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# The effects of fragmentation on fluctuating asymmetry in passerine birds of Brazilian tropical forests

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## Summary

1. Fluctuating asymmetry (FA) refers to the difference between the right and left sides in characters that should otherwise be bilaterally symmetrical, but whose expression is affected by epigenetic stress during development. Forest fragmentation may promote an increase in FA in isolated populations, by either genetic or environmental stress. FA may function as a biomonitor index in conservation biology if increased levels were observed in populations from fragmented habitats.

2. We tested the hypothesis that FA is higher in birds from small tropical forest patches than in large forest tracts. We measured wing and tarsus FA on mist-netted birds from seven fragments and seven continuous areas from south-eastern Atlantic rain forest in Brazil. We performed FA comparisons between fragments and control groups for the whole community, for individual foraging guilds and for the six most abundant species.

**3.** Wing and tarsus FA were significantly greater in fragments than continuous areas for the whole community and were both negatively correlated with forest fragment size. Differences in FA varied among foraging guilds, being more evident for insectivorous species, especially those feeding in or near the understorey.

**4.** FA levels increased significantly in forest fragments in at least one trait for five of the six most abundant species. There was no correlation between tarsus and wing asymmetries for the individuals of any species nor any difference between the degree of asymmetries of these characters.

**5.** We suggest that FA is a useful tool to assess the effects of fragmentation on forest birds, and may be applied in monitoring neotropical birds. FA indices might be profitably developed, particularly in species most threatened by fragmentation effects and when investigated in different morphological characters.

*Key-words:* conservation, deforestation, developmental stability, habitat disturbance, neotropical birds.

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## Introduction

Habitat fragmentation is a major cause of species or population extinctions. It may interrupt gene flow, affect population size and promote inbreeding (Wayne *et al.* 1992). Anthropogenic disturbances to natural habitats create the need for methods to monitor the size and quality of wildlife populations.

Correspondence: Marina Anciães, Natural History Museum, Division of Ornithology, Dyche Hall, University of Kansas, Lawrence, KS 66045–2454, USA (fax 785 864 5335; anciaes@ukans.edu). The effect of fragmentation on neotropical bird communities has been investigated in some depth (Willis 1979; Terborgh & Winter 1980; Lovejoy *et al.* 1984, 1986). Shaffer (1990) reviewed the inverse relationship between forest size and species richness, illustrating the use of island biogeography theory to the design of natural reserves. Other studies have shown that forest clearance affects both habitat selection and movements of birds (Simberloff 1995; Wiens 1995), decreases food supplies and nest site availability (Rappole & Morton 1985; Burke & Nol 1998), and increases nest predation and parasitism (Robinson 1989). Bierregaard & Lovejoy (1989)

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Fluctuating asymmetry in birds showed that bird abundance decreased in Amazonian fragments after isolation, where insectivorous species from the understorey were most affected. Although many studies have focused on disturbances to neotropical bird communities in response to deforestation, there are few studies that evaluate whether fragmentation also promotes alterations in avian morphology.

Fluctuating asymmetry (FA) may be used for monitoring genetic and environmental stress suffered by natural populations (Leary & Allendorf 1989; Parsons 1992; Sarre, Dearn & Georges 1994). FA reflects disturbances during the development of characters that affect an organism's ability to develop uniform traits (developmental stability) (Soulé 1967; Wayne, Modi & O'Brien 1986; Palmer 1994). One possible scenario is that the loss of genetic variability in isolated populations may result in decreased developmental stability and increased levels of FA (Parsons 1990; Clarke 1992; Sherry & Lord 1996). High levels of morphological alteration and FA have been observed where heterozygosity has been depressed (Hutchison & Cheverud 1995). The African cheetah Acinonyx jubatus, for example, has very low genetic variation due to population bottlenecks and apparently has higher FA than other big cats (Wayne, Modi & O'Brien 1986). Other disturbances also increase levels of FA. Greater indices of FA have been observed in fish from areas highly polluted with DDT (Valentine & Soulé 1973) or mercury (Ames, Felley & Smith 1979), and in cell patterns of damselfly wings exposed to the insecticide carbaryl (Hardersen, Wratten & Frampton 1999). It has also been suggested that nutritional stress increases FA in humans (Perzigian 1977). Sarre (1996) concluded that environmental modification caused by habitat destruction was severe enough to increase the developmental instability and FA in Australian lizards.

Because genetic and environmental stress have a cumulative effect, FA may represent a sensitive biological indicator of environmental stress in populations under genetic stress (Clarke 1992; Parsons 1992). Sarre, Dearn & Georges (1994) suggest that FA reflects individual fitness better than life tables, and thus FA may be of value in biological monitoring programmes. Recent studies have demonstrated that fragmentation affects the natural levels of FA. Lizards from small habitat patches present higher levels of FA than those from large ones (Sarre & Dearn 1991; Sarre 1996). Squirrels become slightly more asymmetrical in woodland fragments (Wauters et al. 1996), and Lens et al. (1999) observed increased FA in more degraded remnants of afrotropical forest for seven bird species. The Brazilian Atlantic Forest has been greatly deforested in spite of its high species richness and endemism level (Fonseca 1985; Haffer 1990), being considered a main priority for the conservation of neotropical bird

© 2000 British Ecological Society *Journal of Applied Ecology*, **37**, 1013–1028 diversity (Brawn *et al.* 1998). We compared FA in the wing and tarsus of passerines from forest fragments and large tracts of continuous Brazilian Atlantic Forest. We searched for differences among foraging guilds in FA alteration, aiming to evaluate its potential application as a tool for monitoring neotropical birds.

## Materials and methods

## STUDY SITES AND BIRD CAPTURES

The research was conducted in seven large control areas and seven forest fragments, all within the Brazilian Atlantic Forest biome (Fig. 1 and Table 1). The vegetation of the areas sampled was classified as either 'dense tropical rain forest' or 'semi-deciduous dry tropical forest' according to the Brazilian Institute of Geography and Statistics (IBGE 1988). Control areas were characterized as continuous forest tracts larger than 2000 ha, and fragmented forests were represented by areas of up to 350 ha that had been isolated, by a distance of at least 3000 m from other forests (see exceptions below), for at least 20 years.

Each locality was sampled once during 4–8 consecutive days, in order to measure at least 60 individuals. Field work took place in July 1996, between April and October 1997, and between February and April 1998 (Table 1). Sampling was conducted during these periods in order to avoid birds in moult, which most commonly occurs between November and March (Sick 1993). The sample size was aimed to maximize statistical power and test FA as an index based on a reasonably low sample effort. Rates of individual and species capture usually stabilized only after 5 days.

