

SOME LIFE HISTORY COMPARISONS OF SMALL LEAF-GLEANING BIRD SPECIES OF SOUTH-EASTERN AUSTRALIA

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Breeding biology, longevity and dispersal are compared for six species of thornbills *Acanthiza*, three gerygones *Gerygone*, two pardalotes *Pardalotus* and the Weebill *Smicrornis* from south-eastern Australia. The pardalotes and two thornbills (Buff-rumped and Chestnut rumped) lay relatively large clutches and have the highest nesting success. Incubation and fledging periods are longest for the pardalotes. The breeding season of the Weebill and both pardalotes are much more extensive than those of thornbills of gerygones. There is a pronounced peak in the breeding period for all gerygones (between October and December) and for all thornbills (between August and October). Both pardalotes and two gerygones show seasonal dispersal which is extensive relative to the marked sedentary nature typical of thornbills. Longevity in thornbills may be greater than that for pardalotes. These differences in life history are related to both food availability and nest-site selection.

INTRODUCTION

As a group, the small (6-12 g) leaf-gleaning birds in south-eastern Australia (the thornbills *Acanthiza*, gerygones *Gerygone*, pardalotes *Pardalotus* and Weebill *Smicrornis*) show life history patterns that are distinctly different to those of their ecological counterparts (mainly tits *Parus*, leaf-warblers *Phylloscopus*, warblers *Sylvia*, wood-warblers *Dendroica*, vireos *Vireo* and kinglets *Regulus*) in temperate North America and Europe (Woinarski 1985a). The Australian species have smaller clutch sizes, but longer breeding seasons and longer incubation and fledging periods. They are also more likely to be communal breeders, may have greater longevity and are more sedentary. Woinarski (1985a) has argued that these differences in life history between species of Australia and north temperate areas can be explained by differences in the availability of their invertebrate resource.

In this paper I restrict comparisons to the Australian species of small leaf-gleaning birds, specifically the Weebill *Smicrornis brevirostris*, Brown

Gerygone *Gerygone mouki*, Western Gerygone *G. fusca*, White-throated Gerygone *G. olivacea*, Brown Thornbill *Acanthiza pusilla*, Inland Thornbill *A. apicalis*, Chestnut-rumped Thornbill *A. uropygialis*, Buff-rumped Thornbill *A. reguloides*, Yellow Thornbill *A. nana*, Striated Thornbill *A. lineata*, Spotted Pardalote *Pardalotus punctatus* and Striated Pardalote *P. striatus*. I consider the extent of life history differences between them and whether these differences are associated with resource use. Bell (1983) and Bell and Ford (1986) provided detailed examination of this aspect for three species considered here (Brown, Buff-rumped and Striated Thornbills), and demonstrated a relationship between foraging behaviour, diet, social organization and survivorship. Woinarski (1985b) compared foraging behaviour and diet of all small leaf-gleaning birds of south-eastern Australia, and found that the Weebill and thornbills were the most generalist species, eating a wide range of invertebrates (and also lerps and other carbohydrate sources: Recher *et al.* 1985 and Recher *et al.* 1987).

The pardalotes were relatively specialized, eating mainly the lerp exudate of psyllids. The gerygones included a relatively higher proportion of flying insects in their diet. I examine whether these dietary differences among species within this family are accompanied by differences in life history characteristics.

METHODS

Breeding biology

Data were analyzed from the RAOU Nest Record Scheme to compare clutch sizes, length of breeding season, and incubation and fledging periods. Unless stated otherwise, only records from South Australia, New South Wales and Victoria were considered. This data set was augmented by some personal observations and previous literature reports.

Longevity

Other than the intensive study of Bell (1983), there is no detailed information on survivorship and longevity in this group. Retrap data from the Australian Bird and Bat Banding Scheme were compared with data from only those species for which a minimum of 800 individuals were banded.

Dispersal

To analyse the extent of seasonal shifts in populations, I compared, for every species, summer and winter distributions recorded for the 1° blocks used in the RAOU's *Atlas of Australian Birds* (Blakers *et al.* 1984). Only those blocks with at least ten record sheets per season were included. For each species I calculated a movement index based on the Jaccard similarity index (Smith and MacMahon 1981).

$$M.I. = 100 - \frac{\sum 2w}{a+b}$$

where w is the smaller of the two incidence values (the percent of record sheets in which that species was reported) for each block; a is the sum over all blocks considered of summer incidence values; and b is the sum of winter incidence values. This index varies from 0 (if there is no seasonal change in distribution) to 100 (if summer and winter ranges are totally disjunct).

