

The Adaptive Zone of the Genus *Gerygone* (Acanthizidae) as Shown by Morphology and Feeding Habits

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Summary: Using body morphology, feeding ecology and behaviour, this paper describes the adaptive zone of the species-rich Australo-Pacific genus *Gerygone*. *Gerygone* is a genus of small bodied, specialist insectivores that obtain the majority of their prey by gleaning and snatching it from the foliage. Species tend to be ecologically and morphologically similar. Evolution has mainly taken the form of specialisation to different habitats, to produce a largely allopatric assemblage of species. In this it parallels the larger bodied, foliage-gleaning *Lichenostomus* honeyeaters and contrasts with other species-rich endemic warbler-like gen-

era, such as *Sericornis* and *Acanthiza*, where sympatric species exploit different substrates, forage at different heights above the ground, and use different foraging behaviours. The greatest evolutionary shifts occur in the insular species, *Gerygone igata* and *G. albofrontata*, which are morphologically and ecologically distinct from other *Gerygone*. On the limited data available, it appears that the morphological radiation of *Gerygone* in Australia and New Guinea is constrained by the abundance of other insectivorous genera.

This paper investigates the adaptive zone (Simpson 1953) of, and species roles in, *Gerygone*, a species-rich Australo-Papuan genus of small bodied, warbler-like insectivores in the family Acanthizidae. The work is based on sets of morphological measurements, with data on foraging ecology (feeding substrate use, locomotory feeding movements, flight angles and flight distance during foraging) used to define roles and relate ecology to morphology.

Gerygone, with eight Australian species (three endemics) (Schodde 1975; Christides & Boles 1994) and seven species in New Guinea (three endemics) (Mayr 1941), is one of three highly successful genera of warbler-like birds in the Australo-Papuan region. The other successful genera are *Acanthiza* and *Sericornis*. *Gerygone* probably originally centred in the northern half of Australia and New Guinea (Fig. 1). Of the 17 species of *Gerygone* (19 species, if *modesta* and *insularis* of Norfolk and Lord Howe Islands are accorded species status [Christides & Boles 1994]), only one species, the Golden-bellied Gerygone *Gerygone sulphurea*, has bridged Wallace's Line to reach Malaysia, Thailand and the Philippines (King et al. 1975; van Marle & Voous 1988), one of the few Australasian bird species to achieve this. Eastwards *Gerygone* extends to New Caledonia, the New Hebrides and Rennell Island (Mayr 1978) and south-eastwards to Norfolk Island, New Zealand and the Chathams (Oliver 1955) (Fig. 1).

A feature of *Gerygone* is that, in contrast to *Acan-*

thiza and *Sericornis*, all species are largely allopatric, either in different habitats or geographically (for Australia: Keast 1961; McGill 1970; Blakers et al. 1984; for New Guinea: Rand & Gilliard 1968; Diamond 1972). Hence, evolutionary radiation has taken the form of specialisation for different habitats. In *Acanthiza* and *Sericornis*, by contrast, three or more species often co-occur using different substrates, foraging heights and foraging behaviours (Bell 1985; Ford et al. 1986; Recher 1989). Thus, *Gerygone* poses interesting evolutionary questions. Do all the species have a common morphology and set of foraging habits such that it would be difficult for two or more species to occur together? Has the genus evolved an optimal morphology and set of foraging habits for a set of biological opportunities common to all habitats, such that it has been disadvantageous to change? If so, the morphology and ecology should be relatively stereotyped with changes occurring only with a major shift in the biotic environment.

This paper has two objectives. The first is to explore these ideas at the genus level. The second is to document the morphology and feeding ecology of a range of species and, where shifts are found to occur, to consider these on existing knowledge of functional morphology. Of the species of *Gerygone*, data are available for ten. These span the geographical and habitat distribution of the genus, as well as its morphological variation and are a representative subset of *Gerygone*.

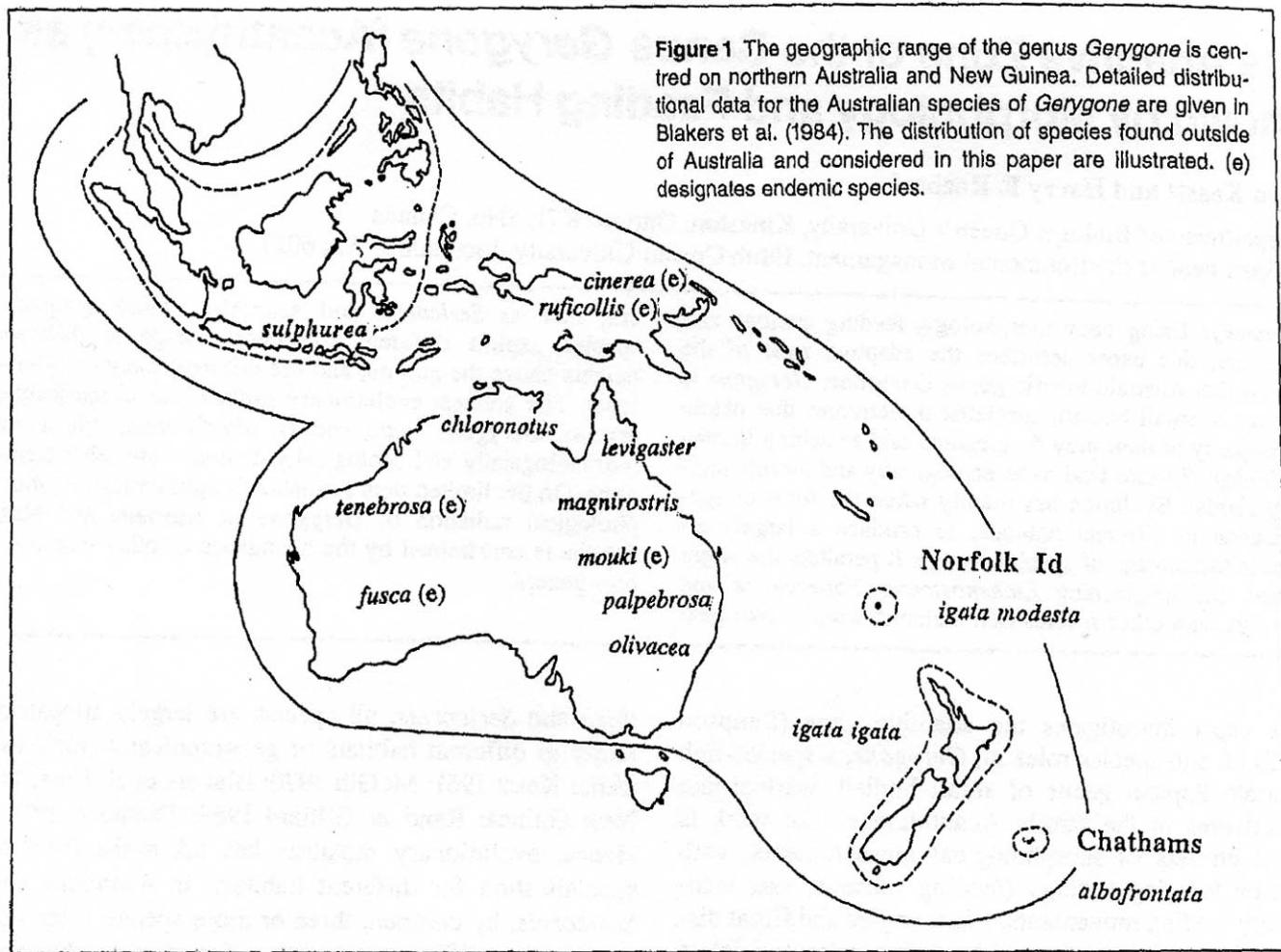


Figure 1 The geographic range of the genus *Gerygone* is centred on northern Australia and New Guinea. Detailed distributional data for the Australian species of *Gerygone* are given in Blakers et al. (1984). The distribution of species found outside of Australia and considered in this paper are illustrated. (e) designates endemic species.

Methods and study sites

Morphological measurements

Morphological measurements were made by AK from museum skins of adult males of each species. Where possible, the populations measured were those from which foraging data were obtained. In the absence of enough Bali specimens of *G. sulphurea*, material from adjacent Indonesian islands was incorporated. For the Grey Gerygone *G. igata*, separate measurements for populations from the North and South Islands of New Zealand were not made because the two are not racially distinct (Kinsey 1970).