Two areas were excluded from community analyses (Table 1) because of their low sample sizes after 8 sampling days. Two fragments had an uncertain isolation distance of approximately 500 m. In spite of the scarce literature about the dispersal ability of forest birds, we included them as fragments because of their area and time since deforestation events in those regions. However, we could not confirm that birds were isolated in these two areas. Historical and topographical information about the study sites was obtained from those institutions that gave permission for the field work (Fundação SOS Mata Atlântica, São Paulo, SP; Fundação J.P. de Oliveira, Campinas, SP; Instituto Florestal do estado de São Paulo; Companhia de Saneamento de Minas Gerais e Instituto Ambiental do Paraná), in the form of satellite imagery, aerial photographs and topographic maps from the forests. Maps from IBGE of 1:50000, 1:100000 and 1:250000 scales were also consulted.



Fig. 1. Geographic location of the control forests and fragments sampled. Detailed information is given in Table 1.

Birds were captured with 36-mm mesh mist-nets (12 m long by 2.5 m high) opened on linear transects in the understorey from 06:30 h in the morning to 17:00 h in the afternoon. Each bird was identified to species and received a metallic ring provided by the Centre for Bird Monitoring, Brazilian Institute for Environmental Affairs (CEMAVE, IBAMA). Nomenclature followed Sick (1993).

#### TYPES OF COMMUNITY ANALYSIS

The communities were analysed using three different procedures. In the first community analysis, all species present in each area were considered (analysis I). In the second analysis, only species present in both forest types (control areas and fragments) were considered, to avoid the effect of different species in the results (analysis II). In the third type, the same species as in analysis II were considered but sample sizes of each species were controlled for, in order to avoid the effect of differences in the abundance of each species among forest types (analysis III).

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## ECOLOGICAL AND BEHAVIOURAL GROUPS

Species were classified according to their degree of dependence on the forest for reproduction, main foraging habitat and diet. Dependence on forest was represented by three categories: 1, independent; 2, semi-dependent; 3, dependent (Silva 1995). The categories of foraging strata were defined as: T, terrestrial; U, understorey; M, medium; C, canopy (Sick 1993; Stotz *et al.* 1996). The main diet of each species was classified as: I, insectivorous; F, frugivorous; O, omnivorous; G, granivorous (Sick 1993).

### FA ESTIMATES

Estimates of FA were calculated following the method of Palmer & Strobeck (1986) adapted following the suggestions of Sarre & Dearn (1991), Evans, Martins & Haley (1995), Sarre (1996) and Wauters *et al.* (1996). Wings and tarsi were measured twice in each individual with dial callipers of 0.02 mm precision, in order to decrease measurement error. Only one researcher took the measurements, with subsequent measurements taken after

© 2000 British Ecological Society *Journal of Applied Ecology*, **37**, 1013–1028 **Table 1.** Characteristics of the study sites: FT, forest type (C = control, F = fragment); Area, approximate forest area in hectares; DCF, minimum distance to the closest forest fragment (m); TSI, approximate time since isolation (years); ALT, altitude (m); *n*, number of birds measured; Faz, Farm; RPAC, Reserve for Environmental Preservation of Companhia de Saneamento de Minas Gerais; RE, Ecological Reserve; PE, State Park; RPPN, Private Reserve; PARNA, National Park; EE, Ecological Station. Most sites names and localities are in Câmara (1991)

SiteStudy siteMIF1Faz. V. BençãoBaF2†RPAC TabooesIbiF3†RE Santa GenebraCaF4†Faz. São JoãoSoF5PE V. R. E.SantoFâF6*Faz. DoraliceJaF7*Faz. RemansinhoIb	Municipality (state) Bananal (SP) Ibirité (MG)	н Г							
F1Faz. V. BençãoBaF2†RPAC TabooesIbiF3RE Santa GenebraCaF4†Faz. São JoãoSoF5FE V. R. E.SantoFãF6*Faz. DoraliceJaF7*Faz. RemansinhoIb	Bananal (SP) Ibirité (MG)	Ц	coordinates	Area (ha)	DCF (m)	(years)	(m)	и	Sampling period
F2†RPAC TabooesIbiF3RE Santa GenebraCaF4†Faz. São JoãoSoF5PE V. R. E.SantoFêF6*Faz. DoraliceJaF7*Faz. RemansinhoIb	[birité (MG)		22°41′ S 44°19′ W	15	3000	30	550	89	28 April–3 May (1997)
F3       RE Santa Genebra       Ca         F4 <sup>+</sup> Faz. São João       So         F5       PE V. R. E.Santo       Fê         F6*       Faz. Doralice       Ja         F7*       Faz. Remansinho       Ib	(HU)	ц	20°01' S 44°03' W	100	500	20	800	80	14 February–20 April (1998)
<ul> <li>F4<sup>†</sup> Faz. São João</li> <li>F5 PE V. R. E.Santo</li> <li>F6<sup>*</sup> Faz. Doralice</li> <li>Ja</li> <li>F7<sup>*</sup> Faz. Remansinho</li> <li>Ib</li> </ul>	Campinas (SP)	ц	22°54' S 47°03' W	250	5000	20	500	120	4–6 July (1996)
F4†Faz. São JoãoSoF5PE V. R. E.SantoFêF6*Faz. DoraliceJaF7*Faz. RemansinhoIb									28–31 July (1997)
F5PE V. R. E.SantoFêF6*Faz. DoraliceJaiF7*Faz. RemansinhoIb	Souzas (SP)	ĹĻ	22°44′ S 46°54′ W	250	500	20	500	67	6-11 August (1997)
F6* Faz. Doralice Jat F7* Faz. Remansinho Ib	Fênix (PR)	ĹĻ	23°54' S 51°58' W	350	3000	50	350	105	14–19 May (1997)
F7* Faz. Remansinho Ibi	Jataizinho (PR)	ĹĻ	23°16' S 51°02' W	150	10000	30	500	13	18–21 June (1997)
	(biporã (PR)	ц	23°15' S 50°58' W	350	10000	30	500	17	21–26 June (1997)
C1 RE Gália Ga	Garça (SP)	C	22°39' S 50°24' W	2180	Ι	Ι	600	115	2-4 August (1997)
C2 Faz. Retiro Pa	Paracambi (RJ)	C	22°36′ S 43°42′ W	$30\ 000$	I	I	420	90	19–26 April (1997)
C3 PE S. Brigadeiro Er	Ervália (MG)	C	20°50' S 42°39' W	13 000	Ι	I	1370	105	1-5 October (1997)
C4 RPPN Salto Morato G1	Guaraqueçaba (PR)	C	25°18' S 48°19' W	120000	I	Ι	40	110	1–6 June (1997)
C5 PE Marumbi Mi	Morretes (PR)	C	25°28' S 48°50' W	150000	Ι	Ι	480	105	25–30 May (1997)
C6 PARNA Itatiaia Ita	Itatiaia (RJ)	C	22°29' S 44°33' W	25000	Ι	Ι	700	107	15–19 July (1997)
C7 EE Juréia Pe	Peruíbe (SP)	C	24°19′ S 46°59′ W	70 000	I	I	20	103	4–8 July (1997)

\*Excluded from the community analysis due to small sample sizes. †Uncertain DCF.