Additionally, I examined all records for those species in the Australian Bird and Bat Banding

Scheme for the number of individuals recovered more than ten kilometres from their banding place.

Species which have a wide dispersal typically have longer and more pointed wings than those of their more sedentary relatives (Gaston 1974). I compared wing shapes of all species in this group, using the ratio of wingtip (distance in folded wing from tip of longest secondary to tip of longest primary: Baldwin *et al.* 1931) to cube root of body weight. All measurements were made by me on wild-caught birds in Victoria.

RESULTS

Breeding biology

The total number of young fledged per nest varied significantly ($F=7.0$, $df=11$ 568, $p<0.01$) between species, from an average of 0.6 per nest for Yellow Thornbill and Brown Gerygone to 2.7 per nest for Striated Pardalote (Figure 1c). Two features in particular contributed to the extent of this difference; the number of eggs laid (Figure 1a: $F=12.9$, $df=11$ 867, $p<0.01$) and the proportion of nests failing (Table 1: $X^2=52.0$, $df=9$, $p<0.001$). Both of these factors are related to the location of nests (Table 2), with those species nesting in more protected locations (hollows) having both higher clutch size and lower failure rates.

The duration and timing of breeding season showed pronounced variation between species (Figure 2). The Weebill and pardalotes have very long breeding seasons. In contrast, the breeding seasons of the thornbills and of the gerygones especially, are brief, with almost all clutches starting within a period of three months for the thornbills, between August and October, and for the gerygones, between October and December.

There are insufficient data available to make comparisons between species in the incidence of multiple broods per season. Nonetheless, double (and perhaps triple) broods seem normal for pardalotes (Bell 1959, Mollison 1960, Woinarski and Bulman 1985) and the interval between successive broods may be very short (2-8 days: Mollison 1960, Woinarski and Bulman 1985). Multiple broods may be regular in the Weebill (North

1901). Double broods have been reported for thornbills (North 1901, Ford 1963), but second clutches typically occur if the initial breeding attempt fails (Bell and Ford 1986). Both incubation and fledging periods are longest in the pardalotes (Table 3), such that the total duration from egg-laying to fledging is about ten days longer than in the Weebill, thornbills and gerygones. On top of this, there may be an additional 2 to 20 days involved in construction of a nesting tunnel (Bell 1959, Mollison 1960, Green 1974), although tunnels are re-used wherever possible (Rogers 1966, Lane 1967, Green 1971, Woinarski and Bulman 1985).

