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WING SHAPE IN INSECTIVOROUS PASSERINES INHABITING NEW GUINEA AND AUSTRALIAN RAIN FORESTS AND EUCALYPT FOREST/EUCALYPT WOODLANDS

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ABSTRACT.—Based on museum skins of 47 bird species in 17 genera, I evaluated the suppositions for members of various taxonomic groups in New Guinea and Australian rain forest compared to open eucalypt forest/eucalypt woodland that in rain forest birds compared to eucalypt forest/eucalypt woodland counterparts in each group: (1) outer primary 9 tends to be proportionately shorter; (2) secondary 1 is proportionally longer; and (3) the longest primary is more proximally placed relative to the body in its series. The postulations are largely confirmed. The results are presaged by the findings of earlier writers that species operating in confined spaces should have broad wings with rounded tips, with low wing loading conferring high manoeuvrability, and that distance flyers should have wings with long wingspans and pointed tips for economy of effort. *Received 1 April 1993, accepted 4 September 1994.*

WHEN MEASURING SKINS of New Guinea and Australian tropical rain-forest insectivorous passerines, and eucalypt forest/woodland counterparts, I found regularly occurring differences in wing form. The former tended to have more rounded wings, with the outer primary 9 relatively short, while the longest primary in the series was placed more proximally than the others in its series relative to the body in the rain-forest species. Examples were found in foliage-gleaning warblers (*Gerygone*), whistlers (*Pachycephala*), ground-feeding robins, and several other groups, suggesting that a general habitat adaptation was operating, as has been shown for several body structures by Winkler and Leisler (1992). In this paper, I quantitatively explored this observation and postulated connection in a diverse set of ecomorphological types of birds.

An early paper by Savile (1957) documented the occurrence of two alternative wing types in small birds—"elliptical" wings found in birds that lived in confined spaces, and "high-speed" wings characteristic of species that remain in the air for long periods. In the former group the wing is curved to increase negative pressure and, hence, lift above, with slotting of the tips serving to minimize turbulence and ensure uniform pressure over the entire surface. The result is high lift, as well as good control and manoeuvrability. By contrast, the high-speed wing has a lower camber, a slender tapering tip, a sweepback of the leading edge, and a short chord. These features reduce drag and conserve power.

Later students of bird flight (Pennycuick 1969, Norberg 1979, 1981, 1990, Norberg and Rayner 1987, Rayner 1988, Thollesson and Norberg 1991) have explored wing design in the more meaningful framework of wingspan, wing loading, and aspect ratio. They have demonstrated that slow-flying species operating in confined spaces should have broad wings with rounded tips and a low wing loading to confer high manoeuvrability. Long-distance-flying migrants, by contrast, should have a long wingspan and high-aspect-ratio wings with pointed tips to reduce profile power and confer economy of effort (see detailed review in Bairlein 1992). Various factors are likely to influence wing shape in birds, including: (1) habitat; (2) feeding zone utilized (e.g. thickets compared to exposed branches); (3) way of life (being aerial feeder vs. undergrowth skulker); (4) relative development of migratory habits; and (5) innate phylogenetic constraints.

All of the species I have evaluated can be allocated readily to a precise habitat category using data for New Guinea birds from Rand and Gilliard (1967), Diamond (1972), Beehler et al. (1986), and for Australian birds from Keast (1961), Hall (1974), Pizzey (1980), and Blakers et al. (1984). Quantitative data on feeding zones and feeding habits of each species are not available, but general information on these characteristics are known (see above references). The need for the former is less critical if the taxonomic groups are considered individually, since in general, members of each share common ecomorphologies and ways of life. Seasonal movements are not a major factor influencing wing shape in these bird species. Only three (the Australian *Pachycephala rufiventris, Gerygone olivacea,* and *G. fusca*) are partial migrants; all other species are residents. It is valid, therefore, to explore habitat as the major variable influencing wing form.

In this paper, I test the hypotheses that congeneric and counterpart species inhabiting tropical rain forest and thickets, compared to those of eucalypt forest/eucalypt woodland, should have: (1) a relatively short primary 9 to give a more rounded tip to wing; (2) a conspicuous, if small, primary 10 (see Averill 1925); (3) secondaries that are relatively long to maximize lift in the proximal part of the wing; and (4) the longest primary in the primary series placed more proximal than the others to the body. The degree to which a feature is developed, of course, will vary with closeness of its link to specific structural features of the alternative habitats.

Materials and Methods

The study covers 47 species in 17 genera (Appendix, Table 1), and includes: foliage-gleaning warblers (*Gerygone*); robinlike birds that are mostly ground feeders; whistlers (*Pachycephala*) that are foliage gleaners and foliage pluckers; aerial-sallying flycatchers (*Rhipidura*); and representatives of four groups of specialist species (Table 1). These are the: thicket-dwelling whipbirds (*Androphobus, Psophodes, Sphenostoma*); trunk- and bark-feeding shrike-tits (*Eulacestoma, Falcunculus*); trunk- and branch-feeding tree-creepers and nuthatches (*Climacteris, Daphoenositta*); and ground-feeding magpie-larks (*Grallina*).

Measurements were made of the wings of six adult males of each species from museum skins. Starting with the outermost primary (i.e. primary 10), the length of each feather was measured by inserting fine dividers between adjacent feathers from point of emergence of each from the skin and measuring to the feather tip. The primaries were measured to primary 5 to contour the outer half of the wing. The first two secondaries (i.e. the distal two in secondary series) were similarly measured. The length of longest primary in each individual was determined. Ratios of the lengths of the primary 10 and primary 9 to longest primary provided a measure of relative degree of pointedness of the wing. Ratios of secondaries 1 and 2 to the longest primary provided an index of breadth of the proximal section of the wing.

The hypotheses were evaluated by comparing the grouped rain-forest, and grouped eucalypt forest/eucalypt woodland members of each taxonomic group using the Mann-Whitney *U*-test (0.05 level of significance; Zar 1984).

