Fluctuating asymmetry increases with habitat disturbance in seven bird species of a fragmented afrotropical forest

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We studied fluctuating asymmetry (FA) in the tarsus length of seven forest-restricted bird species, two of which are globally critically endangered, in three indigenous forest remnants of a recently fragmented, afrotropical biodiversity hot spot. Based on mixed regression analysis and an extension of Levene's test, individuals from the most degraded fragment showed four- to sevenfold higher asymmetry levels compared to those from the least degraded one, with intermediate levels in the moderately disturbed fragment. When comparing contemporary FA levels with measurements of museum specimens collected 50 years ago, we found highly significant increases in asymmetry in the most degraded fragment but no differences in the least degraded one. These strikingly parallel spatial and temporal patterns across species confirm that repeated measurements of FA can provide a sensitive early warning system for monitoring stress effects in highly threatened ecosystems.

Keywords: fluctuating asymmetry; habitat fragmentation; habitat disturbance; museum specimens; afrotropical birds; endemics

1. INTRODUCTION

Disturbance of pristine habitats stresses natural populations in complex ways (Robinson *et al.* 1992). Restricted gene flow and small population sizes in habitat remnants cause between-population divergence through rapid genetic drift and inbreeding (Wayne *et al.* 1992; Saccheri *et al.* 1998). Simultaneously, new and extreme environmental selection pressures are imposed on remnant populations (Sarre 1996), often leading to population extinction (Newmark 1991; Harris & Silva-Lopez 1992). Ecologists are therefore in urgent need of simple methods for measuring the impact of environmental stress. Laboratory experiments suggest that fluctuating asymmetry (FA) could be such a measure (Clarke 1995). Yet, empirical studies supporting its general adequacy for monitoring endangered species or populations are largely lacking or contradictory (e.g. Fowler & Whitlock 1994).

On evolutionary grounds, individuals will be at a selective advantage if they are able to withstand the various perturbations resulting from environmental stress during ontogeny. Because of this range of perturbations, measures of developmental stability (DS) (Palmer & Strobeck 1986; Parsons 1992) are believed to provide a better estimate of the magnitude of stress than estimates of population size, survival or fecundity (Clarke 1992).

FA, the most commonly used estimate of DS, is defined as random deviations from perfect symmetry in a bilaterally symmetrical trait (Palmer & Strobeck 1986). The theoretical argument that stressed individuals should have lower DS and, hence, higher FA is supported by positive relationships between FA and stressors such as inbreeding and pollution, although some studies have indicated that these relationships might not be ubiquitous (e.g. Fowler & Whitlock 1994). Laboratory experiments such as temperature tests (Parsons 1992) suggest further that only severe stresses, which are to be expected in ecologically marginal situations, can increase FA under field conditions and that organisms with enhanced levels of FA may provide sensitive monitors of such stresses before detrimental impacts occur in the population (the 'early warning system'; Clarke 1995). This biomonitoring technique is assumed to be most efficient in the peripheries of species ranges, in marginal habitats or in severely disturbed landscapes.

To examine the sensitivity of FA as a measure of environmental stress, we studied spatial and temporal patterns of asymmetry in seven forest-restricted bird species of a recently fragmented, biodiversity hot spot in south-east Kenya. Major forest loss and degradation have been continuing since the 1960s, restricting the indigenous cloud forest to three forest fragments that differ substantially in their degree of habitat degradation. Elsewhere we have shown tarsus length to be the most

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Table 1. *Vegetation parameters for the three Taita forest remnants*

parameter	MB	NG	CH
altitudinal range (m)	1800–2200	1700–2100	1500
forest area (ha) ^a	200	92	50
mean basal area per m ²	77	58	61
stem density (trees ha ⁻¹)	578	380	297
number of tree species	36	32	17
Shannon–Wiener diversity index, H'	2.75	2.44	1.68
Shannon–Wiener equitability index, $\hat{J}$	0.77	0.70	0.59
mean canopy cover (%)	72	60	51
mean understorey density: 1 m	18	16	12
mean understorey density: 2 m	19	12	11
leaf-litter cover (%)	75	58	47
herbaceous cover (%)	11	34	53

^a Area estimates were based on geographical information system analysis of 1994 1:10 000 aerial photographs and a 1998 ground survey.

appropriate trait for studying FA, because replicated measurements of left and right tarsi are highly repeatable and estimate organism-wide asymmetry across species accurately (Lens & Van Dongen 1999). In this paper we examine patterns in tarsus asymmetry from 849 individuals of seven forest bird species, captured with mist-nets between 1996 and 1998, in relation to the degree of habitat degradation. Based on these contemporary patterns, we test the hypothesis that enhanced levels of asymmetry in the most degraded forest fragment result from a recent increase in environmental stress, by comparing current FA levels with these obtained from the measurement of 50-year-old museum specimens.