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completely closing the callipers. Wing measurements were taken by flattening the wing against a papercovered clipboard, marking the length of both wings, and afterwards measuring them with callipers. Tarsi were measured from the notch at the back of the tibia–tarsus joint to the distal point obtained by bending the toes to an angle of  $90^{\circ}$  to the tarsus. Wings with damaged or moulting feathers, as well as tarsi with anomalies, were not measured. Migratory species and non-passerines were not considered.

The FA of each character was initially calculated for each individual  $(FA_i)$  as:

$$FA_i = (R - L)/[(R + L)/2]$$
 eqn 1

where R = mean of right side measurements, and L = mean of the left side measurements.

This estimate was used for the analysis of the concordance of the pattern to the ideal FA (normal distribution and a mean not significantly different from zero). The values used refer to the relative asymmetry in order to avoid the effect of size variation in the characteristic. Except for comparisons of FA for the whole community, in subsequent analysis unsigned asymmetry values were used (Palmer & Strobeck 1986, 1992; Evans, Martins & Haley 1995; Sarre 1996).

The parameter of FA for each community  $(FA_c)$  was estimated for each characteristic as the variance of the FA estimate described in equation 1:

$$FA_c = V(R - L)/[(R + L)/2].$$
 eqn 2

The index based on the variance of relative FA is recommended because it is sensitive to small FA variations in cases where there is size variation in the characteristic and when directional asymmetry and anti-symmetry are absent (Palmer & Strobeck 1986). Statistical analysis based on this index may, thus, detect small differences among large samples.

#### STATISTICAL ANALYSIS

In order to evaluate the concordance between our data and the 'ideal fluctuating asymmetry', we determined, for each species and community, whether the mean values of the relative asymmetry (equation 1) for each character differed significantly from zero and whether the corresponding frequency distribution departed from normality. This was verified through a one-sample *t*-test and a Kolmogorov– Smirnov (KS) test for known means, respectively (Sokal & Rohlf 1981).

Linear regressions of individual unsigned relative asymmetry, against individual mean trait size, were used to test the linear dependency of the asymmetry on character size, following Evans, Martins & Haley (1995) and Dufour & Weatherhead (1996). This analysis is necessary before comparisons among asymmetries of different species can be made. These tests were conducted separately for each area and each species with a large sample size.

Measurement error (ME) was estimated through both the repeatability of measurements and the significance of FA in relation to ME. We analysed 1-4 species with large sample size (n > 10) in each family or subfamily, in control areas. The repeatability of measurements was estimated on each side of each characteristic in a species through one-way analysis of variance. This approach is described by Sokal & Rohlf (1981) and Lessells & Boag (1987). Palmer & Strobeck (1986) explain that two measurements of each side are enough to considerably reduce the magnitude of ME, allowing a reliable estimate of repeatability of measurements. High repeatability values have been observed in some studies (Swaddle & Witter 1994; Møller 1995a,b; Wauters et al. 1996). In order to attain values as high as possible, we conducted an evaluation of the best measuring technique, based on five different measurements on wings and two on tarsi, collected during 6 months of field work. The gain obtained by using higher precision callipers (0.02 mm compared with 0.05 mm) was also tested prior to collecting data.

A two-way analysis of variance was conducted for each selected species to asses the significance of relative FA in relation to ME, following the protocol described by Palmer (1994). Individuals were the random factor (n - 1 d.f., n = number of individuals) that assessed variation in size or shape among individual birds, and side (1 d.f.) was the fixed factor that assessed directional asymmetry. The individuals-side interaction (n - 1 d.f.) assessed non-directional asymmetry (typically FA) and the error assessed variation in replicate measurements. Swaddle, Witter & Cuthill (1994) argue that estimating the magnitude of measurement error in relation to FA is more appropriate than calculating the repeatability for a trait length, in order to evaluate whether variation in estimated asymmetry is significantly greater than can be accounted for by measurement error. High repeatability values do not imply low error relative to asymmetry.

Comparisons of FA levels among control areas and fragments were conducted through *t*-tests and two-way analyses of variance, following Palmer & Strobeck (1986), Sarre (1996) and Wauters *et al.* (1996). Tukey tests for unequal sample sizes were used to detect the honest significant difference among samples when the effect was significant in the two-way analysis of variance (Sokal & Rohlf 1981). Differences of relative FA levels between communities from large contiguous forests and forest fragments were tested estimating a relative FA index for each community (equation 2) and then running a *t*test to compare the means from each forest type. Each species with a large sample size was analysed based on the individual's relative FA levels on large

Fluctuating asymmetry in birds forests and fragments, through a *t*-test with individuals as sampling units, instead of communities. Analysis of diet and foraging strata influences on relative FA levels were conducted entering each individual bird as an independent datum. Small sample sizes and missing values precluded analysis by mean values on each species or running only a single analysis of variance.

The relationship between relative FA in each characteristic and forest size was achieved through the Pearson correlation coefficient. We conducted linear regressions of the unsigned relative FA in wing and tarsus on each community (equation 2), from the analysis I, against the logarithm of the corresponding forest area (Sokal & Rohlf 1981). The correlation between wing and tarsus asymmetries was tested for each species with large sample size, following Evans, Martins & Haley (1995). Relative asymmetries for each character were plotted, with each point representing one individual, and a linear regression analysis was performed using the Pearson correlation coefficient.

## Results

We measured 1236 individuals from 100 passerine species in the 14 areas, in a total sampling effort of 8093 net hours. The communities comprised between 19 (F4) and 37 species (C4) and the number of individuals sampled in each area varied from 67 to 120, excepting the areas excluded from community analysis (Table 1 and Appendix 1). Net capture rates varied from 2.81 (F3) to 8.87 (C4) species per 100 net hours among the communities.

All communities and species exhibited relative FA on wings and tarsi of individuals. The asymmetry values for wings and tarsi for individual birds were normally distributed (all KS-d > 0.05, P > 0.10) with means equalling zero (all t > 0.08, P > 0.09) in all the analysed cases.

The relative asymmetry values for wings and tarsi of each individual were independent of the mean character size in all communities and species (all r < 0.241, P > 0.078). There were, however, two exceptions: the Pearson correlation coefficient was significant for tarsi in one community (r = 0.06, P = 0.01), but its value was too low and thus did not indicate that a considerable proportion of the variance in character relative asymmetry was explained by mean character size; and results for *Dysithamnus mentalis* indicated that a high proportion of the variance in tarsus relative asymmetry was explained by mean tarsus size, although not significantly (r = 0.94, P = 0.32).

© 2000 British Ecological Society Journal of Applied Ecology, **37**, 1013–1028 All wings and tarsi in the 18 species selected for measurement error analysis (see Appendix 1) showed a high measurement repeatability (all r >0.94) for both right and left sides. Relative FA was significantly higher than the measurement error in both characters for all the 18 species, as verified through the significance of the *F*-values for the individual–side interaction in the analysis of variance (Table 2).