The vegetation features of the contrasting habitat types are summarized in Table 2 (Specht 1981, Webb and Tracey 1981). Tropical rain forest has high structural diversity and compact cover-providing vegetation. The Australian eucalypt forests are classified into: (a) tall open forest; and (b) woodland and dry forest. In both of the latter, the trees and branches are widely spaced. Vines, epiphytes, and thickets are lacking. In woodland, the trees are more widely spaced than in tall forest. The mallee and mangrove habitats, to which *Pachycephala inornata* and *P. lanioides* are confined, have the general structural attributes of woodland (Table 2).

Results

The basic measurements of the 47 species are presented in the Appendix. The Appendix and Table 1 give the longest primary or primaries (on average) for each species, and the ratios of primary 9, primary 10, and secondary 1 to longest primary. Standard deviations are inappropriate for ratios (Atchley et al. 1976). In Table 1, the habitat and feeding zone of each species also are given. Figures 1 and 2 show wing shape for a series of contrasting species in diagrammatic form. The wings of tree-creepers and nuthatches, which do not differ between habitats, are not illustrated.

Gerygone *(Acanthizidae).*—In this group of small-bodied foliage-gleaning warblers (habits documented in Keast and Recher [unpubl. manuscript]), primary 6 is marginally the longest primary. In the Australian rain-forest *G. mouki,* the more inner primary 5 averages slightly longer; in *G. olivacea* and *G. fusca,* both of which are partial migrants found in eucalypt woodlands it is the more distal primary 7 or primary 6 that usually is the longest (see Fig. 1). Primary 9 is relatively longest (83.4% of longest primary) in *G. olivacea;* in *G. fusca,* it is 88.9%, and in *G. ruficollis* 80.4%. Although the latter is a rain-forest inhabitant, it occupies the upper stratum and outer edge (pers. obs. made at Tari, Western Highlands). Primary 10 shows little variation. The secondaries are shortest relative to the longest primary in *G. fusca* and *G. olivacea* (Fig. 1). Thus, in *Gerygone,* trends are in the direction hypothesized.

Robins (Petroicidae).—In the 10 species (six

TABLE 1. Longest primary and means (with ranges in parentheses) of proportionate lengths to longest primary of primary 9, primary 10, and secondary 1 for selected groups of rain-forest and woodland bird species in New Guinea and Australia. Six birds measured for each species.

Species	Habitat[a,b]	Feeding zone[c]	Longest primary[d]	Ratio to longest primary: Primary 10	Primary 9	Secondary 1
Gerygone **warblers (foliage gleaners)**						
G. mouki	RF	G	5	35.4 (33.3–36.6)	78.0 (72.5–87.2)	92.4 (90.0–94.9)
G. cinerea	RF	G	5 (6)	36.1 (34.1–40.5)	71.5 (56.8–76.2)	90.7 (88.4–92.9)
G. palpebrosa	RF	G	6	33.6 (29.3–40.0)	76.0 (71.1–85.0)	93.3 (90.5–97.6)
G. ruficollis	RF	Ubr	6 (5)	32.3 (28.9–34.8)	80.4 (77.3–82.6)	93.3 (88.9–95.5)
G. fusca	EW	Ubr	7 (6)	32.9 (28.3–36.4)	88.9 (82.6–93.8)	85.8 (82.5–88.9)
G. olivacea	EF, EW	Ubr	7 (6)	34.9 (31.8–42.9)	83.4 (77.3–87.2)	79.8 (77.3–83.0)
Robins (ground gleaners and aerial snatchers)						
Poecilodryas albonotata	RF	G	6	38.7 (36.0–41.0)	73.2 (70.4–76.1)	81.1 (74.7–85.2)
Peneothello sigillatus	RF	Th	5	42.0 (40.5–43.1)	74.5 (70.5–78.5)	83.8 (81.1–86.2)
P. cyanus	RF	Th	6	42.5 (40.0–43.8)	81.8 (78.7–83.8)	77.1 (75.0–78.7)
Tregellasia capito	RF	G	5	37.2 (35.5–39.7)	66.5 (63.2–71.0)	80.3 (75.0–85.5)
Eopsaltria australis	RF, EF	G	5	41.1 (39.2–43.8)	76.5 (74.3–80.0)	72.6 (70.7–77.1)
Petroica bivittata	RF	G	6	37.7 (36.1–39.7)	74.9 (72.1–77.6)	81.0 (77.6–83.6)
P. rosea	RF	G	5	27.5 (25.9–30.2)	73.2 (70.4–75.9)	78.1 (77.4–79.6)
P. multicolor	EW	G	6	28.3 (26.2–29.5)	79.6 (75.4–83.6)	74.5 (72.6–75.4)
P. goodenovii	EW	G	7	33.2 (31.4–34.6)	78.0 (74.5–82.4)	76.7 (73.6–80.4)
Melanodryas cucullata	EW	G	7	29.0 (24.7–31.6)	80.5 (77.8–83.5)	75.3 (73.4–77.2)
Pachycephala **(foliage gleaners)**						
P. rufinucha	RF	Th	5	43.5 (41.1–45.3)	72.7 (70.7–74.2)	91.2 (90.5–93.2)
P. olivacea	RF, EF	Th	5	41.4 (39.5–42.3)	72.1 (70.4–74.0)	94.1 (91.4–96.1)
P. soror	RF	G	5, 6	45.3 (43.7–46.5)	80.3 (76.1–84.1)	80.1 (78.9–81.7)
P. schlegelii	RF	G	5	43.2 (41.2–45.1)	75.4 (74.0–76.5)	82.2 (80.6–84.3)
P. aurea	RF	G	5	46.1 (43.7–48.5)	77.7 (74.6–80.3)	84.2 (81.9–86.4)
P. simplex	RF, M	Ubr	5	42.9 (37.9–48.4)	75.3 (72.7–78.5)	83.4 (80.3–87.5)
P. pectoralis	RF, EF	G	6	38.0 (35.9–39.2)	77.9 (75.0–80.5)	82.8 (80.0–84.6)
P. lanioides	M	G	5	48.7 (45.0–51.3)	81.5 (79.5–82.5)	83.1 (79.5–86.3)
P. inornata	L	G	6	46.6 (45.1–49.4)	78.3 (76.2–80.2)	78.5 (76.5–82.7)
P. rufiventris	EW	G	7	36.5 (32.9–38.9)	82.0 (79.7–84.9)	77.0 (75.0–79.5)
Rhipidura **fantails (aerial sallyers)**						
R. threnothorax	RF	Th	5	38.9 (37.3–40.6)	66.5 (65.1–68.3)	86.9 (84.1–88.9)
R. atra	RF	G	6	38.8 (36.1–39.7)	69.1 (67.2–71.0)	84.9 (80.3–88.9)
R. brachyrhyncha	RF	Th	5	34.0 (31.6–36.2)	64.9 (63.8–66.7)	91.7 (89.7–94.7)
R. albolimnata	RF	G	6	35.8 (32.3–40.0)	70.9 (68.2–74.2)	76.3 (72.1–80.0)
R. rufifrons	RF	Th	6	32.9 (23.4–38.1)	71.7 (67.7–75.0)	83.8 (79.4–88.5)

