Assemblage and population-level consequences of forest fragmentation on bilateral asymmetry in tropical montane birds

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Habitat fragmentation has the potential to influence the development and thus the phenotype of organisms. The asymmetry of bilateral traits may be indicative of the extent to which developmental stability is compromised by the stressful conditions underlying fragmentation. Using an assemblage- and population-level approach, we explored asymmetry differences in tarsus and outermost tail feathers of birds inhabiting fragmented landscapes in the tropical Andes of Colombia. More than 2500 individuals of 185 species were mist-netted at nine forest sites representing continuous forest (> 1000 ha), medium- (70–110 ha), and small-sized (8–20 ha) fragments. Feathers showed true fluctuating asymmetry (FA), whereas tarsus presented a mixture of FA and directional asymmetry. Overall, asymmetry was lowest in continuous forest, and highest in small and medium fragments. These patterns remained unchanged when directionality and differences in species composition, abundance, and foraging tactics were considered. The population-level analyses showed a general trend of increased asymmetry variation in fragments, yet the responses were not always in the same direction. Increased asymmetry may represent an outcome of processes that contribute to the persistence of species in changing environments, and to the generation of phenotypic innovation, which suggests individual adjustments of development to deal with stress. This calls into question the deliberated application of FA as a biomonitoring tool for conservation. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **92**, 119–133.

ADDITIONAL KEYWORDS: Andes – Colombia – developmental stability – directional asymmetry – feathers – fluctuating asymmetry – Neotropical birds – tarsus.

INTRODUCTION

Habitat loss and fragmentation stand out as two of the most severe anthropogenic disturbances faced by tropical biotas worldwide (Dirzo & Raven, 2003). Besides modifying the abiotic conditions normally experienced by organisms, habitat loss and fragmentation also affects the biotic resources that they depend upon, and the connectivity of habitats through which they move (Fahrig, 2003). Well documented consequences of these changes are population fluctuations of various magnitudes, including extinctions and invasions (Crooks *et al.*, 2001; Fahrig, 2003). Another consequence, albeit not explored in depth, includes phenotypic changes such as fluctuating asymmetry (FA) (Anciães & Marini, 2000). FA is the random and subtle deviation from perfect symmetry of bilateral traits resulting from errors not buffered during development (Palmer, 1994; Nijhout & Davidowitz, 2003). FA may not only reflect the extent to which genetic and environmental stresses resulting from forest fragmentation impacts developmental stability (Parsons, 1992), but also contribute to the generation of phenotypic variation (West-Eberhard, 2003; Badyaev, Foresman & Young, 2005) providing an explanation for the persistence of species in fragmented habitats (Simons & Johnston, 1997; Price, Qvarnstrom & Irwin, 2003; DeWitt & Scheiner, 2004; Badyaev *et al.*, 2005).

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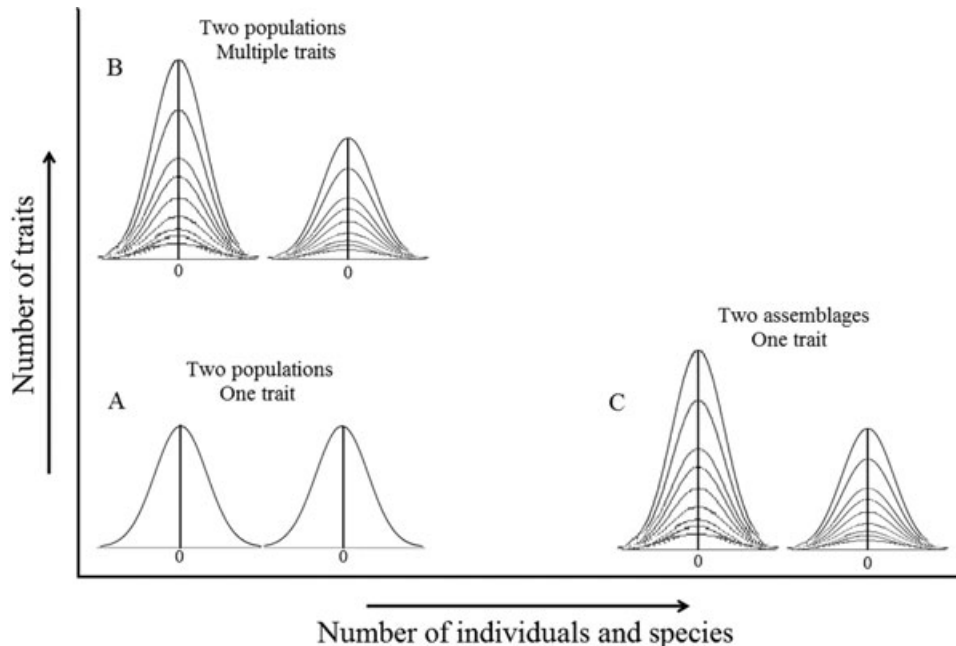
Figure 1. Studies of asymmetry follow different approaches representing trade-offs between the number of traits and number of species and individuals examined. In each panel, the pair of curves depicts the distribution of the signed asymmetries of two groups subjected to contrasting stress environments. A, the two groups represent two populations of the same species and one trait. This approach is fairly simple but is limited in scope. B, the two groups represent two populations of the same species for which multiple traits were measured. Besides allowing intra-individual correlations of asymmetry, this approach allows a robust estimation of developmental stability. This approach is used in most laboratory and some field studies. C, the two groups represent two assemblages for which multiple species and individuals but few traits are evaluated. The assemblage-level approach allows the evaluation of community consequences of phenotypic adjustments to changing environmental conditions.

The impetus for examining the consequences of habitat loss and fragmentation on developmental stability has been provided by several experimental studies that manipulated few environmental variables, targeted particular species, and examined one or multiple traits (Fig. 1A, B). In these studies, the manipulation of temperature (Bubliy, Loeschcke & Imasheva, 2000), water availability (Talloen, Van Dyck & Lens, 2004), pollutants (Graham, Roe & West, 1993b), food (Imasheva et al., 1999), population density (Imasheva et al., 1999), habitat structure (Badyaev et al., 2005), predators (Stoks, 2001), parasites and pathogens (Bize, Roulin & Richner, 2004; Parris & Cornelius, 2004), and degree of inbreeding and hybridization (Waldmann, 1999), resulted in increased levels of FA. These studies also showed that the expression of low developmental stability is often trait specific, and that directional asymmetry (DA), namely consistent asymmetry bias toward one of the sides (Van Valen, 1962; Palmer, 1994), may arise in populations in response to different stresses (Graham, Emlen & Freeman, 2003; but see also Klingenberg, 2003). Habitat loss and forest fragmentation,

however, alter environmental conditions in complex ways, limiting the possibilities of identifying single variables that can affect individuals at different stages during their development. In addition, variation among species, populations, individuals, and traits may result in specific responses that limit our ability to detect a habitat-related effect on developmental stability. This problem may become more acute in highly diverse assemblages because of difficulties associated with the selection of target species (Chase et al., 2000), and the enormous variability in population sizes (Hubbell, 2001).

The majority of field studies addressing the consequences of fragmentation on developmental stability have focused on particular species with conservation problems (Sarre, 1996; Wauters et al., 1996; Lens et al., 1999; Marchand et al., 2003). Overall, these species exhibited increased levels of FA in one (Fig. 1A) or more traits (Fig. 1B) with increasing levels of fragmentation. In some instances, however, it has been difficult to tease apart the effect of forest fragmentation *per se* on developmental stability due to variation in additional factors such as habitat

quality (Lens & van Dongen, 1999). A less conventional approach has been to focus on species assemblages and functional groups (Fig. 1C), such as the study by Anciães & Marini (2000) in the Brazilian Atlantic forest. That study showed increasing levels of FA with forest fragmentation for bird assemblages as a whole, irrespective of species identity, conservation status, or abundance. The importance of this assemblage-level approach (Fig. 1C) is that it links developmental processes occurring at the level of individuals with ecological processes occurring at the level of communities (Callaway, Pennings & Richards, 2003; Werner & Peacor, 2003). Whereas the environment can influence developmental processes and produce variable phenotypes, the latter can influence intra- and interspecific interactions, thus altering community dynamics.