## FRAGMENTATION EFFECTS

The relative FA of both wings and tarsi was larger in forest fragments than in control forests within the Atlantic Forest for all three types of community comparisons. Fragmentation effects were thus evident when communities were controlled for species and sample sizes (Fig. 2 and Table 3). Wing and tarsus asymmetries were both negatively correlated with forest size (wing: r = -0.72, P = 0.04, tarsus: r = -0.83, P = 0.01) (Fig. 3).

Relative FA varied among control forests and fragments independently of foraging habitat for wings, but not tarsi. There was a significant effect of fragmentation and foraging strata only on relative tarsi FA. Tarsi FA was higher in fragments for species foraging from the terrestrial strata to the understorey and also for those foraging from the understorey to the medium strata. The variation of relative FA on wings and tarsi between control forests and fragments depended on the diet of the species. Relative FA on wings was higher in fragments than in control forests for insectivorous species, whereas on tarsi it was higher for both insectivorous and omnivorous species (Table 4). There was no interaction of relative FA on wings and tarsi for combined groups of foraging strata and diet, among control forests and fragments (Table 5).

Only six bird species presented large enough sample sizes (n > 10) in each forest type to be compared separately. Differences in relative FA in characters between control forests and fragments were variable among species. *Conopophaga lineata* exhibited differences in relative FA levels between control forests and fragments only for wings; *Dysithamnus mentalis*, *Turdus albicollis* and *Trichothraupis melanops* only for tarsi; *Platyrinchus mystaceus* for both characters; and *Tachyphonus coronatus* did not show differences in either character (Table 6). All species presented similar levels of relative FA between wings and tarsi in control forests or in fragments, and relative FA in wings was not correlated with relative FA on tarsi in any species (Table 6).

## Discussion

A higher mean level of relative FA in birds' wings and tarsi was found in the forest fragments of the Brazilian Atlantic Forest. This suggests that passerine communities exhibit morphological alterations, expressed as asymmetry, due to habitat fragmentation. Sarre & Dearn (1991) found a negative correlation between FA in lizards and island size, which, in accordance with our results, demonstrates that FA

**Table 2.** The analysis of variance (mean squares, MS, component of variance  $\times 10^2 - \sigma_{1\times S}^2$ , and *F*-values) of wing (W) and tarsus (T) measurements for 18 species. Percentage contribution for error (replicate measurement variation) relative to the interaction of individuals  $\times$  side (I  $\times$  S) source of variation (relative fluctuating asymmetry) in all species for both characters are also given. \*\*All tests were significant at P < 0.01

Species	Trait	$\mathbf{I}\times\mathbf{S}$		Error		FA-error		
Species	Trait	d.f.	MS**	d.f.	MS	F**	$\sigma^2_{I \times S}$	E/FA (%)
Dendrocincla turdina	W	37	1.18	76	0.01	92.93	58.28	2.18
	Т	38	0.02	78	0.00	10.40	0.85	21.28
Lepidocolaptes fuscus	W	32	0.63	66	0.01	47.90	30.89	4.26
	Т	33	0.19	68	0.00	74.84	9.23	2.71
Philydor atricapillus	W	25	1.35	52	0.00	819.10	67.49	0.24
	Т	25	0.02	52	0.00	10.40	0.79	21.28
Automolus leucophthalmus	W	12	1.98	26	0.01	173.00	98.21	1.16
_	Т	13	0.02	28	0.00	18.08	1.15	11.71
Dysithamnus mentalis	W	13	0.35	28	0.00	508.79	17.27	0.39
	Т	15	0.03	32	0.00	63.11	1.61	3.22
Pyriglena leucoptera	W	27	0.87	56	0.00	295.54	43.30	0.68
	Т	30	0.04	62	0.00	40.24	1.94	5.10
Conopophaga lineata	W	12	0.22	26	0.01	24.26	10.45	8.60
	Т	13	0.02	28	0.00	37.43	1.14	5.49
Platyrinchus mystaceus	W	30	0.43	62	0.01	90.18	21.00	2.24
	Т	32	0.09	66	0.00	46.45	4.55	4.40
Chiroxiphia caudata	W	38	0.55	78	0.01	107.75	27.38	1.87
-	Т	38	0.06	78	0.00	28.18	2.99	7.36
Ilicura militaris	W	14	0.68	30	0.00	170.44	33.55	1.18
	Т	16	0.05	34	0.00	42.51	2.53	4.82
Platycichla flavipes	W	13	1.36	28	0.00	2822.46	67.72	0.07
	Т	13	0.03	28	0.00	70.82	1.68	2.87
Turdus albicollis	W	49	1.62	100	0.03	64.84	79.77	3.13
	Т	50	0.06	102	0.01	8.041	2.73	28.40
Basileuterus culicivorus	W	28	0.34	58	0.00	135.99	17.01	1.48
	Т	28	0.04	58	0.00	21.85	1.84	9.59
Tachyphonus coronatus	W	21	0.40	44	0.00	166.58	19.62	1.21
~ 1	Т	20	0.06	42	0.00	96.53	3.17	2.09
Trichothraupis melanops	W	84	0.74	170	0.01	52.38	36.38	3.89
· ·	Т	84	0.03	170	0.00	12.72	1.32	17.07
Habia rubica	W	31	0.55	64	0.01	41.35	26.98	4.96
	Т	31	0.05	64	0.00	19.95	2.41	10.56
Tangara seledon	W	11	0.30	24	0.00	106.92	14.93	1.89
~	Т	11	0.08	24	0.00	49.92	3.88	4.09
Haplospiza unicolor	W	18	0.60	38	0.03	23.68	28.94	8.82
~ ~	Т	15	0.01	32	0.00	18.77	0.49	11.26

may be increased in smaller areas due either to genetic impoverishment, by the reduction of population sizes, or by other environmental changes that increase as the habitat size decreases.

According to Leary & Allendorf (1989), Evans (1991) and Møller (1993), the increase of FA in morphological characters occurs in conditions of genetic stress (high inbreeding, hybridization; Soulé 1967; Parsons 1992) and environmental stress (pollution, parasitism, low food availability; Valentine & Soulé 1973; Ames, Felley & Smith 1979; Swaddle & Witter 1994), with evidence that the effects of both kinds of stress may be cumulative (Parsons 1992).

Our study did not evaluate the genetic variability of the populations studied, thus it was not possible to determine which type of stress most influenced the relative FA levels in these fragments. Populations that have been, in the main, isolated for more

than 20 years may have low genetic variability, or heterozygosity, due to high inbreeding, resulting in lower individual homeostasis (Wayne, Modi & O'Brien 1986; Clarke 1992; Hutchison & Cheverud 1995). Cheverud & Routman (1996), however, explain that epistasis for quantitative phenotypes exhibiting dominance should be considered together with heterozygosity in determining the genetic variability in a population. These authors found that epistasis in this case is added to the additive genetic variance and that it thus may increase the genetic variability. Larry, Routman & Cheverud (1997) showed evidence for the heritability for FA levels among mice lineages and demonstrated the dominance for quantitative trait loci associated with FA, thus high levels of FA may not necessarily reflect low genetic variability.

