

## CHAPTER 12

## MORPHOLOGY

## INTRODUCTION

281. The three species of thornbills have been shown to differ less in what they eat but more in the way and place in which they find it. Therefore it could be expected that they would show morphological adaptations to match these ecological differences. If the morphology did match the feeding ecology then this implies that the differences in feeding habits at Wollomombi are the result of evolutionary processes rather than just local phenomena.

282. The different foraging behaviours of the three thornbills make possible some predictions, based on the literature, of morphological adaptations by them. One would expect Brown Thornbills to have long needle-like beaks for probing into tightly packed foliage, Buff-rumped Thornbills to have long curved beaks suitable for sliding into bark crevices, and the Striated Thornbill to have a relatively unspecialised beak for the flat surfaces on which it mainly forages. Expected aerodynamic differences suggested are good manoeuvrability for the Brown Thornbill which flies among dense foliage and a high aspect-ratio for the Striated Thornbill which hovers more than the other species. One would expect Buff-rumped Thornbills which cling to vertical surfaces and Striated Thornbills which hang from leaves to have longer and more curved claws. The Buff-rumped Thornbill, being a ground forager should have the longest legs and the arboreal Striated the shortest.

283. Many studies have been made on morphological adaptations to specialised feeding habits among birds, such as those of Newton (1967) and Ashmole (1968) on bills; Hartman (1961), Partridge (1976) and Norberg (1979), mainly on wings; and Richardson (1942), Dilger (1956) and Winkler and Bock (1976) mainly on legs and feet. In all

cases species were shown to have one or more morphological adaptations to a specialised feeding role, although in some cases the relation between morphology and feeding habit was debatable (see Partridge 1976 and Norberg 1979 for examples).

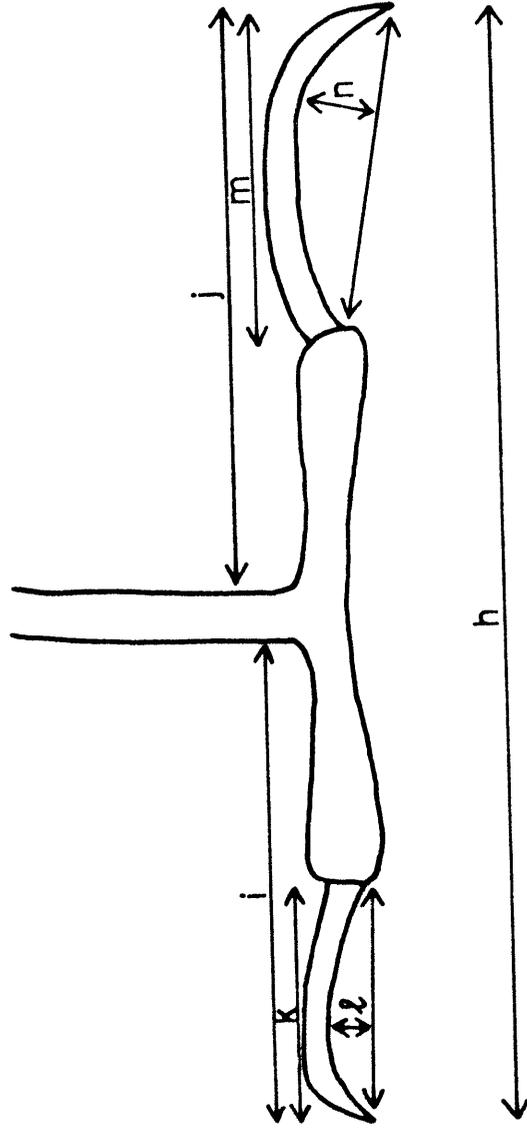
#### METHODS

284. The following measurements were made with dial calipers:

- a. Bill: length from gape to tip.
- b. Bill: length of exposed culmen.
- c. Bill: width at anterior of nares.
- d. Bill: depth at anterior of nares.
- e. Rictal bristles: length of longest bristle.
- f. Wing: length from humero-scapular joint to the tip of the longest primary.
- g. Tail: length from insertion of the two central rectrices to the tip of the longer one.
- h. Foot: span of outstretched right foot from the tip of the middle front claw to the tip of the rear claw. (see Figure 59).
- i. Front toe: length of outstretched right middle front toe from tip of claw to junction of toe and leg. (see Figure 59)
- j. Rear toe: length of outstretched right rear toe from tip of claw to junction of toe and leg. (see Figure 59)
- k. Front claw: length of right middle front claw from tip to junction of top of claw with the toe (see Figure 59).
- l. Curvature of front claw: height of curvature of right middle front claw from top of inside arch to line joining tip of claw with junction of underneath of claw and the toe. (see Figure 59)
- m. Rear claw: as for front claw.
- n. Curvature of rear claw: as for front claw.

Figure 59

Morphological data taken from right feet measured as follows; h: foot span; i: front toe length; j: rear toe length; k: front claw length; l: curvature of front claw; m: rear claw length; n: curvature of rear claw



285. Specimens examined included live birds taken in nets, birds shot for stomach sampling and study skins held in the Australian National Collection at the CSIRO Division of Wildlife Research, Canberra. Shot birds were sexed, if possible. Only those specimens in the National Collection of which the sex was known were used (many specimens of thornbills in all collections are unsexed).

286. Weights were determined by weighing netted birds with a Pe sola Spring balance (100 g capacity, graduated to 0.5 g) and towards the latter part of the study others were also weighed with a Mettler B balance (to 0.01 g sensitivity). The proportion weighed by the two methods was the same for all three species, so a mean of all measurements by both methods was taken. Dr H.A. Ford also supplied weights of live netted birds taken at Eastwood State Forest, near Armidale.

287. Specimens taken by me were dissected, and the severed right wings were pinned and flattened out on metric graph paper, and the outline of the wings traced. This was done three times for each wing. The area covered by the trace was computed by counting the number of 1 mm squares enclosed within the trace and the mean of the three measurements for each wing was the value adopted for later analysis.

288. The head and right leg of specimens were removed and de-fleshed in beakers of water at a temperature of 20°C. The following measurements were taken of the skeletal material:

- a. Cranium length: length of a straight line from a point level with the front of the Foramen Magnum to the tip of the bill.
- b. Upper jaw: length of upper jaw from junction with skull to tip of bill.
- c. Femur, tibio-tarsus and tarso-metatarsus: length between extremities of each bone, not between articulatory surfaces (therefore total length for limb bones longer than intact leg).

289. Ratios computed were:

- a. Tail/wing ratio: length of wing divided by length of tail.
- b. Wing loading: mean weight per species divided by mean wing area (I found it not possible to get accurate measurements of wing area from the live birds from which weights were taken, so wing area of specimens was used).
- c. Aspect ratio: mean wing length per species divided by mean wing area (most wing length measurements were from study skins and wing area from specimens).
- d. Bill length/width ratio: Bill length divided by width at anterior nares.
- e. Bill length/depth ratio: bill length (exposed culmen) divided by depth at anterior nares.
- f. Claw length/curve height ratio (both front and rear claws): height of claw curve (see Figure 59) divided by length.

290. The grasping strength of feet was estimated by the test of Partridge (1976). A piece of wooden dowelling 1 cm in diameter was attached to a Pesola Spring balance (graduated to 1g). The balance was held parallel to the ground and a bird placed so that its feet grasped the dowelling. The bird was then pulled slowly away from the balance until it released its hold on the dowelling, the maximum weight registered on the balance scale being recorded. Each bird was subjected to three pulls and the highest value recorded was taken as the grasping strength of that individual.

291. All measurements were tested for significant difference between sexes within a species, and between each sex with the total sample for each of the other two species. In all cases where species differed significantly this was true for both sexes so data for both sexes were combined.

