlock 1998).

Leptocurtically distributed FA values, however, might also be indicative of the presence of anti-symmetrical individuals in the population (Palmer & Strobeck 1992; Van Dongen 1998b). As anti-symmetry can have a genetic basis, it does not necessarily reflect DS (Palmer & Strobeck 1992; Palmer 1994; but see Graham *et al.* 1993). Whereas FA and anti-symmetry cannot be separated statistically with high power, they can be distinguished reliably through visual inspection of scatter plots depicting between-trait correlation in unsigned FA (see Rowe *et al.* (1997) for a comparable approach).

(d) *Analysis of between-trait correlations in FA*

Between-fragment heterogeneity in average unsigned FA was tested with Levene's test, a one-way ANOVA with unsigned FA as the dependent variable and fragment as the factor. This test is insensitive to departure from normality (Palmer & Strobeck 1992) and was applied because the signed FA showed a leptocurtic distribution (see below). Due to the small number of fragments (three) we could not use standard correlation techniques to assess the population-level association between character asymmetries (the highest exact p -value for Spearman's rank correlation coefficient estimates based on three observations is 0.17; one-tailed). Instead we applied a random effects model and calculated the intraclass correlation coefficient r as the ratio of the between-fragment component to the total variance in unsigned FA (see Lessells & Boag 1987), after correcting for species and trait effects. We further tested whether this correlation differed between species using a heterogeneous variance structure (Littell *et al.* 1996). Average unsigned FA values were log transformed to obtain approximate normality.

To examine whether trait asymmetries were correlated at the individual level, we calculated unbiased individual FA estimates (i.e. deviations of the random slopes from the fixed effects slope in the mixed regression model; Van Dongen *et al.* 1999) and estimated individual-level association with Pearson's correlation coefficients. As the unsigned FA values were not normally distributed, we applied the bootstrap by resampling individuals with replacement (1000 resamples) to construct confidence intervals (percentile method; Efron & Tibshirani 1993). This approach was preferred over non-parametric correlation techniques, since the application of hypothetical repeatability, as a means of correcting downward biases in

Table 1. *Variance components and the distribution of signed and unsigned FA for all species–trait combinations*

(n , sample size; V_{ind} , variance in individual trait size; V_{FA} , variance in signed FA; V_{ME} , variance in measurement error; mean, mean of the signed FA; W , Shapiro–Wilks statistic; K , kurtosis; $V_{|\text{FA}|}$, variance in unsigned FA; R , hypothetical repeatability.)

species ^a	trait ^b	n	V_{ind}	V_{FA}	V_{ME}	mean ^c	W	K	$V_{ \text{FA} }$	R
TT	TL	113	0.97	0.034	0.003	0.00	0.74	16.00	0.027	0.51
	PPW	100	6.76	0.190	0.005	−0.05	0.72	17.20	0.143	0.51
	ORL	73	18.60	0.990	0.082	−0.02	0.80	3.82	0.800	0.52
TW	TL	142	0.49	0.047	0.002	−0.05	0.71	10.80	0.035	0.50
	ERW	121	0.64	0.062	0.009	0.01	0.84	8.40	0.049	0.48
	ERH	121	0.50	0.052	0.007	−0.01	0.79	14.80	0.040	0.47
WR	TL	312	2.01	0.044	0.004	−0.03	0.78	8.50	0.035	0.51
	PSW	176	1.40	0.071	0.006	−0.05	0.84	6.35	0.043	0.36
	PSH	115	0.14	0.029	0.003	−0.03	0.85	5.69	0.019	0.39
OS	TL	309	0.61	0.034	0.005	−0.02	0.80	16.10	0.029	0.52
	PTW	257	4.20	0.130	0.007	0.01	0.79	7.95	0.087	0.43
SG	TL	136	2.89	0.049	0.002	0.01	0.66	23.30	0.037	0.50
	CPW	123	8.29	0.140	0.008	0.00	0.84	6.78	0.120	0.56

^aTT, Taita thrush; TW, Taita white eye; WR, white-starred robin; OS, olive sunbird; SG, stripe-cheeked greenbul.

^b See text for description of the traits.

^c Mean values of the signed FA did not differ significantly from zero; all $p > 0.05$.

between-trait correlations, has been designed for parametric correlation coefficients.

3. RESULTS

(a) *Mixed regression analysis*

The distribution of the signed FA showed no directional component and deviated significantly from normality (see Shapiro–Wilks statistic, W , all $p < 0.0003$) (table 1). The leptocurtic distribution (high kurtosis, K) indicated a high repeatability, R (Van Dongen 1998a,b). The signed FA (V_{FA}) was several orders of magnitude larger than the measurement error (V_{ME}) (table 1) and was highly significant for all trait–species combinations (likelihood ratio tests comparing REML of mixed models with and without random side-effects, all $p < 0.001$).