Two sets of morphological measurements were made. The first were those routinely used by taxonomists to compare species (i.e. bill, wing, tarsus, tail and hallux lengths, and bill width and bill depth). For these measurements, eight adult males of each species were

measured. The second set of morphological measurements were of the functional units represented by leg, wing and bill (see Oxnard 1975; Leisler & Winkler 1985). In this instance, five adult males of each species were measured. The measurements of functional units were those used in the Principal Components Analyses. Measurements of the leg-foot complex were tarsometatarsus, mid-toe, mid-claw, hind toe, hind claw, footspan with claws, and footspan without claws. These measurements relate to perching habits, substrate use, and habitat (Leisler & Winkler 1985). Measurements were also made of total wing length, lengths of successive primaries from outermost tenth down to primary 4, secondaries 1 and 2 (that express breadth of the middle part of the wing), alula, distances from wing tip to primary 10 and secondary 1, and inner- and outer-most rectrices. These flight features are reflective of habitat use, relative importance of aerial feeding, and migratory habits. To define bill form, as it relates to feeding

habits and sizes of prey eaten, bill length, width, and depth, and length of rictal bristles were measured. Unfortunately, skeletal material was not available for *Gerygone*. However, most evolution at the species level is shown in the features that can be measured in skins (Dilger 1956; Leisler & Thaler 1982).

Bill length was taken from the base of the skull to the tip. Bill width and depth measurements were made at the back of the nostrils. Foot measurements were taken following Norberg (1979, Fig. 1). Lengths of the individual flight feathers, that cumulatively define wing shape, and lengths of rectrices were taken from the point of emergence of each feature from the skin to its tip. Length of alula is the distance from its base to the tip.

Foraging ecology

The ecological data were gathered with two major objectives; to describe the adaptive zone of the genus and to describe the use of space and feeding ecology for the species studied. Data on substrate use, foraging behaviour, foraging height and locomotory feeding movements of White-throated *G. olivacea*, Grey *G. igata*, Brown *G. mouki*, Fairy *G. palpebrosa*, Green-backed *G. chloronotus*, Large-billed *G. magnirostris* and

Brown-breasted *Gerygone G. ruficollis* were gathered by AK. He also obtained data on *G. sulphurea* and the Western *Gerygone G. fusca* but did not measure locomotory movements. AK sampled the foraging behaviour of each species or population over a minimum of five mornings within an 8-21 day period. Each individual encountered was followed for 30 seconds and observations of substrate use, foraging behaviour, foraging height and locomotory feeding movements were recorded. Twenty to 40 such periods of observation were made for each species or population. Making consecutive observations on the same individuals was avoided by moving several hundred metres between observations. AK recorded the use of substrate, foraging behaviour, foraging height and feeding movements according to the procedures of Robinson & Holmes (1982), Holmes & Recher (1986) and Recher (1989).

HFR obtained data on substrate use, foraging behaviour and foraging height for *G. olivacea*, *G. mouki* and *G. fusca* using the procedures described in Recher (1989) for data collected before 1986 (i.e. up to five sequential observations on the same individual), and in Recher & Gebski (1989) for data collected after 1985 (i.e. only the second prey-attack was recorded for each individual observed), but did not measure locomotory

Table 1 Morphological measurements of species and populations of *Gerygone*. Apart from body weight (g), measurements are lengths (mm). Numbers are means with standard deviations in parenthesis. Unless indicated otherwise, measurements are based on series of eight adult males taken from museum collections. In the calculation of group means, measurements for *G. albofrontata* have been excluded.

Species	Tarsus	Wing	Bill	Hind toe and claw	Tail	Rictal bristles	Weight*
<i>G. olivacea</i>	15.7 (0.6)	59.6 (2.7)	11.5 (0.5)	8.3 (0.4)	38.4 (2.0)	3.6 (0.9)	7.5
<i>G. fusca</i>	16.8 (0.6)	57.8 (1.1)	10.8 (0.3)	7.9 (0.3)	43.8 (1.1)	2.6 (0.6)	5.8**
<i>G. igata</i> (Norfolk Is.)	18.0 (0.9)	57.4 (0.6)	12.3 (0.3)	10.5 (0.4)	48.2 (0.8)	4.7 (0.5)	6.6
<i>G. igata</i> (North Is., NZ)	18.8 (0.3)	53.4 (1.1)	11.9 (0.3)	8.4 (0.3)	45.0 (2.8)	6.6 (0.6)	6.4**
<i>G. mouki</i>	16.6 (0.5)	51.6 (1.1)	11.3 (0.3)	8.2 (0.3)	43.8 (2.2)	5.4 (0.6)	5.2
<i>G. palpebrosa</i>	15.9 (1.6)	55.2 (1.9)	12.5 (0.3)	8.9 (0.3)	43.6 (3.1)	5.2 (0.2)	7.6
<i>G. chloronota</i>	15.5 (0.4)	51.8 (0.5)	12.3 (0.5)	8.9 (0.5)	34.8 (1.1)	2.6 (0.3)	6.8
<i>G. sulphurea</i>	15.6 (0.5)	52.6 (2.3)	11.3 (0.7)	9.0 (0.4)	35.6 (2.0)	3.2 (1.8)	6.8
<i>G. magnirostris</i>	16.4 (0.5)	56.4 (2.1)	12.3 (0.4)	9.6 (0.5)	41.0 (1.7)	4.0 (0)	7.4
<i>G. ruficollis</i>	16.8 (0.5)	54.7 (2.1)	10.6 (0.2)	8.5 (0.3)	38.7 (1.9)	3.5 (0.5)	7.0***
<i>G. albofrontata</i>	22.4 (0.6)	65.2 (2.1)	15.2 (0.4)	13.3 (0.5)	52.6 (3.6)	4.2 (0.1)	11.8
Group	16.6 (0.1)	54.8 (0.4)	11.6 (0.1)	8.7 (0.1)	40.6 (0.7)	4.4 (0.2)	na

* Weights were derived from the literature (Diamond 1972; Hall 1974; Gill 1982; Robertson & Dennison 1984) and from museum skins where available. Sample sizes range from 1-50. ** Males and females combined. *** Based on a single, unsexed juvenile (Diamond 1972).

movements. HFR's data were used to test the robustness of the conclusions derived from AK's observations.

Study sites

Data on the species sampled by AK were gathered between August and January 1982–92, as follows: *G. mouki*, Macpherson Range, December 1986 and 1988; and Lakes Eacham and Barrine, October 1986; *G. olivacea* Ebenezer, Hawkesbury River (Sydney), October to December 1988 and 1989; *G. magnirostris*, McIlraith Range, Cape York, September 1992; and Cairns, September 1992; *G. sulphurea*, near Denpasar, Bali, September 1982; *G. chloronota*, Darwin, September 1982; *G. palpebrosa*, Byfield, Central Queensland, August 1984 and Lake Eacham, October 1987; *G. ruficollis*, Tari, Western Highlands, New Guinea, September to October 1992; *G. igata*, Norfolk Island, January 1983; North Island, New Zealand, November 1990; and South Island, November to December 1990. Sample sizes are given in Figure 2.

HFR obtained data on *G. olivacea* at Scheyville near Sydney, New South Wales throughout 1984, and during spring 1985. *G. fusca* was sampled by HFR at several locations in Western Australia during 1986 and again in January and November 1989 in Jarrah/Marri *Eucalyptus marginata/E. calophylla* forest at Karragullen near Perth. Data on *G. mouki* were obtained in October 1990 by HFR and W.E. Davis at Clouds Creek, New South Wales. Data from different dates (as those from New Zealand) were grouped, except for those of *G. olivacea* and *G. fusca*. The latter were used to test year-to-year and seasonal differences in foraging behaviour.

Data analysis

Principal Components Analysis was used to define the position of each individual and species in morphological space, defined by 'n' measurements within each of the three groups of morphological variables. All PCAs were based on correlation matrices of raw data scores divided by the cube root mass of each species, the latter being used to minimise size effects. The loadings are correlations between raw variables and new multivariate factors.

AK's data on feeding behaviours (aerial hawking, foliage gleaning, hang-gleaning, and snatching from the foliage), use of substrates, locomotory feeding movements (hops/min, flights/min, prey attacks/min, and hop/flight ratios), and flight distances and angles during feeding were tested for significant differences using

one-factor Analysis of Variance (ANOVA). The test was used to find whether or not there was significant variation within the genus for each of the above behaviours. Scheffe's *F*-test and the Fisher PLSD were used to identify significant differences between pairs of species.

HFR's data were tested using Pearson's χ^2 . The level of significance was set at $P < 0.01$ to avoid errors of significance associated with small sample sizes (i.e. $n < 120$; see Recher & Gebski 1989 for details) and the lack of independence of sequential observations on the same individual.

