Fluctuating Asymmetry as an Early Warning System in the Critically Endangered Taita Thrush

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Abstract: *Environmental and genetic factors increasingly stress natural populations, and conservationists need simple tools to measure the effect of these stresses before populations become irreversibly affected. The inability of an organism to withstand random perturbations during its development—so-called developmental instability—has been proposed as a potential early indicator of stress. To act as a true early warning system, however, stress-mediated changes in developmental instability should be manifest in the phenotype before major changes occur in more direct components of fitness. We tested this hypothesis by estimating the survival probabilities of 260 Taita Thrushes (*Turdus helleri*) inhabiting three differentially disturbed forest fragments (little, moderately, and highly deteriorated) and relating these to individual estimates of tarsus asymmetry (a measure of developmental instability), two other putative indices of expected fitness (size and body condition), and a coefficient of inbreeding. Tarsus symmetry, but not survival, was lower in the moderately disturbed population than in the least disturbed one, whereas both symmetry and survival were lower in the most disturbed population. Thus, higher levels of habitat disturbance were reflected by increased population levels of asymmetry before a decrease in survival became apparent. In contrast, none of the other variables showed a significant response to habitat disturbance. At the individual level, asymmetric thrushes showed lower probabilities of survival than more symmetric ones, and the magnitude of the relationship increased with habitat disturbance. Birds in better condition (i.e., higher residual body mass) survived better, irrespective of the quality of the habitat. The key finding that stress-mediated increase in fluctuating asymmetry may precede decrease in survival suggests that single-trait asymmetry can serve as an early warning system in conservation.*

Fluctuación de Asimetría como un Sistema de Alerta Temprana en el Tordo Taita Críticamente en Peligro

Resumen: *Los factores ambientales y genéticos incrementan la presión sobre poblaciones naturales, y los conservacionistas requieren de herramientas simples para medir el efectos de esas presiones antes de que afecten a las poblaciones irreversiblemente. La incapacidad de un organismo de soportar perturbaciones aleatorias durante su desarrollo, la llamada inestabilidad del desarrollo, se ha propuesto como un potencial indicador temprano de los efectos de la presión. Sin embargo, para funcionar como un verdadero "sistema de alerta temprana" los cambios en la inestabilidad del desarrollo por la presión deben manifestarse en el fenotipo antes de que ocurran cambios mayores en los componentes más directos de la adaptabilidad. Probamos esta hipótesis estimando las probabilidades de supervivencia de 260 tordos Taita (*Turdus helleri*) habitantes de tres fragmentos de bosque perturbados diferencialmente (deterioro bajo, moderado y alto) y las relacionamos con estimaciones individuales de asimetría del tarso (una medida de inestabilidad del desarrollo), con otros dos índices putativos de adaptabilidad esperada (tamaño y condición del cuerpo) y con un coeficiente de endogamia. La simetría del tarso, pero no la supervivencia, fue menor en la población moderadamente perturbada que en la menos perturbada, mientras que tanto la simetría como la supervivencia fueron menores en la población más perturbada. Así, los mayores niveles de perturbación de hábitat reflejaron un incremento en los niveles de asimetría antes de que fuera aparente una disminución en la supervivencia. En contraste, ninguna de las otras variables mostró respuesta significativa a la perturbación del hábitat. A nivel*

individual, los tordos asimétricos tuvieron menor probabilidad de supervivencia en comparación con los simétricos, con lo que la magnitud de la relación se incrementó con la perturbación del hábitat. Aves con mejor condición (es decir, mayor masa corporal residual) sobrevivieron mejor, independientemente de la calidad del hábitat. El hallazgo clave de que el incremento de la asimetría fluctuante debido a la presión puede preceder una disminución de la supervivencia sugiere que la asimetría de un solo carácter puede funcionar como un sistema de alerta tempana en conservación.