TABLE 1. Continued.

Species	Habitat[a,b]	Feeding zone[c]	Longest primary[d]	Ratio to longest primary: Primary 10	Primary 9	Secondary 1
R. spilodora	RF	G	6	36.9 (35.4–38.5)	68.5 (63.6–72.3)	86.5 (83.1–89.4)
R. fuliginosa (Victoria)	RF/EF	G	6	28.3 (25.4–32.1)	70.7 (66.7–75.0)	84.0 (81.4–87.5)
R. javanica	EF/EF	G	6	37.8 (32.8–40.6)	68.4 (64.1–74.2)	86.4 (81.8–90.6)
R. rufiventris	EW	G	6	32.1 (30.8–33.3)	68.8 (67.7–69.7)	71.8 (62.2–80.0)
R. leucophrys (Victoria)	EW, EF	G	6	39.6 (38.0–41.9)	81.3 (79.2–83.8)	82.6 (79.3–84.8)
Whipbirds (thicket dwellers)						
Androphobus viridis	RF	Th	5	41.1 (39.3–42.6)	68.4 (67.9–69.1)	95.1 (92.9–96.4)
Psophodes olivaceus	RF, EF	Th	6	42.6 (40.0–44.6)	71.7 (67.1–74.3)	95.2 (91.0–97.3)
Sphenostoma occidentalis	EW	G	6	50.0 (48.5–51.5)	72.6 (71.2–74.2)	92.7 (89.6–95.5)
Shrike-tits (trunk and bark feeders)						
Eulacestoma nigropectus	RF	Th	5	42.5 (40.4–44.6)	73.9 (72.4–75.4)	94.4 (91.2–96.6)
Falcunculus frontatus	EW, EF	Ubr	5	41.8 (36.6–44.4)	79.8 (75.7–83.3)	82.6 (77.3–87.5)
Tree-creepers and nuthatches (trunk and branch feeders)						
Climacteris leucophaea placens	RF	Ubr	6	38.6 (36.8–40.9)	82.9 (82.1–84.8)	79.5 (77.9–81.8)
C. l. leucophaea	EF	Ubr	6	34.8 (32.8–36.4)	83.8 (80.6–87.9)	77.1 (71.0–81.8)
Daphoenositta miranda	RF	Ubr	7	21.9 (20.3–23.4)	92.5 (87.9–96.8)	73.2 (71.0–74.6)
D. chrysoptera	EF	Ubr	7	20.6 (19.0–21.0)	89.8 (86.9–94.8)	73.3 (69.8–75.9)
Magpie-larks (ground feeders)						
Grallina bruijni	RF	G	5	44.9 (42.2–47.7)	78.5 (75.0–79.5)	88.2 (84.1–92.0)
G. cyanocephala	EF, EW	G	6	42.7 (41.7–43.7)	81.4 (79.6–82.7)	72.0 (69.7–73.4)

[a] RF, rain forest; EF, eucalypt forest; EW, eucalypt woodland; L, mallee; M, mangrove.

[b] For comparisons reported in Table 3, any species with RF listed first was included as species of rain forest. Any species with EW or EF listed first was included as species of eucalypt woodland/eucalypt forest. For *Pachycephala*, two tests conducted with: (test 1) all species as above, with species listed as M or L included tested against distinct eucalypt woodland partial migrant *P. rufiventris*; (test 2) *P. rufiventris* excluded and seven rain-forest species compared with single-habitat-M plus single-habitat-L species.

[c] G, unspecialized; Ubr, upper branches; Th, dense thickets and understory.

[d] When two primary feathers were of identical length, both are listed as "longest." When two were subequal and a second was only marginally shorter than the first, it is shown in parentheses.

TABLE 2. Basic structural features of major New Guinea and Australian bird habitats (derived from Specht [1981] and Webb and Tracey [1981]).

Tropical rain forest.—Dense evergreen closed forest with upper stratum cover of over 70%; several dense intergrading sublayers that include vines, epiphytes, and tree-ferns; often dense thickets along edge; commonly with bare floor with rotting logs, ferns, leaves, mesophyll and notophyll.

Eucalypt tall open forest.—Open evergreen forest with upper stratum cover 50–70%; height variable; trees spaced; open branches; medium to dense low-tree or tall-shrub substratum; variably dense low-shrub cover.

Eucalypt woodland and dry forest.—Evergreen; trees widely spaced; foliage projective cover of upper stratum cover, 30–70% in open forest and 10–30% in woodland; height 10–30 m; medium-dense; small-tree and tall-shrub layer sparse; leaf size notophyll; low shrubs sparse; understory grassy layer.