2. METHODS

(a) Study site and species

The Taita Hills (03° 20' S, 38° 15' E and maximum altitude 2209 m) lie in south-eastern Kenya, 150 km inland from the Indian Ocean and are isolated from other highland blocks by dry plains at 700 m altitude. At present, less than 400 ha of indigenous cloud forest is retained in three larger fragments (Chawia (CH, 50 ha), Ngangao (NG, 92 ha) and Mbololo (MB, 220 ha)) and nine tiny remnants (2–4 ha and one of 12 ha) (Brooks *et al.* 1998; Lens *et al.* 1999). The mutual distances between the three main fragments are NG–MB 11.3 km, CH–MB 19.4 km and CH–NG 10.9 km. The forests are included in an endemic bird area with the Eastern Arc Mountains of Tanzania (Stattersfield *et al.* 1998), although they are biogeographically rather distinct from these (Brooks *et al.* 1999). Indigenous forest loss since the early 1960s has been very substantial and is estimated at 85% for CH, 50% for NG, <50% for MB and 95–99% for some of the smallest remnants (Beentje 1987).

We analysed contemporary and 'ancient' (*sensu* Bouzat *et al.* 1997) FA data from the following forest-restricted bird species inhabiting the three larger fragments: Taita white-eye *Zosterops silvanus* ($n_{\text{field}}=85$, $n_{\text{museum}}=31$), Taita thrush *Turdus helleri* ($n_{\text{field}}=62$, $n_{\text{museum}}=19$), stripe-cheeked greenbul *Andropadus milanjensis* ($n_{\text{field}}=87$, $n_{\text{museum}}=32$), Cabanis's greenbul *Phyllastrephus cabanisi* ($n_{\text{field}}=39$, $n_{\text{museum}}=18$), white-starred robin *Pogonocichla stellata* ($n_{\text{field}}=194$, $n_{\text{museum}}=19$), yellow-throated woodland warbler *Phylloscopus ruficapillus* ($n_{\text{field}}=70$, $n_{\text{museum}}=14$) and olive sunbird *Nectarinia olivacea* ($n_{\text{field}}=212$, no museum specimens). Taita thrush and Taita white-eye are globally, critically endangered

endemics to the Taita forests (Collar *et al.* 1994). The other species have a wider distribution throughout the eastern African region (Brooks *et al.* 1998).

Birds were captured by passive mist-netting (no use of tape luring or artificial feeders) in fragments CH, NG and MB between 1996 and 1998. The museum specimens had been collected by shotgun in fragments CH (1938–1948) and MB (1934–1947) by A. Loveridge and C. G. Williams and were measured during May 1998 in the ornithological collections of the following museums: the National Museums of Kenya (Nairobi, Kenya), American Museum of Natural History (New York, USA), Field Museum of Natural History (Chicago, USA), Harvard University Museum of Comparative Zoology (Cambridge, USA) and Yale Peabody Museum (New Haven, USA).

(b) Vegetation analysis

We established transects of 40 equally spaced points in each of the three forest remnants, which we surveyed using the point-centred quarter method (Cottam & Curtis 1956). For each point we measured the distance to the closest tree (>45 cm circumference) in each quadrant, identified the trees, measured their circumference at 120 cm height and estimated the percentage of canopy cover. All identifications were made with reference to specimens in the East African Herbarium, Nairobi, Kenya (Beentje 1994). From these data we calculated biomass, mean tree size, stem density, number of species, diversity and equitability (Cottam & Curtis 1956; Kent & Coker 1992). We took measurements of shrub layer density at 1 m and 2 m heights to the north and south at each point by counting the number of squares more than half visible on a board that was divided into 25 squares of 8 cm × 8 cm and held at a 5 m distance from the observer (Noon 1980). In addition, we chose three points in a stratified random manner at which to establish five 1 m × 1 m plots. We positioned one plot at the point and the others 14 m to the north-west, north-east, south-west and south-east. In these plots we estimated the percentage cover of leaf litter and herbaceous growth.

