

WING-SHAPE VARIATION IN RELATION TO ECOLOGY AND SEXUAL SELECTION IN FIVE SYMPATRIC LEKKING MANAKINS (PASSERIFORMES: PIPRIDAE)

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Abstract. Size and wing shape, measured for 103 manakins (Pipridae: Passeriformes, Aves) of five sympatric lekking species, are analyzed using multivariate statistical techniques. Specific, sexual, and age differences are contrasted with ecological and behavioral features. Females of each species show attenuated forms of adult male wing loading and wing shape specialization. Immature males occupy an intermediate position between females and adult males. *Manacus manacus* males have rounded wings and high wing loading, presumably adaptations for agile flight among dense vegetation and for wing-snapping. *Corapipo gutturalis* and *Dixiphia pipra* males have dynamic long-hand wings and low wing loading, both required for maneuverable, hovering, and fast agile flight. *Pipra erythrocephala* and especially *Lepidothrix serena* have narrow wings of high aspect ratio, providing agility in fast flight. Female and male wings are presumed to be shaped by physical constraints of the degree of openness of the birds' habitat and the height of their activity. Wings of females appear to be adapted for higher mobility in large home ranges. Intermediate wing shapes of immature males are adapted to progressive changes in their activity, from mobility with females to specific displays with adult males. Wing shapes of adult males provide various flying capacities that help them to perform particular display movements in specific habitats. Accepted 6 May 1997.

Key words: Ecomorphology, sexual selection, flight, niche differentiation, lek, Pipridae, French Guiana, Neotropics.

INTRODUCTION

The aim of this study is to evaluate the interplay between wing design, ecology, and behavior in lekking species. To carry out this evaluation, I have studied size and wing shape variation, and have compared predicted flight potentials with eco-ethological characteristics of females, adult males, and immature males of the five species of manakins (Aves: Passeriformes: Pipridae) inhabiting the tropical moist forest of French Guiana: *Manacus manacus*, *Lepidothrix serena*, *Pipra erythrocephala*, *Dixiphia pipra*, and *Corapipo gutturalis* (nomenclature according to Prum 1992). Manakins were selected for this analysis because all five species are lekking (reviews in Sick 1967; Prum 1990, 1994), and sympatric, presenting an ideal situation where specific display morphology and mating behavior can be related to specific habitats.

Optimal design of animal wings has long stimulated considerable interest, partly in attempts to develop artificial flight (e.g., Mouillard 1881; Marey 1872, 1890). Knowledge of animal flight progressively improved through the comparative study of various flying animals (reviews in Brown 1963; Penny-

cuick 1972, 1975; Greenewalt 1975; Norberg 1981; Norberg & Rayner 1987; Viscor & Fuster 1987; Rayner 1981, 1988; Pennycuick 1989; Thomas 1993; Norberg 1990, 1994, 1995). Although animal wing design is commonly considered to be associated with ecology and behavior, relatively few details are known about the factors affecting wing shape. Habitat, mating system, foraging behavior, migration, territoriality, and predator escape have all been regarded as constraints acting on wing design (Savile 1957; Norberg 1979, 1981; Leisler & Winkler 1985; Norberg & Rayner 1987; Rayner 1988; Chandler & Mulvihill 1990; Tholleson & Norberg 1991; Saunders & Barclay 1992; Wickman 1992; Landmann & Winding 1993, 1995; Norberg 1990, 1994, 1995).

Wing measurements (area, span, length, loading, aspect ratio) are correlated with body mass and flying habit in several groups of flying animals (Greenewalt 1975, Lighthill 1977, Norberg 1981, James 1982, Norberg & Rayner 1987, Viscor & Fuster 1987, Rayner 1988). These correlations provide a baseline that enables one to identify morphological specialization of particular species deviating from the "norm". Because interspecific dissimilarity may simply be

related to body dimensions, size variation of wing parameters should be compared with isometric regression models. Scaling effects also dictate the use of relative measurements of wing design, which should be expressed in aerodynamic or energetic terms. However, single variables such as wing loading or aspect ratio are unlikely to explain flight differences among manakins (Levey *et al.* 1984, Moermond & Denslow 1985) because flight performance is truly multifactorial, involving combinations of size and wing shape variables. Therefore, I also analyzed wing design using other relative measurements selected for their significant influence on flight performance, but not correlated with wing loading or ratio aspects. I have not considered aerodynamic properties of manakin tails because the species I studied all have short tails, and thus do not exhibit dimorphic but aerodynamically costly traits that could be compensated for by sexual differences in wing design (Andersson & Andersson 1994, Balmford *et al.* 1994).

The manakins I studied are lekking species (Prum 1990, 1994), and exhibit marked dispersion and habitat preferences influencing mobility at display sites. Males have relatively small home ranges during the breeding season and are more sedentary than the females, which range more widely and disperse further when not breeding (Snow 1962a, b; Lill 1974a, b, 1976; Graves *et al.* 1983; Martin & Karr 1986; Théry 1992). Female home range size has been found to be correlated with the degree of male clustering (Théry 1992), but little is known about sexual or specific differences in foraging behavior. All five species studied here, and both sexes of each, are known to snatch fruit by short flights (Snow 1962a, b; Levey *et al.* 1984), while hovering in front of the fruit (Moermond & Denslow 1983, 1985). Manakins also take some insects on the wing (review in Marini 1992), a greater proportion being fed to the young than is eaten by adults themselves (Snow 1962a). Marini (1992) found slight sexual differences of foraging tactic and diet in the Helmeted Manakin (*Antilophia galeata*), but similar information is not available for the species studied here.

If intense sexual selection imposes constraints on wing morphology in lekking species, then wing design should result in optimal adult male courtship displays and female mobility or nest building, whereas the acquisition of adult morphology and display behavior may be delayed in immature males (review in Andersson 1994). As flight style and flight performance are dependent on wing design, I used the

ecomorphological studies of Norberg and co-workers (Norberg & Rayner 1987; Norberg 1990; Tholleson & Norberg 1991; Norberg 1994, 1995) to predict how wing shape could be expected to vary among species and between sexes. Species flying within dense vegetation or taking off from the ground are hypothesized to be constrained to have short rounded wings of low aspect ratio. Such wings should be broad to compensate for their shortness, with enough wing area to allow slow flight among dense vegetation. To improve agility in slow flight and facilitate flight path alterations among dense vegetation, the "arm wing" (i.e., the portion of wing between body and humero-scapular joint, Norberg 1981) should be long in relation to total wing length. Manoeuvrable flight, minimizing the radius of turn, would be improved by low wing loading in slow and fast fliers. Hovering capacity and agility in fast flight would be obtained by long "hand wings" (i.e., the portion of wing distal to the humero-scapular joint) and high aspect ratio.