(b) *Population-level asymmetry*

Average unsigned FA values were highly heterogeneous between fragments (figure 1; Levene's tests, all $p < 0.005$). Visual inspection of figure 1 indicates that the FA pattern was highly comparable for all traits in the five species. To measure the association between trait asymmetries, we applied a statistical model with average unsigned FA as the dependent variable (log transformed) and fragment, species and trait as random factors (likelihood ratio tests: fragment $\chi^2_1 = 29.5$ and $p = 0.0001$, trait $\chi^2_1 = 11.71$ and $p = 0.001$, and species $\chi^2_1 = 0.04$ and $p = 0.42$). The intraclass correlation coefficient r , calculated as the between-fragment component to the total variance (i.e. between-fragment component plus within-fragment component) in FA, equalled 0.76, indicating strong between-trait correlation of the population-level FA estimates. The coefficients did not differ between the five species (heterogeneous variance model: $\chi^2_4 = 7.84$ and $p = 0.1$).

(c) *Individual-level asymmetry*

Individual unsigned FA values were positively correlated for all species–trait combinations (table 2). Correlations between tarsus length and feather dimen-

sions (mean $r = 0.34$) were thereby of the same magnitude as those between two dimensions of the same trait (i.e. width and height of the eye ring of Taita white eyes and pre-ocular spot of white-starred robins; mean $r = 0.29$). Visual inspection of the overall between-trait relationship in unsigned FA (figure 2) showed that most observations were located in the lower left corner and close to the x - and y -axes of the graphs. This was in the direction expected, since FA is typically characterized by a large proportion of symmetrical individuals (Whitlock 1996; Rowe *et al.* 1997). In contrast, anti-symmetry would have yielded patterns with a high proportion of observations in the upper right corner, referring to cases where the levels of asymmetry are large in both traits.

No significant between-trait correlation was found for the individual signed FA levels (table 2). The absence of such a correlation allowed us to translate the between-trait correlations in the unsigned FA into correlations in the presumed underlying DS (Whitlock 1998; see table 1 for trait-specific R -values). The resulting between-trait correlations in DS were high (table 2) and the average value ($r = 0.70$) closely resembled the between-trait correlation in FA at the population level, estimated by the intraclass correlation coefficient ($r = 0.76$; see above).

4. DISCUSSION

Populations with the highest levels of unsigned FA in one trait were also more asymmetrical in other traits. Similarly, unsigned FA levels of different traits were significantly correlated between individuals, even for traits that developed at different ages (tarsus versus feather traits). In contrast, no between-trait association was found for the signed FA values, providing evidence that the traits developed independently during ontogeny. This is important, since some traits may have been correlated developmentally (e.g. height and width of eye rings and pre-ocular spots) and correlations between the signed FA levels could hamper the interpretation of between-trait correlations in unsigned FA (Leamy *et al.* 1997). In particular, the absence

Figure 1. Mean unsigned FA values per fragment for all species–trait combinations. (a) Olive sunbird, (b) white-starred robin, (c) Taita thrush, (d) stripe-cheeked greenbul, and (e) Taita white eye. First bar, Mbololo (highest quality as defined by a set of nine vegetation parameters; Wilder *et al.* 1999); second bar, Ngangao (intermediate quality); and third bar, Chawia (lowest quality). Sample sizes and F -statistics of Levene's tests are given above the bars; $^*p < 0.005$, $^{**}p < 0.001$, $^{***}p < 0.0001$. See text for full description of the traits.

of between-trait correlation in signed FA allowed us to translate the observed correlations into patterns of the presumed underlying DS. Unlike between-trait correlations in individual FA, population-level correlates are unbiased and, thus, reflect patterns in DS as well. The close resemblance between individual- (mean $r = 0.70$) and population-level correlation in DS ($r = 0.76$) hence confirms that the use of hypothetical repeatability adequately corrected for sampling and measurement error of individual, single-trait FA estimation.