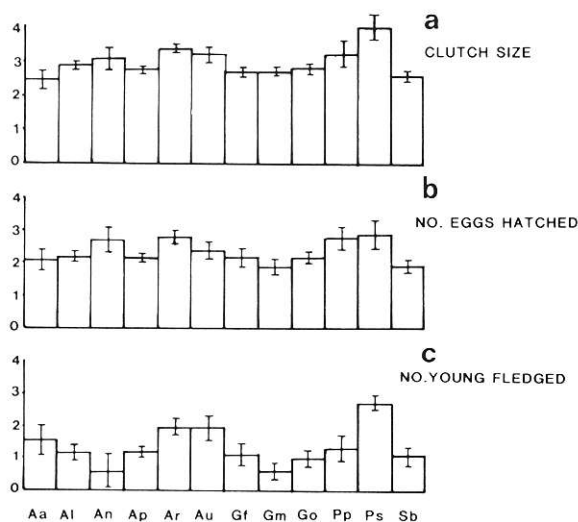


Figure 1. Mean values for (a) clutch size, (b) number of eggs hatched, and (c) number of young fledged per nesting episode for 12 species in south-eastern Australia. Species symbols are sample sizes: Aa=*Acanthiza apicalis* (n=6, 12 and 7), Al=*A. lineata* (n=83, 85, 94), An=*A. nana* (n=7, 9, 5), Ap=*A. pusilla* (n=234, 226, 195), Ar=*A. reguloides* (n=83, 95, 72), Au=*A. uropygialis* (n=16, 20, 8), Gf=*Gerygone fusca* (n=28, 25, 18), Gm=*G. mouki* (n=47, 33, 24), Go=*G. olivacea* (n=101, 71, 58), Pp=*Pardalotus punctatus* (n=5, 12, 19), Ps=*P. striatus* (n=9, 12, 40), Sb=*Smicrornis brevirostris* (n=80, 57, 40). Vertical lines represent one standard error. Differences between species are significant for clutch sizes ($F=12.9$, $df=11$ 867; $p<0.01$), eggs hatched ($F=3.1$, $df=11$ 645; $p<0.01$) and young fledged ($F=7.0$, $df=11$ 568; $p<0.01$).

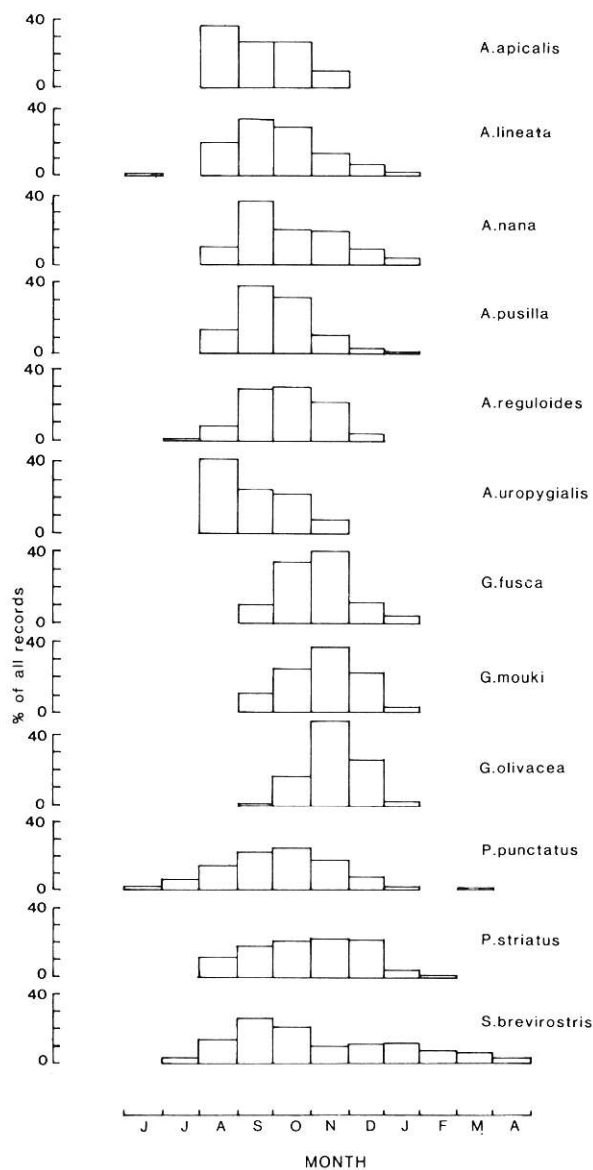


Figure 2. Frequency distribution of first eggs laid per clutch for 12 species in south-eastern Australia. Sample sizes are Aa (n=22), Al (n=200), An (n=21), Ap (n=375), Ar (n=151), Au (n=44), Gf (n=41), Gm (n=60), Go (n=150), Pp (n=146), Ps (n=192), Sb (n=125).

Longevity

For eight species, the total number of individual birds banded exceeded 800 (Table 4). Pooling the data from all of these species, the rate of recovery of birds at least eight years after banding is 0.129 per cent. This recovery rate was used to predict for every species the expected number of

individuals with at least eight years elapsed between banding and recovery (Table 4). Observed rates of recovery were higher than expected for Brown and Striated Thornbills and lower for the two pardalote species. Considering only these four species, which had the highest banding totals, this difference in recovery rate is significant ($X^2=16.2$, $df=3$, $p<0.01$).

TABLE 1

Comparison of rates of nest failure for species in south-eastern Australia. Species with fewer than eight nest record cards (n) are excluded.