Here, we focus on diverse assemblages of tropical montane forest birds and ask how bilateral asymmetry of two different traits, namely tarsus and outermost tail feathers, varies in response to forest fragmentation. The analyses of two traits that differ in their ontogenies provide two complementary assessments of fragmentation effects on birds' phenotype, one that occurs during embryonic and hatchling stages of the individual (i.e. development of tarsus and feather follicles), and the other that occurs repeatedly during its life span (i.e. feather molt and regrowth). Although not every species and trait may respond in the same way, we expect an assemblage-level increase of trait asymmetry in small fragments. Our general expectation is based on the assumption that forest fragmentation results in stressful conditions, and that stress in turn may influence developmental stability and FA (Leung, Knopper & Mineau, 2003). By bringing together an assemblage- and population-approach to examine the developmental consequences forest fragmentation on birds, we aim to contribute to the understanding of the relationship between phenotypic adjustments occurring at the level of individuals and changes in the dynamics of communities in response to the increase influence of humans on the landscape.

MATERIAL AND METHODS

STUDY AREA

This research was conducted at nine sites in the Colombian Cordillera Central of the Andes, municipalities of Anorí and Amalfi, department of Antioquia (upper left corner: 7°15′N, 75°15′W and lower right corner 6°45′N, 74°95′W). This region encompasses elevations between 1420 and 1900 m a.s.l. and is characterized by a persistent cloud cover, a mean annual precipitation of 4000 mm, and a temperature of 22 °C (IGAC, 2003). Accordingly, it is classified as tropical premontane very wet forest (Espinal, 1992). The landscape is composed of patches of mature forest that differ greatly in their size, and includes some of the largest tracts of cloud forests in the Cordillera Central (Etter, 1998). The forest patches are surrounded by a complex matrix of pastures, second growth vegetation, and coffee plantations.

SAMPLING DESIGN

We used aerial photographs (1 : 10 000 and 1 : 20 000) taken in 1997, topographic maps, and ground-truthing to identify nine forest sites belonging to three fragmentation categories (Table 1). The continuous forest (CF) was represented by tracts of forest > 1000 ha in which the matrix surrounding the mist net transects (see below) was also forest. The medium-sized fragments (MF) were represented by forest fragments ranging in area between 70–110 ha and surrounded by pastures, and in less proportion, by coffee plantations. Lastly, the small-sized fragments (SF) ranged in area between 8–20 ha and, like the medium-sized fragments, they were surrounded by pastures. We identified a forest fragment of each type in each of three regions resembling a 3 × 3 complete block design.

The nine study sites were sampled twice in 2002 (January to April and June to August). At each site, we established two transects along which we operated 14–17 mist-nets (mesh: 30 mm and 36 mm; length × height: 12 × 2.6 m). During the first 3–4 days of each sampling period, mist-netting took place along one transect, and resumed along the second transect on the following 3–4 days, for a total of 12–15 days of netting per site. This protocol helped us to reduce the incidence of declining capture rates with continued sampling at the same location. The mist-nets were opened from 06.30 h to 17.00 h and checked at 1.5-h intervals except during rainy mornings when they were opened later and checked more often. Locations of mist-nets were the same in both sampling periods, with the exception of one continuous forest site where mist-nets were operated along only one transect in the first sampling period but during 6 days. This did not appear to affect our results, as shown by the similarity in capture rates (Table 1) and cumulative species curves with respect to the other continuous forests (see Supplementary Material, Fig. S1). The transects were established in a diverse range of microhabitats, including ridges, slopes, tree fall gaps, edges, and the nearby matrix. In total, we completed 13 846 mist-net hours of sampling effort (a mist-net hour equals a 1-h exposure of one mist-net). Each captured bird was identified to species, weighed, mea-

Table 1. Localities, sampling effort, number of species, and number of individuals included in asymmetry analyses

Locality	Region	Fragment type	Fragment size (ha)	Geographic coordinates	Elevation (m)	Sampling effort (MHN)	Capture rates	No. of species/No. individuals for asymmetry analyses	
								Feathers	Tarsus
Sta. Gertrudis	A	CF	>1000	7°08'N 75°09'W	1420–1465	1450	20.4	37/187	37/149
Bodega Vieja	AS	CF	>1000	6°58'N 75°03'W	1505–1550	1798	27.0	63/331	64/308
Guayabito	G*	CF	>1000	6°52'N 75°06'W	1745–1780	1511	21.7	60/227	55/209
Chaquiral	A	MF	103.2	6°58'N 75°08'W	1645–1720	1390	15.6	45/154	44/143
El Abuelo	AS	MF	70.6	6°56'N 75°00'W	1560–1610	1361	21.5	63/214	62/199
La Secreta	G	MF	85.5	6°49'N 75°06'W	1840–1900	1635	17.3	65/197	56/160
Mampuestos	A	SF	14	7°04'N 75°10'W	1460–1500	1806	23.8	50/118	34/68
Las Ánimas	AS	SF	19	6°56'N 75°01'W	1510–1550	1633	9.9	41/116	39/111
Finca Canales	G	SF	8.5	6°49'N 75°05'W	1830–1855	1261	9.3	56/196	51/198

*Continuous forest locality at which only one mist-net line was operated in the first sampling season. MNH, mist-net hours; CF, continuous forest; MF, medium; SF, small forest fragments; Region A, Anorí; AS, Ánimas-Salazar; G, Guayabito. Capture rate is the number of individuals per 100 MNH.

sured to estimate asymmetry (see below), and marked with plastic bands in a unique colour combination. Hummingbirds were marked temporarily by clipping the claw tip of one of its middle toes.

MORPHOLOGICAL MEASUREMENTS

We measured tarsi and the outermost tail feathers to evaluate the effect of forest fragmentation on asymmetry. These two traits have independent ontogenies, show high measurement repeatability, and have been previously used in field studies of trait asymmetry (Lens *et al.*, 1999; Anciães & Marini, 2000; Brown & Brown, 2002). Tarsus measurements were taken from the notch at the tibia-metatarsus joint to the outer corner exposed by bending toes to tarsus for all birds but hummingbirds, Nearctic–Neotropical migrants, or tarsi with conspicuous anomalies. Both tarsi were measured in the field at least three times, alternating the starting side of each measurement at random. We identified the corresponding pair of outermost tail feathers and collected them for further processing in the laboratory. In addition, we only considered feathers that appeared to have completed full growth and that were not worn, folded, or broken. Feather length was measured by lining the proximal and distal end points of the straightened rachis between parallel rulers. This protocol allowed us to take repeatable and highly accurate measurements of feather length. All measurements were made to the nearest 0.01 mm using a digital Mitutoyo Digimatic caliper by one of us (A.M.C.).

MEASUREMENT ERROR AND ASYMMETRY ANALYSES

We took repeated measurements on left and right sides to distinguish the within-side variation (i.e. measurement error) from true asymmetry. For each species with ten or more individuals, we performed a two-way mixed-model analysis of variance (ANOVA) in which individual and side were included as random and fixed effects, respectively (Palmer, 1994). Significance of the interaction term indicates that asymmetry is significantly greater than measurement error (ME), whereas significance of the side term (tested over the interaction mean square) suggests the presence of DA (Palmer, 1994).

In addition to ME, we also inspected the distribution of the signed asymmetry ($R_i - L_i$, difference between right and left sides) which can take one of three forms: normal distribution with zero mean, which represents subtle, random deviations from symmetry (FA); normal distribution with nonzero mean, which reflects a systematic bias towards one of

the sides (DA); and bimodal or platykurtic distribution with zero mean, which represents an unsystematic bias to either side (antisymmetry; Van Valen, 1962; Palmer, 1994). Normality for each trait was evaluated for species with at least ten captures using Kolmogorov–Smirnov tests, and deviation from a zero mean using one sample t-tests. In addition, we generated the probability density functions (PDFs) to visually inspect asymmetry distributions and detect departures from normality associated with kurtosis and skewness. These PDFs were calculated using a Gaussian kernel density estimate based on the method of Sheather & Jones (1991) to select an optimum bandwidth (Venables & Ripley, 1999).