(c) FA measurement

The left and right tarsi of each individual were measured repeatedly (sequence left–right–left–right or right–left–right–left) to the nearest 0.1 mm with the use of slide callipers. In the field, tarsi were measured by four ringers who were unaware of

Table 2. Variance components and the distribution of signed and unsigned FA obtained from tarsus measure 1

(n , sample size; V_{ind} , variation in individual trait size; V_{FA} , variation in signed FA; V_{ME} , variation in ME; mean, mean of the signed FA; W , Shapiro–Wilks’s statistic; K , kurtosis; $V_{[\text{FA}]}$, variation in unsigned FA; R , hypothetical repeatability.)

species ^a	n	V_{ind}	V_{FA}	V_{ME}	mean	W	K	$V_{[\text{FA}]}$	R
TT	62	0.9	0.059	0.004	−0.01	0.80	9.5	0.045	0.50
SG	87	0.7	0.053	0.005	0.00	0.71	25.4	0.043	0.50
CG	139	0.7	0.056	0.004	0.01	0.91	4.0	0.037	0.39
YW	70	0.9	0.047	0.009	0.04	0.82	6.9	0.040	0.49
WR	194	2.1	0.062	0.005	0.03	0.76	23.6	0.050	0.51
TW	85	0.5	0.043	0.002	0.03	0.76	6.6	0.033	0.50
OS	212	0.7	0.037	0.008	0.01	0.77	17.4	0.034	0.52

^aTT, Taita thrush; SG, stripe-cheeked greenbul; CG, Cabanis’s greenbul; YW, yellow-throated woodland warbler; WR, white-starred robin; TW, Taita white-eye; OS, olive sunbird.

the hypotheses being tested and each ringer processed birds in all three fragments. The museum specimens were measured by L.L. Two different tarsus measures were taken: (i) the length 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, hereafter called measure 1; and (ii) the length from the notch on the back of the intertarsal joint to the lower edge of the last complete scale before the toes diverge, hereafter called measure 2 (Svensson 1992). FA levels derived from measure 1 showed smaller measurement errors (MEs) (see below) and so we took this measurement in the field. However, it could not be taken from museum specimens as it involves bending the toes. Therefore, we also took measure 2 in the field as well as in the museums, to allow direct comparison of the FA levels between ancient and contemporary captures.

(d) FA analysis

Repeated and independent tarsus measurements allowed mixed model analysis with restricted maximum-likelihood parameter estimation for distinguishing true asymmetry (i.e. signed FA, L–R tarsus length) from ME (Swaddle *et al.* 1994; Van Dongen *et al.* 1999). We first tested for heterogeneity in ME, which can potentially bias individual and population FA estimates and generate artificial asymmetry patterns (Palmer & Strobeck 1986; Van Dongen *et al.* 1999). Measure 1 showed heterogeneity in ME between the four ringers for five species, while measure 2 showed heterogeneity in ME between the two periods (ancient and contemporary) for two species (likelihood ratio tests, all $p < 0.01$). After correcting for these biases by incorporating the variance in ME into the mixed model (Van Dongen *et al.* 1999), we inspected the distribution of the signed and unsigned FA (i.e. L–R, the magnitude of the signed FA) and calculated the hypothetical repeatability R (see Van Dongen (1998) and Lens & Van Dongen (1999) for details). 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).

Between-fragment and between-period heterogeneity in average unsigned FA was analysed with Levene’s tests (one-way ANOVAs with unsigned FA as the dependent variable and fragment as the factor) which are insensitive to departure from normality (Palmer & Strobeck 1992). For the analysis of spatial patterns in FA we extended this test to a two-way mixed ANOVA by adding the factor ‘species’ and the ‘species $\times$ fragment’

interaction as random effects. For the analysis of temporal patterns we added the factor ‘period’ and all relevant interaction terms to a three-way mixed ANOVA. Since the mean and variance of the unsigned FA are closely linked (Whitlock 1996), differences in the mean unsigned FA between the three fragments co-occur with differences in variance, hence violating the homoscedasticity assumption of Levene’s test. To avoid decreasing the statistical power, we therefore applied a heterogeneous error structure (Van Dongen *et al.* 1999).