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Fig. 2. Relative fluctuating asymmetry (mean and 1 SE) on wings (a) and tarsi (b) of birds from control forests and fragments. I, for all species; II, for species present in both forest types; III, for species present in both forest types with controlled sample sizes. Values refer to the mean  $FA_c$  (equation 1) among control areas and among fragments.

The relative FA levels in birds from fragmented forests may have been increased due to higher environmental stress consequent upon forest clearance. Habitat change may increase pressures from predators, competitors, parasites and disease (Rolstad 1991) and also may decrease food supplies, shelter and nest site availability (Rappole & Morton 1985; Bierregaard & Lovejoy 1989; Tellería & Santos 1993). The level of forest degradation determined FA alteration in seven bird species from other tropical forest fragments that were evenly sized, demonstrating the environmental basis of the stress affecting FA (Lens et al. 1999).

There are large differences among species from different foraging guilds in their susceptibility to fragmentation effects in South American avian communities. These differences are mainly in ecological characteristics, which are the key to understanding and predicting which species will be under the greatest threat (Walters 1998). Most wildlife habitat models that support conservation strategies emphasize the importance of vegetation because selection of vegetative structure is believed to link bird popula-

**Table 3.** Comparisons of relative FA on wings and tarsi between control forests and fragments for the three analyses of communities. Community: I, all species included; II, only species present in both forest types; III, only species present in both forest types and controlled for species abundance. Values refer to the relative  $FA \times 10^2$ 

<b>a</b>	$\mathbf{r}$	<b>T</b>	$Control \times fragment$	nt
Community	Forest type ( <i>n</i> )	Trait	Test	Р
Ι	Control	Wing	t = 4.223	0.004
	(7)	Tarsus	t = 2.501	0.031
	Fragments	Wing		
	(5)	Tarsus		
II	Control	Wing	t = 4.263	0.003
	(7)	Tarsus	t = 2.641	0.039
	Fragments	Wing		
	(5)	Tarsus		
III	Control	Wing	t = 5.801	0.001
	(7)	Tarsus	t = 2.133	0.031
	Fragments	Wing		
	(5)	Tarsus		



Fig. 3. Relationship between relative FA on wings (a) and tarsi (b) for a bird community  $(FA_c)$  and the forest size.  $FA_c$ (equation 2) was estimated as the variance of the FA estimate described in equation 1.

tions with their environments. Changes in vegetation structure greatly affect foraging behaviour, especially in insectivorous birds, which are usually extremely specialized in their prey search and attack tactics (Cody 1985). As foliage distribution and arthropod abundance vary with plant species, the floristic composition of a site may strongly influence the foraging success of insectivorous species in particular habitats (Robinson & Holmes 1984). Lens et al. (1999) observed that environmental degradation influencing FA levels in birds was related to changes in physiognomic and floristic characteristics in the fragments. These variables also influenced selection of nesting sites and avoidance of predation

Table 4. The analysis of variance for foraging strata and diet comparisons among forest type, for relative FA on wings and tarsi. Only forest-dependent species present in both control forests and fragments were analysed. TU, terrestrial to understorey; UM, understorey to medium strata; MC, medium strata to canopy; I, insectivorous; O, omnivorous. \*P < 0.05; \*\*P < 0.01

			Foraging	strata		Diet			
	Trait	Effect	d.f.	F	Tukey's HSD	d.f.	F	Tukey's HSD	
	Wing	Forest type	(1,774)	7.48**	_	(1,760)	4.24*	_	
	-	Foraging strata	(2,774)	0.26	-	_	_	_	
		Diet	_	-	-	(2,760)	1.50	-	
		Interaction	(2,774)	0.77	-	(2,760)	4.77**	I**	
© 2000 British	Tarsus	Forest type	(1,743)	33.90**	-	(1,724)	26.21**	_	
Ecological Society		Foraging strata	(2,743)	1.37	-	_	_	_	
Journal of Applied		Diet	_	_	_	(2,724)	1.62	_	
<i>Ecology</i> , <b>37</b> , 1013–1028		Interaction	(2,743)	3.64*	TU** UM**	(2,724)	1.13*	I** O*	

*Fluctuating asymmetry in birds*  **Table 5.** The analysis of variance for the interaction between foraging strata and diet comparisons among forest type for relative FA on wing and tarsus. Only forest-dependent species present in both control forests and fragments were analysed. TU, terrestrial to understorey; UM, understorey to medium strata; MC, medium strata to canopy; I, insectivorous; O, omnivorous. \*P < 0.05; \*\*P < 0.01

	Factor	Foraging Strata	UM		$TU \times UN$	Λ	$UM \times M$	C
		Diet	I×	0	Ι		0	
Trait	Effect		d.f.	F	d.f.	F	d.f.	F
Wing	Forest type		(1,412)	4.45 *	(1,337)	7.77**	(1,327)	0.45
÷	Foraging strata		_	_	(1,337)	0.03	(1,327)	0.73
	Diet		(1,412)	1.36	_	_	_	-
	Interaction		(1,412)	2.37	(1,337)	0.28	(1, 327)	0.809
Tarsus	Forest type		(1,400)	19.59**	(1,334)	16.79**	(1,306)	7.67**
	Foraging strata		-	_	(1,334)	5.93*	(1,306)	1.02
	Diet		(1,400)	1.25	_	_	_	_
	Interaction		(1,400)	0.00	(1,334)	0.03	(1,306)	0.30

(Tellería & Santos 1994). Decreased humidity observed in fragmented areas (Karr 1982; Tellería & Santos 1993) led to changes in temperature and light incidence in the forest interior, which affected species according to their nesting and foraging requirements (Irwin 1994). Emlen *et al.* (1986) propose that humidity and high temperatures determine the abundance or activity of invertebrates in forests, thus determining the abundance of insectivorous birds. Insectivorous species richness tends to decrease where fragmentation has taken place in both the Atlantic and Amazonian Forests (Willis 1979; Lovejoy *et al.* 1986; Stouffer & Bierregaard 1995). In the same regions, ground and understorey