Introduction

As the loss and deterioration of indigenous habitat increasingly stresses natural populations, ecologists need simple estimators to measure their impact (Cairns et al. 1993). In particular, they are challenged to identify populations subject to stress before these populations are irreversibly affected, because this would greatly increase the effectiveness of conservation programs (Leary & Allendorf 1989; Clarke 1995*a*). Developmental instability, the inability of an organism to withstand random perturbations during its development, could be such an estimator (Leary & Allendorf 1989; Kieser & Groeneveld 1991; Palmer & Strobeck 1992; Parsons 1992; Clarke 1993, 1995*a*; Polak & Trivers 1994). Developmental instability may be a more sensitive estimator than traditional life-history traits such as survival (Clarke & McKenzie 1992) because organisms under stress may need to allocate more energy to processes necessary to survival, hence compromising the maintenance of their developmental stability (Sommer 1996). For developmental instability to predict future stress-mediated changes in direct components of fitness—which are often more cumbersome to measure—and hence use as an "early warning system" (sensu Clarke 1995*a*)—the following assumptions need to be fulfilled: (1) individuals are subject to biologically relevant stress(es) and suffer a significant decrease in fitness under severe stress; (2) increased exposure to stress is reflected in increased levels of developmental instability; and (3) stress-mediated changes in developmental instability are manifest in the phenotype before major changes occur in more direct components of fitness, such as survival or fecundity.

The degree of developmental instability among individuals and populations is most commonly expressed by their level of fluctuating asymmetry (FA; Ludwig 1932). The underlying assumptions of FA analysis are that the development of both sides of bilaterally symmetrical traits is influenced by identical genes, that nondirectional differences between the sides are of environmental origin and reflect accidents during development, and that high levels of FA indicate high levels of developmental instability (Clarke 1993; Palmer 1994; Møller 1997*a*). Because the measurement and analysis of FA is simple, does not require expensive equipment, and is

not destructive, it has become a popular measure of the quality and health of individuals and populations (reviews by Markow 1995; Leung & Forbes 1996; Møller 1997*a*; Clarke 1998*b*; Møller & Thornhill 1998). Although population-level FA generally increases with exposure to stressors of environmental or genetic origin (or underlying processes such as the mating system or population structure that are manifested in a measurable genetic response) (Parsons 1990, 1992; Palmer & Strobeck 1992; Manning & Chamberlain 1994; Polak & Trivers 1994; Møller & Swaddle 1997; but see Bjorksten et al. 2000), relationships between FA and fitness are highly heterogeneous among studies, often weak, and at present poorly understood (Leung & Forbes 1996, 1997*a*, 1997*b*; Clarke 1998*a*; Dufour & Weatherhead 1998; but for a different opinion see Møller 1999).

Inconsistency in the reported relationships of FA with other variables of interest has been attributed to a variety of causes, such as weak between-trait correlation or low repeatability of individual FA estimates (Leamy 1993; Whitlock 1996; Houle 1997; Clarke 1998*b*; Van Dongen 1998*a*, 1998*b*), or an admixture of "true" FA with other types of bilateral asymmetry that may have a genetic basis (Palmer & Strobeck 1992; Palmer 1994; Van Dongen et al. 1999*a*; Lens & Van Dongen 2000). Consequently, it has been argued that FA in individuals may not be a universal measure of quality or fitness and that other phenotypic measures, such as mean or maximum trait size (Hunt & Simmons 1997; Bennett & Hoffmann 1998; David et al. 1998; Van Dongen et al. 1999*c*; Woods et al. 1999; Bjorksten et al. 2000) or measures of organismal condition (Leung & Forbes 1997*b*; Dufour & Weatherhead 1998; Gage 1998), might perform better. Although newly developed programs accommodate most of the statistical problems intrinsic to estimation of individual developmental instability (review by Van Dongen et al. 2002), nonstatistical factors such as trade-offs between different fitness components may further confound attempts at finding universal relationships between asymmetry and fitness (M. Tracy, C. Freeman, T. Huff, A. Alados, & J. Graham, unpublished data). Besides, phenotypic quality is a function of both genetic and environmental factors. Whereas in stressful environments only high-quality individuals might be able to compensate for such stresses, differences in quality may

have little effect on fitness under more benign conditions. Negative relationships between FA and indices of fitness may therefore be measurable only under stressful conditions (Leung & Forbes 1997*b*).