3. RESULTS

(a) Heterogeneity in FA between fragments

The rank order of the fragments was MB > NG > CH for altitude, forest area and ten parameters of forest quality (table 1). Fragment MB had 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 NG (intermediately disturbed) and CH (most disturbed).

The distribution of FA (measure 1) showed no directional component for any species (the means of signed FA did not differ from zero, all $p > 0.1$; table 2) and deviated significantly from normality (see Shapiro–Wilks’s statistic W , all $p < 0.0001$). Overall, the signed FA (V_{FA}) was several orders of magnitude larger than ME (V_{ME}) and was highly significant for all species (likelihood ratio test, all $p < 0.0001$). The leptocurtic distribution of the signed FA (high kurtosis K ; table 2) indicated a high repeatability and, thus, high between-individual heterogeneity in the presumed underlying DS. After sequential Bonferroni correction for multiple testing, the unsigned FA was not significantly correlated with trait size (Taita white-eye: $r_s = 0.11$, $n = 85$, $p = 0.3$; Taita thrush: $r_s = 0.01$, $n = 62$, $p = 0.9$; stripe-cheeked greenbul: $r_s = -0.19$, $n = 87$, $p = 0.08$; Cabanis’s greenbul: $r_s = -0.2$, $n = 139$, $p = 0.02$; white-starred robin $r_s = -0.07$, $n = 194$, $p = 0.4$; yellow-throated woodland warbler: $r_s = 0.01$, $n = 70$, $p = 0.9$; olive sunbird $r_s = 0.06$, $n = 212$, $p = 0.4$). Therefore, no size scaling was performed.

The unsigned FA was highly heterogeneous among fragments (Levene’s test with heterogeneous error structure, $F_{2,840} = 78.6$, $p < 0.0001$; figure 1) and did not differ between species (random species effect; likelihood ratio test, $\chi^2_1 = 3.2$, $p = 0.07$). The increase in FA with habitat

Figure 1. Population levels of unsigned FA in relation to habitat disturbance. Fragments CH, NG and MB are ranked by increasing order of quality based on their levels of habitat disturbance and size. OS, olive sunbird; CG, Cabanis's greenbul; YW, yellow-throated woodland warbler; TT, Taita thrush; SG, stripe-cheeked greenbul; WR, white-starred robin; TW, Taita white-eye.

disturbance was strikingly parallel among species (random species $\times$ fragment interaction not significant; likelihood ratio test, $\chi^2_1 = 0.2$, $p = 0.35$). FA was significantly larger in fragment CH than in NG for all species (all $p < 0.005$) and significantly larger in NG compared to MB for four species (Taita white-eye: $p = 0.002$; Cabanis's greenbul: $p = 0.004$; white-starred robin: $p = 0.01$; olive sunbird: $p = 0.001$). As a result, individuals were four- to sevenfold more asymmetrical in tarsus length in the most degraded fragment compared to the least degraded one.

(b) Change in FA between periods

The variation in ME of measure 2 was 25% larger compared to measure 1. Yet, V_{ME} was still several orders of magnitude smaller than V_{FA} and the signed FA levels were highly significant (likelihood ratio tests, all $p < 0.0003$). The distribution of FA showed no directional component (all time–fragment–species combinations, $p > 0.15$) and the unsigned FA did not differ between specimens from different collectors (F -test, $p > 0.35$). Individual unbiased signed FA estimates for both tarsus measures, as obtained from mixed regression analysis on field captures, were highly significantly correlated ($r^2 = 0.83$, $n = 637$, $p < 0.0001$; values were transformed per species through division by the respective standard deviations).

The ancient (calculated from museum specimens) and contemporary (calculated from field captures) levels of unsigned FA are compared in figure 2. Tarsus asymmetry was significantly larger in contemporary captures from CH (difference in parameter estimates 0.084 ± 0.014 , $t_{489} = 6.13$, $p = 0.0001$) but did not differ between both periods in MB (difference in parameter estimates 0.004 ± 0.016 , $t_{489} = 0.27$, $p = 0.78$). As a result, the period

Figure 2. Ancient (based on museum specimens) and contemporary (based on field captures) levels of unsigned FA in six forest bird species of a recently disturbed and undisturbed forest fragment. Open circles, Taita thrush; filled circles, stripe-cheeked greenbul; open triangles, Cabanis's greenbul; filled triangles, yellow-throated woodland warbler; open squares, white-starred robin; filled squares, Taita white-eye; p -values calculated from a three-way mixed ANOVA with heterogeneous error structure.