Species	% of nests	n	Cause of failure (% of n)				
	failing*		P	PC	FG	ND	OC
Striated Thornbill	52.6	95	36.7	1.0	4.0	10.9	0
Brown Thornbill	54.6	196	32.0	7.3	0	15.3	0
Buff-rumped Thornbill	36.2	72	26.7	1.4	0	8.1	0
Chestnut-rumped Thornbill	12.5	8	0	12.5	0	0	0
Western Gerygone	61.2	18	47.7	0	7.0	7.0	0
Brown Gerygone	75.9	25	48.9	0	10.8	16.2	0
White-throated Gerygone	68.4	57	40.9	3.9	5.5	16.5	1.9**
Spotted Pardalote	31.2	32	25.0	0	0	6.2	0
Striated Pardalote	13.5	37	8.2	0	0	0	5.3***
Weebill	55.0	40	27.6	0	0	27.6	0

*Nest failure rate is the percentage of nests known to have raised no young divided by the total number (n) of nests where the outcome was known.

**Infested by ants.

***Overheated: ejected by kingfisher.

P=predated; PC=parasitised by cuckoo; FG=fell to ground; ND=nest deserted; OC=other cause.

TABLE 2

Position of nest site for species in south-eastern Australia.

Species	percent of nests				n
	in foliage	behind loose bark	tree hollow	ground hole	
Inland Thornbill	100	—	—	—	19
Striated Thornbill	100	—	—	—	200
Yellow Thornbill	100	—	—	—	21
Brown Thornbill	100	—	—	—	379
Buff-rumped Thornbill	68.8*	17.3	13.9	—	144
Chestnut-rumped Thornbill	—	—	100	—	44
Western Gerygone	100	—	—	—	41
Brown Gerygone	100	—	—	—	67
White-throated Gerygone	100	—	—	—	149
Spotted Pardalote	—	—	—	100	141
Striated Pardalote	—	—	53.7	46.3	280
Weebill	100	—	—	—	126

*includes also grass tussocks.

All data from cards of Nest Record Scheme, from Victoria, New South Wales and South Australia, except for Buff-rumped Thornbill and Striated Pardalote which include cards from all states where they occur.

TABLE 3

Nesting periods for species in south-eastern Australia.

Species	Incubation period (days)	Fledging period (days)
Inland Thornbill	18-19	16-18
Striated Thornbill	16-17	18-19
Brown Thornbill	19	14-16
Buff-rumped Thornbill	16-21	17-18
Brown Gerygone	18-19	15-16
Spotted Pardalote	16-22	18-25
Striated Pardalote	16-24	21-25
Weebill	18-21	18-19

All data from RAOU Nest Record Scheme, except for Brown Gerygone (from Marchant 1980).

Bell and Ford (1986) reported annual adult survival rates of 87 percent for Brown Thornbills and 54 percent of Buff-rumped Thornbills. No comparable figures are available for the other species. Woinarski and McEvey (1983) examined information on mortality of Spotted and Striated Pardalotes around Melbourne over a 20 year period and suggested that these species in particular may have very high rates of mortality in some winters.

Dispersal

The species were graded in the extent of their seasonal dispersal (Table 5), from the sedentary Striated and Brown Thornbill to three species with substantial seasonal shifts in distribution, Western and White-throated Gerygones and Striated Pardalote. No species had a totally disjunct summer and winter range and only one species (White-throated Gerygone) had a range for winter populations that overlapped less than half that of the summer range. The pronounced sedentary nature of the thornbill species has been reported at the few sites where local populations have been regularly censused (Lamm and Wilson 1966, Marchant 1982, Bell 1983). Although Brown Gerygones have a relatively low movement index, populations may disperse locally, extending beyond gullies and rainforests to other habitats in the non-breeding season (Hindwood and McGill 1958, Emison *et al.* 1987).

TABLE 4

Banding totals, with expected and observed rates of recovery for individuals at least eight years old.

Species	Number banded	Number of recoveries with >8 year elapsed	
		expected	observed
Inland Thornbill	827	1.1	0
Striated Thornbill	8 430	10.9	19
Yellow Thornbill	852	1.1	1
Brown Thornbill	13 379	17.3	24
Buff-rumped Thornbill	1 834	2.4	0
Spotted Pardalote	3 632	4.7	0
Striated Pardalote	4 189	5.4	0
Weebill	847	1.1	0

Australian totals up to 30 June 1983; from Australian Bird and Bat Banding Scheme. Excludes species with less than 800 individuals banded.