Sexual dimorphism in body size is supposed to be enhanced in polygamous animals, including lekking species, resulting in the selection of large males for combative dominance (Darwin 1871, Hingston 1933). Association between mating system and sexual dimorphism has been studied in several groups of birds, including manakins (e.g., Darwin 1871, Lack 1968, Payne 1984, Höglund 1989, Björklund 1990, Oakes 1992, Webster 1992, Winquist & Lemon 1994). According to Payne (1984), sexual dimorphism in size is expected to vary among manakins, depending on female size and mating system. Höglund (1989) showed that in lekking species where males display on the ground, males are larger than females, while in lekking species with an elaborate flight display, the sexes are monomorphic in size. However, the most recent studies reach opposite conclusions. Björklund (1990) found no differences in dimorphism between polygamous and monogamous species, whereas Oakes (1992) found increased sexual size dimorphism in lekking species.

METHODS

Study sites. Between February 1985 and November 1994 I studied manakins at two sites in the tropical moist forest of French Guiana: (1) the "Nouragues" natural reserve (4°05'N, 52°42'W) around a granite dome 100 km from the coast, and (2) the "piste de Saint-Elie" site (5°04'N, 53°18'W) along a track

20 km from the coast. Both study sites, located 130 km apart in the same unbroken forest block, show similar climate, annual rainfall (Boyé *et al.* 1979), and dominant plant families (Sabatier & Prévost 1990, Poncy *et al.* 1997). At Nouragues, free of human disturbance since the early 1700s, vegetation types vary from high dense *terra firme* old-growth forest to swamp forest, liana forest, bamboo savanna, low forest surrounding the inselberg and rock-savanna (Poncy *et al.* 1997). At Saint-Elie, vegetation types are high dense *terra firme* old-growth forest, swamp forest, and secondary forest. Moderate slopes and forest physiognomy are similar at both sites, except for steeper slopes on the sides of the Nouragues inselberg.

Manakin habitats. The five species of manakins are sympatric at both study sites, and I have previously described their preferred display habitats (Théry 1990a). Male *Manacus manacus* display on and close to the ground, in low inselberg vegetation at Nouragues and in secondary vegetation along the track at Saint-Elie. Their display activity requires a permanent water flow near the lek. *Lepidothrix serena* displays at mid-level of wet understory on slopes of old-growth forest. *Pipra erythrocephala* displays under the canopy of medium and tall trees in old-growth, liana, and secondary forests. Male *Dixiphia pipra* form leks in old-growth and swamp forest, around old gaps or under the canopy of medium and tall trees. Male *Corapipo gutturalis* display on mossy

fallen logs on ridges and on tops of slopes in old-growth forest, their display-site approach beginning from above the canopy (Davis 1982, Prum 1986).

Wing measurement. Data were collected on 103 individually banded manakins, mist-netted in the understory. I measured body mass (BM, to the nearest 0.5 g), wing length (WL, distance from the humero-scapular joint to the tip of the longest primary feather, to the nearest 0.5 mm on the flattened wing), and body width between wings (BWI, along a line perpendicular to the body sagittal axis, to the nearest mm). Contour of the flattened wing was drawn aligning the leading edges with a line perpendicular to the median body sagittal plane (Penny-cuick 1989, Fig. 1). Maximal wing width (MWW) and maximal wing length (MWL) were measured to the nearest mm on the wing contour (Fig. 2). Using these measurements, I computed (Table 1):

- Wing span: the distance between wing tips with wings extended laterally, $WS = 2 MWL + BWI$, measured to the nearest mm.

- Total wing area: the area of both wings plus area of body between wings as projected on the wing chord plane, WA in cm^2 . Measured by planimetry. Relatively large wings are advantageous for highly maneuverable slow flight, whereas small wings bring agility at high speeds (Brown 1963, Norberg & Rayner 1987, Rayner 1988, Norberg 1990, Tholleson & Norberg 1991, Norberg 1994).

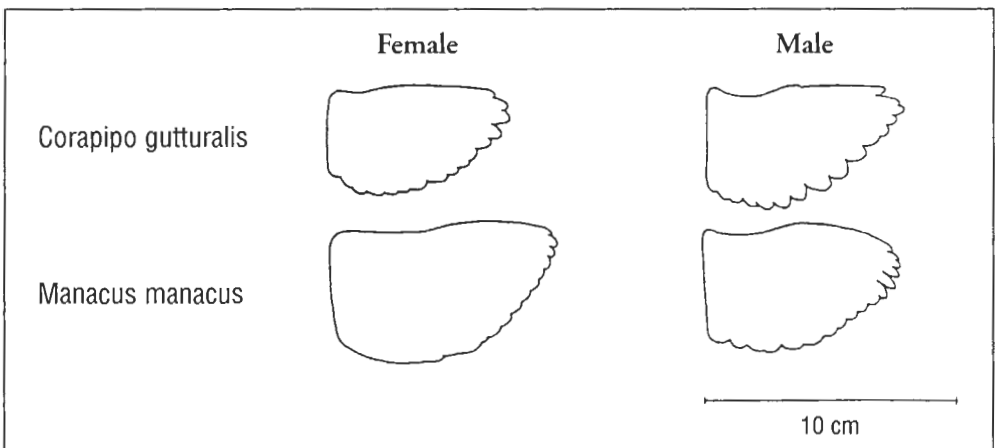


FIG. 1. Examples of wing contours of *Corapipo gutturalis* and *Manacus manacus* measured in French Guiana from February 1985 to November 1994.

TABLE 1. Body mass and wing characteristics of females, and adult and immature males of the five species of manakins (Pipridae) studied in French Guiana from February 1985 to November 1994. Measurements are given as mean \pm SD.