## RESULTS

292. Appendix Q gives means, standard deviations and numbers of each sex from which each mean was derived. Table 31 lists significant differences between each species. Weights were virtually identical. Plate 4 shows the difference in shapes of beaks of the three species. Brown Thornbills had longer tails, proportionately lower tail/wing ratios and longer rectal bristles than the other two species. They had larger wing areas, longer leg-bones and crania, and longer and less deep beaks than Striated Thornbills. Buff-rumped Thornbills had proportionately longer femurs than Striateds, and longer rear toes and more curved rear claws than the other two species. They also had larger wing areas, longer leg-bones and crania, longer and more curved beaks and longer foot-spans than Striated Thornbills. Striated Thornbills had higher wing loadings, higher aspect-ratios, deeper and shorter beaks and longer rear claws than the other two species. They also had longer rectal bristles than the Buff-rumped Thornbill.

293. Results of the grasping test are shown in Table 32. The Yellow-rumped Thornbill, not syntopic with the three species under study, but present on adjacent farmland, is included because it feeds chiefly on the ground. The results show that the Striated Thornbill had by far the greatest grasping ability, Buff-rumped Thornbills had moderate ability and the Brown and Yellow-rumped Thornbills had poor ability.

294. The tongues of six specimens of each species were examined. A representation of typical tongues is shown in Figure 60. All species have bifurcated tongues, but with grooves of different lengths. Only the Brown Thornbill seems to have a fringe of filaments on either side of the tip of the tongue. Another difference is in the fringe of filaments at the back of the tongue, which was absent in the Brown, present in the Buff-rumped and extensive in the Striated. The comparative shortness of the Brown Thornbill's tongue was surprising, given the length of the beak.

Figure 60

Tongues of Brown, Buff-rumped and Striated Thornbills taken at Wollomombi

(top view, tips at right)



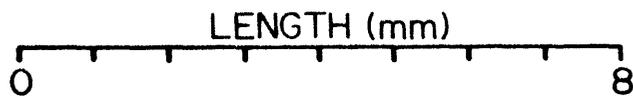
BROWN  
THORNBILL



BUFF-RUMPED  
THORNBILL

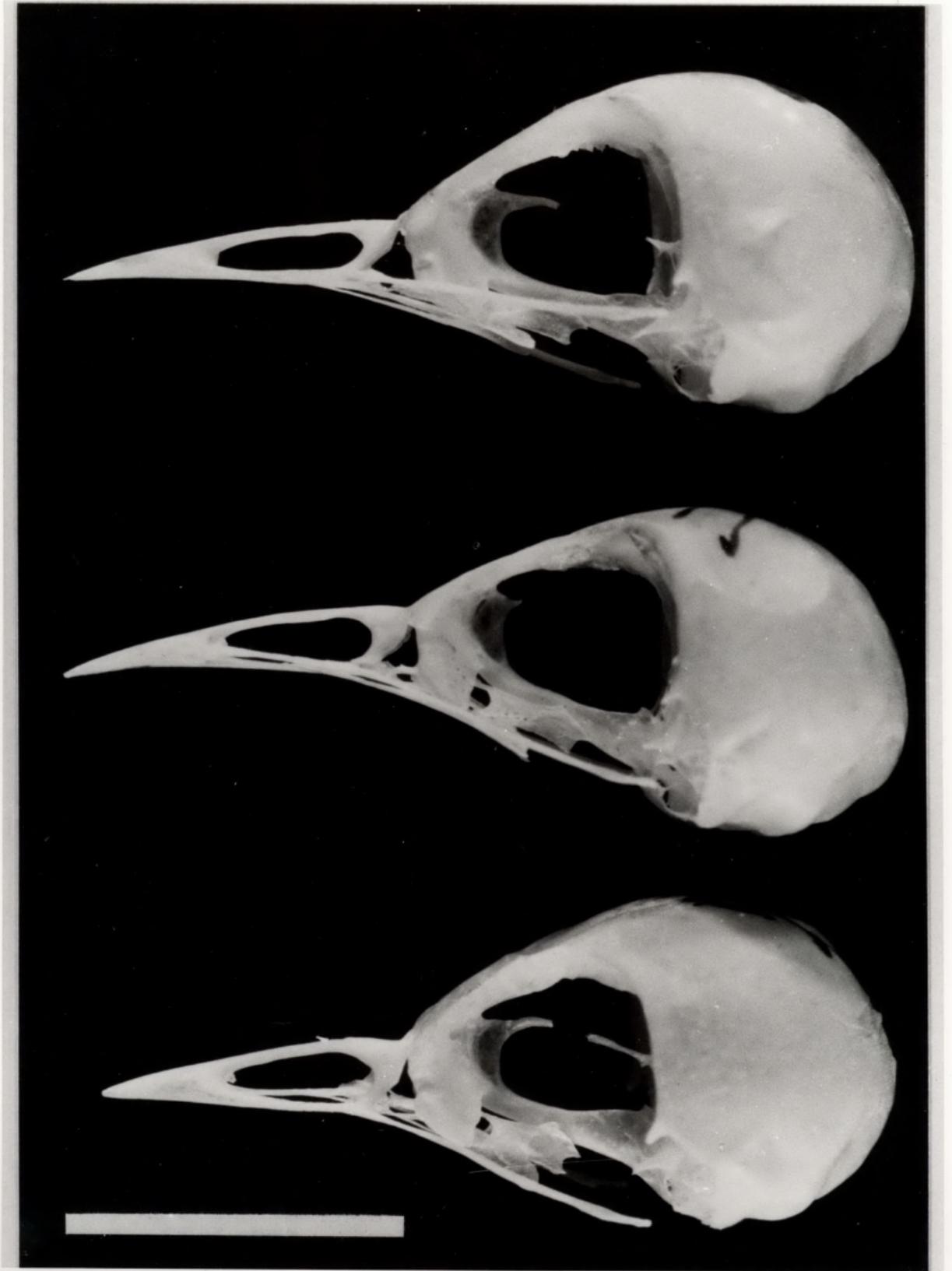


STRIATED  
THORNBILL



## Plate 4

Typical Beaks of (Top) Brown Thornbill, (Centre) Buff-rumped Thornbill  
and (Bottom) Striated Thornbill. Scale line: 1 cm.



Results of Comparisons of Morphological Data Between Species Pairs of Thornbills (each pair compared by T-test except where otherwise shown; \*: Mann-Whitney U-test; \*\*: mere comparison of means for each species)

	compared with: <u>Buff-rumped Thornbill</u>		<u>Striated Thornbill</u>
Wing length	Brown Thornbill	n.s.	n.s.
	Buff-rumped		n.s.
Tail length	Brown Thornbill	Brown longer $F < 0.002$	Brown longer $P < 0.002$
	Buff-rumped		n.s.
Tail/wing ratio (%)	Brown Thornbill	Brown lower $P < 0.005$	Brown lower $P < 0.005$
	Buff-rumped		n.s.
Wing area	Brown Thornbill	n.s.	Brown larger $P < 0.002$
	Buff-rumped		Buff-rumped larger $P < 0.05$
Weight	Brown Thornbill	n.s.	n.s.
	Buff-rumped		n.s.
Wing loading (**)	Brown Thornbill	Little difference	Striated larger
	Buff-rumped		Striated larger
Aspect Ratio(**)	Brown Thornbill	Buff-rumped slightly larger	Striated larger
	Buff-rumped		Striated larger
Bill length at gape	Brown Thornbill	n.s.	Brown longer $P < 0.002$
	Buff-rumped		Buff-rump longer $P < 0.002$
Bill length (culmen)	Brown Thornbill	n.s.	Brown longer $P < 0.002$
	Buff-rumped		Buff-rump longer $P < 0.002$
Bill width	Brown Thornbill	n.s.	n.s.
	Buff-rumped		n.s.
Bill depth	Brown Thornbill	n.s.	Striated deeper $P < 0.01$
	Buff-rumped		Striated deeper $P < 0.01$
Bill width	Brown Thornbill	n.s.	n.s.
	Buff-rumped		n.s.
Bill length/width ratio(*)	Brown Thornbill	n.s.	n.s.
	Buff-rumped		Buff-rump greater $P < 0.01$
Bill length/depth ratio(*)	Brown Thornbill	n.s.	Striated deeper $P < 0.01$
	Buff-rumped		Striated deeper $P < 0.01$
Rictal bristles	Brown Thornbill	Brown longer $P < 0.002$	Brown longer $P < 0.002$
	Buff-rumped		Striated longer $P < 0.002$
Foot span	Brown Thornbill	n.s.	n.s.
	Buff-rumped		Buff-rumped longer $P < 0.01$
Front toe & claw	Brown Thornbill	n.s.	n.s.
	Buff-rumped		n.s.
Front claw	Brown Thornbill	n.s.	n.s.
	Buff-rumped		n.s.
Depth of curve front claw	Brown Thornbill	n.s.	Striated deeper $P < 0.05$
	Buff-rumped		n.s.
Front claw length/depth ratio	Brown Thornbill	n.s.	Striated bigger $P < 0.01$
	Buff-rumped		n.s.
Rear toe & claw	Brown Thornbill	Buff-rumped larger $P < 0.05$	n.s.
	Buff-rumped		Buff-rump longer $P < 0.05$
Rear claw	Brown Thornbill	n.s.	Striated longer $P < 0.01$
	Buff-rumped		Striated longer $P < 0.002$
Depth of curve rear claw	Brown Thornbill	n.s.	n.s.
	Buff-rumped		n.s.
Rear claw length/depth ratio	Brown Thornbill	Buff-rumped greater $P < 0.05$	n.s.
	Buff-rumped		Buff-rump greater $P < 0.05$
Femur length	Brown Thornbill	Buff-rumped longer $P < 0.05$	n.s.
	Buff-rumped		n.s.