We tested the stress dependency of relationships between fluctuating asymmetry and fitness and the applicability of FA as an early warning system in biological monitoring, relative to other putative indices of expected fitness. We studied the effects of variation in FA, trait size, residual body mass, and coefficient of inbreeding on the probability of survival of Taita Thrushes (*Turdus helleri*) inhabiting a highly degraded, moderately degraded, or virtually undegraded forest fragment. In previous studies we showed that population levels of FA were positively related to the extent of habitat degradation in *T. helleri* and six sympatric bird species (Lens & Van Dongen 1999; Lens et al. 1999*b*; for comparable patterns in immature *T. merula*, see Møller 1995) and that more inbred thrushes from the most degraded fragment were more asymmetric (Lens et al. 2000). By analyzing individual capture-recapture histories over a 3-year period, we modeled relationships between the individual covariates and recapture and survival rates.

Methods

Study Species and Site

The Taita Thrush (*Turdus helleri*) is a shy, forest-restricted bird species, endemic to the Taita Hills forest of southeastern Kenya (lat. 03°20'S, long 38°15'E) and listed as critically endangered globally (Collar et al. 1994), the highest category of threat. Within its tiny range, the species prefers the shady, interior understory of intact forest (Brooks 1997; Brooks et al. 1998). Its habitat has been severely reduced in size and fragmented since the 1960s and currently covers <400 ha in 12 fragments (map in Lens et al. 1999*a*). At present, the species survives in three forest fragments only: Chawia (50 ha), Ngangao (90 ha), and Mbololo (200 ha). Detailed comparison of the composition and structure of the vegetation (Wilder et al. 2000) show that forest degradation is lowest in fragment Mbololo, intermediate in Ngangao, and highest in Chawia. The number of individuals is estimated at 1059 for Mbololo, 250 for Ngangao, and 38 for Chawia (Galbusera et al. 2000).

Survival and Recapture Rates

Between January 1997 and January 2000, we captured 260 *Turdus helleri* with mistnets (no use of feeders or playback). Each of the three thrush populations was sampled 12 times, with a mean (±SD) capture session of 19 (±7) days and a mean (±SD) between-capture interval of 70 (±38) days. Only one individual was recaptured in a fragment different from its original capture site, compared with 289 within-fragment recaptures. During 1850 hours of observation, no additional dispersal events were recorded, and genetic assignment tests did not positively identify migrants in the current generation (Galbusera et al. 2000). Recapture and survival rates were estimated with the program MARK (White & Burnham 1999). Because time intervals between consecutive capture sessions were comparable and adjustment of the intervals (on a pilot data set) did not affect the outcome of the modeling, all time intervals were set to one time unit.

We computed estimates of model parameters via numerical maximum-likelihood techniques. We used a parametric bootstrap procedure to test if a starting model with time dependence in both recapture and survival rates adequately fit the data. We accomplished this goodness-of-fit (GOF) testing by running 1000 simulations and testing whether the observed model deviance (i.e., deviance from the fit of the model to the original data) fell within the distribution of the deviances from the simulated data (i.e., simulated in absence of overdispersion or any violation of model assumptions). If so, we estimated the overdispersion quasi-likelihood parameter ($\hat{c}$) and calculated quasi-likelihood AIC values (QAICc) based on the number of estimable parameters. We formally tested the significance of a variable by comparing nested models with and without the variable of interest with likelihood-ratio tests. First, we tested whether recapture and/or survival rates were time dependent by comparing different models, those in which either survival or recapture—or both—varied with time and those in which both rates were kept constant with respect to time. By applying a stepwise forward procedure, we next tested the significance of each grouping variable (age, sex, population), individual covariate (FA, size, condition, inbreeding coefficient), and two-way interaction between these variables. Based on population-specific survival rates (*S*), estimated over 70-day intervals, mean life span (MLS) was computed as $MLS = 1/-\ln S^{365/70}$, with $\sigma^2_{MLS} = ((365/70)/(S*\ln S^2)^2)^{2}*\sigma^2_S$ (delta method; Lynch & Walsh 1998).