Mallee open shrub.—Evergreen; spare and open, stunted small-tree and tall-shrub stratum; medium dense; foliage projective cover 30–70%; ground cover incomplete and of sparse hummock grass clumps.

Mangroves.—Evergreen estuarine formation varying structurally from closed forest to woodland and tall shrubland; branches sparse; substratum absent; intertidal.

genera) of robins evaluated, primaries 6 and 5 characteristically are the longest, but in the ground-feeding Australian woodland *Petroica goodenovii* and *Melanodryas cucullata*, primary 7 and 6 are the longest (Appendix, Fig. 1). These species and the Australian dry-forest-dwelling *Petroica multicolor* have relative to this group of robins the greatest ratio of primary 9 to the longest primary except for the *Peneothello cyanus*, which is characteristic of rain forest. *Petroica goodenovil, Melanodryas cucullata* and *Petroica multicolor*, as well as the Australian rainforest *P. rosea*, have relatively the shortest primary 10. The first secondary is relatively the

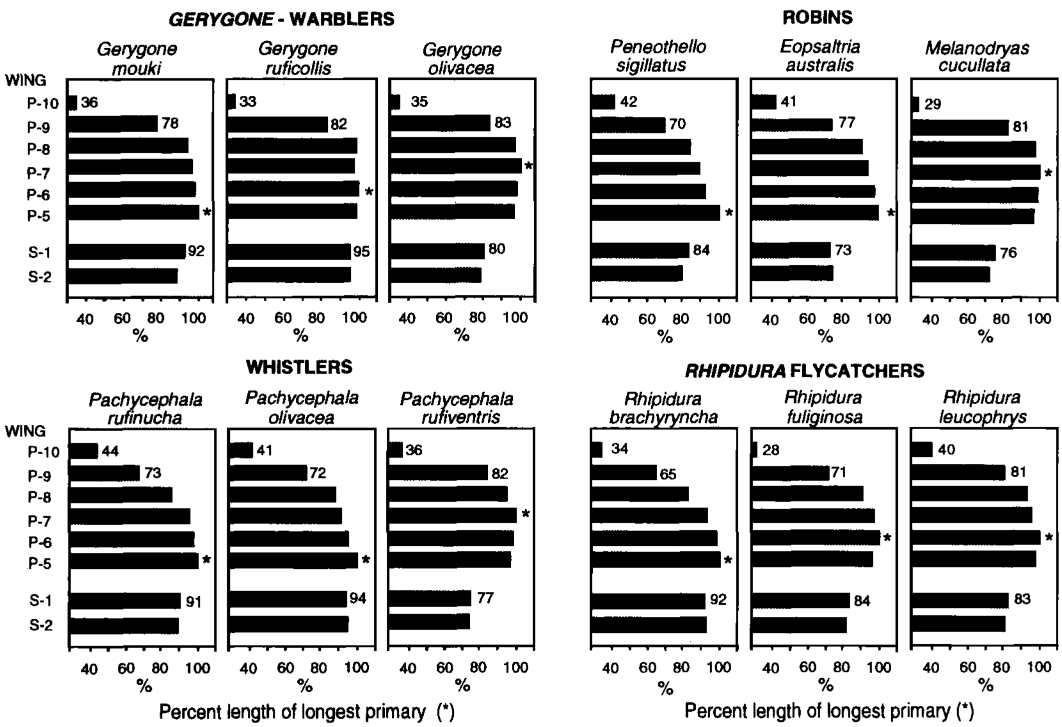

Fig. 1. Wing shape based on lengths of individual primary and secondary feathers for representative species of *Gerygone* warblers, robins, *Pachycephala*, and *Rhipidura* fantails. Longest primary (on average) for each species indicated by asterisk. Figures beside primary 10, primary 9, and secondary 1 are percentages of longest primary in series. Data based on averages of six adult males for each species.

shortest in the first three species and in the Australian eucalypt-forest *Eopsaltria australis.*

Thus, for the robinlike birds, the hypotheses are largely supported, although in relative size of primary 10 in *Petroica rosea* groups with those of the other Australian species. Feeding data that might suggest why *Peneothello cyanus* has a long primary 9 are lacking.

Pachycephala *(Pachycephalidae).*—In the 10 members of this genus, which variously feed by foliage gleaning and plucking prey from the leaves (see data on *P. rufiventris* and *A. pectoralis* in Recher and Holmes 1985, Recher et al. 1985), or largely by the former method (my observations on *P. rufinucha*), the longest primary is characteristically primary 6 or primary 5. The exception is the partly-migratory Australian-woodland *P. rufiventris,* where the outer primary 7 is longest. Primary 9 is proportionately long in this species and in the Australian mangrove- and mallee-inhabiting *P. lanioides* and *P. inornata.* It is also long in the Australian rain-forest/eucalypt-forest *P. pectoralis,* and its close New Guinea rain-forest relatives, *P. soror* and *P. aurea.* Primary 10 tends to be shortest in *P. rufiventris* and *P. pectoralis.* The secondaries are shortest in *P. rufiventris* and *P. inornata,* and longest in the thicket-dwelling *P. rufinucha* and *P. olivacea* (habitat data in Beehler et al. [1986], plus pers. obs.).

Pachycephala rufiventris, the only true open-country dweller, stands apart from the others. The contrasting wing shape relative to those of *P. rufinucha* and *P. olivacea* are shown in Figure 1.

Rhipidura *(Rhipiduridae).*—These insectivorous fantail flycatchers feed mainly by sallying into the air for prey. The feeding habits of the various species are closely similar (pers. obs., Diamond 1972, Cameron 1985, Beehler et al 1986).

Primaries 6 and 5 are the longest. In the unique large-bodied open-terrain ground-feeding *R. leucophrys,* the ratio of the primary 9 to longest primary ratio is 81.3%, compared to 64.9 to 71.7% in the others. *Rhipidura leucophrys* also has a long primary 10 and somewhat short outer secondaries. *Rhipidura rufiventris* has a short primary 10 and the shortest secondary in the series.