**Table 6.** Species comparisons and correlations (Pearson correlation coefficient) of relative FA on wings and tarsi. Comparisons were conducted for FA among control forests (C) and fragments (F) and among characters within each forest type. Correlations were conducted among characters within each forest type. Means refers to relative  $FA \times 10^2$ 

a .	Forest type Trait		Control × fragmen	Control × fragment					Wing × tarsus			
Species	Forest type	Trait	Mean $\pm 1$ se ( <i>n</i> )	t	Р	t	Р	r	Р			
Dysithamnus mentalis	С	Wing	$0.86 \pm 0.17$ (14)	0.10	0.33	1.21	0.24	0.18	0.54			
		Tarsus	$0.63 \pm 0.19$ (16)	2.19	0.04							
	F	Wing	$1.18 \pm 0.18$ (14)			0.2	0.87	0.31	0.28			
		Tarsus	$1.20 \pm 0.21$ (14)									
Conopophaga lineata	С	Wing	$0.52 \pm 0.11$ (13)	2.02	0.03	0.86	0.40	0.14	0.66			
		Tarsus	$0.61 \pm 0.12$ (14)	0.47	0.64							
	F	Wing	$0.89 \pm 0.12$ (35)			0.95	0.35	0.06	0.77			
		Tarsus	$0.79 \pm 0.14$ (31)									
Platyrinchus mystaceus	С	Wing	$0.78 \pm 0.16$ (31)	2.15	0.04	0.88	0.38	0.02	0.90			
		Tarsus	$0.80 \pm 0.13$ (33)	2.07	0.05							
	F	Wing	$1.26 \pm 0.20$ (21)			0.17	0.86	0.29	0.22			
		Tarsus	$1.21 \pm 0.16$ (20)									
Turdus albicollis	С	Wing	$0.80 \pm 0.12$ (50)	1.10	0.28	1.89	0.06	0.13	0.38			
		Tarsus	$0.52 \pm 0.08$ (51)	1.86	0.04							
	F	Wing	$0.94 \pm 0.15$ (34)			1.51	0.14	0.21	0.33			
		Tarsus	$0.69 \pm 0.10$ (31)									
Tachyphonus coronatus	С	Wing	$0.67 \pm 0.12$ (22)	0.41	0.68	0.46	0.65	0.10	0.68			
		Tarsus	$0.66 \pm 0.21$ (21)	1.24	0.22							
	F	Wing	$0.87 \pm 0.15$ (40)			1.03	0.31	0.03	0.90			
		Tarsus	$0.85 \pm 0.13$ (31)									
Trichothraupis melanops	С	Wing	$0.87 \pm 0.08$ (85)	0.66	0.51	1.83	0.07	0.08	0.48			
* *		Tarsus	$0.64 \pm 0.06$ (85)	2.26	0.03							
	F	Wing	$0.90 \pm 0.01$ (34)			1.48	0.15	0.24	0.20			
		Tarsus	$1.17 \pm 0.24$ (30)									

foraging birds are among those most affected by habitat loss (Willis 1979; Bierregaard & Lovejov 1989).

The effects of forest fragmentation on relative FA levels varied among species according to their foraging guilds. This result also seems to be in accordance with the pattern of their wing and tarsus use in feeding and breeding behaviour. In general, insectivorous species from the terrestrial and understorey strata are the most sensitive to relative FA changes. Thereafter, the greater the importance of a character (wing or tarsus), the less it shows alteration on its relative FA level. The absence of a correlation between wing and tarsus relative FA is in agreement with the results found by Evans, Martins & Haley (1995) on hummingbirds Trochilus polytmus. It shows that stress does not affect all structures similarly, nor do asymmetries in different characters reflect the instability in different developmental periods (Palmer & Strobeck 1986). The relative FA in an individual character should not be taken as a measure of phenotypic quality for a bird because the genetic control occurs separately for different characters, with individuals having, for example, symmetric wings but asymmetric tarsi (Evans 1993; Palmer 1994; Dufour & Weatherhead 1996). Evans, Martins & Haley (1995) concluded that alteration in wing asymmetry might be more representative of disruption of developmental stability than asymmetry in another character, for example the tarsus. However, selective pressure for symmetry is stronger on more important functional characters, which vary considerably across species (Balmford, Jones & Thomas 1993). It should also be considered that increased FA in tarsus and wing might represent fragmentation effects from different origins, as tarsus development occurs only once in an individual's lifetime but feather moults occur every year. Tarsus FA could better estimate long-term genetic effects, while wing FA could better indicate short-term environmental effects. However, the time scale analysed in this study does not allow a differentiation between these two processes.

Platyrinchus mystaceus, Dysithamnus mentalis and Conopophaga lineata are insectivorous species that showed alteration of relative FA levels. Platyrinchus mystaceus was found in both forest types and it is usually observed in the lower parts of the understorey (Sick 1997). This species has disappeared from the 250-ha Santa Genebra fragment in São Paulo state (Aleixo & Vielliard 1995), indicating that it is sensitive to habitat reduction and isolation, supporting our findings of increased relative wing and tarsus FA.

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Dysithamnus mentalis was present in only two fragments in this study. Decreased population sizes and local extinctions have been observed in isolated forests (Aleixo & Vielliard 1995), and fragment size appears to limit the species' distribution at Viçosa region Minas Gerais state, where it occurred in only 34% of the areas studied by Ribon (1998). These data are congruent with the greater relative FA observed in fragments, while alteration of FA only in the tarsus may reflect the stronger selection pressure for symmetry on the wing than on the tarsus. Dysithamnus mentalis forages in the medium strata (Stotz et al. 1996) and may follow army ants (Willis 1984), which indicates that wings are relatively important for the species' activities. However, studies on specific foraging tactics would provide more reliable information in this respect.

Conopophaga lineata is common in some fragments in São Paulo (Aleixo & Vielliard 1995) and Minas Gerais states (Ribon 1998), although Willis (1979) observed low abundance in previous studies in the localities studied by Aleixo & Vielliard (1995). Changes in wing relative FA may reflect less selection pressure for symmetry on this characteristic than in the tarsus, because it is a terrestrial species that builds its nest and forages close to the ground (Sick 1993). Competition for food seems to play an important role in regulating the population dynamics in this species. Competition may, thus, be a source of environmental stress accounting for the increased FA level observed in the fragments. Individuals travel widely within their territories, through horizontal, vertical and diagonal low perches, where they forage on small insects from the litter. During the non-breeding season individuals feed solitarily, probably in order to increase prey capture rates. However, litter does not offer an abundant food resource for this species, being better exploited by arthropods that also forage on small insects (Willis, Oniki & Silva 1983), and, in fragmented forests, competition between insectivorous birds is expected to be greater as resource availability decreases.

The most abundant frugivorous species sampled in this study (Chiroxiphia caudata, Manacus manacus and Ilicura militaris) were commonly found in altered forest patches (Aleixo & Vielliard 1995; Stotz et al. 1996; M. Anciães, unpublished data). This feature demonstrates that these species probably have not been affected by fragmentation, in agreement with the pattern shown by FA analyses. These species feed on fruit plants commonly found on forest edges and other secondary growth areas, which represent an abundant food resource for these birds (Foster 1987; M. Anciães, personal observation).