Results

Morphological characteristics and variation

Excluding the Chatham Island Gerygone *G. albofrontata*, *Gerygone* are small birds with weights of most species in the 6.0–7.0 g range (Table 1). Excluding *G. albofrontata* because of its exceptional large size from the following calculations, mean tarsus length in the genus is 16.6 mm (range, 15.5–18.8), with a 21% difference between the species with the shortest tarsus and the species with the longest tarsus (Table 1). Mean wing length is 54.8 mm (51.6–59.6), with a difference between the smallest and largest species of 15.5%. Mean bill length is 11.6 mm (10.6–12.5), a difference between the shortest and longest of 17.9%. In other features the variation between the smallest and largest is greater; hind toe and claw, 32.9%; tail length, 38.5%; and rictal bristles, 153%. While some adaptive differences in proportions between different structures are indicated, the per cent differences between species and group means are generally small and show the genus to be relatively homogeneous (Table 2).

Feeding ecology

The species of *Gerygone* are specialist insectivores of the foliage. For most species, more than 80% of prey was taken from foliage, mainly in the canopy, by gleaning, hang-gleaning or snatching (Fig. 2, Table 3). Hawking (aerial prey) accounted for up to 12% of prey attacks. Bark was a minor foraging substrate, accounting for up to 10% of prey attacks in *G. mouki*, *G. sulphurea* and *G. magnirostris*, but exceeded 20% with *G. igata* on Norfolk Island. The taking of prey from low shrubs was recorded in *G. igata* (New Zealand) and *G. mouki*. The former also took prey from the ground, a substrate not used by any other species (Fig. 2).

Table 2 The per cent difference from the group mean of basic morphological measurements for 10 species of *Gerygone*. In the calculation of group means, measurements for *G. albofrontata* have been excluded.

Species	Tarsus	Wing	Bill	Hind toe and claw	Tail	Rictal bristles
<i>G. olivacea</i>	-5.2	8.7	0	-4.8	-5.3	-17.8
<i>G. fusca</i>	1	5.4	-6.9	-10.1	8	-40.6
<i>G. igata</i> (Norfolk Island)	8.2	4.7	6.4	19.7	18.9	19.7
<i>G. igata</i> (North Island, NZ)	13.4	-2.6	2.9	-3.4	11	50.7
<i>G. mouki</i>	0	-5.9	-2.8	-6.2	8	23.3
<i>G. palpebrosa</i>	-4.4	6.6	8.1	2.3	7.5	17.8
<i>G. chloronota</i>	-6.6	-5.5	6.2	1.4	-14.2	-40.2
<i>G. sulphurea</i>	-6.1	-4.1	-2.2	3	-12.2	-26.9
<i>G. magnirostris</i>	-1.4	2.8	6.2	9.4	1.1	-8.7
<i>G. ruficollis</i>	1	0	-8.4	-2.5	-4.6	-20.1
<i>G. albofrontata</i>	34.9	18.9	31	51.9	29.7	-5

With some exceptions discussed below, most species did not appear to select between the tree species in which they foraged. In eucalypt habitats and mulga *Acacia aneura* woodland, Recher (1989, unpubl. data) found that *G. olivacea*, *G. mouki* and *G. fusca* used all common tree and understorey plant species including *Eucalyptus*, *Casuarina*, *Acacia*, *Hakea* and *Banksia*.

Differences in foraging ecology between species and populations

Although much of our data is limited to single populations and seasons, it is compensated for by the spread of species, locations and times of year data were collected. We can therefore ask the following question.

Table 3 Foraging behaviour and substrate use of three species of *Gerygone* in New South Wales and Western Australia. Data are presented as the per cent of prey-attacks attempted (N); Sp = spring, Su = summer, W = winter.

Species/location	Year	Season	(N)	Substrate			Prey-attack behaviour			
				Foliage	Bark	Air	Glean	Snatch	Hover	Hawk
<i>G. mouki</i> (Clouds Creek, NSW)	1990	Sp	237	86	9	5	46	42	7	5
<i>G. olivacea</i> (Scheyville, NSW)	1984	Sp	115	84	3	13	43	35	13	9
	1984	Su	202	89	3	8	40	45	8	7
	1985	Sp	95	95	0	5	29	53	13	5
<i>G. fusca</i> (Dryandra, WA)	1986	Sp	54	100	0	0	50	25	15	10
(Kings Park, WA)	1986	All	439	86	6	8	46	26	19	9
(Kellerberrin, WA)	1986	W/Sp	102	82	6	12	44	34	11	11
(Karragullen, WA)	1986	All	74	89	4	7	31	50	12	7
	1989	Sp	53	94	6	0	40	55	12	7
	1989	Su	66	92	2	6	57	29	8	6

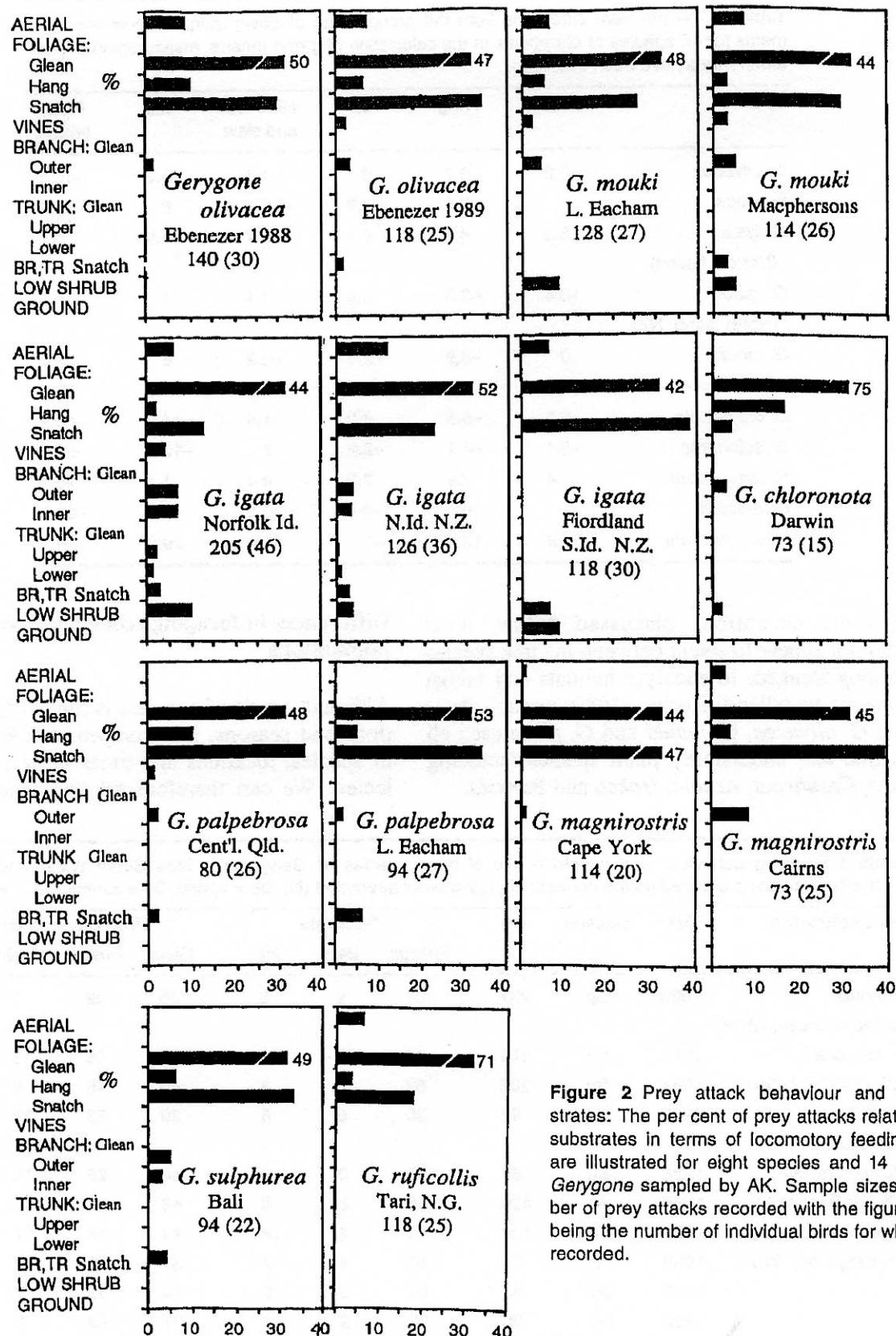


Figure 2 Prey attack behaviour and foraging substrates: The per cent of prey attacks relative to different substrates in terms of locomotory feeding movements are illustrated for eight species and 14 populations of *Gerygone* sampled by AK. Sample sizes are the number of prey attacks recorded with the figures in brackets being the number of individual birds for which data were recorded.