Fluctuating Asymmetry

Four persons, each unaware of the hypothesis tested to ensure objectivity, made two independent measurements of left and right tarsus length per capture to the nearest 0.1 mm (sequence left-right-left-right or right-left-right-left, with slide callipers reset to zero after each measurement). We selected this trait for the study of asymmetry because tarsus FA correlates with asymmetry in a suite of other bilateral traits (Lens & Van Dongen 1999) and, among these, showed the highest level of between-capture repeatability (data not shown). Levels of FA are usually subtle, typically in the order of 1% or less

of the size of the trait (e.g., Møller & Swaddle 1997). Because the degree of asymmetry is so small and some traits cannot be measured with high accuracy, measurement error can be expected to cause an upward bias in the between-sides variance if not appropriately corrected (Palmer & Strobeck 1986; Merilä & Björklund 1995; Van Dongen 1999, 2000). Therefore, tarsus asymmetry was analyzed through mixed-regression analysis with REML parameter estimation, which allows separation of measurement error from the analysis of left-right asymmetry (Van Dongen et al. 1999*b*). First, we examined whether variance due to measurement error was heterogeneously distributed between the three populations. Because this was not the case (likelihood-ratio test: $p > 0.05$), we estimated a single error component. Second, we separated measurement error from "real" FA (i.e., variance components of the random side effect), and tested for the presence of directional asymmetry by *F* statistics (adjusting the denominator degrees of freedom by Satterthwaite's formula; Verbeke & Molenberghs 1997). Third, we tested the significance of FA by comparing the likelihood of models with and without random side effect. Fourth, we calculated unbiased FA values per individual as the variance components of the slopes of the individual regression lines in the mixed-regression model. Because individual, unsigned FA levels did not vary with tarsus length ($r_s = 0.05$, $n = 255$, $p = 0.43$), no size scaling was performed.

Other Phenotypic and Genotypic Measures

Upon first capture, individuals were aged as juvenile or fully grown on the basis of their plumage characteristics (Zimmerman et al. 1996) and were sexed on the basis of their highly conserved *W* chromosome–linked gene CHD-W (Lens et al. 1998). We assessed individual size by tarsus length, obtained by averaging all repeats over left and right tarsi within each individual. Body mass was measured to the nearest 0.2 g. To reduce the possible effects of time of capture on body mass, we analyzed only weights obtained between 0900 and 1200 hours. Body mass significantly increased with tarsus length, and we estimated condition using the residuals derived from the regression of $\log_e$(body mass) on $\log_e$(tarsus length) for all individuals pooled (Packard & Boardman 1987; Jakob et al. 1996).

A total of 237 *T. helleri* was genotyped with six polymorphic microsatellite–DNA markers. Details on DNA extraction and PCR amplification conditions are described by Galbusera et al. (2000). Genotypes were scored on a 6% acrylamide gel in an automated sequencer (ALF express, Pharmacia Biotech). No allelic disequilibrium was detected between any two loci, and all locus-population combinations were in Hardy-Weinberg equilibrium. Given the absence of a heterozygote deficit, null alleles were assumed to be absent. Characteristics of the six polymorphic microsatellite loci are described by Lens et

al. (2000). The probability that both alleles at any locus are identical by descent (i.e., inbreeding coefficient *f*; Falconer & Mackay 1996) is traditionally estimated by the proportion of homozygous loci in an individual. However, estimates of the probability of identity-by-descent calculated from mean homozygosity at loci with different expected levels of identity-by-state are biased downward. Instead, we applied an unbiased estimator for individual inbreeding coefficients ($\hat{f}$), originally developed by Ritland (1996), that combines information on the number and frequency of all alleles for each marker loci into a single coefficient as a weighted sum (for assumptions and calculations see Ritland 1996; and Lens et al. 2000). Ritland estimates are typically hampered by large errors of inference (Ritland 1996; Lynch & Ritland 1999) that lead to conservative estimates of relationships with other variables of interest such as FA (e.g., Bollen 1989).