Species	Sex-age (n)	Wing length (cm)	Body mass (g)	Wing span (cm)	Total wing area (cm ²)	Aspect ratio	Wing loading (g/cm ²)	Wing elongation index	Wing dynamism index
<i>Campylopterus curvipennis</i>	Female (7)	5.59 \pm 0.16	8.57 \pm 0.35	17.10 \pm 0.73	62.63 \pm 3.44	4.67 \pm 0.20	0.137 \pm 0.008	1.66 \pm 0.07	153.12 \pm 6.40
	Ad. male (9)	5.79 \pm 0.05	7.94 \pm 0.17	18.03 \pm 0.68	69.06 \pm 1.71	4.71 \pm 0.24	0.115 \pm 0.004	1.59 \pm 0.05	155.60 \pm 5.59
	Immat. male (4)	5.70 \pm 0.08	8.38 \pm 0.25	17.78 \pm 0.29	65.62 \pm 3.43	4.82 \pm 0.13	0.128 \pm 0.009	1.61 \pm 0.04	155.92 \pm 0.38
	Female (4)	5.57 \pm 0.05	16.00 \pm 0.41	18.70 \pm 0.08	83.11 \pm 0.84	4.21 \pm 0.01	0.192 \pm 0.003	1.75 \pm 0.04	167.87 \pm 0.86
<i>Manacus manacus</i>	Ad. male (4)	5.33 \pm 0.05	18.88 \pm 1.31	18.20 \pm 0.46	74.23 \pm 2.29	4.46 \pm 0.10	0.254 \pm 0.012	1.61 \pm 0.05	170.88 \pm 3.67
	Immat. male (3)	5.40 \pm 0.10	17.50 \pm 0.50	18.47 \pm 0.25	77.27 \pm 4.24	4.42 \pm 0.14	0.227 \pm 0.014	1.65 \pm 0.06	171.02 \pm 3.13
	Female (5)	6.02 \pm 0.13	12.68 \pm 0.31	18.24 \pm 1.07	73.49 \pm 3.52	4.53 \pm 0.35	0.173 \pm 0.008	1.69 \pm 0.05	151.46 \pm 7.59
	Ad. male (4)	5.78 \pm 0.05	11.75 \pm 0.31	18.80 \pm 0.16	72.40 \pm 1.08	4.88 \pm 0.07	0.162 \pm 0.005	1.72 \pm 0.03	162.78 \pm 2.00
<i>Disciphia pipra</i>	Immat. male (4)	6.00 \pm 0.12	12.50 \pm 1.47	18.60 \pm 0.29	73.31 \pm 0.33	4.72 \pm 0.14	0.170 \pm 0.020	1.70 \pm 0.01	155.07 \pm 5.13
	Female (22)	6.49 \pm 0.10	13.15 \pm 1.56	20.25 \pm 0.70	89.55 \pm 1.81	4.58 \pm 0.26	0.147 \pm 0.018	1.67 \pm 0.08	156.08 \pm 6.49
	Ad. male (6)	6.51 \pm 0.08	11.17 \pm 0.61	20.05 \pm 0.41	88.47 \pm 2.37	4.55 \pm 0.14	0.126 \pm 0.009	1.63 \pm 0.02	154.02 \pm 1.66
	Immat. male (12)	6.55 \pm 0.40	12.00 \pm 1.28	20.40 \pm 0.66	88.87 \pm 4.10	4.69 \pm 0.21	0.135 \pm 0.010	1.67 \pm 0.06	156.35 \pm 10.52
<i>Lepidobrotis serena</i>	Female (6)	5.57 \pm 0.08	10.97 \pm 0.50	17.70 \pm 0.58	68.06 \pm 2.69	4.60 \pm 0.14	0.161 \pm 0.010	1.64 \pm 0.07	158.97 \pm 4.00
	Ad. male (9)	5.23 \pm 0.11	10.72 \pm 0.75	17.87 \pm 1.53	61.83 \pm 4.85	5.16 \pm 0.50	0.175 \pm 0.021	1.75 \pm 0.13	170.70 \pm 14.24
	Immat. male (7)	5.51 \pm 0.16	10.71 \pm 0.86	17.67 \pm 0.26	64.59 \pm 5.11	4.86 \pm 0.34	0.167 \pm 0.018	1.64 \pm 0.08	160.31 \pm 3.61

• Wing loading WLO = BM / WA, in g/cm². Low wing loading reduces the cost of flight and consequently is advantageous for slow flight, hovering and maneuverability (Brown 1963; Norberg 1979, 1981; Norberg & Rayner 1987; Rayner 1988; Thollessen & Norberg 1991; Norberg 1994).

• Aspect ratio: the ratio of wing span to mean width of the wing, calculated as AR = WS² / WA (Pennycuik 1972, Greenewalt 1975, Lighthill 1977). Narrow wings of high aspect ratio, particularly in combination with low wing loading, reduce the cost of flight (Pennycuik 1969, 1975, Hails 1979, Norberg & Rayner 1987, Rayner 1988). Agility is increased by relatively long broad wings of low AR in slow fliers (combined with rounded wing tips), and by short narrow and pointed wings of high AR in fast fliers (Thollessen & Norberg 1991, Norberg 1994).

• Wing-elongation index WE = MWL / MWL. This variable expresses the lengthening of the longest primary feathers (WL) and of the arm (WS-2WL-BWI) in relation to the lengthening of the longest secondary feathers (MWI). High values of WE characterize pointed (long primaries), elongated (long arm), or narrow wings (short secondaries). Short or rounded wings exhibit low WE values.

• Wing-dynamism index WD = (WS / 2) / WL. Without osteological measurements, this index expresses the relative importance of the bird's "hand", essential for flight dynamics, and of the bird's "arm" and body that mostly bring lift. Low values of WD characterize long hand wings, adapted to hovering flight (Norberg 1979) or agile fast flight (Thollessen & Norberg 1991, Norberg 1994); gliding, soaring and high agility at low flight speed require high values of WD in long arm wings.

Data analysis. I conducted multivariate analyses on the following dimensional and relative measurements, given with their abbreviations in the text: total wing area = WA, wing loading = WLO, aspect ratio = AR, wing-elongation index = WE, wing-dynamism index = WD.