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Tibia length	Brown Thornbill Buff-rumped	n.s.	Brown longer P<0.01 n.s.
Tarsus length	Brown Thornbill Buff-rumped	Brown longer P<0.05	Brown longer P<0.002 n.s.
Total length of leg bones	Brown Thornbill Buff-rumped	n.s.	Brown longer P<0.05 n.s.
% of total leg length that is femur (**)	Brown Thornbill Buff-rumped	Buff-rumped greater P 0.05	Buff-rumped greater P<0.05 n.s.
% of total leg that is tibia (**)	Brown Thornbill Buff-rumped	n.s.	n.s. n.s.
% of total leg that is Tarsus	Brown Thornbill Buff-rumped	Brown greater P<0.05	Buff-rumped greater P<0.05 n.s.
Cranium length (includes bill)	Brown Thornbill Buff-rumped	n.s.	Brown longer P<0.01 Buff-rumped longer P<0.01

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Table 32

Results of Grasping-strength Tests on Thornbills at Wollomombi  
 (value for each individual in g)

Brown Thornbill	Buff-rumped Thornbill	Striated Thornbill	Yellow-rumped Thornbill
20.0	42.3	60.0	16.0
23.3	28.0	50.3	26.3
24.0	30.0	59.0	31.3
15.0	40.3	60.3	11.0
19.3	40.0	51.0	17.0
16.0		59.3	17.3
			17.0
			14.3
			9.0
			8.0

Results of paired comparisons by Wilcoxon's Sum of Ranks Test  
 (\*\* :  $P < 0.002$ ; \* :  $P < 0.01$ )    Striated \*\* > Buff-rumped \* >  
 Brown n.s. > Yellow-rumped.

## DISCUSSION

295. The weights of individual birds are known to vary between seasons and even time of day (Fisher 1955). Specimens of the three species of thornbills were taken in approximately the same proportions by both season and by time of day. I have therefore accepted the values given for weights in Appendix Q as showing that the three species are virtually of the same weight. This weight, *ca.* 7.1 g is fairly close to the lower limits known for passerines, about 5 g (Kendeigh 1972). This similarity violates Hutchinson's (1959) theory on size ratios between sympatric congeners where two species in the same trophic level can co-exist if their size ratios are more than 1.2. For reasons given earlier (paragraph 8) the theory is suspect, at least for insectivorous birds.

296. The wing-loadings of 0.21-0.27 g/cm<sup>2</sup> seems to fall within the data for birds of similar size elsewhere (Poole 1938, Hartman 1961). Birds with high aspect-ratios appear to be more efficient aerodynamically in that proportionately less of the wing is subject to tip vortices than in a wing of a low aspect-ratio (Patridge 1976). This may account for the Striated Thornbill, which has the highest aspect-ratio, hovering significantly more than the other two species and sallying more than the Buff-rumped Thornbill (Figure 53). Moreover, the Striated Thornbill's propensity for hanging on outer leaves may require, in the final approach to the leaf, hovering ability of a high order. The Brown Thornbill has the lowest wing/tail ratio of the three species. A long tail in proportion to wing length is considered by Hartman (1961) to aid manoeuvrability in flight, and the Brown Thornbill is the one species of the three to habitually fly through the foliage of dense understorey. The Buff-rumped Thornbill frequents mainly bare bark surfaces or the the ground, while the Striated Thornbill feeds mainly in the rather open canopy of eucalypts. Nevertheless, despite the significant differences in aerodynamic properties, the difference in values between the three species are not very great. Foraging habits that are dependent on aerodynamic qualities (ie. sallying, hovering, snatching, and perhaps hanging) make up only a small minority of the foraging techniques used by thornbills.

297. The differences in the bills of the three species appear related to differences in foraging habits. Both the Brown and Buff-rumped Thornbills have long thin bills, with the Buff-rumped being wider at the nares and being slightly decurved (see Plate 4). The Striated Thornbill, however, has a short deep bill. Newton (1967), Löhrl (1974) and Partridge (1976) found that species with long thin bills were those which probed into crevices or into finely-divided dense foliage such as the needles of conifers. The Brown Thornbill certainly probed into finely-divided dense foliage (e.g. bipinnate *Acacia*) which tended to be ignored by the other two species, and significantly, only the Brown out of the three species, readily adapts to plantings of exotic conifers (e.g. Pawsey 1966, Gepp 1979). The Buff-rumped Thornbill probed into fissures of bark, particularly on Stringybarks. A long and curved bill would be an advantage, enabling the bird to get at prey in deep and convoluted fissures. There is a possible explanation as to why the Buff-rumped Thornbill should have a bill which is wider at the base than that of the Brown Thornbill. Snow (1954) pointed out that a slender bill facilitates the picking up of food items much in the same way that forceps are easier to steer when picking up objects. Thicker instruments may partially obscure the object. Ludescher (1968) showed by photographs that titmice *Parus* spp kept their eyes open when picking up food and suggested that the tip of the bill was being controlled by sight. Following on from this Partridge (1976) demonstrated that a wider and/or longer bill could partially obscure vision, particularly of small items. Therefore the Brown Thornbill that takes insects from dense foliage, but apparently from the surface of leaves, may require to see the prey being taken. However the Buff-rumped Thornbill, which presumably can often not see the prey being extracted out of a deep fissure in the bark, need not have a slender bill. The shorter deeper bill of the Striated Thornbill is probably related to its main foraging site, the surface of *Eucalyptus* leaves, where there are no crevices. As Partridge (1976) further showed, a shorter bill enables a bird to take smaller prey, and it is noteworthy that the stomach samples taken from Striated Thornbills contained insects of a smaller mean size (although not significantly so) than those from the other two species.

298. The differing sizes of rictal bristles are difficult to explain. Rictal bristles have long been regarded as aids to aerial feeding i.e. by acting as sweeps to guide prey into an open bill (Van Tyne and Berger 1976), and certainly most families that are obligate aerial feeders (e.g. Apodidae, Caprimulgidae) have very large bristles. However Lederer (1972) produced evidence, for one family, that rictal bristles were not used in the capture of prey. Stettenheim (1973) suggested that rictal bristles may assist in retaining prey already held in the bill or that they might protect the eyes during flight. Whatever the reasons for rictal bristles, Cameron (1975) showed among three sympatric fantails *Rhipidura* spp the size of the bristles related to the extent of aerial feeding. Similarly Bell (1982b) showed that in a species with marked sexual difference in ecology, the Frilled Monarch *Arses telescopthalmus*, the female, which strongly favoured aerial feeding, had much larger bristles than the male, which rarely sallied. The amount of sallying by Brown and Striated Thornbills, although not great, was significantly higher than that of the Buff-rumped Thornbill, which has fewest bristles. However the Brown has much longer bristles than the Striated, even though they both sallied to the same extent. Perhaps the Brown, when inserting its bill into dense foliage, uses the long rictal bristles, in conjunction with the foliage, as a cage in which to entrap prey. Against this, the Striated, foraging on bare smooth *Eucalyptus* leaves would seem to have little opportunity to use its moderately long bristles in such a fashion.