Results

Signed FA estimates showed no directional component, in that population means of the signed FA did not significantly differ from zero (*F* tests: Chawia, $p = 0.95$; Ngangao, $p = 0.77$; Mbololo, $p = 0.38$). The leptokurtic distribution patterns indicated substantial between-individual variation in DI in the three populations (Kurtosis: $1.18 < K < 6.08$; Shapiro-Wilks's statistic: $0.74 < W < 0.86$; all $p < 0.0001$). Variance in the signed FA was consistently larger than variance in measurement error (Chawia: $V_{FA} = 0.16$, $V_{error} = 0.006$; Ngangao: $V_{FA} = 0.05$, $V_{error} = 0.002$; Mbololo: $V_{FA} = 0.02$, $V_{error} = 0.003$) and was highly significant in all three populations (likelihood-ratio tests: all $p < 0.0001$). Population levels of the unsigned FA were lowest in fragment Mbololo, intermediate in Ngangao, and highest in Chawia (Fig. 1: $F_{2,244} = 4.08$, $p = 0.018$). In contrast, mean tarsus length and residual body mass did not differ between the three sites (Fig. 1: male tarsus length, $F_{2,150} = 0.26$, $p = 0.77$; female tarsus length, $F_{2,95} = 0.68$, $p = 0.51$; residual body mass, $F_{2,257} = 1.32$, $p = 0.27$). As described by Galbusera et al. (2000), mean inbreeding coefficients did not differ between the three populations either ($F_{2,234} = 1.61$, $p = 0.20$), despite a substantial decrease in allelic variability in population Chawia. Mean FA, residual body mass, or inbreeding coefficients did not differ between sex and age classes, and none of the individual covariates were significantly correlated after Bonferroni correction (data not shown; all $p > 0.05$).

A fully time-dependent model fit the data sufficiently well (probability of observing the deviance of the fitted model: $p = 0.21$) and was used as starting model. The level of overdispersion was low ($\hat{c} = 1.25$) and was adjusted by calculation of QAICc values. Neither recapture nor survival rates showed significant time dependence, so they were kept constant with respect to time (Table 1). Recapture
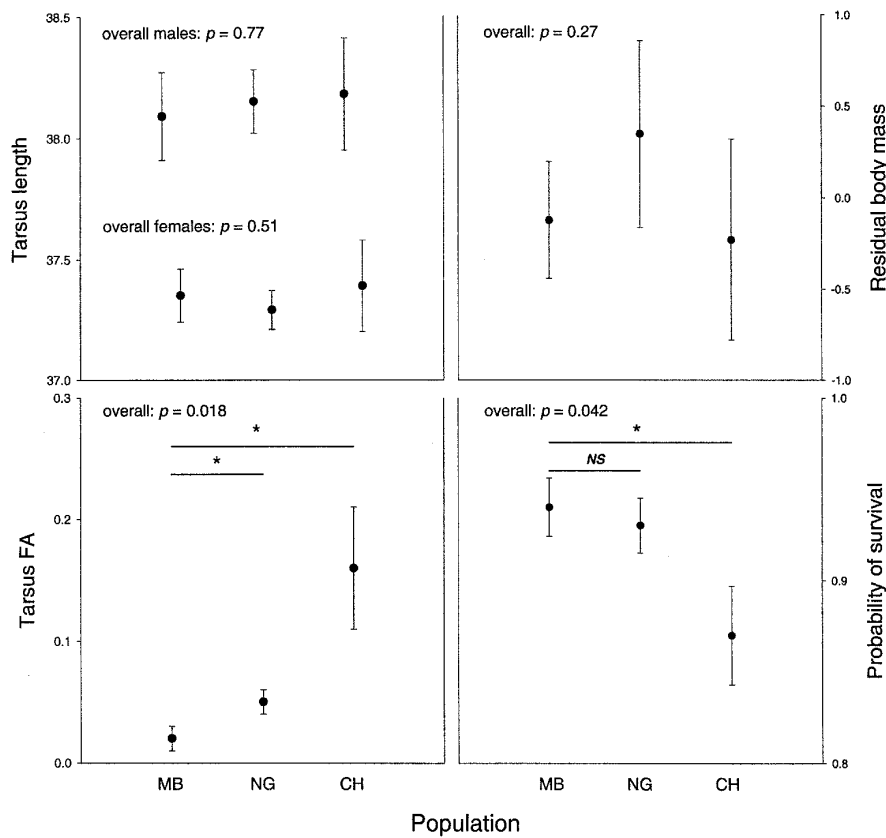
Figure 1. Mean levels (±SE) of survival during 70-day intervals and of three putative indices of expected fitness in three T. helleri *populations exposed to increasing levels of habitat disturbance. Because tarsus length significantly differed between sexes, population means are depicted separately for males and females (*, p < 0.05; NS, p > 0.05). Populations: MB, Mbololo; NG, Ngangao; CH, Chawia.*