I log-transformed all variables to meet the normality requirement for parametric statistical tests. I used multiple analysis of variance to provide statistical evidence that wing size and shape vary among species, and between age and sex classes within species. I generated uncorrelated morphological axes accounting for most of the variance using principal components analysis of correlation matrices, therefore

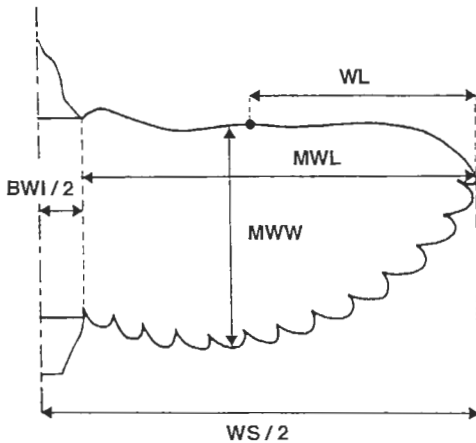


FIG. 2. Measurements of the wing contour of five manakin species studied in French Guiana from February 1985 to November 1994. WL = wing length (longest primary feather), MWL = maximal wing length, MWW = maximal wing width, BWI = body width between wings, WS = wing span (see text for further details).

weighting all variables equally (Leisler & Winkler 1985, Norberg & Rayner 1987). The accepted level of significance for statistical tests is 95%. Principal components analyses were performed between mean values for females, adult males and immature males. I computed specific means as the average of adult male and female means, which may have been calculated on different sample sizes. First-year males having the same plumage as females, I considered green birds as "females" if they remained in female plumage for more than one year, or if they typically behaved as females when visiting leks. Among males, adults were distinguished from intermediate-plumaged immature males.

RESULTS

Isometric dimensional relationships and patterns of wing shape variation. The five species in the group do not conform to the main isometric relationships found between wing morphology and body weight in other bird species (Greenewalt 1975, Viscor & Fuster 1987, Rayner 1988). Only wing span is correlated with wing area:

$$WS = 3.673 WA^{0.375}$$

($WS = 2.221 WA^{0.531}$ for 139 Passeriformes, Greenewalt 1975).

Body mass, wing loading, aspect ratio, and wing length are independent of dimensional scaling, and the computed equation deviates from the geometric similarity hypothesis. Therefore, no global trend of size variation emerges from interspecific comparison. Multiple analyses of variance, computed among species and between sex and age classes within species, provide statistical evidence of consistent variation among studied groups (all P values < 0.001). These results justify focusing on variation in size and wing shape among sex and age classes, and allow one to proceed with principal component analysis, keeping wing area and wing loading as size descriptors.

Wing size and shape for females, adult males and immature males of the five species. The two principal components, collectively, explain 73.5% of the total sample variance. The first component, PC1 which accounts for 40.2% of the total variance, essentially expresses variance in wing loading and wing dynamism (Table 2, Fig. 3). The second axis, PC2 (33.3% of the total variance), contrasts wing area with aspect ratio. These two principal components reveal two significant associations between variables: wing loading is positively correlated with wing dynamism index ($r = 0.749$, $n = 15$, $P < 0.01$), and aspect ratio is negatively correlated with wing area ($r = -0.578$, $n = 15$, $P < 0.05$). The first association makes sense in aerodynamic terms: dynamic wings and low wing loading are both advantageous for the hovering flight and fast aerial displays of *Corapipo gutturalis* and *Dixiphia pipra*, whereas long arm wings allow the slow agile flights of *Manacus manacus* within dense vegetation. The second correlation reveals that large

TABLE 2. Contributions (in percent) to the principal components of the five variables selected in the multivariate analysis of wing design of five manakin species studied in French Guiana from February 1985 to November 1994.

Variable	% contribution	
	PC 1	PC 2
Total wing area	2.9	45.2
Aspect ratio	12.8	37.7
Wing loading	40.7	1.4
Wing elongation index	10.7	6.5
Wing dynamism index	32.9	9.2

wings are wide instead of long (*Manacus manacus*, *Dixiphia pipra*), and that small wings are narrow rather than short (*Lepidothrix serena*).

The first component separates *Manacus manacus*, characterized by high wing loading and long arm wing, from *Conapipo gutturalis* and *Dixiphia pipra*, with low wing loading and long hand wing (Fig. 3). Females of each species show attenuated forms of adult male specialization in wing loading and wing shape (Tables 1 and 3): *C. gutturalis* and *D. pipra* show low wing loading in females, and even lower values in males (14–16 % lower than in females). These two species also exhibit the longest hand wings (lowest WD). Contrary to *Conapipo*, *Manacus* shows high wing loading in males and females. In males of

Manacus manacus, wing loading is 32% higher than in females (Table 3), and twice as high as *Conapipo* males (Table 1). *Manacus* males are also characterized by longest arm wings (highest WD).

The second component shows that males of *Pipra erythrocephala*, and especially of *Lepidothrix serena*, present high aspect ratios, through reduction of wing width in *L. serena*, which induces higher wing loading. Despite having the highest aspect ratio, *L. serena* males show relatively little wing dynamism but long arm wings. Female *L. serena* and *P. erythrocephala* show little wing shape or wing area specialization.

Immature males are all positioned between females and adult males of their respective species.