Movements documented through banding studies are extraordinarily meagre, probably reflecting both the very low likelihood of recovery of these small birds at places other than where intensive banding is undertaken and a real lack of movement of most individuals of those species with highest banding totals (Brown and Striated Thornbills). Only one individual of one species has been recovered more than ten kilometres from its banding point (a Spotted Pardalote that moved 590 km: Recovery Round-up 1980).

TABLE 5

Dispersal and wing-shape for species in south-eastern Australia.

Species	Movement Index*	Wingtip/cube root of weight
Inland Thornbill	25.2	4.1
Striated Thornbill	11.4	5.5
Yellow Thornbill	20.8	3.7
Brown Thornbill	11.7	4.0
Buff-rumped Thornbill	23.6	4.5
Chestnut-rumped Thornbill	27.6	4.4
Western Gerygone	39.6	6.1
Brown Gerygone	20.6	4.9
White-throated Gerygone	55.2	6.6
Spotted Pardalote	28.6	8.5
Striated Pardalote	33.2	9.2
Weebill	24.6	5.7

*Index varies from 0 (distribution of populations in summer = distribution of populations in winter) to 100 (completely disjunct summer and winter range).

Wing-shape was positively correlated with the extent of seasonal dispersal (Table 5: $r=0.52$, $n=12$, $p<0.05$), with long and pointed wings for the two pardalotes, White-throated and White-tailed Gerygones, and short and rounded wings for the thornbills, Weebill and Brown Gerygone. This suggests that the current patterns of dispersal may be long-standing.

DISCUSSION

Bell's (1983) intensive study of the social systems and ecology of three species of thornbill provides an example of the research needed to describe life history parameters and the factors that shape them. Unfortunately that study is one of the few such examples, and detailed knowledge is lacking on the life histories of most Australian birds. Accordingly, to compare life histories in the group of birds considered here, I have tried to relate information from a wide variety of sources. This database is fragmentary, which consequently frustrates some of the interpretations.

For the species considered, there are significant differences in some life history characteristics. Thornbills and gerygones have, relative to pardalotes, low annual reproductive output, both in terms of number of young raised per clutch and number of clutches raised per season. The two thornbills, the Weebill and the Brown Gerygone are sedentary or make seasonal movements which are limited and local. The pardalotes and two gerygones show a more extensive seasonal dispersal. Thornbills may be longer lived than pardalotes, although unfortunately the comparative data on survivorship are especially meagre. I have used information on the number of banded birds recovered long after banding (in this case, eight years) and such data may be misleading if the species compared vary in the extent to which they are sedentary. Nonetheless, some differences between species in terms of survivorship are effectively a corollary of comparable differences between species in their reproductive output. As further support, the analysis of Woinarski and McEvey (1983) suggested that spectacular episodes of mortality may be characteristic for pardalotes, whereas Bell and Ford (1986) found annual adult survival rates of Brown Thornbills to be very high.

These differences can be related to two factors: choice of nest site and diet. Nest location is probably the less important of the two factors, and indeed nest location may be more a consequence than a cause of the life history traits discussed here. Lack (1968) demonstrated a general relationship between the degree of protection of the nest site, breeding success, and incubation and fledging periods. This holds true also for the species considered here, with those species nesting in holes and hollows (the pardalotes and Chestnut-rumped Thornbill) having a lower rate of predation than foliage-nesting species (0-25% compared with 28-49% respectively). Consequently, the former species produce more young per nesting event (averages of 1.4-2.7 compared with 0.6-1.6). The hollow-nesting species also had larger clutches (averages of 3.2-4.0) than the foliage-nesting species (2.5-3.1). This difference in clutch-size may be determined by nest location and resultant differences in predation pressures. Relative to small clutches, large clutches may attract more attention from predators through increased noise and more frequent visits from parents. If the nest location is readily accessible to predators then smaller clutches may prove more successful.