rate did not differ between populations, ages, or sexes and was not related to any of the individual covariates. Hence, recapture rate was kept constant when survival rates were modeled (Table 1). The probability of survival did not differ between ages or sexes, but was lower in the Chawia population than in those of Ngangao and Mbololo (Fig. 1). Given that survival rates differed between populations but were constant in time, mean expected life spans (±SE) were estimated at 1.4 ± 2.4 years (Chawia), 2.6 ± 2.3 years (Ngangao), and 3.0 ± 2.2 years (Mbololo).

When the individual covariates and two-way interactions with factor population were added to the model, the probability of survival increased with condition and decreased with FA (Table 1). Individuals with higher residual body masses survived better, irrespective of the population involved (Fig. 2a). The negative relationship between FA and survival, in contrast, differed between populations, as was shown by a significant interaction between FA and population (Table 1). This interaction term remained significant after we tested for outlier ef-

Table 1.   Likelihood-ratio statistics describing the effects of fluctuating asymmetry (FA) in tarsus length and other variables of interest on recapture and survival rates of 260 individuals of *T. helleri*.

		Recapture rate			Survival rate		
Factor	n	χ^2	df	p	χ^2	df	p
Time	260	15.30	10	0.12	14.95	10	0.13
Age	260	0.15	1	0.70	0.03	1	0.87
Sex	251	0.73	1	0.39	0.11	1	0.74
Population	260	3.24	2	0.20	6.34[a]	2	0.042[a]
FA	255	0.96	1	0.33	2.69	1	0.10
Size	259	2.59	1	0.11	0.45	1	0.50
Condition	260	0.57	1	0.45	6.24[a]	1	0.012[a]
Inbreeding coefficient	237	1.03	1	0.31	0.02	1	0.89
Population × FA[b]	255	0.17	2	0.92	7.17[a]	2	0.028[a]
Population × size[b]	259	0.32	2	0.85	0.55	2	0.76
Population × condition[b]	260	0.28	2	0.87	0.47	2	0.79