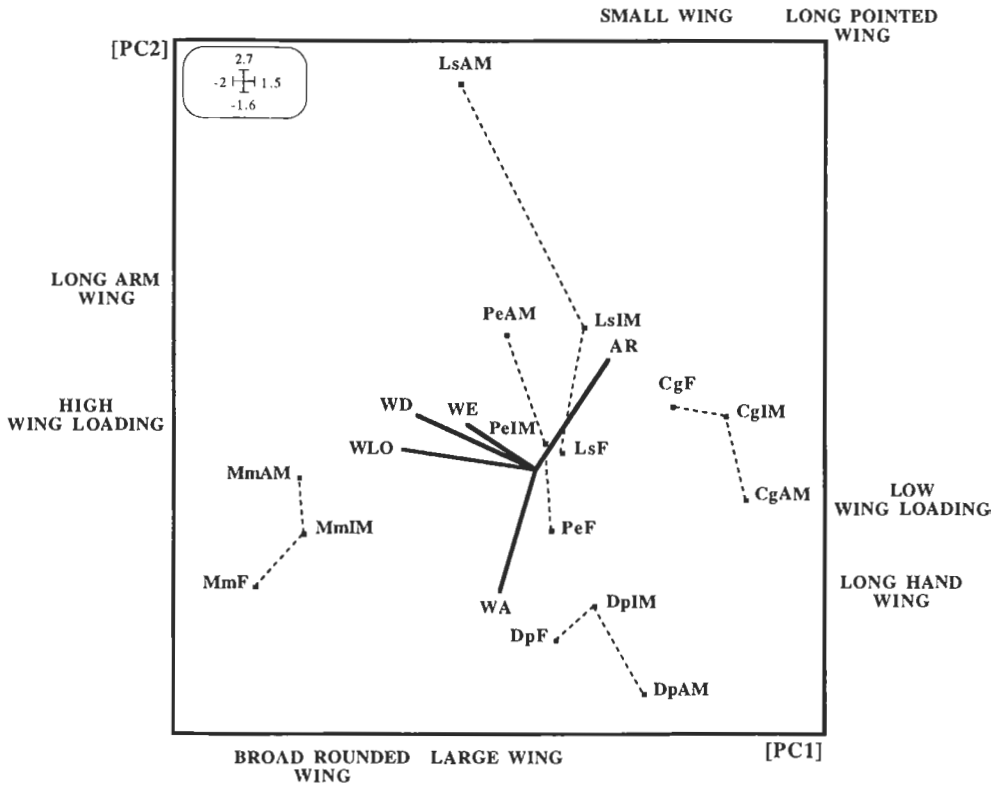


FIG. 3. Bivariate plot of the principal components, PC1 and PC2, in the sex and age dimorphism analysis of five manakin species studied in French Guiana from February 1985 to November 1994. Dashed lines are connecting subgroups of the five species. Cg = *Conapipo gutturalis*, Dp = *Dixiphia pipra*, Ls = *Lepidothrix serena*, Mm = *Manacus manacus*, Pe = *Pipra erythrocephala*; F = female, IM = immature male, AM = adult male; WA = total wing area, WLO = wing loading, AR = aspect ratio, WE = wing elongation index, WD = wing dynamism index. Notes indicate wing shapes in different sections of the plot.

TABLE 3. Mean body mass and wing characteristic ratios (adult males/females) of five manakin species studied in French Guiana from February 1985 to November 1994.

Species	Ratio adult males/females							
	Wing length	Body mass	Wing span	Total wing area	Aspect ratio	Wing loading	Wing elongation index	Wing dynamism index
<i>Conopipo gutturalis</i>	1.04	0.93	1.05	1.10	1.01	0.84	0.96	1.02
<i>Manacus manacus</i>	0.96	1.18	0.97	0.89	1.06	1.32	0.92	1.02
<i>Pipra erythrocephala</i>	0.96	0.93	1.03	0.99	1.08	0.94	1.02	1.07
<i>Dixiphia pipra</i>	1.00	0.85	0.99	0.99	0.99	0.86	0.98	0.99
<i>Lepidothrix serena</i>	0.94	0.98	1.01	0.91	1.12	1.08	1.07	1.07

Wing design and ecological factors. Wing loading and wing shape variations were compared with heights of male displays and female nests in an attempt to identify ecological factors constraining wing design. Although differences in vegetation density were not measured, descriptions of lek habitat and extensive field observations show that *M. manacus* displays in the densest habitat, *L. serena* and *P. erythrocephala* in more open sites, and *C. gutturalis* and *D. pipra* in the most open sites. In each species, male and female show a preference for display or nesting height which may be related to habitat openness. Thus, I compared wing loading and wing shape, as expressed by PC1 (Fig. 3), with mean height of nests and displays (Fig. 4). Principal components scores of adult males and females are positively correlated with nest or display heights (Spearman rank correlation $r_s = 0.745$, $n = 10$, $P < 0.05$). In *M. manacus*, characterized by long arm wings and high wing loading (low PC1 score), males display close to the ground and females build the lowest nests. In *C. gutturalis* and *P. pipra* (high PC1 score), long hand wings and low wing loading are correlated to elaborate aerial displays in more open space, and to higher nests.

DISCUSSION

Dimensional relationships. The sizes of the studied manakins are consistent with the correlation of wing area with wing span found by Greenewalt (1975) among other Passeriformes. Wing area is the most efficient size descriptor and may be used to scale species and sexes.

Payne (1984) contrasted male combative dominance, selecting males for larger size, with female choice, selecting males for smaller size and increased

agility in aerial displays. Using male vs. female ratios of wing length and body mass, Payne showed that sexual dimorphism in size varies among species of manakins with female size and mating system. My results are not consistent with Payne's (1982) conclusions, neither for female size (wing length: $r = 0.163$, body mass: $r = 0.588$; $n = 5$, $P > 0.05$ in both cases) nor for male dispersion (with female long wings either in concentrated leks or in dispersed leks). Using a difference of more than 5% in mean wing length and more than 10% in mean body mass to define dimorphism, Höglund (1989) showed that in lekking species where males display on the ground, males are larger than females. This is confirmed by *M. manacus* males being 18% heavier than females (Table 3). Moreover, my results fit Höglund's prediction that size monomorphism may be explained by the selection of small agile males with elaborate flight display: *C. gutturalis* and *P. erythrocephala* are monomorphic for wing length and body mass, *D. pipra* for wing length. Höglund stated that size dimorphism never evolved among the manakins. Nevertheless, his appendix presents five size-dimorphic manakins. In addition, analyses of size dimorphism from the literature give different results (e.g., *M. manacus* shows more than 10% body mass dimorphism in Snow & Snow 1963). Using Höglund's criterion for size dimorphism, my study of sympatric living individuals shows that three of the five species can be considered to show size dimorphism (Table 3).