To determine whether a size-scale correction was necessary, we evaluated the relationship between trait size and the unsigned asymmetries ($|R_i - L_i|$, absolute value of the difference between sides) using the whole data set. Trait length was a poor predictor of asymmetry, explaining only 7.3% for tarsus and 6.2% for feathers (Pearson correlation coefficients: 0.27 and 0.25, respectively). Repeating the analyses with the size-scaled values produced the same results as with the untransformed data; therefore, all the analyses are based on the untransformed asymmetry values.

We used ANOVA of the unsigned asymmetry $|R_i - L_i|$ (FA1; Palmer, 1994) to evaluate differences in bird asymmetry among fragment types (CF, MF, SF), including region as blocking factor. This 3×3 complete block design (Table 1) minimizes the experimental error variance that might exist due to regional variation in bird composition and morphology. Because the distribution of the unsigned asymmetry is truncated and skewed to the right, its mean and variance are highly correlated (Palmer & Strobeck, 2003). Therefore, analysing mean differences of unsigned asymmetry with ANOVA is equivalent to Levene's tests for variance differences of signed asymmetry (Palmer & Strobeck, 2003).

We followed a four-step approach to evaluate the assemblage-level consequences of forest fragmentation on trait asymmetry. First, we subset the data to include all captured species and individuals in the analysis (analysis A), only those species captured in the three fragment types though not necessarily in all regions (analysis B), and only those species captured in the three fragment types in each of the three regions, thus present in all nine sites (analysis C). This approach eliminated, in successive steps, the possibility that differences in species composition of samples could have biased the results. Second, we subset the data to include species with low capture rates ($N < 10$ individuals) in one group, and the rest of species ($N \geq 10$ individuals) in a second group and repeated analyses A and B. This approach ruled

out the possibility that asymmetry differences were driven by differences in the number of captured individuals among fragments, especially because the majority of species were represented by few individuals. Third, analyses A and B were repeated grouping species according to different types of asymmetry (FA versus DA) to assess whether directionality influenced the assemblage-level results for tarsus. Lastly, species were classified in five groups based on major foraging tactics (see Supplementary Material, Table S1) to rerun a modified analysis A by including the 'foraging tactic' as a fixed factor in the ANOVA model. The way that birds obtain food may reflect the extent to which different morphological traits are used (Naoki, 2003). In turn, differences in the relevance of a trait for foraging may determine the amount of selection pressure acting on that particular trait.

To evaluate the population-level consequences of forest fragmentation on asymmetry, we analysed separately species captured at least in two fragment types with a minimum of five individuals per fragment type. We used a two-sample t-test (if present in just two fragment types) or one-way ANOVA (if present in three fragment types) to evaluate population differences in asymmetry. We conducted Tukey's post-hoc pairwise comparisons at the 0.05 significance level for the analyses that were significant. All the statistical analyses were carried out using S-Plus, version 6.1 (Insightful Corporation, 2002).

RESULTS

Overall, 2533 individuals belonging to 185 species were captured. In general, while the number of species was approximately similar among fragment types, the number of captured individuals was greater in continuous than in medium and small fragments (Table 1). Data on feather asymmetry was collected for a total of 142 species (1545 individuals) for which 48 had at least ten individuals captured. Similarly, data on tarsus asymmetry was collected for 158 species (1740 individuals) for which 49 species had at least ten individuals. Sample sizes were not the same for both traits because, for many individuals, one trait could not be measured due to worn, molting, or missing feathers, or lack of tarsi data for hummingbirds. For both traits, species with ten or more individuals represented approximately 32% of the total captures.

MEASUREMENT ERROR AND THE DISTRIBUTION OF SIGNED ASYMMETRY

Feather and tarsus asymmetry was significantly larger than ME for each subset of species analysed as indicated by the significance of the individual–side

interaction term (ANOVAs, $P < 0.0001$ for each test; see Supplementary Material, Table S1), suggesting high measurement repeatability. The error variance had a low contribution to the observed asymmetry (ME in Supplementary Material, Table S1), yet it varied among species, particularly for tarsus data (ME was in the range 0.2–17.4% for tarsi and 0.02–1.4% for feathers). In addition, ME of tarsus and feathers did not differ significantly among fragments (results not shown); therefore, subsequent analyses did not require a correction for ME.

The distribution of feather signed asymmetry in 41 species did not depart from normality with mean zero (Kolmogorov–Smirnov tests, $P > 0.06$; t-tests, $P > 0.06$; see Supplementary Material, Table S1). For the remaining seven species, the distribution differed from a normal distribution suggesting high leptokurtosis (K tests, $P < 0.032$; Wilcoxon $Z < 1.9$, $P > 0.06$; see Supplementary Material, Table S1). Additional support for these results is shown by the nonsignificant effect of the side term in the mixed-model ANOVAs (see Supplementary Material, Table S1). In conclusion, asymmetry of tail feathers among the assessed species resembled FA.

Unlike feathers, we found a mixture of FA and DA in tarsus. For 25 out of 49 species (51%), the distribution of signed asymmetry did not differ from normality with mean zero (Kolmogorov–Smirnov tests, smallest $P > 0.06$; t-tests, smallest $P > 0.07$; see Supplementary Material, Table S1) resembling FA. For a second group of 21 species (43%), however, the distribution was normal with a mean different from zero (Kolmogorov–Smirnov D-tests, $P > 0.11$; t-tests, $P < 0.02$; see Supplementary Material, Table S1), indicating DA. The significance of the side term in the mixed-model ANOVAs for these species agrees with these results (see Supplementary Material, Table S1). Finally, for a group of three species (*Trogon collaris*, *Machaeropterus regulus*, and *Euphonia xanthogaster*; see Supplementary Material, Table S1) the distribution of asymmetry of tarsus could not be reliably characterized as FA, DA, or antisymmetry either statistically or by inspection of the PDFs.

ASSEMBLAGE LEVEL ASYMMETRY

Forest fragmentation affected feather and tarsus asymmetry in different ways. Feather asymmetry differed significantly among forest fragment types (Table 2, analysis A; Fig. 2) even when restricting the analysis to include species present in all fragment types but not all regions (Table 2, analysis B). A post-hoc Tukey's test showed that asymmetry variation (mean unsigned asymmetry ± SD) was highest in birds from medium-sized fragments (0.548 ± 0.753 mm) compared to birds from small-sized

fragments (0.517 ± 0.664) and continuous forests (0.432 ± 0.612) (Fig. 2). When the analysis was restricted to the five species present in all nine study sites, no differences in feather asymmetry were found (Table 2, analysis C). Unlike feathers, tarsus asymmetry was markedly different among fragments in all the three analyses (Table 2; Fig. 2). In general, variation in tarsus asymmetry was larger in birds from small- (0.094 ± 0.097) and medium-sized (0.096 ± 0.099) fragments than from continuous forests (0.069 ± 0.096) (Fig. 2).

Given that the many species (119 and 93 for feathers and tarsus, respectively) with low capture numbers ($N < 10$) could have introduced a sampling error effect, we repeated analyses A and B with these alone ($N < 10$) and the rest ($N \geq 10$). Feather asymmetry differed significantly among fragment types when considering species with ten or more captures, but not those with few captures (Table 2). In species with ten or more captures, asymmetry was lower in continuous forests (0.410 ± 0.560) and higher in medium-sized fragments (0.512 ± 0.729). Tarsus asymmetry differed among fragments for each group of species, showing the same pattern as when all species were considered together (Table 2). These consistencies suggest that results are not an artefact of the inclusion of the multiple species with low capture rates. Because several species exhibited DA in tarsus, we repeated analyses A, B and C without them. The results did not change (Table 2), suggesting that the observed patterns are not an artefact of the presence of directionality. Moreover, we corrected the data for directionality by standardizing to FA following Palmer (1994) and, again, the conclusions were the same as with the uncorrected asymmetry data (two-way ANOVA $F_{2,700} = 4.59$, $P = 0.0104$). Grouping species by foraging tactics showed that tarsus but not feather asymmetry differed among fragment types but in relation to the foraging group (Table 3). Tarsus asymmetry was lower in continuous than fragmented forests for gleaners, probers, and salliers (Fig. 3).

The data on feather and tarsus asymmetries failed to show any correlation between them whether we used individual ($r = 0.04$, $P = 0.23$, $N = 1059$ individuals) or species averages ($r = 0.023$, $P = 0.80$, $N = 127$ species) values. This suggests a lack of organism-wide asymmetry.