Whipbirds (Cinclosomatidae).—The relictual New Guinea *Androphobus* and Australian *Psophodes* live in dense thickets near the ground, while the Australian interior *Sphenostoma* inhabits desert shrubbery. The longest primary in *Androphobus* is, marginally, primary 5; in the others, the longest is primary 6. *Andophobus* has relatively the shortest primary 9. *Sphenostoma* has the longest primary 10 and shortest secondary 1. Wing shape in the three is relatively similar (Fig. 2).

Shrike-tits (Pachycephalidae).—Feeding in the eucalypt-forest *Falcunculus* is largely from the branches and hanging bark (Recher and Holmes 1985, Holmes and Recher 1986). The rain-forest *Eulacestoma* feeds in vines and thickets, commonly hanging its head downwards (Beehler et al. 1986). *Eulacestoma* has the shorter primary 9 and longer secondary 1 (Fig. 2).

Tree-creepers and nuthatches.—Tree-creepers (*Climacteris,* Climacteridae) and nuthatches (*Daphoenositta,* Neosittiae) are unrelated trunk and branch feeders of the upper stratum. There was little difference in wing form in the two pairs of New Guinea and Australian counterparts considered here. However, in the Australian-woodland *Climacteris picumnus,* primary 7 is marginally the longest primary, the primary 9 to longest primary ratio averages 94% (90–97), and ratio of secondary 1 to the longest primary averages 79%.

Magpie-larks (Grallinidae).—Comparison of the wings of the New Guinea mountain-stream inhabiting *Grallina bruijni* and larger-bodied Australian open-country *G. cyanoleuca* show that the former has a more rounded wing and longer secondaries (Fig. 2).

Statistical analysis.—Are the seeming differences between the counterparts in rain forest and eucalypt forest/eucalypt woodland statistically significant? Table 3 compares them. Ratios of primary 9 to the longest primary are significantly different in six of the eight groups (exceptions are whipbirds and tree-creepers/nuthatches). Ratios of secondary 1 to the longest primary are significantly different in seven groups (but not in tree-creepers and nuthatches). In each case, the differences lie in the direction hypothesized. There is some intragroup variation. Differences in body sizes being evaluated must, of course, be borne in mind when weighing the validity of the statistics. The hypothesis that the diminutive primary 10 should be smaller in more actively flying birds (Averill 1925) is not confirmed.

Discussion

The predictions are supported for most of the taxonomic groups. Wing shapes of rain-forest

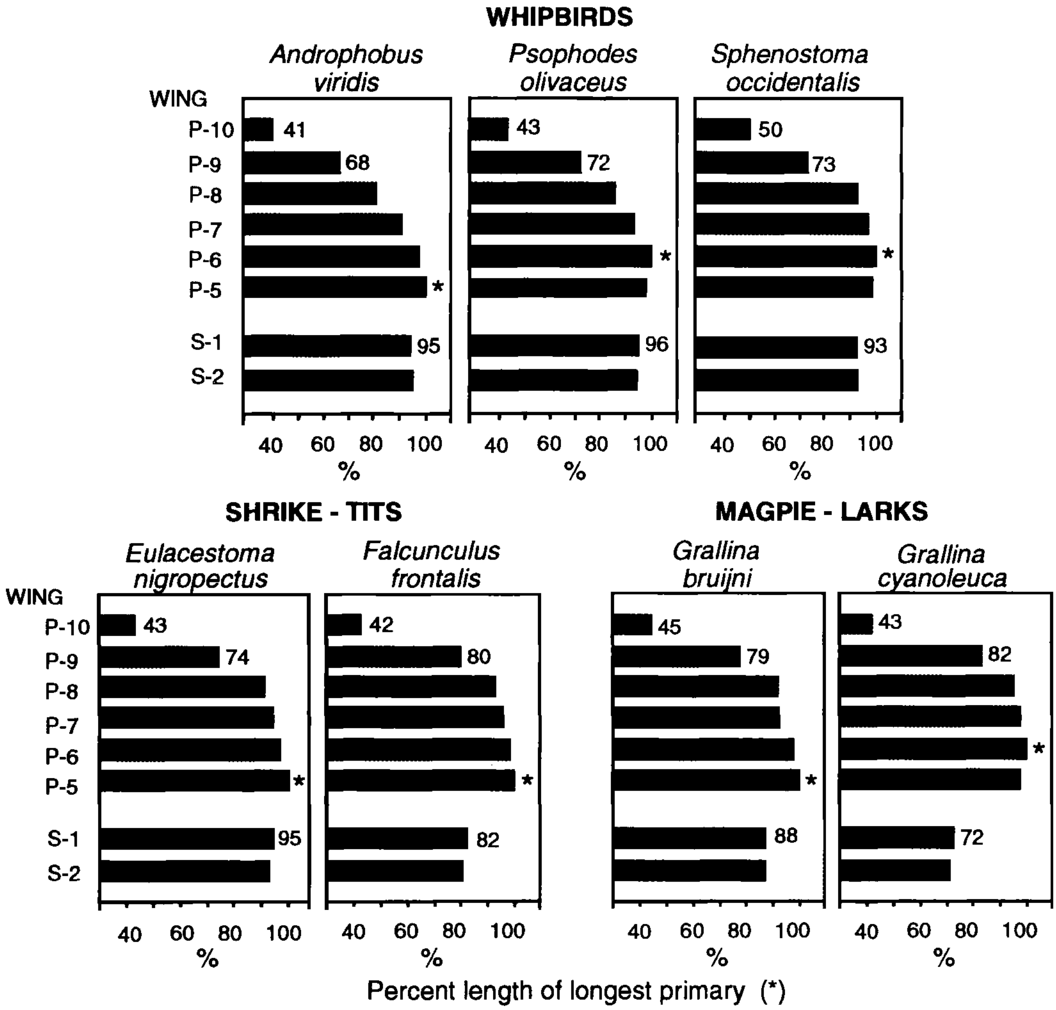

Fig. 2. Wing shape based on lengths of individual primary and secondary feathers for representative species of whipbirds (*Androphobus, Psophodes, Sphenostoma*), shrike-tits (*Eulacestoma* and *Falcunculus*), and magpie-larks (*Grallina*). Longest primary (on average) for each species indicated by asterisk. Figures beside primary 10, primary 9, and secondary 1 are percentages of longest primary in series. Data based on averages of six adult males for each species.