Table 4 Foraging behaviours, pairs of species compared, one-factor ANOVA (statistic shown) for each of the following four variables: A/a = aerial hawk ($F_{13,299} = 2.24, P = 0.0081$); G/g = foliage gleaning ($F = 6.11, P = 0.0001$); H/h = hang gleaning ($F = 2.22, P = 0.0091$); S/s = snatch ($F = 2.31, P = 0.0001$). In each case, lower case letters indicate significance with Fisher PLSD, upper case with the more rigid Scheffé's F -test. All tests: 95% confidence level; ns = not significant.

	<i>igata</i>	<i>lgata</i>	<i>lgata</i>	<i>mouki</i>	<i>mouki</i>	<i>palpebrosa</i>	<i>palpebrosa</i>	<i>chloronota</i>	<i>sulphurea</i>	<i>magnirostris</i>	<i>magnirostris</i>	<i>ruficollis</i>
	Norfolk	NZ N	NZ S	Eacham	Macph.	Eacham	C. Qld.	Darwin	Bali	Cairns	CY	Tari NG
<i>olivacea</i> , 1988 Ebenezer	h,s	h,s	ns	ns	h	a	ns	g,s	ns	h	s	g,s
<i>olivacea</i> , 1989 Ebenezer	s	s	ns	ns	ns	a	a	a,g,h,s	a	ns	a,s	g,s
<i>lgata</i> , Norfolk Island		ns	s	s	s	a,s	a,s	a,g,h	a,s	s	s	g
<i>lgata</i> , NZ North Island			s	a	s	a,s	a,h	a,g,h,s	a,s	a,s	a,s	g
<i>lgata</i> , NZ South Island				ns	ns	ns	h	g,h,s	ns	ns	ns	g,s
<i>mouki</i> , Lake Eacham					ns	ns	ns	g,h,s	ns	s	s	g
<i>mouki</i> , Macphersons						ns	ns	g,h,s	ns	ns	s	g,s
<i>palpebrosa</i> , Lake Eacham							ns	g,h,s	ns	ns	ns	a
<i>palpebrosa</i> , Central Qld.								g,s	ns	ns	ns	g,s
<i>chloronota</i> , Darwin									g,h,s	g,h,s	g,h,s	ns
<i>sulphurea</i> , Bali										ns	ns	g,s
<i>magnirostris</i> , Cairns											ns	g
<i>magnirostris</i> , Cape York												g,s

Are there significant differences between species and populations in foraging behaviour and substrate use?

AK's observations on substrate use by three populations of *G. igata*, and two of each of *G. mouki*, *G. palpebrosa*, *G. magnirostris* and *G. olivacea* at Ebenezer in two years, plus HFR's data on *G. fusca* in Western Australia and *G. olivacea* at Scheyville near Sydney, allow some comparisons within a species.

The foraging data collected by AK and HFR were tested separately for differences between species and populations. The analyses of AK's data are presented in Table 4 and described below followed by a description of differences between species and populations for HR's data.

Keast's observations

Foliage gleaning was used to a significantly greater extent by *G. chloronota* and *G. ruficollis* (75% and 71% of prey attacks), than by the other species (Fig. 2, Table 4). Hang-gleaning was used by *G. chloronota* significantly more (17%) than other species except *G. olivacea* at Ebenezer in 1988 (12%) and the central Queensland population of *G. palpebrosa* (12%) (Fig. 2, Table 4). *G. olivacea* (1988 series) hang-gleaned significantly more than the three *G. igata* populations, *G. mouki* (Macphersons), *G. magnirostris* (Cairns) and *G. ruficollis*. *G. palpebrosa* (central Queensland) hang-gleaned to a significantly greater extent than the *G. igata* North and South Island populations.

Snatching prey from the foliage was used as a feeding mode to a significantly lesser extent by *G. chloronota* and *G. ruficollis* than most species other than *G. igata* (Fig. 2, Table 4). *G. igata* on Norfolk Island and the North Island of New Zealand also snatched less often than most other species and the South Island population of *G. igata* (Fig. 2, Table 4). Snatching was used proportionately more often by *G. magnirostris* than most other species.

Hawking was used to a significantly greater degree by *G. olivacea* (Ebenezer 1988, 1989) and *G. igata*; *G. palpebrosa*, *G. chloronota*, *G. sulphurea* and *G. magnirostris* (all populations) seldom hawked (Fig. 2, Table 4).

There were also some differences in the use of sub-

strates. Although foliage was the most commonly used substrate (Fig. 2), an ANOVA revealed significant differences in the use of some less commonly used substrates: upper trunk ($F = 12.299 = 3.93, P = 0.0001$); lower trunk ($F = 1.83, P = 0.0379$) inner branch gleaning ($F = 5.43, P = 0.0001$); and outer branch feeding ($F = 1.85, P = 0.036$) (Table 4). In general, use of these less commonly exploited substrates was predominantly by *G. igata* (Norfolk Island population). *G. igata* on Norfolk Island fed significantly more often than other species on both the upper and lower trunk. Inner branch gleaning characterised the feeding of *G. igata* (both Norfolk and North Island populations) to a significantly greater extent than in other forms. *G. igata* (Norfolk Island) and *G. mouki* (Lake Eacham) fed significantly

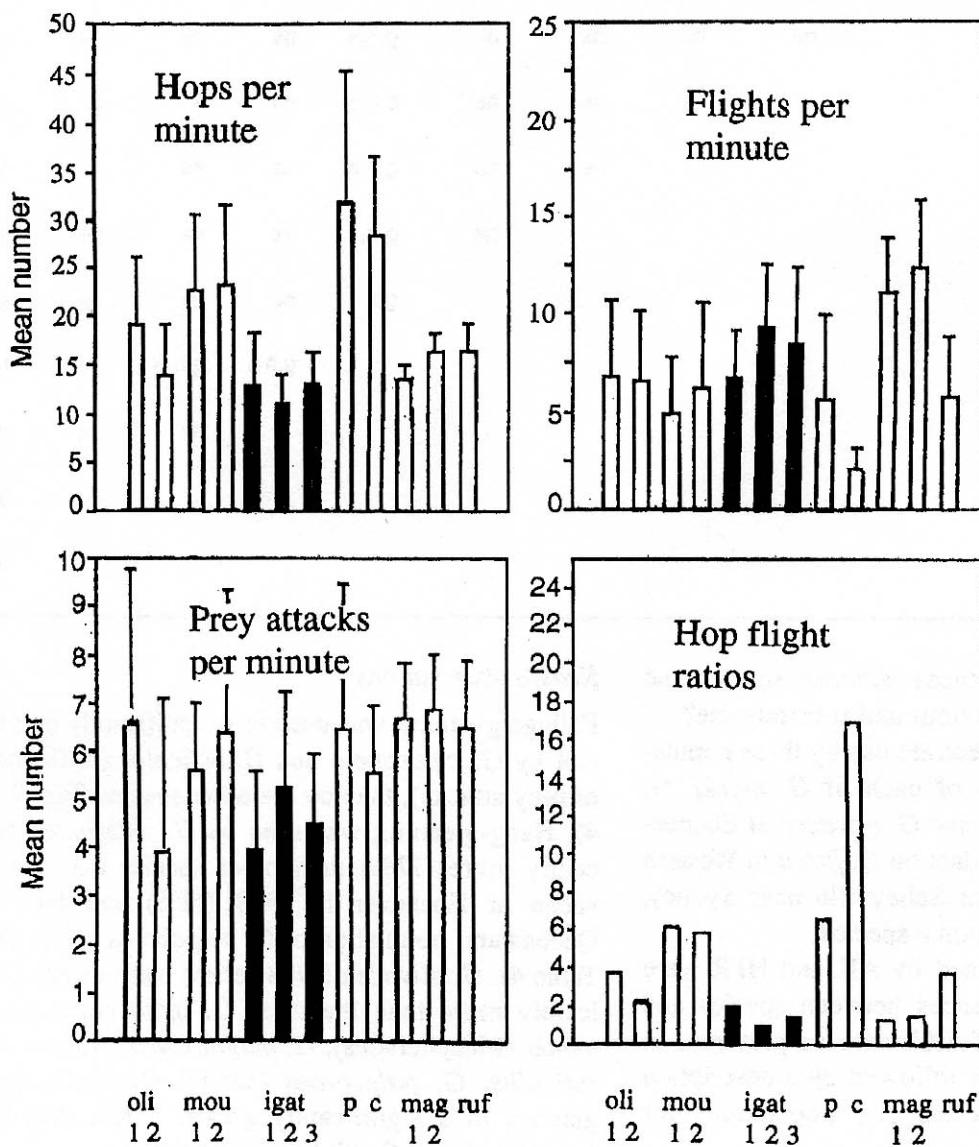


Figure 3 Foraging activity patterns of *Gerygone*: The hops, flights, and prey attacks per minute, and hop/flight ratios of foraging birds are shown for seven species and 12 populations of *Gerygone* sampled by AK. Sample sizes are those given in Figure 2 in brackets. Species key: oli *G. olivacea*; mou *G. mouki*; igat *G. igata*; p *G. palpebrosa*; c *G. chloronota*; mag *G. magnirostris*; ruf *G. ruficollis*.