POPULATION LEVEL ASYMMETRY

The variability of tarsus but not feather asymmetry showed a general trend of increase from continuous to small-sized forest fragments (Figs 4, 5). For feathers, only three out of 31 species exhibited significant differences in FA across fragments

Table 2. Summary of two-way analyses of variance of the unsigned asymmetry of feathers and tarsus for the assemblage-level analyses

Analysis	Source of variation	Feathers d.f.	F	P	Tarsus d.f.	F	P
Complete data set:							
A	Fragment type	2	4.999	< 0.01	2	20.73	< 0.001
	Region	2	3.788	< 0.05	2	23.95	< 0.001
	Error	1735			1540		
B	Fragment type	2	3.629	< 0.05	2	19.07	< 0.001
	Region	2	4.321	< 0.05	2	19.19	< 0.001
	Error	1460			1170		
C	Fragment type	2	0.585	0.558	2	6.373	< 0.01
	Region	2	0.380	0.685	2	3.278	< 0.05
	Error	180			196		
Only including species with $\geq$ 10 individuals:							
A	Fragment type	2	3.791	< 0.05	2	15.3	< 0.001
	Region	2	2.664	0.070	2	18.52	< 0.001
	Error	1415			1232		
B	Fragment type	2	2.846	0.058	2	16.78	< 0.001
	Region	2	2.763	0.063	2	17.27	< 0.001
	Error	1355			1099		
Only including species with < 10 individuals:							
A	Fragment type	2	0.496	0.610	2	4.878	< 0.01
	Region	2	0.520	0.595	2	4.644	< 0.05
	Error	315			303		
B	Fragment type	2	0.595	0.550	2	3.554	< 0.05
	Region	2	0.230	0.800	2	3.687	< 0.05
	Error	100			125		
Excluding species showing DA in tarsus:							
A	Fragment type				2	15.600	< 0.001
	Region				2	9.230	< 0.001
	Error				834		
B	Fragment type				2	11.040	< 0.001
	Region				2	6.387	< 0.01
	Error				492		

Analysis A, all species captured included; Analysis B, all species captured in each fragment type included; Analysis C, only the species captured in the three fragment types of the three regions included. d.f., degrees of freedom.

(Fig. 4; see Supplementary Material, Table S2). Two of these three species (*Syndactyla subalaris* and *Phaethornis guy*) had the lowest FA in continuous forests, whereas the third (*Doryfera ludovicae*) showed the opposite pattern. Because 5% of the species would show a significant effect by chance alone, three out of 31 species with feather FA differences is likely to be the result of a Type I error (binomial test, $P = 0.201$).

For tarsi, six out of 33 species showed significant differences in asymmetry across fragments (Fig. 5). The asymmetry in four of these species appeared to be FA (Fig. 5A) whereas, in the other two, it appeared to be DA (Fig. 5B). In all but one species, *Masius*

chrysopterus, asymmetry was lower in the continuous forests (Fig. 5; see Supplementary Material, Table S2). The probability of observing asymmetry differences in six out of 33 species as a result of Type I error is very low (binomial test, $P = 0.005$), indicating that our results may indeed reflect an effect of forest fragmentation on developmental stability.

DISCUSSION

The present study demonstrates assemblage- and population-level effects of forest fragmentation on bilateral asymmetry in birds. Feather and tarsus asymmetry was lowest in bird assemblages inhabiting
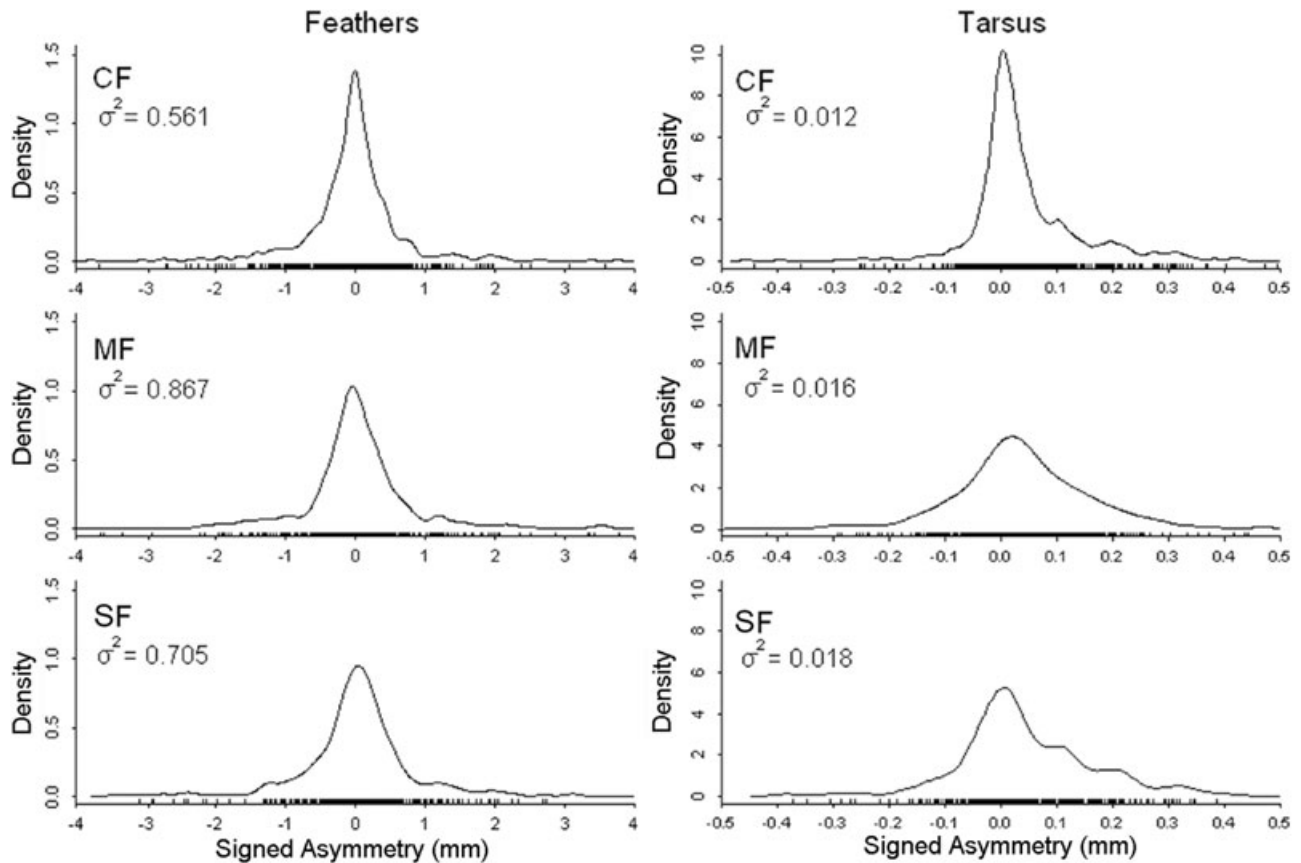
Figure 2. Probability density functions (PDF) of the signed asymmetry of tarsus and feathers. Fragmentation categories include: CF, continuous forest; MF, medium; SF, small forest fragments. Note the increase in asymmetry variation in tarsus with fragmentation. Both traits exhibit different magnitudes of asymmetry, with feathers having a more spread out range than tarsi.