forms compared to congeners inhabiting eucalypt forest/eucalypt woodland tend to be different. However, New Guinea and Australian counterparts in the trunk-and-branch-feeding *Climacteris* and *Daphoenositta* are no different. All *Daphoenositta* have long pointed wings, which might be associated with high mobility and life in the upper branches. The forms of *Climacteris* measured represent a conspecific pair (*C. leucophaea*). Wing form in *Rhipidura*, except in the large-bodied *R. leucophrys*, shows little variation; most are rain-forest dwellers. Possibly, the needs of aerial feeding dictates wing shape in this group. Note, for example, that the relative length of primary 9 in the woodland *R. rufiventris* is similar to that of the rain-forest species.

Although I have identified and shown the longest primary for each species, it often differs from adjacent ones by as little as 1 to 2 mm (Appendix). Often in a particular individual, two or three feathers are nearly equally long. When averages are struck, one emerges as the longest. For present purposes minor differences in lengths of individual primates serve mainly to identify trends. Differences in relative lengths

TABLE 3. Results of Mann-Whitney U-tests for differences in proportionate lengths relative to longest primary of primary 10, primary 9, and secondary 1. Comparisons of species in eight taxonomic groups in tropical rain forest (RF) vs. open eucalypt forest (EF) and eucalypt woodland (EW). U represents ranking done from low to high, U' the reverse.

No. species compared[a]		Primary 10			Primary 9			Secondary 1		
RF	EF/EW	U	U'	P	U	U'	P	U	U'	P
				Gerygone warblers (foliage gleaners)						
4	2	128.0	160.0	ns	27.5	260.5	***	3.5	284.5	***
				Robins (ground gleaners and aerial snatchers)						
7	3	85.0	671.0	***	131.0	625.0	***	161.5	594.5	***
				Pachycephala (test 1; foliage gleaners)						
9	1	11.0	313.0	***	29.0	295.0	***	15.5	308.5	***
				Pachycephala (test 2; foliage gleaners)						
7	2	51.0	453.0	***	82.0	422.0	***	125.0	379.0	**
				Rhipidura fantails (aerial sallyers)						
8	2	273.5	302.5	ns	112.0	392.0	**	68.5	411.5	***
				Whipbirds (thicket dwellers)						
2	1	0.0	72.0	***	17.0	55.0	ns	14.0	58.0	*
				Shrike-tits (trunk and bark feeders)						
1	1	16.0	20.0	ns	0.0	36.0	**	0.0	36.0	**
				Tree-creepers and nuthatches (trunk and branch feeders)						
2	2	44.5	99.5	ns	66.5	77.5	ns	57.5	86.5	ns
				Magpie-larks (ground feeders)						
1	1	7.0	29.0	ns	0.0	36.0	**	0.0	36.0	**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, $P > 0.05$.

[a] Number of species from rain forest (RF) compared with number from eucalypt forest/eucalypt woodland (EF/EW). Species compared indicated in Table 1. For *Pachycephala* tests 1 and 2, see Table 2.

of primary 9 and secondary 1 are more clearcut. Wing features should be viewed as part of a composite. This is obvious when contrasting wing types are diagrammed (Figs. 1 and 2).

The significance of differences in relative length of the diminutive primary 10 remains to be resolved. In an early study, Averill (1925) found that the length of this feather, which is commonly regarded as "vestigial," actually varied inversely with the length of the wing. It was short, if not absent, in migratory members of the Vireonidae and Turdinae, but showed no regression in the Troglodytidae, few species of which are migrants. He found that it was not reduced in the large-bodied crows and ravens and, hence, he suggested that in these species, it must function in flight. A much more comprehensive study than the present one would be necessary to explore the role of the tenth primary in Australo-Papuan birds. It is reduced in size in only one of the three migratory species, *Pachycephala rufiventris.*

It would be fruitful to extend my study to incorporate data on wingspan, wing loading, and aspect ratio. Such information would greatly improve understanding and interpretation. Unfortunately, many of the species covered here are relatively inaccessible and, since these measurements can only be made on live material, the repeat study may have to be based on a smaller subset of species.

The avifaunas of New Guinea and Australia represent twin, but quite differently adapted, radiations from a common stock. The bulk of New Guinea birds inhabitat rain forest and montane forest; most Australian species are found in open eucalypt forest and eucalypt woodland (Keast 1981). The features documented here presumably have evolved repeatedly in the two faunas.

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APPENDIX. Means (± SD) of lengths (mm) of primaries 10 (outermost) to 5, and secondaries 1 and 2, for bird species in rain forest and eucalypt forest/eucalypt woodland in New Guinea and Australia. Measurements for each species taken from six adult males.