The pattern found for Turdus albicollis and Trichothraupis melanops may reflect their foraging habit. These species are omnivorous, eating fruit, insects and seeds from the understorey to the medium strata (Foster 1987; Sick 1993; Galetti & Stotz 1996). They seem to be less sensitive to fragmentation, probably because as more generalist species they rely on a greater variety of food sources, and, in fact, they have persisted in fragmented areas

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(Willis 1979; Laurance 1991). Tachyphonus coronatus showed no differences in relative FA levels among forest types, which may be an effect of its foraging strata. It is also omnivorous (Sick 1993; Galetti & Stotz 1996) but forages from the medium strata to the canopy, and species occupying these strata are among those less affected in fragmented habitats (Willis 1979; Bierregaard & Lovejoy 1989; Laurance 1991).

The ability to disperse has been considered the principal characteristic determining the sensitivity of a species to fragmentation (Walters 1998). There are few data available regarding movement patterns of insectivorous species. Dysithamnus mentalis and Platyrinchus mystaceus have been recorded moving a maximum of 700 and 300 m, respectively, in fragmented landscapes from Minas Gerais state, whereas the frugivore Antilophia galeata is known to have crossed about 700 m in the same region as Platyrinchus mystaceus (Andrade 1999; M. Â. Marini, unpublished data). It is not known whether insectivore species are more affected by isolation distances than other groups.

Our results, nevertheless, show that species have been influenced by fragmentation more strongly than has been previously documented in the literature (Terborgh 1974; Willis 1979; Bierregaard & Lovejoy 1989). Karr (1982) noticed that even relatively abundant species of undergrowth forests are lost as a result of fragmentation, in contrast to the general correlation between rarity and extinction probability (Terborgh & Winter 1980). The relative FA levels shown by those species indicates that there has been a disruption in developmental stability even in species commonly found in fragmented forests. Consequently, FA may be used to detect species that are being affected by fragmentation but have not been identified by studies relying on indexes such as the relative abundance. Indeed, Clark (1995) suggested that FA could be used as an early warning system, because it may detect problems in the environment prior to it becoming obvious through other methods, or by species extinction.

The susceptibility of species to environmental alteration predicted by other studies seems to be reflected in the relative FA. This provides further support for the application of FA in detecting ecological requirements of more threatened species, identifying those disturbance factors that are affecting bird populations in fragmented forests. FA may also be an appropriate tool to verify the conservation value of a particular forest patch. The phenotypic quality (FA) measured in the birds from any given area may indicate the average fitness of the populations overall, and the use of several morphological characteristics may prove to be more effective in detecting the effects of stress on FA levels. Additional studies may be helpful in choosing traits and

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species most suited for the application of FA as conservation indices, as well as in verifying the genetic and environmental contribution to the origin of increased FA.

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## Appendix 1

Relationship between species sampled in each locality and their characteristics. HD, habitat dependence; FS, foraging strata; DT, diet type. See Table 1 and text for locality and characteristic codes. Scientific authorities followed Hellmayr (1924–1938). \*Species analysed for measurement error estimates.

Taxa	HD	FS	DT	Localities
FAMILY DENDROCOLAPTIDAE				
Dendrocincla turdina (Lichtenstein 1818) *	3	U/M	Ι	C1,C2,C5,C7
Sittasomus griseicapillus (Temminck 1821)	3	Μ	Ι	C1,C2,C3,C6,C7,F2
Xiphocolaptes albicollis (Vieillot 1818)	3	М	Ι	C3
Dendrocolaptes platyrostris (Spix 1824)	3	М	Ι	C1,C3,C5,C6
Campilorhamphus falcularius (Vieillot 1822)	3	U/M	Ι	F1
Lepidocolaptes fuscus (Vieillot 1818)*	3	U/M	Ι	C1,C2,C3,C4,C5,C6,C7,F2,F4
FAMILY FURNARIIDAE				
Synallaxis spixi (Sclater 1856)	3	U	Ι	C3
Synallaxis ruficapilla (Vieillot 1819)	3	U	Ι	C4,F4
Phacellodomus erytrophthalmus (Wied 1821)	2	U/M	Ι	F1
Anabazenops fuscus (Vieillot 1816)	-	М	Ι	C6
Philydor atricapillus (Wied 1821)*	3	М	Ι	C2,C4,C5,C6,C7
Philydor lichtensteini (Cabanis & Heine 1859)	3	Μ	Ι	C1
Philydor rufus (Vieillot 1818)	3	Μ	Ι	C3,C5
Automolus leucophthalmus (Wied 1821)*	3	U	Ι	C1,C2,C5,C6,C7,F2,F4,F5
Xenops minutus (Sparrman 1788)	3	U/M	Ι	C4,C7
Xenops rutilans (Lichtenstein 1823)	3	U/M	Ι	F1,F4,F5
Sclerurus scansor (Ménétriès 1835)	3	Т	Ι	C1,C2,C3,C4
Lochmias nematura (Lichtenstein 1823)	3	Т	I	C3
FAMILY FORMICARIIDAE	2	TT	т	C1
<i>Mackenziana severa</i> (Lichtenstein 1823)	3	U	I	CI
Thamnophilus dollatus (Hellmayr 1903)	2	U/C	I	F5
Thamnophilus punctatus (Helimayr 1885)	3	U/M	I	
<i>I namnophilus caerulescens</i> (Pelzein 1868)	3	U/M	I	C1, C3, F2, F3, F4
<i>Dystinamnus mentalis</i> (Temminck 1823)*	3	U/M	I	C1,C4,C0,C7,F2,F4
Myrmoinerula guiaris (Spix 1825)	3	U M	I T	$C_{3}, C_{6}, C_{7}$
<i>Myrmotherula unicolor</i> (Melletties 1855)	2	IVI	I T	$C_{2}, C_{4}, C_{3}, C_{7}$
Drymophila ochropyga (Heilillayi 1900) Drymophila sayamata (Boycord & Borlonsoh 11802)	2	U	I T	$C_{3}$
Drymophila squamula (Boucard & Benepsen 11892)	2	U	T	$C_{2}, C_{4}, C_{7}$
Murmaciza laricata (Lichtenstein 1823)	3	U T	I	$C_{1}, C_{2}, C_{3}, C_{4}, \Gamma_{2}$
Myrmeciza sayamosa (Pelzeln 1868)	3	Т	I	C4 C7
Formicarius colma (Boddaert 1783)	3	Т	I	C4
FAMILY CONOPOPHAGIDAE	5	1	1	64
Conononhaga lineata (Wied 1831)*	3	I	т	C1 C3 C4 C6 F1 F2 F3 F4
Conopophaga melanops (Vieillot 1818)	3	Ŭ	Ī	C2 C5 C6 C7
FAMILY TYRANNIDAE	5	U	1	02,00,00,07
Phyllomvias virescens (Allen 1889)	3	С	T	F5
Camptostoma obsoletum (Temminck 1824)	1	Č	I	F5
Myiopagis caniceps (Swainson 1837)	1	U	Ι	F5
Elaenia spectabilis (Pelzeln 1868)	3	U	0	F5
Mionectes rufiventris (Cabanis 1846)	3	U/M	0	C2,C3,C4,C6,C7,F1,F2,
Leptopogon amaurocephalus (Tschudi 1846)	3	U/M	Ι	C2,C4,C6,C7,F1,F2,F5
Corythopis delalandi (Lesson 1830)	3	T	Ι	C1,F1,F2,F4,F5
Hemitriccus diops (Temminck 1822)	3	М	Ι	C3
Hemitriccus orbitatus (Wied 1831)	3	T/C	Ι	C1,C2,F4
Tolmomyias sulphurescens (Spix 1825)	_	_	Ι	C1,C3,C6
Platyrinchus mystaceus* (Vieillot 1818)	3	M/C	Ι	C1,C2,C3,C4,C5,C6,C7,F1,F2,F4
Myiobius barbatus (Wied 1821)	3	C	Ι	C4,C6,C7
Myiobius atricaudus (Lawrence 1863)	3	U/M	Ι	C3
Myiophobus fasciatus (Ihering 1907)	3	U	Ι	F1,F5
Lathrotriccus euleri (Cabanis 1868)	3	U/M	Ι	C3,F2,F4
Cnemotriccus fuscatus (Wied 1831)	3	U/M	Ι	F5
Knipolegus cyanirostris (Vieillot 1818)	3	Μ	Ι	C3
Satrapa icterophrys (Vieillot 1818)	3	С	I	F5
Rhytipterna simplex (Lichtenstein 1823)	3	M/C	Ι	C7