Ecomorphology and male displays. Wing design appears to be primarily related to the physical constraints of the degree of habitat openness and activity height, which constitute selective pressures on male and

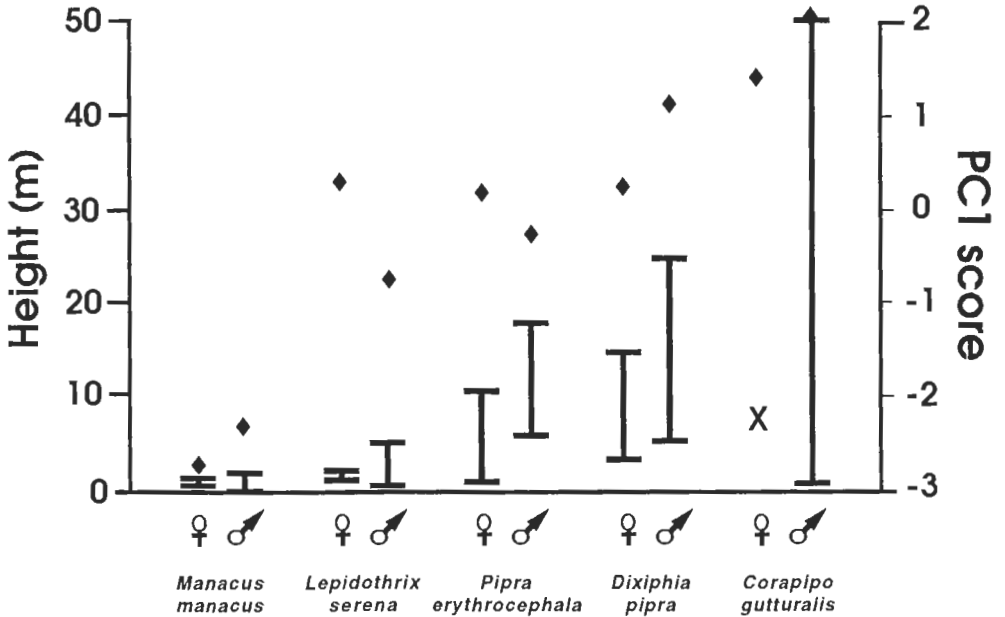


FIG. 4. Height ranges for nests and displays of the five lekking species of manakins, compared with wing designs (PC1 scores) as measured by principal component analysis of sexual dimorphism of the same species studied in French Guiana from February 1985 to November 1994. Height ranges compiled from Snow (1961, 1962a, b), Lill (1974a, b, 1976), Davis (1982), Prum (1985, 1986), Dujardin (1987), Tostain (1988a, b), Théry (1990a, b, and unpubl. personal observation), are figured as bars for each species and sex, except for the only nest-height data known in *Corapipo gutturalis* (X). ♦ represents female and male values of PC1 on the x axis of Fig. 3, which contrast low wing loading and long hand wing of *Corapipo* with high wing loading and long arm wing of *Manacus*.

female wing morphology (Savile 1957, Brown 1963, Kokshaysky 1973, Rayner 1988). Manakins with elongated wings occur in more open spaces, whereas those with broad rounded wings live in closed habitats. Long hand wings are present in species performing agile aerial displays or hovering, long arm wings in species that fly slowly among dense vegetation. All these wing shapes bring various display potentials to males in their display site habitat, and appropriate flying capacities to wider-ranging females building nests and feeding young alone. The intermediate wing shapes of immature males may represent an adaptation to progressive changes in their activity, from mobility with females to specific displays with adult males.

Males of each lekking manakin species display in a particular habitat, which can be defined by vegetation structure, height, and number and diameter of display perches. Courtship behaviors consist of

rapid movements, combined in certain species with slower elements (e.g., butterfly-flight display of *D. pipra* and *C. gutturalis*) or mechanical noises (e.g., wing "pop" of *C. gutturalis* and snap-jump of *M. manacus*), which all involve specialized wing shape or modified flight feathers. Among the studied species, *L. serena* and especially *D. pipra* show relatively simple display repertoires, whereas *M. manacus*, *P. erythrocephala* and *C. gutturalis* exhibit more complex courtship behaviors (Prum 1990).

What is the relationship between male display and wing configuration? *C. gutturalis* produces a wing "pop" without the wing-feather specialization used by some other manakin species (e.g., *M. manacus*), performs like *D. pipra* a butterfly-flight display with deep, slow exaggerated wing beats (Prum 1986, 1990; Théry 1990b), and is the only manakin species to begin its display-site approach from above the canopy. The wing "pop" is produced by rapidly snapping the

wing tips against the air, creating something like a “whip” of low pressure behind the wing (Prum 1986), at a speed of 100-120 km/h (Théry & Vehrencamp 1995). In adult, but not immature males, the two outermost primary feathers are lanceolate; i.e., narrow and pointed along both webs. This feather specialization, combined with a long hand wing and high-speed flight, is responsible for the wing “pop”. Indeed this noise is much softer in immature males and the removal of these feathers, or even only the single outermost, renders the adult male unable to produce the usual “pop” (pers. observ.). Multivariate analyses showed that *C. gutturalis* and *D. pipra* are characterized by low wing loading and a long hand wing. Maneuverability in fast flight and hovering are typical display features in these species, and are dependent upon this wing design. Following the wing “pop”, males of *Couripipo* perform an about-face in flight above the female before copulation (Théry 1990b), and both *C. gutturalis* and *D. pipra* hover in their butterfly-flight display. Therefore, it is consistent that males of these two species have evolved lower wing loading than females and other males, given their frequent aerial displays. As predicted from observations of ecology and behavior, low wing loading and long hand wings were found in *C. gutturalis* and *D. pipra*, in accordance with requirements for maneuverable, hovering or fast and agile displays.

M. manacus is the only manakin species known to exhibit a snap-jump display (Prum 1990), the result of hypertrophied muscles holding the wings stiff and rigid in order to form a fixed support for still more specialized movements of the highly modified secondaries (Lowe 1942). This hypertrophied musculature, specialized to produce wing noises, increases wing loading. High wing loading also helps to create strong pressure under the wing to aid the snapping of stiff secondaries and the whirring of primaries. Contrary to Payne (1984:31), the wing feathers of immature males and females are not modified and give softer wing noises (Snow 1962a, pers. observ.). My predictions of rounded wings and high wing loading are verified in *Manacus*. Similarly, short flights and perching are typical of *Manacus* displays (Snow 1962a), and were expected from the low flight performance inherent in this wing design. I also found long arm wings, as expected, since they improve agility among dense vegetation.

As predicted, *L. serena* is characterized by high aspect ratio, particularly in males which also exhibit high values of wing elongation and wing dynamism

indices. These values are higher in males than in females, as is wing loading. High aspect ratio and wing loading increase agility in fast flight for to-and-fro displays and also make a wide range of speeds available. Similarly, long arm wings improve agility in the slow flight required for S-curve flight displays in dense understory before copulation (Théry 1990b).