Table 3. Asymmetry among landscape types and foraging tactics

Source of variation	Feathers			Tarsus		
	d.f.	F	P	d.f.	F	P
Fragment type	2	0.417	0.659	2	9.465	< 0.0001
Foraging technique	4	17.204	< 0.0001	4	9.805	< 0.0001
Interaction	8	0.713	0.680	8	2.831	< 0.01
Error	1725			1530		

Summary of two-way analyses of variance of the unsigned asymmetry of feathers and tarsus among fragment treatments and foraging techniques.
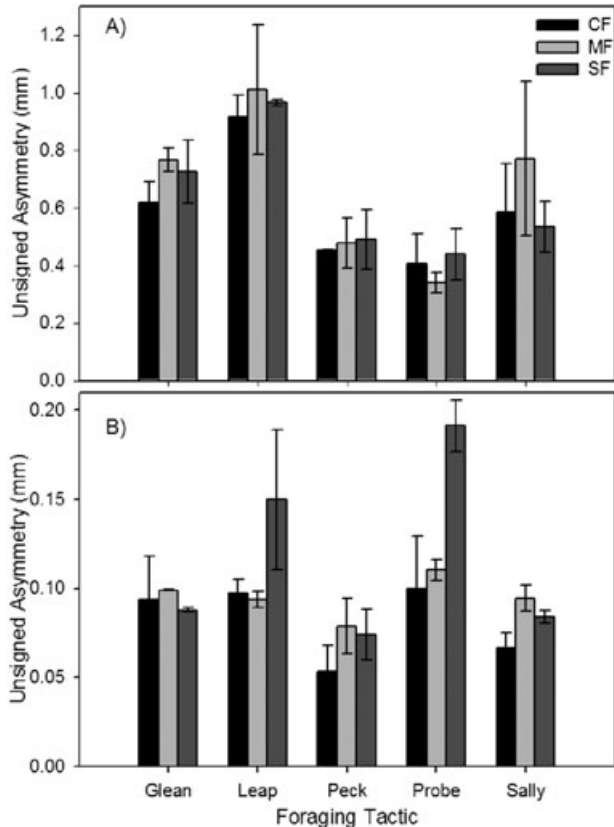CF, continuous forest; MF, medium; SF, small forest fragments.
d.f., degrees of freedom.

continuous forest; this pattern remained unchanged when directionality and differences in species composition, abundance, and foraging tactics were considered. Furthermore, feather and tarsus asymmetry differed among fragment types in 19% of the species analysed at the population-level, yet the responses were not always in the same direction. However, there was a general trend of increased asymmetry

Figure 3. Mean unsigned asymmetry of birds classified in five foraging tactics by fragment type. Error bars depict the standard deviation. A, feathers; B, tarsus; CF, continuous forest; MF, medium; SF, small forest fragments.

variation of populations in fragments other than continuous forest. That fragmentation-related factors influence bird developmental stability is intriguing in several ways. First, in the assemblage-level analyses, species with low and high captures rates showed similar trends. Second, several species that showed significant effects of fragment size on asymmetry are known to thrive in disturbed habitats. These two results suggest that increased levels of asymmetry may represent an outcome of other processes that may contribute to persistence of organisms in changing environments. Third, tarsi showed a mixture of FA and DA, which also increased with fragmentation in agreement with the notion that DA is also an indicator of developmental stability. Lastly, the range of asymmetry variation was greater in feathers than in tarsi suggesting that the developmental origin and degree of integration of traits influence the magnitude of observed changes. The general trend of increased asymmetry in fragments is revealing even though the effect sizes were low (6–10%). This is in agreement with a theoretical maximum of approxi-

mately 20% that is not only biologically significant, but also comparable to other field and laboratory studies of asymmetry because asymmetry is a variance rather than a mean (Houle, 2000; Palmer & Strobeck, 2003).

ASSEMBLAGE- AND POPULATION-LEVEL PATTERNS OF ASYMMETRY IN FRAGMENTED HABITATS

To our knowledge, the only other study that has examined the assemblage-level consequences of forest fragmentation on developmental stability was conducted in the Brazilian Atlantic forest, another tropical mountainous region (Anciães & Marini, 2000). That study showed that FA of wings and tarsi in passerine birds increased with fragmentation in patches that ranged in size from 15 to 70 000 ha. In the present study, we focused on tail feathers and tarsi, and we used a different experimental design (i.e. complete block design versus linear regression) to test the hypothesis of increasing levels of FA with fragmentation. Except for the incidence of DA, our results for tarsi are in general agreement with those from Brazil. Furthermore, separate analyses based on the number of captured individuals indicate that differences in asymmetry were not influenced by differences in species composition and abundance. Similarly, birds grouped according to their foraging tactics, which may reflect differences in the importance of hind limb and tail feathers, revealed consistent results especially for tarsi (Fig. 3). Although these two regions only share 7.2% of the bird species, taken together, both studies suggest an overall similar phenotypic response to forest fragmentation of multiple individuals of multiple species. This variability may be indicative of a broader set of phenotypic adjustments to changing environments (West-Eberhard, 2003; Badyaev *et al.*, 2005).

As mentioned earlier, the population-level analyses showed that levels of asymmetry differed among fragments in up to 19% of the species analysed. For feathers, the number of significant tests is what would be expected by chance alone but, for tarsi, the number of significant asymmetries appeared to represent a real effect. Differences in feather asymmetry among fragment types were observed in two species (*P. guy* and *D. ludovicae*), in tarsus asymmetry in five species (*Sittasomus griseicapillus*, *Mionectes olivaceus*, *M. chrysopterus*, *Buarremon brunneinucha*, *E. xanthogaster*), and in both traits in one species (*S. subalaris*), and these were not necessarily in the predicted directions. The results of two other fragmentation studies that examined several species simultaneously agree in general terms with ours. In the Brazilian study, only six out of a total of 100 passerine species were amenable for a population-
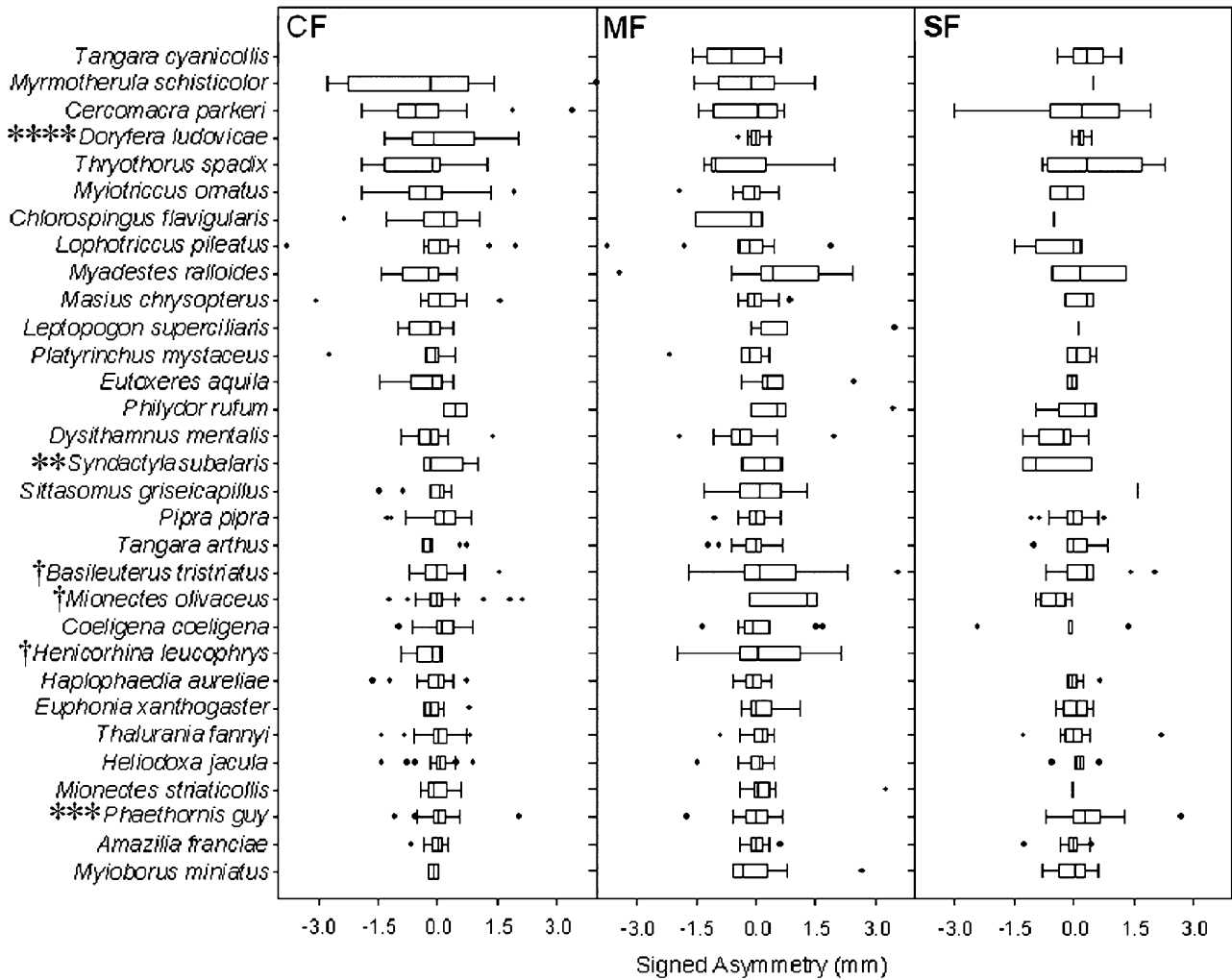
Figure 4. Box whisker plots of fluctuating asymmetry (FA) of feathers for species with enough sample sizes for statistical analyses (see text and see Supplementary Material, Table S2). Species were arranged in increasing order of asymmetry variance in CF. CF, continuous forest; MF, medium fragments; SF, small forest fragments. One-way ANOVA †$P < 0.1$, **$P < 0.05$, ***$P < 0.01$, ****$P < 0.001$.