$\times$ fragment interaction was highly significant (Levene's test with heterogeneous error structure, $F_{1,489} = 18.2$, $p < 0.0001$) while the random effects species, species $\times$ period, species $\times$ fragment and species $\times$ period $\times$ fragment were not significant (likelihood ratio tests, all $p > 0.27$). Although much weaker than in contemporary captures, the ancient FA levels were significantly higher in CH than in MB (difference in parameter estimates 0.068 ± 0.016 , $t_{489} = 5.92$, $p = 0.0001$; figure 2).

4. DISCUSSION

Despite the potential use of measures of DS in conservation issues (Leary & Allendorf 1989; Clarke 1995), few studies have examined FA patterns of critically endangered species in relation to assumed environmental or genetic stress. The present variation in FA levels between the three Taita forest remnants of significant size, as observed across seven bird species, is among the highest recorded in natural populations (Møller & Swaddle 1997). As the species sample represented 92% (2170 out of 2353 individuals) of all birds captured in the study area, our results can be considered indicative for the low- and mid-canopy bird community of the Taita forests.

Given the fact that FA patterns were highly consistent across species, increased asymmetry levels, as recorded in this study, are believed to reflect stresses that may negatively affect the bird community. As inferred from the comparison with ancient FA levels, these stresses appear to be, at least in part, the result of recent habitat deterioration. Our results therefore support the hypothesis that population-level FA estimation can be a very sensitive indicator of environmental stress and can thus act as an early warning system which allows remedial conservation action to be taken (Clarke 1995). When interpreting spatial patterns of FA, alternative explanations, such as ecological or behavioural mechanisms that force individuals of poor

physical quality to settle in inferior sites, should, however, not be neglected. Yet, as tarsus length is fully grown at fledging (Lens & Van Dongen 1999) and most study species showed very low levels of between-fragment dispersal (Lens *et al.* 1999), such interpretation is disproved in this case. Nevertheless, determining causality from these data remains difficult without knowledge of the underlying developmental pathways causing variation in asymmetry. Increased asymmetry in the most disturbed fragment may have resulted from inbreeding depression (as a consequence of small population sizes; Lens *et al.* 1998) or from high levels of homozygosity. Alternatively, it may have resulted from various sources of environmental stress or from the cumulative effect of both genetic and environmental factors (Parsons 1992). Given the degree of recent forest disturbance in the Taita Hills (Beentje 1987) and the longevity of many afrotropical bird species (Mann 1985; Gichuki & Schifter 1990), strong effects on genetic variability seem less obvious.

While the use of museum collections as a source of baseline data for natural experiments is well-established, for example through Ellegren *et al.*'s (1997) study of albinistic feathers in *Hirundo rustica* before and after the nuclear accident at Chernobyl, Swaddle *et al.* (1994) put forward a number of arguments against its use in the study of FA.

- (i) It would rarely be possible to separate between-year, between-site and between-individual variation in museum specimens.
- (ii) Museum collectors seeking 'typical' specimens might be biased towards collecting more symmetrical individuals.
- (iii) Wear and damage asymmetry may not be separable from FA.

The analyses presented in this study, however, are believed to overcome these problems. First, between-year and between-fragment variation in FA is explicitly tested for, while between-individual variation in asymmetry does not bias the population-level FA (Van Dongen 1999). Second, FA is typically very small relative to the size of the trait (Møller & Pomiankowski 1993), only 0.68% for our measures and would thus only be visible by a collector at very close range, if at all. As specimens from the Taita Hills were collected by shotgun, it is unfeasible that the samples were biased with respect to asymmetry. Obviously, FA could indirectly affect 'shootability' through correlated plumage or behavioural traits that would make symmetrical individuals more conspicuous or attractive for collection. However, analysis of FA for eight conspicuous feather traits of the same species (Lens & Van Dongen 1999) did not show any correlation with trait size. Finally, the levels of unsigned FA did not differ between specimens from different collectors, while wear, damage or skin preparation can be expected to increase rather than decrease asymmetry between tarsi regardless of collection site, thus making our tests more conservative.

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