Table 5 Locomotory feeding movements, pairs of species compared, one-factor ANOVA (statistic shown) for each of the following four variables: H/h = hops/min ($F_{12,289} = 5.79, P = 0.0001$); F/f = flights/min ($F = 5.79, P = 0.0001$); P/p = prey attacks/min ($F = 7.81, P = 0.0001$); and X/x = hop/flights ratios ($F = 31.97, P = 0.0001$). In each case, lower case letters indicate significance with Fisher PLSD, upper case with the more rigid Scheffe's F-test. All tests: 95% confidence level; ns = not significant

	olivacea	igata	Igata	igata	mouki	mouki	palpebrosa	chloronota	magnirostris	magnirostris	ruficollis
	1989	Norfolk	NZ N	NZ S	Eacham	Macph.	Eacham	Darwin	Calrns	CY	Tari NG
olivacea, 1987 Ebenezer	h,p	h,p	h,f,p,x	h,f,p,x	x	x	H,x	h,f,X	h,F,x	F,x	ns
olivacea, 1989-Ebenezer	ns	f	f	h,p	h,p,x	H,p,x	H,f,X	f,p	F,p	p	
Igata, Norfolk Island		f	f	h,p,x	h,p,x	H,p,x	H,f,X	F,p	p	p	
Igata, NZ North Island				ns	H,F,X	H,f,p,X	H,f,X	H,F,X	f,p	h,f,p	h,f,x,p
Igata, NZ South Island					H,F,X	H,f,p,x	H,f,p,X	H,F,X	f,p	f,p	f,p,x
mouki, Lake Eacham						ns	h	h,f,X	h,F,X	h,F,X	h,x
mouki, Macphersons							h	h,f,X	H,F,x	h,F,x	h,x
palpebrosa, Lake Eacham								f,X	H,F,X	H,F,X	H,x
chloronota, Darwin									H,F,X	H,F,X	H,F,X
magnirostris, Cairns									ns	F,x	
magnirostris, Cape York										F,x	

more in low shrubs. *G. igata* (South Island) was the only population recorded feeding on the ground (Fig. 2).

Recher's observations

There were no significant differences in prey-attack behaviours between *G. mouki* at Clouds Creek and *G. olivacea* at Scheyville (1984 and 85 combined) ($\chi^2 = 5.635, d.f. = 3, P > 0.1$). Both species differed significantly from *G. fusca* in King's Park ($\chi^2 = 27.023$ and 27.827 respectively, $d.f. = 3, P < 0.0001$). *G. mouki* and *G. olivacea* snatched prey more often and hovered less often than *G. fusca* in Kings Park. *G. mouki* at Clouds Creek took significantly more prey from bark and less from the air than *G. olivacea* at Scheyville (1984 data) ($\chi^2 = 14.811, d.f. = 3, P < 0.001$) (Table 3). Other comparisons between species and populations were not significant ($\chi^2, P > 0.01$).

G. olivacea at Scheyville used tree species in the same proportion as the abundance of their foliage (Recher 1989). However, in both 1986 and 1989, *G. fusca* at Karragullen used Marri more often and Jarrah less often than expected from the relative abundances of their foliage ($\chi^2 = 54.240$ and 25.612 respectively, $d.f. = 1, P < 0.0001$). Annual and seasonal differences in the use of Marri and Jarrah by *G. fusca* at Karragullen are described more fully below.

Locomotory feeding movements, and flight angles and distances while foraging

The major locomotory feeding movements (hops/minute; flights/minute; prey attacks/minute; and hop/flight ratios) are documented in Figure 3. They were tested to determine whether there was significant variation across species for each (Table 5). The hops per minute rate ranged from 11.6 to 31.1; flights from 2.0 to 2.4; prey attacks from 3.9 to 6.9; and hop/flight ratios from 1.2 to 16.8. The hops/minute rate and hop/flight ratios were significantly greater in *G. chloronota* and *G. palpebrosa* than in all other species. The former was significantly less in *G. mouki* than in these two, but significantly higher than in all others. *G. chloronota* had the lowest flights/minute rate, while in *G. magnirostris* it was significantly more than in all other species, followed by the North and South Island populations of *G. igata*.

Flight angles and distances used during foraging are shown for a subset of species in Figure 4. As is the case for most foliage gleaning birds, horizontal and upward-directed flights, either at 45 degrees or vertical, were prominent. Much of the snatching of prey from foliage involved an upward angle of flight. Mean distances of feeding flight for the entire series was 1.3 m. In all species most flights were in the 0.3-1.0 m range, relatively few being greater than 2.0 m. Mean flight dis-

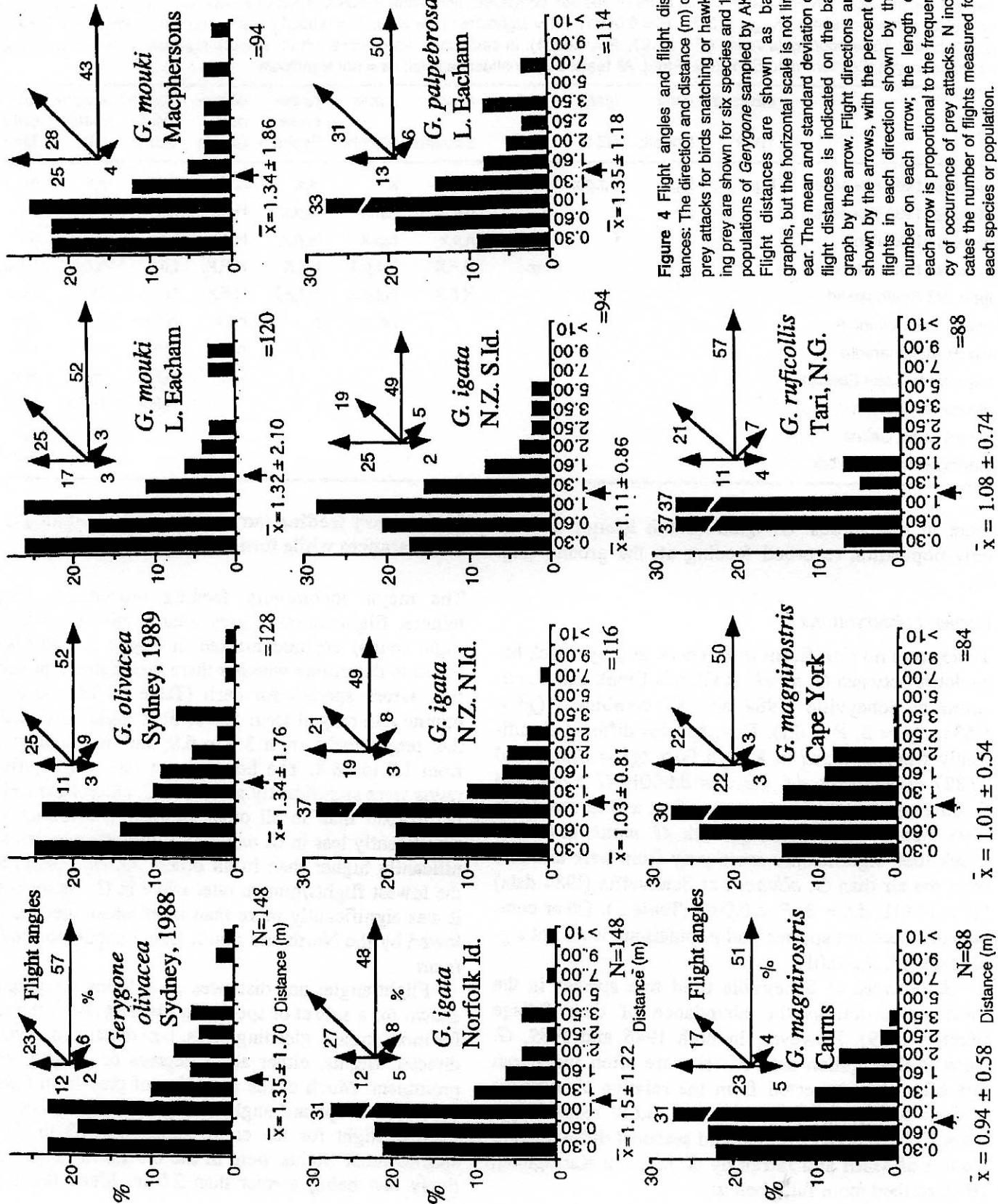


Figure 4 Flight angles and flight distances: The direction and distance (m) of prey attacks for birds snatching or hawking prey are shown for six species and 11 populations of *Gerygone* sampled by AK. Flight directions are shown as bar graphs, but the horizontal scale is not linear. The mean and standard deviation of flight distances is indicated on the bar graph by the arrow. Flight directions are shown by the arrows, with the percent of flights in each direction shown by the number on each arrow; the length of each arrow is proportional to the frequency of occurrence of prey attacks. N indicates the number of flights measured for each species or population.