[a]*Statistically significant.*
[b]*All other two-way interactions were not significant (p > 0.05).*
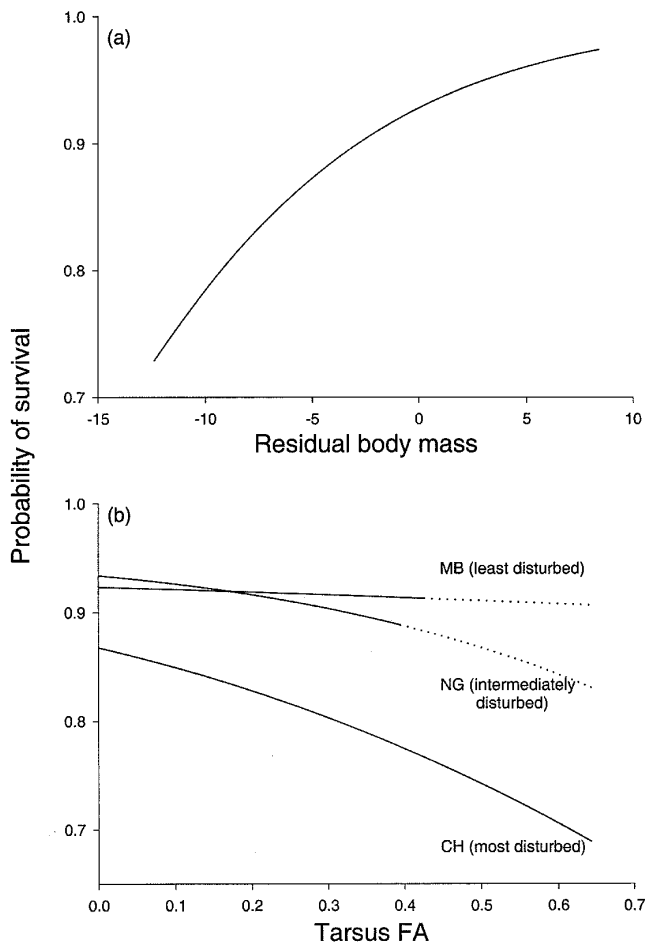
Figure 2. Probability of survival of 260 individuals of T. helleri *during 70-day intervals in (a) relation to residual body mass and (b) tarsus fluctuating asymmetry (FA). Solid lines depict the estimated survival rates within the range of observed values of body mass and FA in each population. Dotted lines depict the predicted relationship in populations at Mbololo (MB) and Ngangao (NG) for FA values observed in Chawia (CH).*

fects by excluding the two most asymmetric individuals from each population (FA × population: $\chi^2_2 = 6.54$, $p = 0.038$). In the Chawia population, survival was significantly inversely related to FA ($n = 18$, $\chi^2_1 = 5.64$, $p = 0.018$; Fig. 2b). In the less disturbed populations, Ngangao and Mbololo, more asymmetric individuals tended to have lower survival prospects, albeit not significantly (Ngangao: $n = 70$, $\chi^2_1 = 3.44$, $p = 0.064$; Mbololo: $n = 167$, $\chi^2_1 = 1.24$, $p = 0.27$; Fig. 2b).

Discussion

In agreement with our hypothesis, tarsus symmetry, but not survival, was lower in the moderately disturbed population (Ngangao), whereas both symmetry and survival

were lower in the most disturbed population (Chawia) than in the least disturbed population (Mbololo). In contrast, none of the other individual covariates showed a significant response to habitat disturbance. At the individual level, survival was lower in more asymmetric individuals, but the magnitude of the relationship decreased with increasing forest quality. In the most degraded fragment, FA and survival were strongly, inversely related, whereas in the least degraded one they were not significantly related. Because more asymmetric individuals from the most disturbed population may have lower probabilities of survival before being sampled (e.g., Møller 1997b), the degree of FA in Chawia can be expected to be even larger than inferred from our capture data. Thrushes with higher residual body masses survived better, irrespective of the degree of habitat deterioration, whereas size and inbreeding coefficients were not significantly related to survival. Given the positive relationship between individual FA and coefficients of inbreeding in the Chawia population (and, to a lesser extent, that at Ngangao) (Lens et al. 2000), the latter may have had an indirect effect on survival in these populations.

The generality of the association between FA and fitness and the potential of FA to predict the fitness consequences of changes in ambient stress levels have been the subject of intense debate (e.g., Clarke 1995a, 1995b; Markow 1995; Leung & Forbes 1996, 1997a, 1997b; Møller 1997a; Clarke 1998a; Dufour & Weatherhead 1998; Bjorksten et al. 2000). Fluctuating asymmetry is generated by random developmental processes, and developmentally unstable (i.e., low-quality) individuals may therefore display low FA by chance. Consequently, relationships between FA and fitness have been predicted to typically show triangular bivariate distributions: high variation in fitness at low FA and reduced fitness in a small number of highly asymmetric individuals (Leung & Forbes 1997a). If so, low levels of FA would have little predictive power, because they might either refer to "true" high-quality individuals or "lucky" low-quality ones (Palmer 1994; Whitlock 1996). But the various relationships with tarsus FA, observed in this and earlier studies of *T. helleri*, do not support such a pattern, given the lack of symmetrical individuals with high inbreeding coefficients in the Chawia population (Lens et al. 2000), and the fact that removing the most asymmetric individuals from the three populations did not affect the relationships between FA and survival (this study). Our study design does not allow rigorous testing of the correlation among levels of stress, asymmetry, and fitness, because it is based on only three statistically independent observations—three surviving populations. Hence, to examine whether the concept of FA as an early warning system can be generalized to other biological systems, future studies should include population replicates within disturbance-treatment levels, whereby interactions between

population-level factors and individual covariates can be tested.