level analysis comparing FA in fragments and continuous forests. Wing asymmetry in one species (*Conopophaga lineata*), tarsus asymmetry in three species (*Dysithamnus mentalis*, *Turdus albicollis*, and *Trichothraupis melanops*), and asymmetry in both traits in one species (*Platyrinchus mystaceus*) was significantly lower in continuous than in fragmented forests (Anciães & Marini, 2000). In another study conducted in the Taita Hills of Kenya, all of the seven forest-dependent bird species studied (*Zosterops silvanus*, *Turdus helleri*, *Andropadus milanjensis*, *Phyllastrephus cabanisi*, *Pogonocichla stellata*, *Phylloscopus ruficapillus*, *Nectarinia olivacea*) showed an increase of tarsus asymmetry in the smallest fragment (Lens *et al*., 1999). Unlike other studies

on FA that have targeted taxa with local conservation problems and found increased levels of FA in populations from fragmented forests (Sarre, 1996; Wauters *et al*., 1996; Marchand *et al*., 2003), the species listed above appear to persist in fragmented forests, and several of them even use second growth and disturbed forests.

TRAIT ASYMMETRY

The two traits examined in the present study showed marked differences in terms of the range of variability exhibited across fragment types, and the type of asymmetry. The variance of signed FA for tail feathers was 0.70, which lies within the range of variation
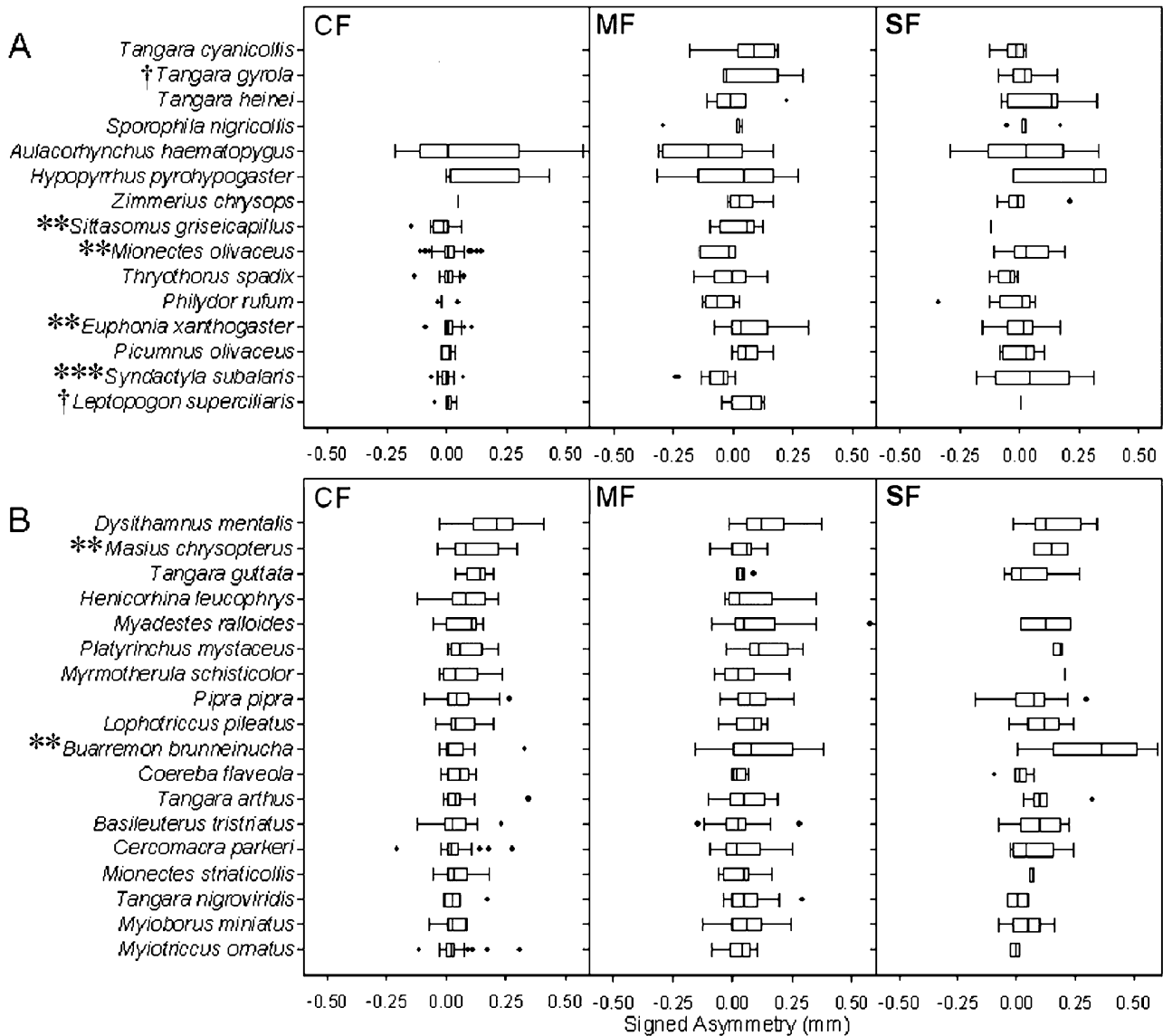
Figure 5. Box whisker plots of signed asymmetry of tarsus for species with enough sample sizes for statistical analyses. A: species showing tarsus FA, B: species showing tarsus DA. Species were arranged in increasing order of asymmetry variance in CF. Note the general trend of increasing asymmetry variation with fragmentation. CF: continuous forest, MF: medium, and SF: small forest fragments. One-way analysis of variance: †$P < 0.1$, **$P < 0.05$, ***$P < 0.01$.

for feather asymmetry reported in previous studies (Lens & van Dongen, 1999; Anciães & Marini, 2000; Bize *et al.*, 2004). On the other hand, the variance of tarsus asymmetry was 0.015, which is lower than that of feathers, in agreement with reported values (Lens & van Dongen, 1999; Anciães & Marini, 2000).

The above differences in the range of natural variation in tarsi and feather asymmetry may be explained in terms of their developmental origin, degree of integration (Aparicio & Bonal, 2002; Badyaev &

Foresman, 2004), as well as mode of selection (Balmford, Jones & Thomas, 1993). Tarsus is an osteological structure involving the fusion of the distal tarsals and metatarsals (Dingus & Rowe, 1998) and completes its development once and before fledging. On the other hand, feathers are branched integumentary appendages made of keratin (Prum & Williamson, 2001) that grow multiple times during the life time of a bird from the same follicles. Furthermore, in each molting season, feathers of each side may grow asynchronously; thus, they may experience slightly different

growth conditions. We might expect then that magnitude of asymmetry change throughout the life of a bird but the available evidence for this is inconclusive (Swaddle, 1997; Stige, Slagsvold & Vollestad, 2005). Therefore, tarsus asymmetry may only reflect stresses during embryonic and hatchling stages, whereas feathers may in addition reflect stresses throughout the life span of the bird (Swaddle, 1997; Aparicio, 2001; Stige *et al.*, 2005).