Those species that nest in more sheltered sites do better in terms of breeding success than those that nest in more exposed sites. Saunders *et al.* (1982) showed that, relative to passerines in other continents, there are very few Australian passerines which do nest in hollows. Why then do not more species (and specifically more of the species considered here) use hollows or holes for breeding?

It is unlikely that there is a phylogenetic reason for this comparative lack of hollow-nesting species as (i) hollow-nesting has evolved independently across a very broad range of bird species (Lack 1968, Saunders *et al.* 1982) and, (ii) within the one genus *Acanthiza*, species range from obligate hollow-nesters (Chestnut-rumped Thornbill) to facultative hollow-nesters (Buff-rumped Thornbill) to obligate foliage-nesters (most other species). The substantial domed nest built in the nesting chamber of pardalote hollows suggests a relatively recent derivation of hollow-nesting from an ancestral foliage-nesting habit although Pardalotes have white eggs, which is characteristic

of hollow-nesting species of longer standing. In swallows, hollow-nesters have white eggs, cup/retort-nesters (*Hirundo*) have marked eggs; the hollow nesting Tree Martin *Cecropis nigriceps* have marked eggs, apparently having recently 'reverted' to this practice. (W. Boles pers. comm.). Pardalotes may have retained some potential for foliage-nesting, since there is recent record of a Spotted Pardalote nesting in a bush (Richards and Richards 1978).

One disadvantage of hollow-nesting is the prerequisite of trees with suitable hollows, and hence restriction to habitats with some old trees (Woinarski and Bulman 1985). Emancipation from this restriction may be possible if birds make their own hollows or show some flexibility in nest-siting requirements. Spotted Pardalotes construct their nest hollows independent of trees, but may suffer more predation (Hill 1911) as a consequence of increased accessibility (and may take longer in preparation of hollows). Striated Pardalotes may be able to switch nest-siting according to availability of tree hollows but their ground-nesting is limited to only a narrow range of soil and bank types (Woinarski 1974). In contrast the nesting flexibility of Buff-rumped Thornbills may enable them to nest in a wider range of environments, while still being able to gain the advantages of hollow-nesting where suitable hollows are abundant.

The lack of use of tree hollows by most of the species considered here may be because the general advantages that hollows convey (specifically the capacity for increased output per brood and the relaxation of growth rates of fledglings) may not be realized unless food resources are abundant and available over a relatively long period.

Differences in diet among species in this group relate reasonably well to the life history patterns discussed here. For pardalotes the preferred food item, lerps, may show dramatic fluctuations in density and reach superabundant levels in areas of outbreak (Clark 1962, White 1971). Such outbreaks may be unpredictable in time (season or year), duration and location (Clark 1962, Journet 1980). Dispersal ability and the potential for high and prolonged reproductive output are characteristics most suitable for exploiting such resources.

In contrast, in south-eastern Australia other foliage invertebrates may occur typically at low densities (Ohmart *et al.* 1983), show little seasonal fluctuation (Woinarski and Cullen 1984) and outbreak rarely (Neumann and Marks 1976, Ohmart 1985). Thornbills and the Weebill, which feed upon such invertebrates, show adaptations in life history well suited to this availability. Flying insects are a significant component in the diet of gerygones, and differences in life histories between gerygones and the other foliage-gleaning birds can be related to the availability of such prey items. In seasonal south-eastern Australia, adult flies, wasps and butterflies show a more marked decline over winter than do their larvae (Woinarski and Cullen 1984).

To maintain a diet in which flying insects are an important component, gerygones should disperse in winter to either aseasonal areas (such as inland Australia) or areas with a milder winter (for example, north-eastern Australia). Flying insects reach their peak in abundance later than do their non-flying larvae. Consequently birds which specialize in feeding on flying insects have delayed breeding seasons (Ricklefs 1973, Davies 1979). Gerygones show this typical late breeding.

This analysis shows that, within a fairly compact group (the small predominantly insectivorous leaf-gleaning species), differences in diet between species may also influence, through food availability, a wide range of life history characteristics. This relationship extends also to distribution, foraging behaviour and morphology. Some life history features, however, appear not to fit the general pattern: notably, the sedentary nature of Brown Gerygones relative to other gerygones of south-eastern Australia, and the obligate hollow-nesting of Chestnut-rumped Thornbills. Such anomalies merit more intensive study.

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