299. The longer foot-span of the Buff-rumped Thornbill does not accord with findings elsewhere that a reduction in ground pressure, because of a greater foot-span relative to weight, enables a bird to perch on lighter substrates (e.g. titmice, Paridae, Palmgren 1932). Buff-rumped Thornbills perched mainly on the ground or on trunks and branches, much firmer perches than the outer leaves of bipinnate *Acacia* so favoured by the Brown Thornbill, which has a smaller foot-span. A possible explanation, discussed in the next paragraph, relates to the Buff-rumped Thornbill's predilection for perching on trunks.

300. Norberg (1979) showed that longer toes and curved claws assisted greatly in clinging to vertical surfaces. The two species with longer toes and claws and more curved claws, the Buff-rumped and Striated Thornbills, were the two that clung most to vertical surfaces (trunks in the case of Buff-rumped, hanging leaves for the Striated). Winkler and Bock (1976) showed that a longer foot-span greatly aided a bird clinging to a trunk. The claws of upwardly-directed toes tend to be pulled away from the bark and the backwardly-directed toes, as well as the tail, are pushed against it. Therefore the longer the foot-span, the smaller is the horizontal force away from the trunk on the forwardly-directed claws. This is possibly the explanation for the Buff-rumped Thornbill having the longest foot-span. Winkler and Bock also pointed out that a longer tail would assist a bird clinging to a trunk where the bark was smooth. The Buff-rumped Thornbill lacks the long tail but this would not be a disadvantage because the species clings to trunks of Stringybarks and Boxes (Chapter 9) which have rough bark, and does not seem to use its tail as a prop.

301. Various studies (e.g. Promptov 1956) have established that birds that are predominantly ground-feeders have longer legs than the more arboreal species. Also, other studies have shown that ground-feeders have relatively longer tarsi and shorter femurs (Dilger 1956, Newton 1967, Fretwell 1969). Conversely, birds that hang from vegetation have been found to have relatively short tarsi (Palmgren 1932, Grant 1965, Sturman 1968, Norberg 1979). However Partridge (1976) did not find these correlations in her studies of English titmice *Parus* spp. She found that the Great Tit *P. major* which fed more on the ground had a low tarsus: femur ratio whereas the Blue Tit *P. caeruleus*, which hung the most, had a relatively short femur and long tarsus. This was in contrast to Norberg (1979) who found that two hanging species, the Coal Tit *P. ater* and Willow Tit *P. montanus* had relatively short tarsi.

302. My data on thornbills agree with those of Partridge in that they contradict all the other references given above. Not only has the Brown Thornbill the longest legs; it also has a disproportionately long tarsus. One would expect it to be a ground-feeder. However it

is clearly much less a ground-feeder (ca. 3%) than the Buff-rumped Thornbill (ca. 34%). The Striated Thornbill does appear to conform with expectation in that it has the shortest legs and is the most arboreal of the three. However, although by far the greatest hanger of the three, it has a shorter femur than the Buff-rumped, which virtually never hangs. Obviously the conflicting findings of various workers overlook other factors, such as muscle thickness and strength, which may compensate for less well-adapted bone structures.

303. The results of the grasping-strength experiments supported Partridge (1976) in that the species that hung the most, the Striated Thornbill, had the strongest grasp. The Buff-rumped performed the next best, and it often clings to the sides of trunks and limbs. The Brown Thornbill which hung more than the Buff-rumped Thornbill had a surprisingly weak grasp. However, it hung disproportionately less on eucalypts than did the Striated (Chapter 10) and hung mostly on *Acacia*, *Cassinia* and *Olearia* where foliage structure would make hanging easier (no smooth surfaces and thus more friction). The ground-foraging Yellow-rumped Thornbill also had, not surprisingly, a weak grip.

304. Leg adaptations appear to be a compromise between conflicting pressures. If long legs are desirable for ground-feeders, as world-wide evidence suggests, then the Buff-rumped Thornbill should have long legs. However it also clings to bark surfaces as often as it feeds on the ground and for bark-feeders long legs would be disadvantageous (Norberg 1979). Thus a possible reduced efficiency in ground feeding may be outweighed by access to other resources (i.e. on bark) which would have become totally unavailable to a longer-legged bird. The seasonal change in feeding by the Buff-rumped Thornbill, between ground and arboreal feeding (Chapter 9) is no doubt related to this apparent 'trade-off'. Why the Brown Thornbill should have legs seemingly adapted for ground-feeding and not for hanging when it hung more than it fed on the ground is unclear. However for reasons given in paragraph 303, the sites on which it hangs may not have demanded strong adaptation to hanging.

305. The tongues of all three species seem typical of those for small insectivores illustrated by Gardner (1925). Of interest is the differing degrees of bifurcation among the three thornbills; exactly the situation found by Noske (1978) among the three tree-creepers *Climacteris* spp found at Wollomombi. Although Noske found that all three tree-creepers ate ants extensively, the ground-feeding *C.picummus*, which had the least bifurcation, fed on ants the most. Similarly the ground-feeding Buff-rumped Thornbill fed on ants more and had the least bifurcation of the thornbills. Gardner (1925) considered that the fringe at the back of the tongue was to prevent escape by insects being swallowed. Because the Striated Thornbill appears to feed on smaller (and more active?) insects, particularly dipterans, than the other thornbills, the extensive fringe at the back of its tongue may well serve this purpose. Overall, however, the usefulness of tongue morphology, in identifying adaptations to niches, has been strongly questioned (e.g. Gardner 1925, Rand 1967, McKean 1969).

306. The morphological differences between the three species, though in each comparatively minor, seem to be in most cases adaptations that enable the species to forage in ways or in places more efficiently than its congeners. All three species eat substantially the same things, with perhaps the Striated Thornbill taking slightly smaller prey. Therefore their adaptations enable the three to share virtually identical resources but substantially, in each case, from foraging sites less readily available to the others.

## PART IV

## CHAPTER 13

## FOOD LIMITATIONS IN THORNBILLS

## INTRODUCTION

307. As mentioned previously (paragraph 10, Chapter 1), there have been few studies in which the foraging behaviour of potentially competing species has been compared between periods of abundance and scarcity of food. None, so far as I know, has monitored such information for continuous extended periods, i.e. over one year or more. However, sufficient evidence, drawn from groups as diverse as fish (Zaret and Rand 1971), large African ungulates (Jarman 1971) and doves (Morel and Morel 1974), exists to show that feeding behaviour of syntopic species diverges as food becomes scarce. The aim of this chapter is to show the interaction between behaviour and the food supply over a continuous period, using the data obtained in the preceding chapters.

308. If insectivorous birds are regulated by availability of food we can make the following predictions:

- a. When arthropods are scarce insectivorous birds should leave the area or turn to non-insectivorous foods (Lack 1947)
- b. With sedentary species mortality should be highest when food is scarcest (Lack 1947)
- c. Interference competition, i.e. physical denial of food to other birds, should be more frequent when food is scarcest (Ripley *et al.* 1959, Wolf 1978)
- d. Breeding should take place at, or just before, periods of peak abundance of food (Murton and Westwood 1977, Nix 1976)
- e. Foraging rates should be greatest when food is scarcest, because birds will need to work harder to find food (Gibb 1950, Kluijver 1950)

- f. Size-ranges of arthropods taken should be smaller, or the prey less palatable, when food is scarce (Krebs and Davies 1981)
- g. Morphological differences should be related to specialisations in foraging (Lack 1947, Cody 1974)
- h. Each species' specialisation in foraging should, at times of scarcity, be related to diet (Lack 1947, Cody 1974)
- i. Specialised foraging techniques of each species should be used more often in time of scarcity (Baker and Baker 1973, Schoener 1982)
- j. (1) Overlaps between species should be lowest when food is scarcest, as each species specialises in those foraging techniques at which it is most efficient (Lack 1947, Schoener 1974); or:
  - (2) Overlap should increase when food is scarce as each species should have to extend its range of food to less acceptable items and in so doing visit a wider range of foraging sites (Emlen 1966, Svårdson 1947, Krebs and Davies 1981)
- k. Overlaps should be higher when species associate in mixed-species feeding flocks (MSF) and MSF should be more frequent in times of scarcity (Morse 1970).