tances ranged from 0.9–1.0 m in *G. magnirostris* to 1.4 m for *G. palpebrosa* at Lake Eacham.

A one-factor ANOVA revealed no significant differences in angle directions and distances.

Temporal differences in foraging behaviour

How characteristic are the kinds of differences in foraging ecology described above? Specifically, does the use of substrates, plant species, and foraging behaviours differ between populations of species? Do they change within a population seasonally or between years?

For *G. olivacea* in open forest near Scheyville, New South Wales, Recher (1989) found no significant differences between seasons (spring vs summer 1984) or years (spring 1984 vs spring 1985) in prey attack behaviour, or in the use of substrate and plant species ($\chi^2, P > 0.2$). Studies of *G. fusca* in Jarrah/Marri forest at Karragullen also show no significant differences between seasons (including in winter relative to other seasons) or years (1986 vs 1989) in the use of substrates ($\chi^2, P > 0.05$). In 1989, *G. fusca* were observed more often in Marri in summer (48% of prey taken from eucalypt foliage) and less often in spring (33%), while Jarrah was used less often in spring (52%) than summer (66%), but the differences were not significant ($\chi^2 = 2.10, d.f. = 1, P = 0.15$). Jarrah was used significantly more often in 1989 than in 1986, while Marri was used less often ($\chi^2 = 19.209, d.f. = 1, P < 0.0001$). However, as noted above, at all times Marri was the preferred substrate. The differences in the use of Jarrah and Marri between years almost certainly reflects temporal differences in prey kind and abundance on these two species of eucalypts (see Recher et al. 1996 for a description of seasonal patterns of arthropod abundances on Jarrah and Marri at Karragullen).

In the following comparisons, the observations of *G. fusca* at Karragullen from 1986 and 1989 were combined. This was done because the data from other sites in Western Australia were collected throughout the year with no one season having enough observations for separate analysis. There were significant differences in the prey-attack behaviour of *G. fusca* between birds foraging in Jarrah/Marri forest at Karragullen and those foraging in banksia/casuarina woodland at Kings Park ($\chi^2 = 22.646, d.f. = 3, P < 0.001$). At Karragullen, *G. fusca* snatched more often and used other prey-attack behaviours less often than in other habitats (Table 3). Other comparisons between populations and sites were not significant ($\chi^2, P > 0.01$). Despite a smaller proportion of observations of prey being taken from bark and air in

Marri/Jarrah forest (Table 3), there were no significant differences in the use of substrates by *G. fusca* between habitats ($\chi^2, P > 0.10$) with most prey (> 80%) taken from foliage.

Seasonal differences in foraging height were also studied by HR. With *G. olivacea* at Scheyville it was found that the birds foraged significantly higher in the canopy in spring than summer. Recher (1989) attributed this to the behaviour of singing males seeking a high song perch in spring while advertising territories. There was no significant difference in foraging height between spring and summer of *G. fusca* at Karragullen in 1989 ($\chi^2 = 4.032, d.f. = 1, P > 0.01 < 0.05$). Foraging height data for other sites and years were inadequate for seasonal comparisons.

The relationship between species morphology and ecology and behaviour

Potential correlations between morphology and ecology in *Gerygone* can be best developed relative to the background of what is known, or has been postulated, about the relationships between morphology and function in small birds.

(1) *Body size, geographic range and Bergmann's Rule* Body size influences physiology and ecology in various ways (Maurer 1991). Body weight is the best indicator of size.

Size variation in wide-ranging species commonly expresses itself in terms of Bergmann's Rule which states that populations of species inhabiting colder areas are larger-bodied (Mayr 1956). Populations within *G. fusca* and *G. palpebrosa* show this (see measurements in Ford 1981). The generality does not necessarily apply between species (Mayr 1956) and this is the case in *Gerygone*. Some northern tropical lowland species (*G. chloronota* and *G. sulphurea*) have a small body biomass (Table 1), but the smallest species, *G. mouki*, ranges well to the south. The New Zealand *G. igata* is small-bodied, but *G. albofrontata* is large (Table 1). Presumably in the cold wet Chatham Islands the demands of heat conservation favour large size whereas the habitats occupied by *G. mouki* in eastern Australia are warm temperate. *G. mouki* may also leave the highest elevations when it becomes cold and move into warm coastal habitats during winter (HFR pers. obs.).

(2) *Leg and foot features* The tarsus is long in ground-feeding birds. Among arboreal passerines, it is commonly longer in insular forms. This is a trend that Grant (1971) suggested may be linked to use of a wider range of perching and feeding substrates. An increase in

Table 6 Principal Components Analysis: factor loadings for leg and foot, flight and bill features of *Gerygone*.

LEG AND FOOT FEATURES		FACTORS				
Components		1	2	3	4	5
Tarsus length		0.77	0.16	0.59	0.04	-0.12
Mid-toe length		0.23	0.94	0.04	0.14	-0.03
Mid-claw length		0.56	-0.76	0.13	0.28	0.10
Hind-toe length		0.89	-0.06	0.10	-0.39	0.18
Hind-claw length		0.86	-0.22	-0.25	-0.08	-0.37
Foot span		0.89	0.27	-0.25	0.08	0.15
Foot span without claw		0.95	0.08	-0.19	0.13	0.07
Per cent of total variance		59.7	23.1	7.7	4.0	3.2
FLIGHT FEATURES		FACTORS				
Components		1	2	3	4	5
Wing length		0.81	0.20	-0.23	-0.26	-0.08
Alula length		0.36	0.11	-0.67	0.18	0.38
Length of primary 10		0.37	-0.12	-0.50	0.33	0.46
Length of P9		0.60	0.50	0.17	-0.40	0.18
Length of P8		0.80	0.41	0.13	-0.13	0.11
Length of P7		0.88	0.31	0.03	-0.13	0.07
Length of P6		0.87	0.15	0.10	0.05	-0.09
Length of P5		0.83	0.01	0.13	0.32	0.01
Length of P4		0.72	-0.26	0.11	0.30	0.09
Length of S1		0.42	-0.52	0.64	0.01	0.16
Length of S2		0.35	-0.54	0.62	0.09	0.28
Distance from wing tip to P10		0.04	0.82	0.43	0.24	-0.14
Distance from wing tip to S1		0.42	-0.56	-0.20	-0.62	0.09
Length of outer rectrices		0.73	-0.20	-0.27	0.20	-0.44
Length of inner rectrices		0.65	-0.40	0.20	0.03	-0.56
Per cent of total variance		40.6	16.1	13.1	7.2	7.1
BILL FEATURES		FACTORS				
		1	2	3	4	5
Bill length		0.83	0.41	0.02	-0.29	-0.24
Bill width		-0.58	0.62	0.29	-0.42	0.13
Bill depth		-0.39	0.60	0.17	0.39	-0.16
Length of rictal bristles		0.48	-0.17	0.85	0.12	0.08
Per cent of total variance		36.6	32.7	18.3	8.9	3.4