Apart from laboratory studies on developmentally related traits (Atchley *et al.* 1984; Leamy & Atchley 1984; Leamy 1993) and a recent field study on traits located in different body regions (Dufour & Weatherhead 1996), the vast majority of studies have failed to detect individual-level concordance in unsigned FA (see Palmer & Strobeck 1986; Leamy 1993; Möller & Swaddle 1997). In view of

this, how can we explain the significant patterns found in this study? FA estimates stemmed from a statistical model that tests for non-zero directional asymmetry and heterogeneity in FA and ME among samples (Van Dongen *et al.* 1999). Such a procedure generates unbiased estimates of individual FA levels, which is a first prerequisite for detecting between-trait correlations. Second, the estimated levels of hypothetical repeatability measured were high, with 10 out of 13 values ranging between 0.47 and 0.56 ($R_{\max} = 0.637$; Whitlock 1998). High repeatability is assumed to be a second prerequisite for detecting between-trait correlation in individual FA levels. Whereas most individual-level studies do not present R -values, Dufour & Weatherhead (1996) did find low levels (mean $R = 0.16$ and range = 0–0.44 as calculated from their table 2) and, indeed, weak between-trait correlations in individual FA. A third possibility for differences between studies is that

Table 2. Measures of association between-trait asymmetries within individuals

(R_{signed} , Pearson correlation coefficient (with probability p) of the signed FA; R_{unsigned} , Pearson correlation coefficient of the unsigned FA; CI = 95% obtained by resampling individuals with replacement (percentile method; Efron & Tibshirani 1993); DS, transformed correlation in presumed underlying DS by applying the hypothetical repeatability R .)

species ^a	trait ^b	R_{signed}	p	R_{unsigned}	CI	DS
TT	TL × PPW	−0.09	0.37	0.35	0.14–0.61	0.69
	TL × ORL	0.12	0.31	0.45	0.21–0.66	0.88
	PPW × ORL	−0.01	0.91	0.27	0.13–0.54	0.52
TW	TL × ERW	0.03	0.74	0.23	0.06–0.43	0.52
	TL × ERH	−0.03	0.74	0.35	0.07–0.63	0.83
	ERW × ERH	0.11	0.24	0.42	0.32–0.58	0.88
WR	TL × PSW	−0.02	0.79	0.28	0.19–0.40	0.67
	TL × PSH	0.08	0.40	0.31	0.17–0.51	0.69
	PSW × PSH	0.11	0.26	0.18	0.01–0.38	0.48
OS	TL × PTW	−0.02	0.75	0.32	0.22–0.45	0.68
SG	TL × CPW	0.07	0.44	0.42	0.15–0.63	0.77

^aTT, Taita thrush; TW, Taita white eye; WR, white-starred robin; OS, olive sunbird; SG, stripe-cheeked greenbul.

^bSee text for description of the traits.

Figure 2. Pairwise relationship between standardized unsigned FA for all species–trait combinations. Individual FA values were transformed per species and trait by dividing the individual estimates by the respective standard deviations. As FA values from different species and traits were pooled, the data are not statistically independent. Therefore no significance tests were performed.

the occurrence of individual-level concordance in unsigned FA could be trait, species or population specific, for reasons as yet unknown.

Laboratory experiments (e.g. temperature tests; Parsons 1992) predict that only extreme stressors, which are to be expected in marginal or disturbed environments, can increase FA under field conditions. Yet, the extent to which FA can be expected to reflect exposure to stress may largely depend on which trait is chosen for analysis. In particular, ‘appropriate’ traits should have a functional basis for symmetry and be able to withstand minor fluctuations in symmetry without concomitant

significant losses in individual fitness (Clarke 1995). Between-trait correlation in FA, as demonstrated in this paper, permits the selection of traits largely based on rapidly verifiable properties such as high repeatability and ease of measurement. The resulting gain in time can be crucial, particularly when dealing with critically endangered organisms.

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REFERENCES

- Atchley, W. R., Herring, S. W., Riska, B. & Plummer, A. A. 1984 Effects of the muscular dysgenesis gene on developmental stability in the mouse mandible. *J. Cranial Gen. Dev. Biol.* **4**, 179–189.
- Badyaev, A. V. 1998 Environmental stress and developmental stability in dentition of the Yellowstone grizzly bears. *Behav. Ecol.* **9**, 339–344.
- Beentje, H. J. 1987 An ecological and floristic study of the forests of the Taita Hills, Kenya. *Utafiti* **1**, 23–66.
- Brooks, T., Lens, L., Barnes, J., Barnes, R., Kihuria, J. K. & Wilder, C. 1998 The conservation status of the forest birds of the Taita Hills, Kenya. *Bird Conserv. Int.* **8**, 119–139.
- Clarke, G. M. 1995 The genetic basis of developmental stability. II. Asymmetry of extreme phenotypes revisited. *Am. Nat.* **146**, 708–725.
- Clarke, G. M. 1998a Developmental stability and fitness: the evidence is not quite so clear. *Am. Nat.* **152**, 762–766.
- Clarke, G. M. 1998b The genetic basis of developmental stability. IV. Individual and population asymmetry parameters. *Heredity* **80**, 553–561.
- Clarke, G. M., Oldroyd, B. P. & Hunt, P. 1992 The genetic basis of developmental stability in *Apis mellifera*: heterozygosity vs. genic balance. *Evolution* **46**, 753–762.
- Dufour, K. & Weatherhead, P. J. 1996 Estimation of organism-wide asymmetry in red-winged blackbirds and its relation to studies of mate selection. *Proc. R. Soc. Lond. B* **263**, 769–775.