In terms of function, the tarsus is a functional structure on its own and plays a critical role in daily activities (e.g. locomotion, perching, preening, foraging) whereas the pair of outermost feathers is one component of the tail, a structure composed of five to six feather pairs used for flight and communication, among other activities (Balmford *et al.*, 1993). This functional difference may explain to some extent why tarsus, but not feather asymmetry, differed with fragmentation for some of the foraging guilds considered. Gleaning and probing are foraging tactics that rely heavily on hind limb movements, which suggests that even under different selection pressures, the tarsus may reflect developmental stresses in fragmented habitats. Accordingly, there was little evidence for a correlation between feather and tarsus asymmetry regardless of whether individual values or species means were used. This result is in general agreement with most FA studies that fail to find individual wide asymmetry (Dufour & Weatherhead, 1996; Sarre, 1996; Anciães & Marini, 2000).

Feathers and tarsi also differed in the type of asymmetry. Although asymmetry of feathers appeared to represent solely FA, that of tarsus consisted of a mixture of FA and DA. For feathers, our results are consistent with those of other studies examining asymmetry of tails and wings (Balmford *et al.*, 1993; Aparicio & Bonal, 2002; Brown & Brown, 2002). For tarsus, however, our results showing a mixture of asymmetries are consistent with some studies (Lens & van Dongen, 2000; Kark, 2001), but not with others (Anciães & Marini, 2000). The increasing reporting in recent years of DA in different traits and organisms (Graham *et al.*, 1998; Gallant & Teather, 2001; Marchand *et al.*, 2003; Marques, Costa & Cabral, 2005) suggests either the recent application of rigorous analyses to distinguish among asymmetry forms or biases toward reporting only FA results. Although DA may well have a genetic basis (Palmer & Strobeck, 1992), environmental stress after drastic habitat changes may induce DA (Lens & van Dongen, 2000). Both empirical and theoretical research has argued that developmental errors can also result in DA (Graham, Freeman & Emlen, 1993a) and in transitions between asymmetry types (Graham *et al.*, 2003) as has been documented in natural populations (Kark, 2001).

ASYMMETRY, FOREST FRAGMENTATION, AND CONSERVATION

Mechanisms leading to increased asymmetry in birds from fragmented forests may stem from the multiple local and regional changes in abiotic (e.g. understory temperature, and luminosity) and biotic factors (e.g. parasitism, territory density, and life history traits) induced by fragmentation (Saunders, Hobs & Margules, 1991; Karlsson & Van Dyck, 2005). Some of these changes are thought to affect bird development (Brown & Brown, 2002; Bize *et al.*, 2004), such as through changes in incubation time patterns that might lead to tarsus or feather asymmetry, ultimately affecting fitness.

A negative correlation between high levels of asymmetry and individual fitness has often been assumed in the literature (Clarke, 2003). However, we and others have shown that species that are abundant, and even thrive in fragmented forests, appear to exhibit increased levels of asymmetry. Discrepancies between the long-held view that asymmetry is detrimental and the results of this and other studies suggest several alternative explanations about the meaning of asymmetry in fragmented and, more broadly speaking, heterogeneous habitats. First, it suggests no, or at most a weak, direct relationship between asymmetry and fitness. Species that are known to persist in fragmented habitats and show high levels of asymmetry in these habitats may provide support for this explanation. Second, increased levels of asymmetry may represent developmental-driven adjustments to stressful conditions (Badyaev *et al.*, 2005). Variation in developmental stability has been viewed as a bet-hedging strategy because of its ability to produce a diversity of phenotypes from the same genotype depending on the environment (Simons & Johnston, 1997). According to this, differences in asymmetry may be advantageous under different environmental changes. Third, new environments may induce phenotypic plasticity that may impose costs at the expense of developmental stability (DeWitt, Sih & Wilson, 1998). If canalization and developmental stability share the same set of underlying developmental mechanisms, then adaptive phenotypic plasticity may produce increasing levels of asymmetry. Fourth, developmental stability in natural populations is not only affected by local stressors, but also by processes varying geographically across species distributions (Kark, 2001). For example, unlike our results for *D. mentalis* and *P. mystaceus*, Anciães & Marini (2000) demonstrated asymmetry differences with fragmentation for these passerine birds in Brazil. These possibilities call into question the notion that variation in developmental stability is strictly detrimental and suggest that its

applications for monitoring populations under conservation threats (Leary & Allendorf, 1989) may be taken with caution. Instead, changes in developmental stability under different conditions may be seen as a contribution to phenotypic variation expressed in multiple individuals and species at once. This may not only have the potential for evolutionary innovation (West-Eberhard, 2003), but also enable the persistence of species in changing environments, providing a link between individual adaptation to stress and the evolution of stress resistance (Badyaev *et al.*, 2005).

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REFERENCES

Anciães M, Marini MA. 2000. The effects of fragmentation on fluctuating asymmetry in passerine birds of Brazilian tropical forests. *Journal of Applied Ecology* **37:** 1013–1028.

Aparicio JM. 2001. Patterns of growth and fluctuating asymmetry: the effects of asymmetrical investment in traits with determinate growth. *Behavioral Ecology and Sociobiology* **49:** 273–282.

Aparicio JM, Bonal R. 2002. Why do some traits show higher fluctuating asymmetry than others? A test of hypotheses with tail feathers of birds. *Heredity* **89:** 139–144.

Badyaev AV, Foresman KR. 2004. Evolution of morphological integration. I. Functional units channel stress-induced variation in shrew mandibles. *American Naturalist* **163:** 868.

Badyaev AV, Foresman KR, Young RL. 2005. Evolution of morphological integration: developmental accommodation of stress-induced variation. *American Naturalist* **166:** 382–395.

Balmford A, Jones IL, Thomas ALR. 1993. On avian asymmetry: evidence of natural selection for symmetrical tails and wings in birds. *Proceedings of the Royal Society of London Series B, Biological Sciences* **252:** 245–251.

Bize P, Roulin A, Richner H. 2004. Parasitism, developmental plasticity and bilateral asymmetry of wing feathers in alpine swift, *Apus melba*, nestlings. *Oikos* **106:** 317–323.

Brown CR, Brown MB. 2002. Ectoparasites cause increased bilateral asymmetry of naturally selected traits in a colonial bird. *Journal of Evolutionary Biology* **15:** 1067–1075.

Bubliy OA, Loeschcke V, Imasheva AG. 2000. Effect of stressful and nonstressful growth temperatures on variation of sternopleural bristle number in *Drosophila melanogaster*. *Evolution* **54:** 1444–1449.

Callaway RM, Pennings SC, Richards CL. 2003. Phenotypic plasticity and interactions among plants. *Ecology* **84:** 1115–1128.

Chase MK, Kristan WB, Lynam AJ, Price MV, Rotenberry JT. 2000. Single species as indicators of species richness and composition in California coastal sage scrub birds and small mammals. *Conservation Biology* **14:** 474–487.

Clarke GM. 2003. Developmental stability-fitness relationships in animals: Some theoretical considerations. In: Polak M, ed. *Developmental instability: causes and consequences*. New York, NY: Oxford University Press, 187–195.

Crooks KR, Suárez AV, Bolger DT, Soulé ME. 2001. Extinction and colonization of birds on habitat islands. *Conservation Biology* **15:** 159–172.

DeWitt TJ, Scheiner SM. 2004. Phenotypic variation from single genotypes: a primer. In: DeWitt TJ, Scheiner SM, eds. *Phenotypic plasticity: functional and conceptual approaches*. New York, NY: Oxford University Press, 1–9.

DeWitt TJ, Sih A, Wilson DS. 1998. Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* **13:** 77–81.

Dingus L, Rowe T. 1998. *The mistaken extinction, dinosaur evolution and the origin of birds*. New York, NY: WH Freeman.

Dirzo R, Raven PH. 2003. Global state of biodiversity and loss. *Annual Review of Environment and Resources* **28:** 137–167.

Dufour KW, Weatherhead PJ. 1996. Estimation of organism-wide asymmetry in red-winged blackbirds and its relation to studies of mate selection. *Proceedings of the Royal Society of London Series B, Biological Sciences* **263:** 769–775.

Espinal LS. 1992. *Geografía ecológica de Antioquia: Zonas de Vida*. Medellín, Editorial Léalon.

Etter A. 1998. Mapa general de ecosistemas de Colombia (1: 1.500.000). In: Chaves ME, Arango N, eds. *Informe Nacional Sobre El Estado de la biodiversidad*. Bogotá: Instituto Alexander von Humboldt, PNUMA, and Ministerio del Medio Ambiente.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **34:** 487–515.