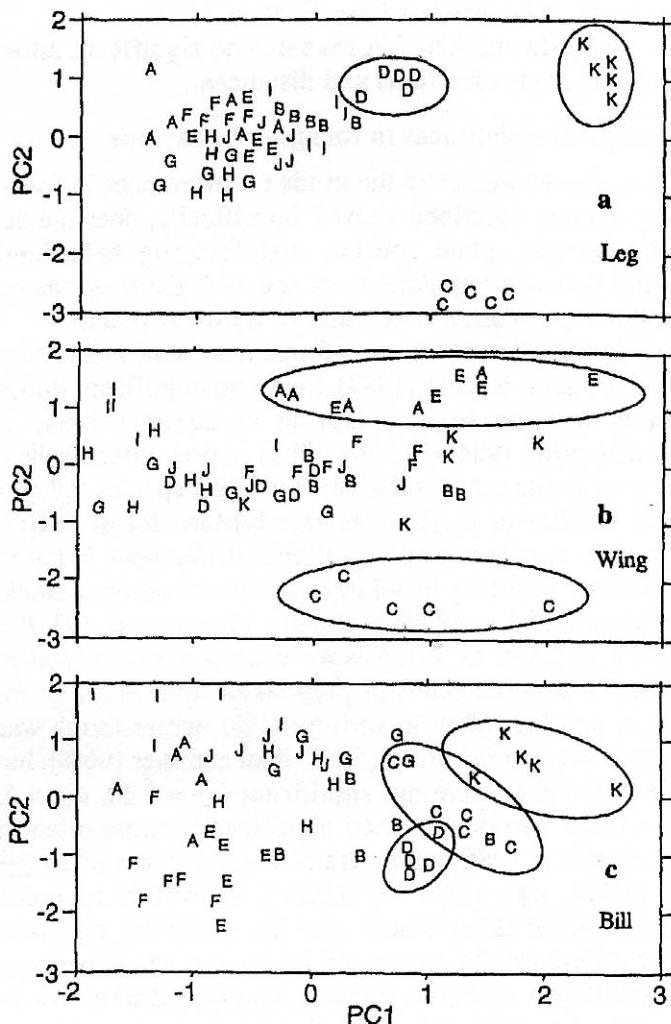


Figure 5 Principal Components Analysis of morphological features: Plots of the first two principal-components for (a) leg and foot features; (b) flight features; and (c) bill features are illustrated. The features measured and used in the PCA analysis are described in the text. Species key: A. *G. olivacea*; B. *G. mouki*; C. *G. igata*, NLK; D. *G. igata*, NZ; E. *G. fusca*; G. *G. palpebrosa*; H. *G. chloronota*; I. *G. sulphurea*; J. *G. magnirostris*; K. *G. albifrons*.

the relative length of the hind toe and claw can be linked to an increase in the climbing or hanging habit (Palmgren 1932).

In the PCA plots (Fig. 5), factor 1, accounting for 59.7% of the variance, loads heavily for tarsus length, hind toe and hind claw lengths, and footspan with and without claw lengths (Table 6). Factor 2 (23.1% of the variance) loads positively for middle toe length and negatively most heavily with mid-claw length and hind-claw length. Factor 3 (7.7% of the variance) is positive

for tarsus length, but negative for hind claw length, footspan and footspan without claw (Table 6). Most species of *Gerygone* cluster together (Fig. 5).

The aberrant, large-bodied *G. albifronsata*, however, separates out strongly on both factors (Fig. 5); it has a long tarsus and long hind-toes, mid-toes and footspan. The Norfolk Island *G. igata* parallels this trend, but has a short mid-toe. The New Zealand *G. igata* is intermediate. The 'insular effect' is thus demonstrated; a longer tarsus is matched by a greater diversity of substrate use (Fig. 2). It may, however, be linked to increased use of trunks and branches in feeding, a habit that entails increased clinging in a vertical position. Foraging data on *G. albifronsata* on Southeast Island in the Chathams (O'Donnell & Dilks 1993) shows that in this species 53% of prey attacks are on bark, and 26% on twigs. Early settlers on the Chatham Islands called this bird 'the woodpecker', from its readily observed trunk-feeding habits (Oliver 1955). Trunk-feeding, as noted, is virtually absent in typical *Gerygone*.

Apart from the above, no ready correlations between changed leg morphology and specialised perching or feeding habits can be drawn. This is presumably because in neither feature do the species depart far from a common or central theme. *G. chloronota* and *G. palpebrosa* hang-gleaned more than other species, but the habit still represented only a minor component of their feeding. Hence, there should not be selection for a longer hind toe. *G. chloronota* has a high hop rate and low flight rate while foraging (Fig. 3) and does relatively less foliage gleaning and foliage snatching (Fig. 2). *G. palpebrosa* and *G. mouki* also have high hop rates (Fig. 2), which is in accordance with their small body size and/or with a shorter mid-toe. A more extensive study would be necessary to confirm these relationships.

(3) *Flight features* Factors governing wing morphology are varied and complex. A wing that is shorter, more rounded and of low aspect ratio characterises birds which aerial feed in confined spaces that require slow flight and an ability to turn tightly (Rayner 1988; Norberg 1979, 1990). The necessary economy of effort required for long flights can be best achieved by a high aspect ratio wing (Pennycuik 1969, 1989; Rayner 1988; Norberg 1990; Winkler & Leisler 1992; Bairlein 1992). The wing of migratory species and populations is characteristically longer and more pointed than equivalent sedentary species or populations (Gaston 1974). A recent comprehensive study of the wing shape of New Guinean and Australian rainforest passerines compared to eucalypt forest/woodland species showed that in the

former the outer primary 9 tends to be proportionately shorter, secondary 1 proportionally longer, and that the longest primary is placed closer to the body in the series (Keast 1996). Presumably this difference has evolved because rainforest vegetation tends to be closed, requiring shorter flights and closer manoeuvring than in the relatively more open eucalypt habitats.

In the PCA analysis of flight features (Fig. 5), factor 1, accounting for 40.6% of the variance, loads most heavily for wing length, the lengths of primaries 7 to 5 (middle primaries) (Table 6). It is also positive for the outer and inner remiges (Table 6). Factor 2 (16.1% of the variance), loads heavily for outermost primaries 9 and 8, distance from wing tip to primary 10 and negatively for wing tip to secondary 1 (giving a more pointed wing), and inner and outer remige lengths (i.e. a shorter tail). Factor 3 (13.1% of the variance) loads positively for length of secondaries 1 and 2 and negatively for alula length and the length of primary 10 (i.e. a broader middle section of the wing with increased lift) (see Keast 1996). Factor 4 (7.2% of variance) loads positively for primary 10 (the functional role of this feather is uncertain, see Averill 1925) and negatively for wing length, outer primary lengths and distance from wing tip to secondary 1 (Table 6). Factor 5 is positive with respect to alula length and the length of primary 10, and negative for the lengths of the remiges again pointing to the functional importance of wing length and shape in conjunction with tail length.

Separating out positively on factor 1 (total wing length) is the large-bodied *G. albifronsata*, the Norfolk *G. igata*, and the Australian open country dwelling *G. olivacea* and *G. fusca* (Fig. 5). The long wing of *G. ruficollis* is, at first sight, anomalous. However, it feeds high in the treetops and has been observed flying long distances between trees which may account for the longer wing length (Keast 1996). Separating out most clearly on Factor 2 are *G. olivacea* and *G. fusca*, the only *Gerygone* that are migratory (Ford 1981; Blakers et al. 1984). Separating negatively on Factor 2 (having a more rounded wing) is the Norfolk *G. igata*. Towards the end of the plotted series and having relatively short wings are the small-bodied rainforest edge and mangrove *G. chloronota*, *G. sulphurea*, and *G. palpebrosa*. These species, as noted, tend to fly less and hop more in feeding. In Malaya, Noske (1995) found that *G. sulphurea* feeds mainly by gleaning (67% of prey attacks) and 36% by hovering and snatching, closely paralleling the figures of 57% gleaning, 7% hang-gleaning and 38% snatching recorded by AK in his Bali observa-

tions of *G. sulphurea*. The above findings accord with predictions based on Keast (1996).

Tail length and shape are influenced by many factors. Recent studies of tail aerodynamics using wind-tunnel experiments show that: (i) the tail acts as a device for maintaining longitudinal and lateral stability and control; (ii) longitudinal motion is elicited by deflections, with up and down movements changing lift and pitching moment; and (iii) lateral control is achieved by twisting (Hummel 1991). The effectiveness of these controls is governed by the size and aspect ratio of the tail. Other roles of the tail include functioning as a brake during sudden twisting manoeuvres, as in the aerial 'tumble feeder' *Rhipidura* (Cameron 1985) and insect flushing by 'pumping' the tail (Robinson & Holmes 1982, 1984). It may also be a display structure. The latter two roles do not apply in *Gerygone*.

With the tail potentially functioning as a steering device a longer tail might be expected for species which aerial feed. Aerial feeding, however, is a minor feeding mode in *Gerygone* (Fig. 2, Table 3) and no correlation with tail length is found. Instead, tail length is correlated with body size.