309. For predictions a. to h. the answers can be found from the data presented in Chapters 5-11. Therefore, in this chapter, the methods and results will deal with only predictions i., j. and k. Following this all predictions will then be discussed in turn.

#### METHODS

310. Various measures of overlap have been used, the most common and the one I use here being that of Schoener (1968):

$$\alpha = 1 - \frac{1}{2} \sum_{i=1}^S |p_{x_i} - p_{y_i}|$$

where  $\alpha$ : overlap,  $p_{x_i}$  and  $p_{y_i}$  are frequency of use of category  $i$  by species  $x$  and  $y$ . Cody (1974) has suggested two ways in which overall overlap can be calculated: the overlap values for two or more dimensions can be averaged (mean  $\alpha$ ) or multiplied together (product  $\alpha$ ). In the former case the assumption is that the resources are totally dependent upon each other, i.e. all gleaning is in leaves, all probing is on bark etc. In the latter case it is assumed that they are independent, i.e. frequency of gleaning in bark-foraging is the same as in leaf-foraging. In nature, resource dimensions are to some degree dependent on each other and so the actual overlap will be somewhere between mean  $\alpha$  and product  $\alpha$ . In this study I have calculated overall overlap directly, i.e. I have taken the  $w$  substrate,  $x$  plant species,  $y$  height, and  $z$  foraging method as representing resources along a single dimension ( $w \times x \times y \times z$ ). Overlaps between all species were calculated along this single dimension for each month. One possible problem was that for the first seven months all eucalypts were grouped (Chapter 8) and therefore, having fewer variables the data for those months could have shown overlaps higher than would otherwise have been the case. As a check I combined data for all three eucalypt groups for the remaining 29 months, but found that monthly overlaps were increased by only 0-2%, so I did not adjust data for the first seven months when eucalypts were grouped.

## RESULTS

311. Among the three thornbills the relatively exclusive resources (i.e. feeding sites) available to each species were: Brown Thornbill, dense foliage of the understorey; Buff-rumped Thornbill, the ground and vertical bark surfaces; Striated, tips of hanging eucalypt leaves (reached by hovering or hanging). If Schoener (1982) is correct, then those seasons in which thornbills significantly used their 'exclusive' resource more than at other times should be those in which food was least abundant. For the overall study this was not so, except for the

Striated Thornbill. However the drought, in the last two years of the study had probably distorted the picture, in particular that of abundance of arthropods (see paragraph 51, Chapter 2). Table 33 shows the situation in the first year (1978/79) of the study, as a 'normal' one, i.e. with a summer peak and a winter low in insects.

312. No species used its specialized behaviour significantly more in times of high abundance (summer). All three used their specialised behaviour significantly during the period of least abundance (winter), except that the Striated Thornbill hung more in autumn, which however was a period of moderate scarcity. The significant use of specialised foraging by Brown and Buff-rumped Thornbills during spring, when food appears to have been moderately abundant, can be explained. Comparative values of abundance in spring were 0.04, 0.06, and 0.38 respectively for September, October and November, so the combined value of 0.48 disguises what was in fact mainly a very lean period.

313. Figures 61 and 62 show comparisons between monthly overlaps of each pair of species with the Plantgrowth Index (PGI) (see Figure 2, Chapter 2) and with the abundance of arthropods on foliage (see Figure 7, Chapter 3). Values shown for overlaps include those for all foraging data and those for data taken when the species were not in MSF. For correlations I have used the data taken not in MSF. Also, in the case of the Brown/Buff-rumped combination, that part of the overlap not in MSF, which was contributed by ground-foraging, is shown separately.

314. Correlations between PGI and overlaps are poor though significant in two cases (Spearman Rank Correlation: Brown/Buff-rumped,  $r: 0.400$ ,  $P < 0.05$ ; Brown/Striated,  $r: 0.214$ ,  $P$  n.s.; Buff-rumped/Striated  $r: 0.401$ ,  $P < 0.05$ ). Overall, however, as shown by t-test in Table 34, when the PGI is low ( $< 0.2$ ) the mean for overlap also tends to be low i.e. when primary productivity was low, bird species diverged in foraging behaviour. One reason for the poor correlation was that although overlaps dropped when productivity fell, there was a marked increase in overlap, in almost every case, well before the PGI began

Figure 61

Comparison of foraging overlaps between species pairs of thornbills  
with PGI (overlaps: x: all observations; y: all those not  
in MSF; shaded part of Brown/Buff-rumped overlap is  
ground-foraging not in MSF)