- Efron, B. & Tibshirani, R. J. 1993 *An introduction to the bootstrap*. New York and London: Chapman & Hall.
- Evans, M. R., Martins, T. L. F. & Haley, M. P. 1995 Inter- and intra-sexual patterns of fluctuating asymmetry in the red-billed streamtail: should symmetry always increase with ornament size? *Behav. Ecol. Sociobiol.* **37**, 15–23.
- Fowler, K. & Whitlock, M. C. 1994 Fluctuating asymmetry does not increase with moderate inbreeding in *Drosophila melanogaster*. *Heredity* **73**, 373–376.
- Graham, J. H., Freeman, D. C. & Emlen, J. M. 1993 Antisymmetry, directional asymmetry, and dynamic morphogenesis. *Genetica* **89**, 121–137.
- Leamy, L. 1993 Morphological integration of fluctuating asymmetry in the mouse mandible. *Genetica* **89**, 139–153.
- Leamy, L. & Atchley, W. R. 1984 Morphometric integration in the rat (*Rattus* sp.) scapula. *J. Zool. (Lond.)* **202**, 43–56.
- Leamy, L., Routman, E. & Cheverud, J. M. 1997 A search for quantitative trait loci affecting asymmetry of mandibular characters in mice. *Evolution* **51**, 957–969.
- Lessells, C. M. & Boag, P. T. 1987 Unrepeatable repeatabilities: a common mistake. *Auk* **104**, 116–121.
- Littell, R. C., Milliken, G. A., Stroup, W. W. & Wolfinger, R. D. 1996 *SAS[®] system for mixed models*. New York: SAS Institute Inc.
- Manning, J. T. & Chamberlain, A. T. 1994 Fluctuating asymmetry in gorilla canines: a sensitive indicator of environmental stress. *Proc. R. Soc. Lond. B* **255**, 189–193.
- Møller, A. P. 1990 Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Anim. Behav.* **40**, 1185–1187.
- Møller, A. P. & Swaddle, J. P. 1997 *Asymmetry, developmental stability, and evolution*. New York: Oxford University Press.
- Palmer, A. R. 1994 Fluctuating asymmetry analyses: a primer. In *Developmental stability: its origins and evolutionary implications* (ed. T. A. Markow), pp. 335–364. Dordrecht: Kluwer Academic Publishers.
- Palmer, A. R. & Strobeck, C. 1986 Fluctuating asymmetry: measurement, analysis and patterns. *A. Rev. Ecol. Syst.* **17**, 391–421.
- Palmer, A. R. & Strobeck, C. 1992 Fluctuating asymmetry as a measure of developmental stability: implications of non-normal distributions and power of tests. *Acta Zool. Fenn.* **191**, 57–72.
- Parsons, P. A. 1992 Fluctuating asymmetry: a biological monitor of environmental and genomic stress. *Heredity* **68**, 361–364.
- Rowe, L., Repasky, R. R. & Palmer, A. R. 1997 Size-dependent asymmetry: fluctuating asymmetry versus antisymmetry and its relevance to condition-dependent signalling. *Evolution* **51**, 1401–1408.
- Svensson, L. 1992 *Identification guide to European passerines*. Stockholm: Naturhistoriska Riksmuseet.
- Thornhill, R. 1992 Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*: Mecoptera). *Behav. Ecol.* **3**, 277–283.
- Van Dongen, S. 1998a How repeatable is the estimation of developmental stability by fluctuating asymmetry? *Proc. R. Soc. Lond. B* **265**, 1423–1427.
- Van Dongen, S. 1998b The distribution of individual fluctuating asymmetry: why are the coefficients of variation of the unsigned FA so high? *Ann. Zool. Fenn.* **35**, 79–85.
- Van Dongen, S., Molenberghs, G. & Matthysen E. 1999 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.
- Whitlock, M. 1996 The heritability of fluctuating asymmetry and the genetic control of developmental stability. *Proc. R. Soc. Lond. B* **263**, 849–854.
- Whitlock, M. 1998 The repeatability of fluctuating asymmetry: a revision and extension. *Proc. R. Soc. Lond. B* **265**, 1428–1430.
- Wilder, C. M., Brooks, T. M. & Lens, L. 1999 Vegetation structure and composition of the Taita Hills forests. *J. E. Afr. Nat. Hist. Soc.* (In the press.)