Species	Geographic range[a]	Primary feather 10	9	8	7	6	5	Secondary feather 1	2
				***Gerygone* warblers (foliage gleaners)**					
G. mouki	A	14.3 ± 0.8	31.5 ± 1.6	37.8 ± 1.2	39.0 ± 1.3	39.8 ± 1.5	40.2 ± 1.6[b]	37.3 ± 0.8	35.8 ± 1.7
G. cinerea	NG	15.3 ± 1.0	30.3 ± 2.9	38.7 ± 2.6	41.0 ± 1.9	42.0 ± 1.1	42.3 ± 1.5[b]	38.5 ± 0.6	38.2 ± 0.4
G. palpebrosa	A, NG	14.2 ± 1.3	32.0 ± 1.3	38.5 ± 2.5	40.5 ± 1.8	42.2 ± 1.9[b]	41.3 ± 2.4	39.3 ± 1.6	38.5 ± 1.6
G. ruficollis	NG	14.3 ± 1.2	35.7 ± 1.5	43.3 ± 1.2	42.7 ± 1.0	43.7 ± 1.0[b]	43.3 ± 2.0	41.3 ± 0.8	41.3 ± 0.8
G. fusca	A (migr)	14.8 ± 1.2	40.2 ± 2.6	43.7 ± 1.0	44.8 ± 1.7[b]	44.3 ± 1.2	43.3 ± 1.6	38.3 ± 1.0	38.5 ± 0.5
G. olivacea	A (migr)	15.5 ± 1.4	36.7 ± 2.3	43.5 ± 2.6	44.3 ± 2.2[b]	44.0 ± 2.3	42.3 ± 2.1	35.5 ± 1.9	34.8 ± 1.6
				Robins (ground gleaners and aerial snatchers)					
Poecilodryas albonotata	NG	34.3 ± 2.0	65.0 ± 2.1	81.8 ± 1.3	87.7 ± 2.2	88.7 ± 1.4[b]	85.2 ± 2.7	72.0 ± 2.9	71.3 ± 2.3
Peneothello sigillatus	NG	30.8 ± 1.6	54.7 ± 1.9	64.2 ± 3.3	68.5 ± 2.1	70.8 ± 3.1	73.3 ± 5.0[b]	61.5 ± 3.1	61.0 ± 2.7
P. cyanus	NG	31.8 ± 1.0	60.7 ± 1.2	67.0 ± 0.6	72.0 ± 0.9	74.7 ± 1.5[b]	69.5 ± 2.4	57.7 ± 0.8	57.2 ± 1.2
Tregellasia capito	A	24.3 ± 2.0	43.3 ± 0.5	58.3 ± 2.7	63.3 ± 1.7	64.8 ± 2.7	65.2 ± 3.1[b]	52.3 ± 0.8	51.3 ± 0.5
Eopsaltria australis	A	30.0 ± 1.5	55.8 ± 0.7	66.8 ± 1.2	69.2 ± 3.1	71.8 ± 2.5	72.7 ± 1.6[b]	53.0 ± 0.9	54.0 ± 1.8
Petroica bivittata	NG	22.5 ± 0.5	44.7 ± 1.0	56.2 ± 0.7	57.8 ± 0.7	59.7 ± 1.4[b]	58.7 ± 2.2	48.3 ± 2.1	48.2 ± 2.2
P. rosea	A	14.8 ± 0.7	39.5 ± 1.2	48.8 ± 1.2	51.8 ± 0.4	52.7 ± 1.0	54.0 ± 0.6[b]	42.2 ± 0.7	41.7 ± 0.8
P. multicolor	A	17.3 ± 0.8	48.8 ± 1.9	55.8 ± 0.4	59.0 ± 1.3	61.0 ± 1.1[b]	60.5 ± 0.8	45.7 ± 0.5	44.8 ± 0.7
P. goodenovii	A	17.3 ± 0.8	40.7 ± 1.5	49.3 ± 1.0	51.8 ± 1.6[b]	51.3 ± 0.5	49.5 ± 1.0	40.0 ± 0.9	40.2 ± 1.0
Melanodryas cucullata	A	23.0 ± 2.4	64.0 ± 1.3	77.0 ± 0.9	78.8 ± 0.4[b]	78.7 ± 1.5	76.2 ± 1.3	59.8 ± 1.2	58.3 ± 1.2
				***Pachycephala* (foliage gleaners)**					
P. rufinucha	NG	32.2 ± 1.8	53.7 ± 2.1	64.5 ± 1.9	70.7 ± 2.3	72.8 ± 2.9	73.8 ± 2.1[b]	67.3 ± 1.8	66.8 ± 1.7
P. olivacea	A	32.3 ± 0.5	56.3 ± 0.8	70.0 ± 1.1	71.7 ± 0.8	74.8 ± 1.3	78.2 ± 1.7[b]	73.5 ± 1.2	74.0 ± 1.3
P. soror	NG	32.2 ± 0.8	57.0 ± 1.6	64.0 ± 1.4	69.3 ± 2.2	70.7 ± 1.2[b]	70.7 ± 1.0[b]	56.8 ± 0.7	55.7 ± 0.5
P. schlegelii	NG	30.7 ± 1.6	53.5 ± 0.8	64.8 ± 0.7	69.5 ± 2.2	70.8 ± 1.6	71.0 ± 1.8[b]	58.3 ± 1.8	58.0 ± 1.7
P. aurea	NG	31.8 ± 0.7	53.7 ± 0.8	61.5 ± 0.8	64.8 ± 1.0	67.3 ± 1.6	69.2 ± 2.6[b]	58.2 ± 1.3	58.2 ± 1.3
P. simplex	NG, A	28.0 ± 2.4	49.2 ± 1.5	60.5 ± 1.4	61.7 ± 2.0	64.0 ± 1.1	65.0 ± 1.3[b]	54.5 ± 1.4	54.7 ± 1.4
P. pectoralis	NG, A	29.8 ± 1.2	61.2 ± 1.0	70.0 ± 0.6	74.5 ± 0.8	78.5 ± 1.0[b]	75.5 ± 1.5	65.0 ± 0.9	64.0 ± 0.6
P. lanioides	A	38.8 ± 1.9	65.0 ± 0.9	74.0 ± 1.7	76.7 ± 0.8	78.7 ± 1.6	79.8 ± 1.8[b]	66.3 ± 1.6	66.0 ± 1.3
P. inornata	A	39.0 ± 1.4	65.5 ± 2.1	76.2 ± 2.3	82.2 ± 2.8	83.7 ± 1.8[b]	79.5 ± 1.6	65.7 ± 0.8	65.0 ± 0.6
P. rufiventris	A (migr)	26.7 ± 1.5	60.0 ± 1.4	69.5 ± 1.5	73.2 ± 0.7[b]	71.8 ± 0.4	70.5 ± 1.9	56.3 ± 1.5	56.2 ± 1.8

APPENDIX. Continued.