Like *L. serena*, *P. erythrocephala* males show increased aspect ratio, which was expected to make a wide range of speed available and to increase male agility in fast flight when executing S-curve flight displays.

Conclusion. In manakins, the evolution of lekking and lek spatial organization are strongly constrained by phylogeny, limiting the influence of adaptive individual plasticity and subsequent behavioral evolution (Prum 1994). Secondary sexual characters, display elements, and specialized wing morphologies all evolved and diversified following the evolution of lekking in the group. Prum (1990) also showed that “derived male plumage traits in manakins have evolved subsequent to the behavioral novelties in which they are prominently featured”, and that “the opposing hypothesis that novel plumage results in the evolution of derived displays can be rejected”. If behavioral diversification is indeed “driving” male morphological specialization, then lekking and courtship behaviors adapted to specific lek sites before the evolution of derived morphological characters. Therefore, courtship displays, plumage colors (Endler & Théry 1996), and wing shapes were all constrained under sexual selection to evolve in a specific lek habitat. The same process applies at the ontogenetic level, with the specialized wing shapes and flight feathers involved in courtship appearing in males long after displays and molt into adult plumage, as does male coloration.

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REFERENCES

- Andersson, M. 1994. Sexual selection. Princeton.
- Andersson, S., & M. Andersson. 1994. Tail ornamentation, size dimorphism and wing length in the genus *Euplectes* (Ploceinae). *Auk* 111: 80–86.
- Balmford, A., Jones, I.L., & A.L.R. Thomas. 1994. How to compensate for costly sexually selected tails: the origin of sexually dimorphic wings in long-tailed birds. *Evolution* 48: 1062–1070.
- Björklund, M. 1990. A phylogenetic interpretation of sexual dimorphism in body size and ornament in relation to mating system in birds. *J. Evol. Biol.* 3: 171–183.
- Boyé, M., Cabaussel, G., & Y. Perrot. 1979. Climatologie. Pp. 1–4 in *Atlas de la Guyane*. C.N.R.S. and ORSTOM, Paris.
- Brown, J.H. 1963. The flight of birds. *Biol. Rev.* 38: 460–489.
- Chandler, C.R., & R.S. Mulvihill. 1990. Wing-shape variation and differential timing of migration in dark-eyed juncos. *Condor* 92: 54–61.
- Darwin, C.R. 1871. The descent of man, and selection in relation to sex. London.
- Davis, T.H. 1982. A flight-song display of the white-throated manakins *Copapto gutturalis*. *Ibis* 99: 146–147.
- Dujardin, J.L. 1987. Découverte du nid et de la ponte du manakin à front blanc *Pipra serena*. *Oiseau R.F.O.* 57: 57–58.
- Endler, J.A., & M. Théry. 1996. Interacting effects of lek placement, display behavior, ambient light and color patterns in three neotropical forest-dwelling birds. *Am. Nat.* 148: 421–452.
- Graves, C.R., Robbins, M.B., & J.V. Remsen, Jr. 1983. Age and sexual difference in spatial distribution and mobility in manakins Pipridae: inferences from mist-netting. *J. Field Ornithol.* 54: 407–412.
- Greenewalt, C.H. 1975. The flight of birds. *Trans. Am. Phil. Soc.* 65: 1–67.
- Hails, C.J. 1979. A comparison of flight energetics in hirundines and other birds. *Comp. Biochem. Physiol.* 63A: 581–586.
- Hingston, R.W.G. 1933. The meaning of animal colour and adornment. London.
- Höglund, J. 1989. Size and plumage dimorphism in lek-breeding birds: a comparative analysis. *Am. Nat.* 134: 72–87.
- James, F.C. 1982. The ecological morphology of birds: a review. *Ann. Zool. Fennici* 19: 265–275.
- Kokshaysky, N.V. 1973. Functional aspects of some details of bird wing configuration. *Syst. Zool.* 22: 442–450.
- Lack, D. 1968. Ecological adaptations for breeding in birds. London.
- Landmann, A., & N. Winding. 1993. Niche segregation in high-altitude Himalayan chats (Aves: Turdidae): does morphology match ecology? *Oecologia* 95: 506–519.
- Landmann, A., & N. Winding. 1995. Guild organisation and morphology of high-altitude granivorous and insectivorous birds: convergent evolution in an extreme environment. *Oikos* 73:237–250.
- Leisler, B., & H. Winkler. 1985. Ecomorphology. *Curr. Ornithol.* 2:155–186.
- Levey, D.J., Moermond, T.C., & J.S. Denslow. 1984. Fruit choice in Neotropical birds: the effect of distance between fruits on preference patterns. *Ecology* 65: 844–850.
- Lighthill, M.J. 1977. Introduction to the scaling of aerial locomotion. Pp. 365–484 in Pedley, T.J. (ed.). *Scale effects in avian locomotion*. London.
- Lill, A. 1974a. Sexual behavior in the lek-forming White-bearded Manakin, *M. manacus trinitatis* Hartert. *Z. Tierpsychol.* 36: 1–36.
- Lill, A. 1974b. Social organization and space utilization in the lek-forming White-bearded Manakin, *M. manacus trinitatis*. *Z. Tierpsychol.* 36: 513–530.
- Lill, A. 1976. Lek behavior in the Golden-headed Manakin *Pipra erythrocephala* in Trinidad West Indies. *Z. Tierpsychol. Adv. Ethol.* 18.
- Lowe, P.R. 1942. The anatomy of Gould's manakin *Manacus vitellinus* in relation to its display. *Ibis* 6: 50–83.
- Marey, E.J. 1872. Mémoire sur le vol des insectes et des oiseaux. Paris.
- Marey, E.J. 1890. Le vol des oiseaux. Paris.
- Marini, M.A. 1992. Foraging behavior and diet of the Helmered Manakin. *Condor* 94: 151–158.
- Martin, T.E., & J.R. Karr. 1986. Temporal dynamics of Neotropical birds with special reference to frugivores in second-growth woods. *Wilson Bull.* 98: 38–60.
- Moermond, T.C., & J.S. Denslow. 1983. Fruit choice in Neotropical birds: effects of fruit type and accessibility on selectivity. *J. Anim. Ecol.* 52: 407–420.
- Moermond, T.C., & J.S. Denslow. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. *Orn. Monogr.* 36: 865–897.
- Mouillard, L.P. 1881. L'empire de l'air: essai d'ornithologie appliquée à l'aviation. Paris.
- Norberg, U.M. 1979. Morphology of the wings, legs and tail of three coniferous forest tits, the goldcrest, and the treecreeper in relation to locomotor pattern and feeding station selection. *Phil. Trans. R. Soc. London B287*: 131–165.
- Norberg, U.M. 1981. Flight, morphology and the ecological niche in some birds and bats. *Symp. Zool. Soc. London* 48: 173–197.