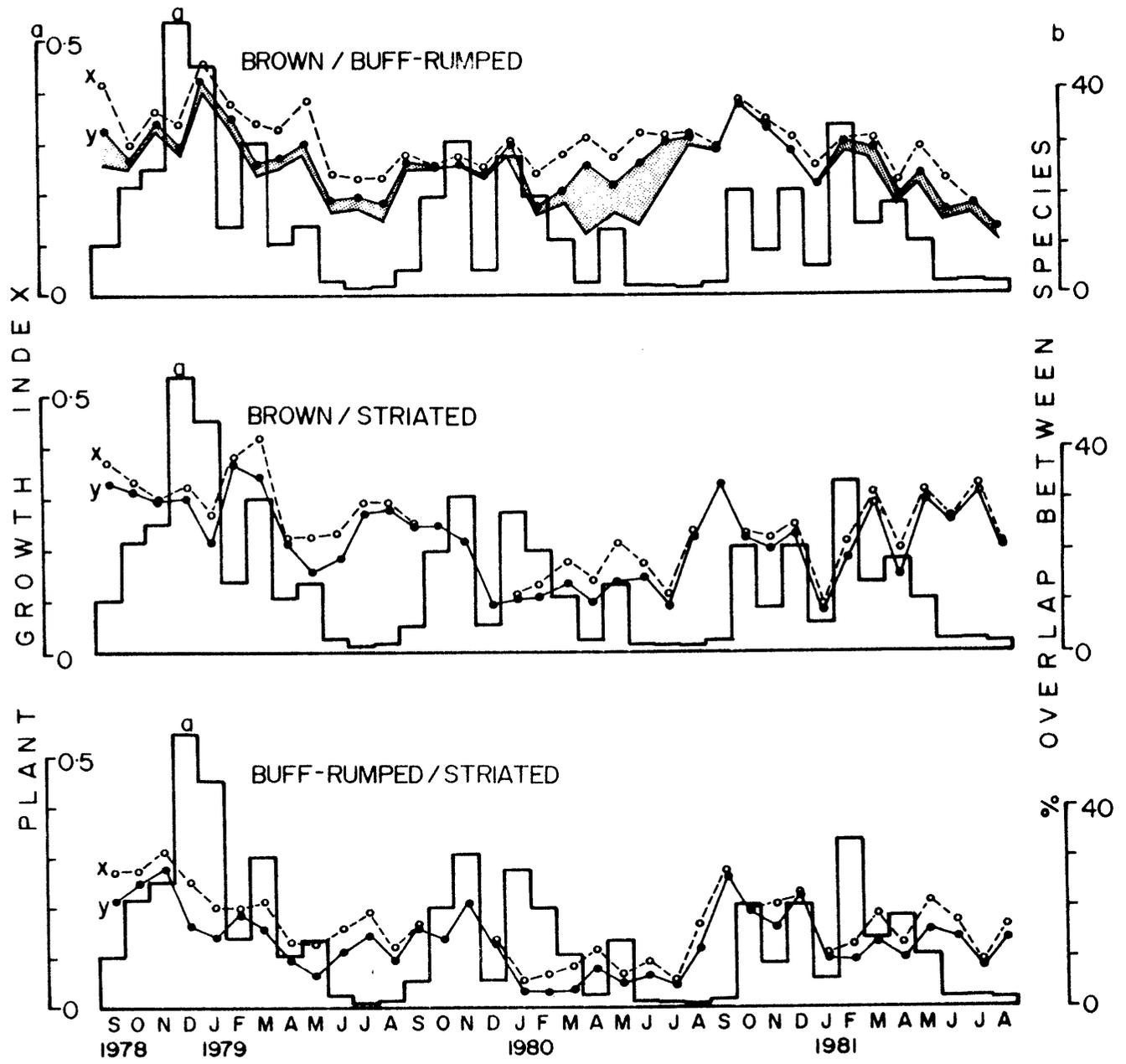


Figure 62

Comparison of foraging overlaps between species pairs of thornbills  
with abundance of arthropods on foliage overlaps: x: all  
observations; y: all those not in MSF; shaded part  
of Brown/Buff-rumped overlap is ground-foraging  
not in MSF)

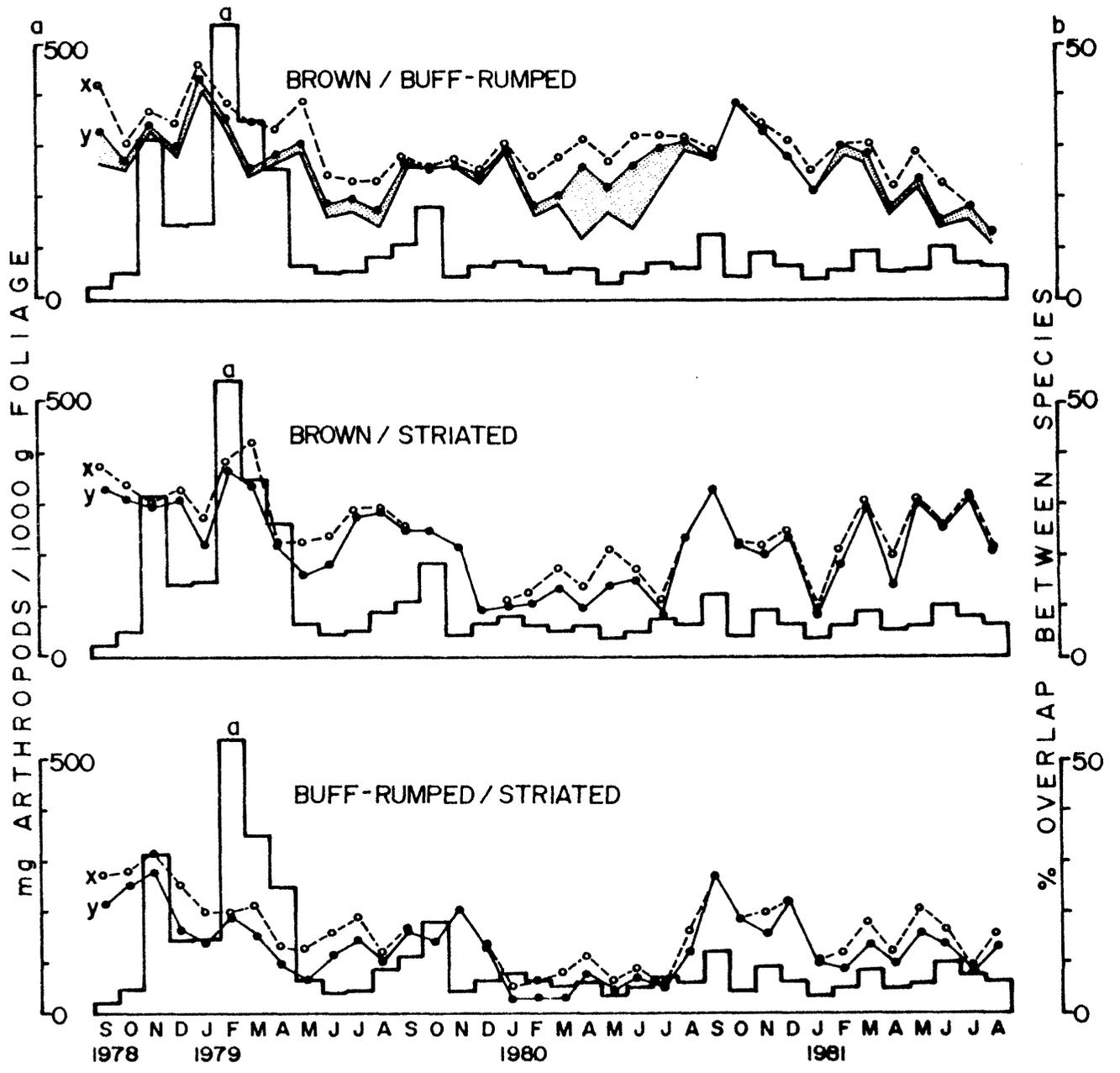


Table 33

Comparison of the Seasons in Which Each Thornbill Species Carried  
Out its Specialized Foraging Behaviour Significantly More Than  
Expected and the Availability of Arthropods by Seasons,  
September 1978-August 1979

	Spring	Summer	Autumn	Winter	Data source
Comparative Abundance of food	0.48	1.00	0.38	0.04#	
Brown Thornbill					
Foraged more in dense understorey	***	#		**	Chapter 9
Buff-rumped Thornbill					
Foraged more on ground				***	Chapter 7
Foraged more on trunks	***	#		**	Chapter 7
Striated Thornbill					
Hovered more				***	Chapter 10
Hung more			***		Chapter 10

\* X<sup>2</sup> Test results, values for foraging type by season against mean for that type for whole year: \*\*\*: P<0.005; \*\*: P<0.01): data from Figures 35 and 47 and Table 24.

# Values for abundance of food taken from figure 8. N.B. that in spring monthly values were 0.04, 0.06 and 0.38, therefore the overall value gives an unrealistic picture of abundance for the greater part of the season.

Table 34  
Comparison, by T-test, of Mean Overlaps (and S.D.) Between  
Thornbill Species, in Months of Scarce and  
Abundant Resources

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Overlaps compared to Plant Growth Index %

Species pair	Mean overlap when:		Significance by T-test
	PGI over 0.20	PGI under 0.20	
Brown/Buff-rumped	31.27 ± 5.76	24.38 ± 5.86	P<0.002
Brown/Striated	24.34 ± 7.18	21.19 ± 8.60	P<0.05
Buff-rumped/Striated	17.35 ± 7.49	11.92 ± 5.62	P<0.002

Overlaps compared to abundance of arthropods on foliage %

Species pair	Mean overlap when values per 1 kg leaves:		Significance by T-test
	Over 100mg	Under 100mg	
Brown/Buff-rumped	30.67 ± 5.86	24.41 ± 6.17	P<0.01
Brown/Striated	28.71 ± 5.51	18.90 ± 7.32	P<0.002
Buff-rumped/Striated	17.87 ± 6.10	11.02 ± 5.36	P<0.002