				***Rhipidura* fantails (aerial sallyers)**					
R. threnothorax	NG	25.2 ± 0.7	43.0 ± 1.3	54.7 ± 2.8	58.0 ± 2.3	63.2 ± 1.2	64.7 ± 1.6[b]	56.2 ± 2.3	56.2 ± 2.3
R. atra	NG	23.8 ± 1.2	42.8 ± 1.2	52.7 ± 1.0	60.7 ± 0.5	62.0 ± 0.9[b]	61.3 ± 1.0	52.7 ± 2.5	52.0 ± 1.4
R. brachyrhyncha	NG	19.7 ± 1.0	37.5 ± 0.5	48.2 ± 0.7	54.5 ± 1.0	57.0 ± 0.6	57.8 ± 0.4[b]	53.0 ± 1.1	53.7 ± 1.9
R. albolimnata	NG	23.3 ± 2.2	46.2 ± 1.0	61.2 ± 1.5	63.8 ± 1.9	64.8 ± 2.7[b]	61.2 ± 3.6	49.8 ± 2.2	50.5 ± 2.4
R. rufifrons	A, NG	20.5 ± 3.2	44.8 ± 2.3	55.3 ± 1.5	61.2 ± 1.8	62.3 ± 1.2[b]	59.2 ± 2.4	52.3 ± 1.4	50.7 ± 1.9
R. spilodora	Fiji	24.2 ± 0.7	44.8 ± 2.3	58.8 ± 2.3	64.8 ± 1.0	64.8 ± 1.0[b]	64.5 ± 0.5	55.7 ± 1.2	55.7 ± 1.0
R. fuliginosa (Victoria)	A	16.7 ± 0.8	41.7 ± 1.4	53.8 ± 1.5	57.7 ± 3.1	59.0 ± 2.8[b]	57.2 ± 2.1	49.5 ± 2.0	48.8 ± 2.6
R. javanica	Bali	23.8 ± 1.9	44.3 ± 2.7	52.8 ± 1.2	63.0 ± 0.9	64.5 ± 1.4[b]	64.3 ± 0.5	56.0 ± 1.9	56.0 ± 1.9
R. rufiventris	A	22.2 ± 1.7	47.5 ± 2.9	64.2 ± 2.1	68.3 ± 3.0	69.0 ± 3.8[b]	67.0 ± 4.5	49.3 ± 2.8	49.7 ± 3.1
R. leucophrys (Victoria)	A, NG	31.0 ± 0.9	63.7 ± 2.2	73.8 ± 2.2	75.7 ± 3.0	78.3 ± 2.7[b]	77.0 ± 3.3	64.7 ± 1.7	64.5 ± 1.5
				Whipbirds (thicket dwellers)					
Androphobus viridis	NG	22.5 ± 0.5	37.5 ± 0.5	45.2 ± 1.5	49.8 ± 1.5	53.5 ± 1.9	54.8 ± 1.0[b]	52.2 ± 1.0	52.5 ± 1.6
Psophodes olivaceus	A	32.0 ± 1.3	53.8 ± 1.7	65.0 ± 1.8	70.0 ± 1.7	74.8 ± 1.8[b]	74.5 ± 1.6	71.5 ± 0.8	71.3 ± 1.0
Sphenostoma occidentalis	A	33.2 ± 1.0	48.2 ± 0.8	61.5 ± 1.0	64.2 ± 1.5	66.0 ± 0.6[b]	65.5 ± 1.4	61.5 ± 1.0	61.3 ± 0.8
				Shrike-tits (trunk and bark feeders)					
Eulacestoma nigropectus	NG	24.2 ± 1.0	42.0 ± 0.6	51.8 ± 0.4	54.5 ± 0.8	55.5 ± 0.8	56.8 ± 0.7[b]	53.7 ± 1.4	53.0 ± 0.9
Falcunculus frontatus	A	30.3 ± 2.2	57.8 ± 2.7	68.5 ± 2.1	71.2 ± 2.3	72.0 ± 1.8	72.5 ± 1.9[b]	59.8 ± 2.9	59.0 ± 1.7
				Tree-creepers and nuthatches (trunk and branch feeders)					
Climacteris leucophaea placens	NG	26.0 ± 0.9	55.8 ± 1.2	63.0 ± 0.6	66.5 ± 0.6	67.3 ± 0.8[b]	64.8 ± 1.3	53.5 ± 0.6	52.5 ± 0.5
C. l. leucophaea	A	23.2 ± 0.7	55.8 ± 1.6	63.2 ± 0.7	65.7 ± 1.0	66.0 ± 2.2[b]	60.7 ± 2.4	51.3 ± 1.8	51.5 ± 1.6
Daphoenositta miranda	NG	14.0 ± 0.9	59.2 ± 0.8	63.5 ± 1.0	63.8 ± 1.6[b]	63.3 ± 1.8	62.8 ± 1.3	47.0 ± 1.7	46.5 ± 1.6
D. chrysoptera	A, NG	12.7 ± 0.8	55.3 ± 1.6	57.8 ± 3.0	61.7 ± 2.0[b]	59.3 ± 1.2	49.7 ± 1.0	45.2 ± 1.0	44.0 ± 1.9
				Magpie-larks (ground feeders)					
Grallina bruijnii	NG	40.0 ± 1.7	70.0 ± 0.6	82.3 ± 1.7	84.5 ± 1.5	87.0 ± 3.0	89.0 ± 1.3[b]	78.7 ± 3.4	78.7 ± 3.4
G. cyanocephala	A	60.2 ± 1.5	114.7 ± 1.0	134.5 ± 2.2	139.0 ± 2.0	140.2 ± 1.7[b]	138.7 ± 1.6	101.3 ± 1.2	100.5 ± 1.1

[a] A, Australia; NG, New Guinea; NZ, New Zealand; migr, species a partial migrant.

[b] Longest primary.