(4) *Bill features* There is a general correlation between bill size and size of prey consumed (Hespenheide 1971; Lederer 1972). This does not, however, always apply (Wiens & Rotenberry 1980). A larger bill can be closed more quickly (Beecher 1962) and should favour the capture of fast-moving (including aerial) prey. A wider bill suggests increased aerial feeding (Leisler & Winkler 1985). A deeper and, hence, a stronger bill may be linked to taking larger and/or harder-bodied prey. Insular populations commonly have longer bills (Grant 1968) and should favour the taking of a wider range of prey sizes.

In the PCA on bill morphology (Fig. 5), Factor 1, (accounting for 36.6% of the variance) loads heavily for bill length and negatively for bill width and depth (Table 6). Factor 2 (32.7% of variance) is positive for bill length, depth and width, but is negative for length of rictal bristles. Factor 3 (18.3% of variance) is positive for rictal bristle length, but only weakly positive for bill length, depth and width (Table 6). Factor 4 (8.9% of variance) loads positively for bill depth, but negatively for bill length and width and is only weakly positive for rictal bristle length. Thus, long bills tend to be narrow and shallow and are associated with long rictal bristles, while wider beaks tend to be short and relatively deep. These characteristics accord with different feeding habits, with long billed birds expected to probe or glean

more often, while wider beaked birds should snatch and hawk prey more frequently. Separating positively on factor 1 (long bill) are the large *G. albifronsata*, *G. igata* Norfolk and *G. igata* New Zealand North Island, followed by *G. palpebrosa* (Fig. 5). At the other end of the series, with a relatively shorter bill, are *G. ruficollis* and *G. olivacea*. Having the deepest and widest bills are *G. sulphurea*, *G. magnirostris*, *G. olivacea* and *G. fusca*. Generally the prey-attack behaviours and substrates exploited fit the predictions based on bill morphology (Fig. 2, Table 3), but confirmation would require the recording of finer details on behaviour and substrates (e.g. depth of bark substrates and a longer series of observations under different conditions).

In the absence of comprehensive data on the diets of the different species, it is difficult to interpret these differences. The Lederer-Hespenheide, Beecher, and Grant hypotheses cannot, accordingly, be tested. The long bills of *G. albifronsata* and *G. igata* accords with the predictions about insular forms. They may also, however, be an adaptation to trunk-probing. Aerial feeding is probably too uncommon in *Gerygone* to influence bill form.

Long rictal bristles, projecting outwards on either side of the bill, commonly characterise aerial feeders. However, alternative functions have been suggested (Lederer 1972; Stettenheim 1974; Conover & Miller 1980). In *Gerygone*, the longest rictal bristles are found in *igata* from New Zealand, *mouki*, Norfolk Island *igata*, and *palpebrosa* (Table 1). They are shortest in *fusca*, *chloronota* and *sulphurea*. An anticipated correlation between rictal bristle length and degree of aerial feeding is not indicated; presumably again because aerial feeding is too uncommon to elicit a morphological response.

Discussion

Gerygone occupies a clearly defined adaptive zone. They are a group of small-bodied warbler-like birds that obtain prey by gleaning or snatching from foliage. As a group, they are morphologically and ecologically homogeneous. The inter-habitat and inter-year data suggests a high level of consistency in the foraging ecology of *Gerygone*, but with some variation. The latter is to be expected and, as suggested by the differential use of Jarrah and Marri between years by *G. fusca*, occurs in response to changes in the distribution, abundance and kinds of prey. As shown by the differences in foraging behaviour of *G. fusca* between the populations in Kings Park and that at Karragullen, *Gerygone* also responds to differences in habitat structure and plant morphologies.

How discrete is the adaptive zone of *Gerygone*? How does it differ from that of taxonomic groups with which it occurs? The data available on the prey of *Gerygone* show that they take a variety of small-bodied invertebrates (Lea & Gray 1935; AK & HFR pers. obs.). They are not dependent on lerp-producing psyllid insects as an energy source and are rarely seen to take lerp, nectar, or sap (AK & HFR pers. obs.). In this they contrast with the small-bodied and short-billed *Smicrornis brevirostris*, *Pardalotus* spp., and *Acanthiza lineata*, and the larger-bodied foliage-gleaning honeyeaters (e.g. *Melithreptus* spp. and *Lichenostomus* spp; Paton 1980; Woinarski 1985; Recher 1989; Recher et al. 1991; Recher & Majer 1994).

Potential competitors and 'invaders' of the adaptive zone of *Gerygone* are *Acanthiza* and *Sericornis*, and meliphagids, such as *Melithreptus* and *Lichenostomus*. *Acanthiza* and *Sericornis* have radiated in a basically different way from *Gerygone*, producing clusters of differently adapted species that are sympatric, not allopatric. *Lichenostomus* honeyeaters have a continent-wide distribution with many allopatric species (Keast 1961) and a radiation pattern similar to *Gerygone*. Cohabiting species of *Lichenostomus* and *Melithreptus* also differ in their use of substrates (Keast 1968; Recher & Holmes 1985; Ford et al. 1986). The honeyeaters are, however, over twice as large in body size as *Gerygone* and glean prey from the foliage or bark; they seldom snatch or hawk and are unlikely to compete with *Gerygone*.

We posed two questions about *Gerygone*: (1) Do all species have a common morphology such that it would be disadvantageous for more than one species to co-occur? (2) Has *Gerygone* evolved an optimal morphology and set of foraging behaviours for specific sets of biological opportunities common to all habitats, such that it would be disadvantageous to change? Our study suggests that the answer to the first question is 'yes' and to the second a probable 'yes'.

The morphological and ecological versatility of *Gerygone* is such as to suggest that there is no reason why *Gerygone* could not expand into the adaptive zones of *Sericornis* and *Acanthiza*. This then raises the question of whether or not these genera constrain *Gerygone* ecologically, and hence morphologically. The answer is probably 'only partially', because the ranges are somewhat different. *Acanthiza* and *Sericornis* are primarily southern and eastern Australian forms and are rainforest dwellers in New Guinea (Blakers et al. 1984); *Gerygone* is largely northern Australian and New Guinean and tropical, with an extensive peripheral insu-

lar distribution beyond the continent (Fig. 1). It is possible that *Gerygone* has been prevented from radiating more widely in southern and eastern Australia by the abundance of other acanthizid genera in eucalypt forests and woodlands. Similarly *Gerygone* (together with *Smicrornis*) may constrain the radiation of *Acanthiza*, in particular, in more open woodlands and tropical forests where *Gerygone* (with *Smicrornis*) fills the arboreal, small insectivore role.

In support of the thesis that inter-group competition has had a role in the evolution of contemporary *Gerygone* is the fact that the greatest departures from its generalised features occur on islands with impoverished avifaunas. Thus, on Norfolk Island, *G. igata* could be said to fill the roles of mainland *G. mouki*, *Sericornis magnirostris*, *Acanthiza pusilla* and *A. lineata*. In New Zealand there are also few competitors. Note that *Acanthisitta*, which commonly co-occurs with *Gerygone igata*, also uses a wide range of substrates but uses different foraging behaviours (Hunt & McLean 1993). In any comparison of island and mainland forms, the two environments (island and mainland) are different, and so are the range of ecological opportunities available and the variety of co-occurring species. Reduced interspecific competition, resulting in ecological release, may not be the major factor in moulding an island ecology.

The present survey shows broad links between morphology, ecology, environment, and behaviour. In doing so, it supports some of the correlations between habitat and morphology suggested by previous authors. That more cannot be demonstrated is presumably because *Gerygone* is generalised in morphology and ecology. None of the species more than marginally enter the aerial-feeding adaptive zone of the flycatchers as do some warbler-like birds in other faunas (Keast et al. 1995) and none have developed the exaggerated clinging habit of some *Parus* (Palmgren 1932). Apart from this, the most aberrant species, *G. albofrontata*, shows the predicted correlations between an island form and ecological/morphological adaptation quite well.

There is one over-riding reason why we did not, and should not necessarily expect, clear-cut correlations between the various morphological structures measured by us and foraging behaviour. Evolution works on entire functional complexes, for example the entire hind-limb, multiple dimensions of the wing or the entire body of the bird, to achieve an 'adaptive end' (Leisler & Thaler 1982). Our morphological studies were restricted by the material available. The subject needs further study with a more comprehensive data set, specifi-

cally including the skeleton (Leisler & Thaler 1982) and components of the wing such as wingspan and aspect ratio (Pennycuik 1989).

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