- Norberg, U.M. 1990. Vertebrate flight. Berlin.
- Norberg, U.M. 1994. Wing design, flight performance, and habitat use in bats. Pp. 205–239 in Wainwright, P.C., & S.M. Reilly (eds.). *Ecological morphology*. Chicago.
- Norberg, U.M. 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Funct. Ecol.* 9: 48–54.
- Norberg, U.M., & J.M.V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. London B316*: 335–427.
- Oakes, E.J. 1992. Lekking and the evolution of sexual dimorphism in birds: comparative approaches. *Am. Nat.* 140: 665–684.
- Payne, R.B. 1984. Sexual selection in birds. *Orn. Monogr.* 33: 1–52.
- Pennycook, C.J. 1969. The mechanics of bird migration. *Ibis* 111: 525–556.
- Pennycook, C.J. 1972. *Animal flight*. London.
- Pennycook, C.J. 1975. Mechanics of flight. Pp. 1–75 in Farner, D.S., & J.R. King (eds.). *Avian biology*, Vol. 5. London.
- Pennycook, C.J. 1989. *Bird flight performance*. Oxford.
- Ponce, O., Riéra, B., Larpin, D., Belbenoit, P., Jullien, M., Hoff, M., & P. Charles-Dominique. In press. 1997. The permanent field research station "Les Nouragues" in the tropical rain forest of French Guiana: current projects and preliminary results on tree diversity, structure and dynamics. In Dallmeier, F., & J. Comiskey (eds.). *Forest biodiversity in North, Central and South America and the Caribbean: research and monitoring*. Washington.
- Prum, R.O. 1985. Observations of the White-fronted Manakin *Pipra serena* in Suriname. *Auk* 102: 384–387.
- Prum, R.O. 1986. The displays of the White-throated Manakin *Corapipo gutturalis* in Suriname. *Ibis* 128: 91–102.
- Prum, R.O. 1990. Phylogenetic analysis of the evolution of display behavior in the Neotropical manakins (Aves: Pipridae). *Ethology* 84: 202–231.
- Prum, R.O. 1992. Syringeal morphology, phylogeny, and evolution of the Neotropical manakins (Aves: Pipridae). *Am. Mus. Novit.* 3043: 1–65.
- Prum, R.O. 1994. Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves: Pipridae). *Evolution* 48: 1657–1675.
- Rayner, J.M.V. 1981. Flight adaptations in vertebrates. *Symp. Zool. Soc. London* 48: 137–172.
- Rayner, J.M.V. 1988. Form and function in avian flight. *Curr. Ornithol.* 5: 1–66.
- Sabatier, D., & M.-F. Prévost. 1990. Quelques données sur la composition floristique et la diversité des peuplements forestiers de Guyane française. *Bois et Forêts des Tropiques* 219: 31–55.
- Saunders M.B., & R.M.R. Barclay. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. *Ecology* 73: 1335–1345.
- Savile, D.B.O. 1957. Adaptive evolution of the avian wing. *Evolution* 11: 212–224.
- Sick, H. 1967. Courtship behavior in manakins (Pipridae): a review. *Living Bird* 6: 5–22.
- Snow, D.W. 1961. The displays of the manakins *Pipra pipra* and *Tyrannetes virescens*. *Ibis* 103: 110–113.
- Snow, D.W. 1962a. A field study of the Black and White Manakin, *Manacus manacus*, in Trinidad. *Zoologica* 47: 65–104.
- Snow, D.W. 1962b. A field study of the Golden-headed Manakin, *Pipra erythrocephala*, in Trinidad, WI. *Zoologica* 47: 183–198.
- Snow, D.W., & B.K. Snow. 1963. Weights and wing-lengths of some Trinidad birds. *Zoologica* 48: 1–12.
- Théry, M. 1990a. Influence de la lumière sur le choix de l'habitat et le comportement sexuel des Pipridae (Aves: Passeriformes) en Guyane Française. *Rev. Ecol. (Terre Vie)* 45: 215–236.
- Théry, M. 1990b. Display repertoire and social organization of the White-fronted and White-throated Manakins. *Wilson Bull.* 102: 123–130.
- Théry, M. 1992. The evolution of leks through female choice: differential clustering and space utilization in six sympatric manakins. *Behav. Ecol. Sociobiol.* 30: 227–237.
- Théry, M., & S.L. Vehrencamp. 1995. Light patterns as cues for mate choice in the lekking White-throated Manakin *Corapipo gutturalis*. *Auk* 112: 133–145.
- Tholleson, M., & U.M. Norberg. 1991. Moments of inertia of bat wings and body. *J. Exp. Biol.* 158: 19–35.
- Thomas, A.I.R. 1993. On the aerodynamics of birds' tails. *Phil. Trans. R. Soc. London B340*: 361–380.
- Tostain, O. 1988a. Nouvelles données sur la nidification de quatre manakins Pipridae de Guyane Française: *Pipra pipra*, *P. serena*, *P. aureola* et *P. erythrocephala*. *Alauda* 56: 159–170.
- Tostain, O. 1988b. Description du nid et de la ponte du manakin à gorge blanche, *Corapipo gutturalis*, Pipridae. *Alauda* 56: 176–177.
- Viscor, G., & J.F. Fuster. 1987. Relationship between morphological parameters in birds with different flying habits. *Comp. Biochem. Physiol.* 87A: 231–249.
- Webster, M.S. 1992. Sexual dimorphism, mating system and body size in New World blackbirds (Icterinae). *Evolution* 46: 1621–1641.
- Wickman, P.-O. 1992. Sexual selection and butterfly design: a comparative study. *Evolution* 46: 1525–1536.
- Winkler, T., & R.E. Lemon. 1994. Sexual selection and exaggerated male tail length in birds. *Am. Nat.* 143: 95–116.