Gallant N, Teather K. 2001. Differences in size, pigmentation, and fluctuating asymmetry in stressed and non-stressed northern leopard frogs (*Rana pipiens*). *Ecoscience* **8:** 430–436.

Graham JH, Emlen JM, Freeman DC. 2003. Nonlinear dynamics and developmental instability. In: Polak M, ed. *Developmental instability: causes and consequences*. New York, NY: Oxford University Press, 35–50.

Graham JH, Emlen JM, Freeman DC, Leamy LJ, Kieser JA. 1998. Directional asymmetry and the measurement of developmental instability. *Biological Journal of the Linnean Society* **64:** 1–16.

Graham JH, Freeman DC, Emlen JM. 1993a. Antisymmetry, directional asymmetry, and dynamic morphogenesis. *Genetica* **89:** 121–137.

Graham JH, Roe KE, West TB. 1993b. Effects of lead and benzene on the developmental stability of *Drosophila melanogaster*. *Ecotoxicology* **2:** 189–195.

Houle D. 2000. A simple model of the relationship between asymmetry and developmental stability. *Journal of Evolutionary Biology* **13:** 720–730.

Hubbell SP. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton, NJ: Princeton University Press.

IGAC. 2003. *Atlas de Colombia*. Bogotá: Instituto Geográfico Agustín Codazzi and Imprenta Nacional de Colombia.

Imasheva AG, Bosenko DV, Bubliy OA, Lazebny OE. 1999. The effect of three ecological stresses on variation of morphological traits in *Drosophila melanogaster*. *Russian Journal of Genetics* **35:** 1188–1193.

Insightful Corporation. 2002. *S-Plus 6.1 for Windows*. Seattle, WA: Insightful Corporation.

Kark S. 2001. Shifts in bilateral asymmetry within a distribution range: the case of the chukar partridge. *Evolution* **55:** 2088–2096.

Karlsson B, Van Dyck H. 2005. Does habitat fragmentation affect temperature-related life-history traits? A laboratory test with a woodland butterfly. *Proceedings of the Royal Society of London Series B, Biological Sciences* **272:** 1257–1263.

Klingenberg CP. 2003. A developmental perspective on developmental instability: theory, models, and mechanisms. In: Polak M, ed. *Developmental Instability: causes and consequences*. New York, NY: Oxford University Press, 14–34.

Leary RF, Allendorf FW. 1989. Fluctuating asymmetry as an indicator of stress: implications for conservation biology. *Trends in Ecology and Evolution* **4:** 214–217.

Lens L, van Dongen S. 1999. Evidence for organism-wide asymmetry in five bird species of a fragmented afrotropical forest. *Proceedings of the Royal Society of London Series B, Biological Sciences* **266:** 1055–1060.

Lens L, van Dongen S. 2000. Fluctuating and directional asymmetry in natural bird populations exposed to different levels of habitat disturbance, as revealed by mixture analysis. *Ecology Letters* **3:** 516–522.

Lens L, van Dongen S, Wilder CM, Brooks TM, Matthysen E. 1999. Fluctuating asymmetry increases with habitat disturbance in seven bird species of a fragmented afrotropical forest. *Proceedings of the Royal Society of London Series B, Biological Sciences* **266:** 1241–1246.

Leung B, Knopper L, Mineau P. 2003. A critical assessment of the utility of fluctuating asymmetry as a biomarker of anthropogenic stress. In: Polak M, ed. *Developmental instability: causes and consequences*. New York, NY: Oxford University Press, 415–426.

Marchand HL, Paillat G, Montuire S, Butet A. 2003. Fluctuating asymmetry in bank vole populations (Rodentia, Arvicolinae) reflects stress caused by landscape fragmentation in the Mont-Saint-Michel Bay. *Biological Journal of the Linnean Society* **80:** 37–44.

Marques JF, Costa JL, Cabral HN. 2005. Variation in bilateral asymmetry of the Lusitanian toadfish along the Portuguese coast. *Journal of Applied Ichthyology* **21:** 205–209.

Naoki K. 2003. Evolution of ecological diversity in the Neotropical tanagers of the genus Tangara (Aves: Thraupidae). PhD Thesis, Louisiana State University.

Nijhout HF, Davidowitz G. 2003. Developmental perspectives on phenotypic variation, canalization, and fluctuating asymmetry. In: Polak M, ed. *Developmental instability: causes and consequences*. New York, NY: Oxford University Press, 3–13.

Palmer AR. 1994. Fluctuating asymmetry analyses: a primer. In: Markow T, ed. *Developmental instability: its origins and evolutionary implications*. Dordrecht: Kluwer Academic Publishers, 335–364.

Palmer AR, Strobeck C. 1992. Fluctuating asymmetry as a measure of developmental stability: Implications of non-normal distributions and power of statistical tests. *Acta Zoologica Fennica* **191:** 55–70.

Palmer AR, Strobeck C. 2003. Fluctuating asymmetry analyses revisited. In: Polak M, ed. *Developmental instability: causes and consequences*. New York, NY: Oxford University Press, 279–319.

Parris MJ, Cornelius TO. 2004. Fungal pathogen causes competitive and developmental stress in larval amphibian communities. *Ecology* **85:** 3385–3395.

Parsons PA. 1992. Fluctuating asymmetry: a biological monitor of environmental and genomic stress. *Heredity* **68:** 361–364.

Price TD, Qvarnstrom A, Irwin DE. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society of London Series B, Biological Sciences* **270:** 1433–1440.

Prum RO, Williamson S. 2001. Theory of the growth and evolution of feather shape. *Journal of Experimental Zoology* **291:** 30–57.

Sarre S. 1996. Habitat fragmentation promotes fluctuating asymmetry but not morphological divergence in two geckos. *Researches on Population Ecology* **38:** 57–64.

Saunders DA, Hobbs RJ, Margules CR. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5:** 18–32.

Sheather SJ, Jones MC. 1991. A reliable data-based bandwidth selection method for kernel density estimation. *Journal of the Royal Statistical Society B* **53:** 683–690.

Simons AM, Johnston MO. 1997. Developmental instability as a bet-hedging strategy. *Oikos* **80:** 401–406.

Stige LC, Slagsvold T, Vollestad LA. 2005. Individual fluctuating asymmetry in pied flycatchers (*Ficedula hypoleuca*) persists across moults, but is not heritable and not related to fitness. *Evolutionary Ecology Research* **7:** 381–406.

Stoks R. 2001. Food stress and predator-induced stress shape developmental performance in a damselfly. *Oecologia* **127:** 222–229.

Swaddle JP. 1997. Within-individual changes in developmental stability affect flight performance. *Behavioral Ecology* **8:** 601–604.

Talloen W, Van Dyck H, Lens L. 2004. The cost of melanization: Butterfly wing coloration under environmental stress. *Evolution* **58:** 360–366.

Van Valen L. 1962. A study of fluctuating asymmetry. *Evolution* **16:** 125–142.

Venables WN, Ripley BD. 1999. *Modern applied statistics with S-Plus*. New York, NY: Springer-Verlag.

Waldmann P. 1999. The effect of inbreeding and population hybridization on developmental instability in petals and leaves of the rare plant *Silene diclinis* (Caryophyllaceae). *Heredity* **83:** 138–144.

Wauters LA, Dhondt AA, Knothe H, Parkin DT. 1996. Fluctuating asymmetry and body size as indicators of stress in red squirrel populations in woodland fragments. *Journal of Applied Ecology* **33:** 735–740.

Werner EE, Peacor SD. 2003. A review of trait–mediated indirect interactions in ecological communities. *Ecology* **84:** 1083–1100.

West-Eberhard MJ. 2003. *Developmental plasticity and evolution*. New York, NY: Oxford University Press.

SUPPLEMENTARY MATERIAL

The following material is available for this article online:

Figure S1. Cumulative number of species represented by captured individuals at each study site as a function of capture effort based on days mist-netting samplings.
Table S1. Results of the two-way mixed model ANOVAs of feathers and tarsus for species with at least ten individuals.
Table S2. Summary of population level comparisons of mean unsigned asymmetry.

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