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Appendix 1 (cont'd)

Taxa	HD	FS	DT	Localities
FAMILY PIPRIDAE				
Pipra fasciicauda (Hellmayr 1915)	3	U/M	F	F5
Antilophia galeata (Lichtenstein 1834)	3	M/C	F	F2
Chiroxiphia caudata (Shaw & Nodder 1793)*	3	U/M	F	C1,C2,C3,C4,C5,C6,C7,F1,F2,F3,F4
Ilicura militaris (Shaw & Nodder 1808)*	3	M/C	F	C2,C3,C4,C5,F2
Manacus manacus (Desmarest 1806)	3	U	F	C2,C4,F1,F3
Schiffornis virescens (Lafresnaye 1838)	3	U	Ι	C1,C2,C3,C4,C6
FAMILY COTINGIDAE				
Laniisoma elegans (Thunberg 1823)	3	M/C	0	C7,F2
FAMILY TROGLODYTIDAE				
Thryothorus longirostris (Vieillot 1819)	3	U	Ι	F1
Troglodytes aedon (Vieillot 1807)	1	T/U	0	F1
FAMILY MUSCICAPIDAE				
Subfamily Turdinae				
Platicychla flavipes (Vieillot 1818)*	3	M/C	0	C6,C7
Turdus rufiventris (Vieillot 1818)	1	T/C	0	C1,C4,F1,F2,F3,F4
Turdus leucomelas (Vieillot 1818)	2	T/C	0	F1,F2,F5
Turdus amaurochalinus (Cabanis 1851)	2	T/C	0	C1,F3,F5
Turdus albicollis (Vieillot 1818)*	3	U/M	0	C1,C2,C3,C4,C5,C6,C7,F1,F3, F5
FAMILY EMBERIZIDAE				
Subfamily Parulinae				
Geothlypis aequinoctialis (Vieillot 1807)	1	U	Ι	F5
Basileuterus flaveolus (Baird 1865)	3	T/U	Ι	C1,F2,F3
Basileuterus culicivorus (Swainson 1837)*	3	U/M	Ι	C1,C2,C3,C4,C5,C6,C7,F1,F5
Basileuterus hypoleucus (Swainson 1837)	3	U/M	Ι	F2,F3,F4
Phaeothlyps rivularis (Wied 1821)	3	Т	Ι	C4,C5
Subfamily Coerebinae				
Coereba flaveola (Cabanis 1851)	1	С	0	C4,F3
Subfamily Thraupinae				
Pyrrhocoma ruficeps (Strickland 1844)	3	U	I	F5
Thlypopsis sordida (Lafresnaye & d'Orbigny 1837)	2	U/C	0	F1,F3
Hemithraupis guira (Linnaeus 1766)	3	С	0	F5
Tachyphonus cristatus (Spix 1825)	3	C	0	C2,C7
Tachyphonus coronatus (Vieillot 1822)*	3	M/C	0	C1,C3,C4,C5,C6,C7,F1,F3,F4,F5
Trichothraupis melanops (Vieillot 1818)*	3	U/M	0	C1,C2,C3,C4,C5,C6,C7,F2,F3,F4,F5
Habia rubica (Vieillot 1817)*	3	U/M	0	C1,C2,C4,C5,C6,C7,F3
Ramphocelus bresilius (Linnaeus 1766)	2	U/M	0	C4,F1
Thraupis sayaca (Linnaeus 1766)	2	C	0	FI
Thraupis cyanoptera (Vieillot 1817)	3	C	0	C4
Stephanophorus diadematus (Temminck 1819)	3	U/C	0	
Pipraeidea melanonota (Vieillot 1819)	3	M/C	0	FS
Euphonia violacea (Linnaeus 1758)	3	C	F	
Euphonia pectoralis (Latham 1801)	3	C	F	C4,C5,C6
Tangara seledon (Muller 1//6)*	3	C	0	C4
Tangara cyanocephala (Muller 17/6)	3	C	0	
Tangara desmaresti (Vieillot 1819)	3	C	0	
Tangara cyanoventris (Vieillot 1819)	3	C	0	C6,F1
Tangara cayana (Linnaeus 1766)	1	U/C	0	
Controstrum speciosum (Temminck 1824)	_	C	0	F5
Sublamily Emberizinae	2	MC	C	$C_1 C_2 C_4 C_5 C(E_2)$
<i>Amaging a moesta</i> (Haptleyb 1952)	3		G	$C_{1}, C_{3}, C_{4}, C_{3}, C_{0}, F_{3}$
Snovonkila agomilosoons (Visillot 1833)	5 1		0	C1,C4 F2
Arramon somitorquetus (Suciesce 1927)	1	U T	U T	1°5 C5
Arremon Semuorqualus (Swainson 1837)	3	I T	I T	
Saltaton similis (Lafresnaus & d'Orbieny 1927)	3 2		I C	C1 C1 C2 C2 C4 C6 E1 E2 E4 E5
EAMILY VIPEONIDAE	2	IVI/C	U	U1,U2,U3,U4,U0,F1,F3,F4,F3
Cuolarhis guianansis (Tschudi 1945)	2	MC	0	F2
<i>Cyciarnis gujanensis</i> (1seniudi 1645) Hylophilus poggilotis (Tammingk 1922)	23		0	1 <sup>-2</sup> C3
Hytophilus poecuotis (Tenninick 1822)	5	IVI/C	0	05