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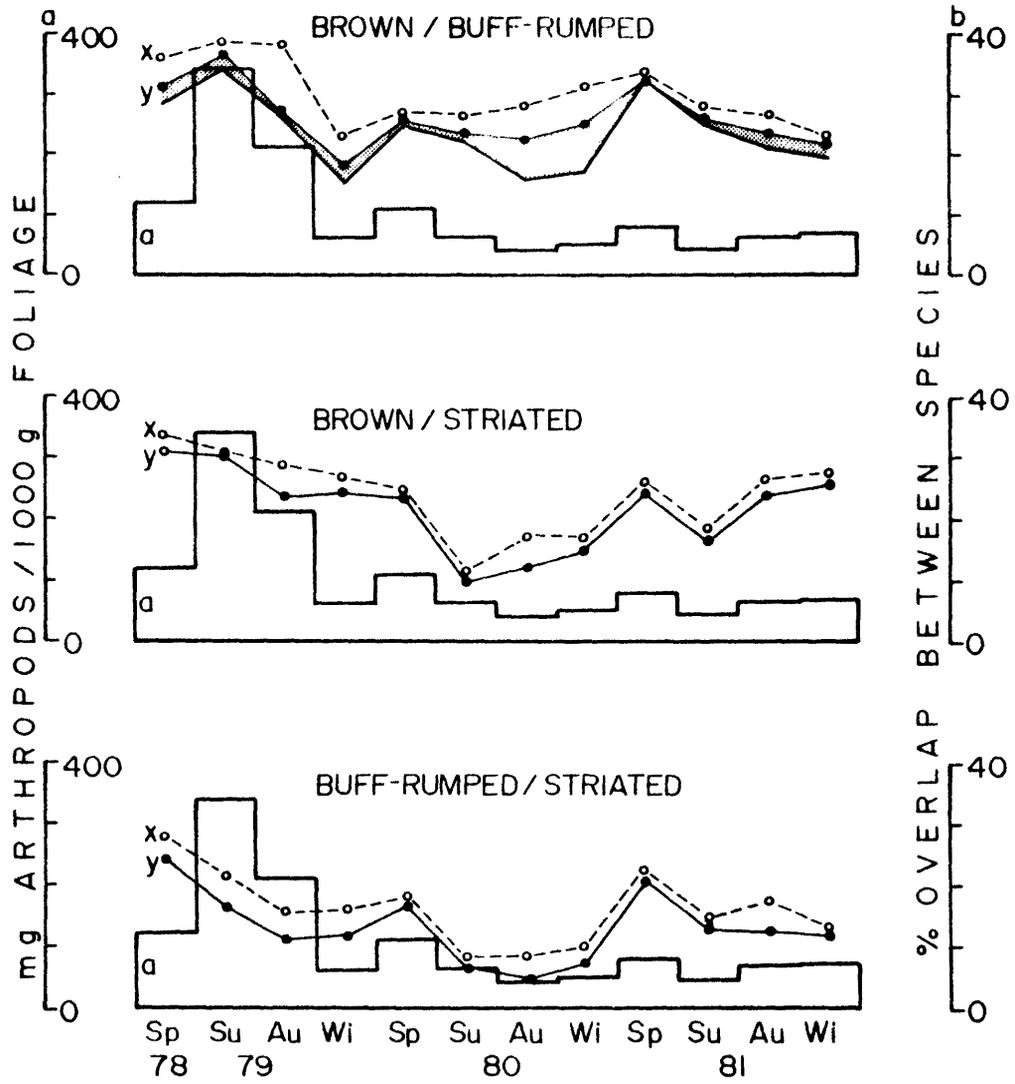
to rise. In the case of the Brown/Buff-rumped combination much of the unexpected rise in overlap during the autumn and winter of 1980, at the height of the drought, was contributed by the abnormal behaviour of the Brown Thornbill in switching to ground-foraging (see Chapter 7).

315. As shown in Figure 62 correlation between overlaps and abundance of arthropods was also poor (Spearman Rank Correlation: Brown/Buff-rumped,  $r: 0.259, P < 0.05$ ; Brown/Striated,  $r: 0.442, P < 0.05$ ; Buff-rumped/Striated,  $r: 0.490, P < 0.01$ ). Similarly to the comparison between overlap and PGI, there were rises in overlap well before any increase in the food supply, and also the same contribution to increased overlap by the Brown Thornbill's switch to ground-foraging. Table 34 also shows by T-test that, overall, low levels of food supply ( $< 100 \text{ mg}/1000 \text{ g}$  of leaves) give lower overlaps than periods of higher abundance. The usefulness of a rank correlation was minimised by the uniform levels of (low) abundance in the second and third years. Therefore data in Figure 63 are presented by seasons, as opposed to months, in Figure 62. Here abundance of food accounts for a greater proportion of variance in overlap than it does in the monthly samples (Spearman Rank Correlation: Brown/Buff-rumped,  $r: 0.707, P < 0.05$ ; Brown/Striated,  $r: 0.728, P < 0.01$ ; Buff-rumped/Striated,  $r: 0.651, P < 0.05$ ). Once again, with the Brown/Buff-rumped combination the comparatively high degree of overlap in the very lean period of autumn and winter of 1981 was contributed to heavily by the Browns' change to ground-foraging.

316. Abundance values for insects taken in grass sweeps (see Figure 7) are not compared with overlap. The only species that feeds on the ground to any great extent, the Buff-rumped Thornbill, showed an inverse correlation between ground-feeding and the values for arthropods taken in grass sweeps (Spearman Rank Correlation,  $r: -0.689, P < 0.01$ ), suggesting that factors other than food abundance at ground level influence its trend to ground-feeding in winter (see Chapter 9). The Brown Thornbill also switched to extensive ground feeding in the winter of 1980 when the values for sweeps were low.

## Figure 63

Comparison, by seasons, of overlaps between species pairs of thornbills with abundance of arthropods on foliage (a) (overlaps: x: all observations; y: all those not in MSF; shaded part of Brown/Buff-rumped overlap is ground-foraging not in MSF)



317. When overlaps include observations taken in MSF (Figures 61, 62 and 63) the situation is not much different from that for data taken when not in MSF, except for the Brown/Buff-rumped combination. Brown Thornbills increased their overlaps with Buff-rumped Thornbills more in autumn and winter than at other times. The comparatively low MSF component in the overlaps shown for the other two species combinations is because little of the Striated Thornbill's activity in MSF was with those species. However, at those times when thornbill species were associated in MSF their overlaps greatly increased. Table 35 summarises the data from Figures 38, 45 and 52, which showed changes in behaviour by the species, for substrate, plant species and height respectively. Foraging method (Chapter 10) was not included because it did not change when birds joined MSF. Table 35 shows that with all combinations overlap greatly increased when in MSF except when flocks of Buff-rumped and Striated Thornbills joined.

#### DISCUSSION

318. The discussion in this chapter will be presented as an answer to the predictions detailed in paragraph 308 above.

Prediction a: (birds should leave the area or turn to other foods in time of scarcity)

319. Monthly values for the biomass of insectivorous birds present at Wollomombi showed no correlation with the supply of arthropods (Figure 7, Chapter 2). Indeed the biomass present showed fairly regular annual peaks and troughs apparently unrelated to the supply of food. No thornbills left the study area other than the usual young of the previous season, these tended to be replaced by immigrants, also probably young birds (Chapter 5).

320. There is a suggestion (Chapter 11) that thornbills may turn to other foods in times of scarcity. Only two stomach samples contained seeds but both were taken in times of scarcity (August 1979, July 1981). One of these stomachs contained 40 seeds, as well as insects, which suggests that ingestion of seeds is not accidental. Unfortunately

Table 35

Percentage Overlaps Between Species Pairs of Thornbills When  
and When Not in MSF

Species combination		Substrate	Plant species	Height	Mean
Brown/Buff-rumped	in MSF	95	71	85	84
	not in	51	52	42	48
Brown/Striated	in MSF	95	67	72	78
	not in	88	32	28	49
Buff-rumped/Striated (both in flocks)	in MSF	35	53	46	44
	not in	38	39	25	34
Buff-rumped/Striated (1-3 Buff-rumped in flock of Striated)	in MSF	60	64	46	60
	not in	38	39	25	34
Buff-rumped/Striated (1-3 Striateds in flock of Buff-rumped)	in MSF	35	52	59	49
	not in	38	39	25	34

there are no data on consumption of nectar, but as shown in Table 29 it is possible that Brown and Striated Thornbills could turn to nectar. There were, however, very few sources of nectar at Wollomombi during the study period, although honeydew may have been freely available. Generally prediction a. was not supported by the available data, though there is a little circumstantial evidence.