A strong association between fitness and asymmetry under stressful conditions but not under more relaxed ones might result from stress-mediated shifts in an admixture of FA with other types of bilateral asymmetry (for a similar rationale see Rowe et al. 1997). Based on predictions stemming from reaction-diffusion theory, Graham et al. (1993) hypothesized transitions from fluctuating to directional asymmetry, and/or antisymmetry, with severe environmental or genetic stress. Increased admixture of FA with directional asymmetry was shown earlier in stressed populations of four other bird species of the Taita Hills, for which larger sample sizes allowed the use of powerful mixture analysis (Lens & Van Dongen 2000). But the potential mechanisms underlying these transitions between asymmetry types, such as nonlinear feedback between left- and right-trait sides (Graham et al. 1993), are at present poorly understood. Alternatively, the stress dependency of relationships between FA and fitness might result from the fact that both low- and high-quality individuals—characterized by high and low levels of FA, respectively—survive well in the absence of strong environmental stress, whereas low-quality ones succumb under more stressful conditions (Leung & Forbes 1997b). Irrespective of the mechanism(s) involved, the above results complement the consistent association between FA and stress (Lens et al. 1999b, 2000) and between FA of different traits (Lens & Van Dongen 1999) observed in *T. helleri* and a suite of sympatric forest birds. They further confirm that patterns of bilateral trait asymmetry can predict fitness consequences in populations of conservation concern.

When data from case studies such as the present one are used to assess the applicability of FA in conservation planning, it is crucial to take the level of analysis into account. In the majority of cases, the "population" is the level of interest to conservationists, who aim to select the most appropriate targets for conservation if resources are restricted or to assess the extent and rate of recovery after conservation action has been undertaken (Cairns et al. 1993). Population levels of FA have repeatedly responded to distinct stressful events in free-living populations (e.g., Jagoe & Haines 1985; Zakharov & Yablokov 1989; Pankakoski et al. 1992; Schandorff 1997; Badyaev 1998; Lens et al. 1999b). Because our study provides evidence that stress-mediated changes in asymmetry can actually precede detectable changes in more direct fitness components, population FA should be regarded as a potential early warning system (sensu Clarke 1995a). From a statistical perspective, the accuracy of population FA estimation is determined by the number of individuals and the number of repeated measures within individuals relative to measurement error (Van Dongen & Lens 2000b). Because the study of asymmetry does not require recaptures, adequate sample sizes are relatively easily obtained,

and estimation accuracy can be expected to be sufficiently high in most population-level studies.

In specific cases, however, conservation needs to be targeted to individuals rather than populations (e.g., during the planning of translocation experiments to restore demographic or genetic balances) (e.g., Tarr & Fleischer 1999; Galbusera et al. 2000), and accurate individual FA estimates may be required. Unlike population FA, individual estimates are generally hampered by low repeatability due to high sampling variability (Whitlock 1996) or proportionally large measurement error (Van Dongen 1998a) and are therefore considered crude estimates of underlying developmental instability (Whitlock 1996; Houle 1997; Van Dongen & Lens 2000a). Due to recent statistical developments, various sources of bias in the estimation of individual developmental instability can now be detected and corrected for (reviewed by Van Dongen et al. 2001). Yet the degree of error usually remains substantial. The study of multiple traits could further reduce this problem, but only at the cost of intensified fieldwork. Increased use of powerful statistical tools, in combination with the study of synergistic interactions between stresses (e.g., Parsons 1992; Palmer 1994; Lens et al. 2000), will further improve our knowledge about the conditions under which fluctuating asymmetry reliably reflects individual quality.

Acknowledgments

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