Prediction b: (mortality should be highest in times of scarcity)

321. Mortality of thornbills was strongly correlated with scarcity of arthropods (Figure 26, Chapter 5). As has been earlier discussed (Chapter 5) this correlation seems unrelated to the rigours of temperature and short day-length of those seasons (winters of 1979 and 1980) in which deaths were most frequent. In the winter of 1981, when insects become relatively more abundant than in the previous summer, and when thornbills had become fewer (Figure 26) losses were small. Prediction b. is supported by the data.

Prediction c: (interference competition should be greatest in times of scarcity)

322. Data on interference competition are too few for analysis, and for reasons discussed earlier, the diets of thornbills are such that there are few opportunities to defend a clumped resource (Chapter 5). However, on occasions thornbills will attempt to exclude other species from food resources. The most important observations of interference competition (Chapter 5) were at a time of great scarcity. Prediction c. is not supported by sufficient data, but some evidence for it does exist.

Prediction d: (Breeding should occur at or near periods of peak abundance of arthropods)

323. Data on breeding (Figure 13, Chapter 4) show that nesting is timed to coincide with abundance of arthropods. The peak of egg-laying tended to be about one month ahead of peak abundance which would ensure that most young fledged at that time. Prediction d. is supported by the data.

Prediction e: (Foraging rates should be fastest when food is scarcest)

324. Foraging rates increased and distances covered per move were less in times of scarcity (Figure 54, Chapter 10). This indicates that as food becomes scarce birds have to work harder to find it. This is further corroborated by Table 27, Chapter 10, which showed that foraging rates increased and distances covered were less in mornings than at other times. During mornings birds would be under pressures, to replace energy lost during the night. Also lower morning temperatures would necessitate a faster replacement of energy loss than in the warmer times of the day. Insects could also be more difficult to find as they would be less active and therefore less conspicuous at low temperatures. Prediction e. is supported by the data.

Prediction f: (size of prey taken is smaller in times of scarcity)

325. The evidence on sizes of arthropods taken (Table 30, Chapter 11) shows that Striated Thornbills took smaller prey in lean (i.e. cooler) months. Brown and Buff-rumped Thornbills appeared not to show a change in length of prey taken. However they did switch to ants in the cooler seasons, even though ants were much more abundant in summer (Figure 9, Chapter 3). Although thornbills took mostly prey of 3-4 mm in length (Figure 57, Chapter 11) they generally took no ants below 5 mm long, even though most ants were under that length (Figure 58, Chapter 11). This suggests that ants may be less palatable or less profitable as food. If ants are excluded from seasonal comparisons of diets then both Brown and Buff-rumped Thornbills, as well as Striateds, showed significant decreases in size of prey taken during lean periods. However the mean lengths of arthropods available in cooler seasons is also smaller than that in warmer periods (Figure 12, Chapter 3) so the changes by thornbills may merely reflect availability rather than a need to take sub-optimal items because food is scarce. Prediction f., therefore, is generally supported by the data, although alternative explanations are possible.

Prediction g: (morphological differences should be related to foraging behaviour)

326. The specialised foraging behaviours shown by the three species (Table 33), i.e. those mostly exclusive to one species, were related to morphological differences (Chapter 12). Brown Thornbills have adaptations to their beaks and aerodynamics that enable them to forage efficiently in dense vegetation with tightly-packed foliage. Striated Thornbills have adaptations to their legs, feet and wings, which enable them to forage at the hanging tips of eucalypt foliage. Buff-rumped Thornbills have adaptations to beaks and feet which fit the species for bark-foraging. Adaptation to the most specialised foraging behaviour, that of ground-foraging by Buff-rumped Thornbill, is not strongly supported by the morphological evidence, in that the legs, which should be relatively long for a ground-feeder (see Chapter 12) are no longer than those of the Brown Thornbill, not usually a ground forager. At least the legs of the Buff-rumped are better adapted for ground-feeding than the short ones of the arboreal Striated Thornbill. Overall, Prediction g. is supported by the data.

Prediction h. (specialised foraging should relate to diet in time of scarcity)

327. The evidence for diet (Table 30, Chapter 11) of Buff-rumped Thornbills and Brown Thornbills shows an apparent change to ants and seeds at the same period (cooler seasons) when the Buff-rumped Thornbill changes to predominantly ground-feeding and the Brown Thornbill joins it in MSF. Similarity in stomach contents showed a great drop during the cooler period (Table 30), except for the Brown/Buff-rumped combination which associate closely. Overall the decrease in overlap indicates that specialisation by each species becomes greater in times of scarcity. Prediction h. is considered to be supported by the evidence.

Prediction i: (specialised foraging should be employed more in times of scarcity)

328. As shown in Table 33 each species used its specialised foraging behaviour significantly more frequently when food was scarcest. Thus, in times of scarcity each was able to gain access to resources either inaccessible or not readily available to the others. The one exception was the major shift to ground-feeding by the Brown Thornbill during the autumn and winter of 1980, to which the species, by virtue of its long legs, is at least not ill-adapted. However, on balance, Prediction i. is supported by the evidence.

Prediction i. (1): (overlaps should be lowest when food is scarcest)

329. Seasonal comparisons of overlaps and abundance of arthropods (Figure 63) show strong correlation between low overlaps and scarcity of food. Monthly correlations between abundance of arthropods and overlap were, as in the case of PGI and overlaps, less significant, even though, overall, periods of scarcity produced a lower mean overlap than periods of abundance. Lack of a better correlation is hardly a surprise. Abundance of arthropods was based on mg/1000 g of leaves from small samples of leaves. There were, however, by the summer of 1979/80, far fewer leaves. Thus the values for abundance of arthropods, during the drought period, greatly understate the scarcity. When the period of massive defoliation (November 1979 to March 1981) is ignored then correlation between overlaps and abundance of food are much better i.e. overlaps high when food is abundant.

330. The inverse correlation between feeding on the ground by Buff-rumped Thornbills and the abundance of arthropods in the grass sweep samples may arise from several factors. Firstly, many of the insects taken in grass sweeps must have been taken off the grass itself, where thornbills rarely forage, and the values may not reflect what was really on the ground. However the patterns of litter fall, build-up and decay for eucalypt woodlands in the Armidale area (Pressland 1982) suggest that the ground surface was likely to have harboured few arthropods at the times (in winter) when grass sweep samples were low.

Secondly the peaks in sweep samples may have been influenced by a few large locusts as found in other studies (e.g. Dingle and Khamala 1972) and thus the differences between peaks and troughs, of food used by very small birds, may not have been as marked as the sweep data suggest. Thirdly, social factors or risk of predation may predominate.. Buff-rumped Thornbills, which flock in the cooler, less productive months, may feed less on the ground at other periods because they would be vulnerable to predation (see Chapter 5 for social organisation and Figure 49 for ground-feeding vs. flock size). This raises the question whether they feed on the ground because they have reconstituted their non-breeding flocks, or do they form flocks because they need to feed on the ground? The non flock-forming Scarlet Robin also switches to ground feeding in autumn (Huddy 1979), although it does tend to join mixed-species flocks when so doing and Huddy suggested that the switch was related to greater abundance of food on the ground relative to other substrates in winter. My opinion is that Buff-rumped Thornbills feed on the ground at the time of food scarcity because the scarcity is less severe on the ground than in the foliage.

331. The rather poor correlations of overlaps with the PGI, even though months of low PGI produced lower mean overlaps than periods of high PGI, can possibly be explained. Fitzpatrick and Nix (1970) designed the PGI programme mainly for application to pasture growth, and it is noteworthy (see Chapter 3) that the PGI correlates well with the abundance of arthropods on grass, but not so well with those on leaves. H.A. Nix (pers. comm.) has informed me that there are delay factors associated with the application of the PGI to trees, mainly related to the ability of trees to tap ground-water not available to grasses or shrubs. The main discrepancy between overlap and PGI values are the sudden drop in overlap values in the middle of comparatively high values for PGI during the summer of 1979/80, and the sudden rises in overlap well before the PGI rose in spring of each year. Perusal of the PGI values for 1979/80 show a low value for December 1980, when a combination of high temperatures and little rainfall may have seriously reduced the insect population to below the level where it could exploit the flush of growth that followed rain

in January and February and thus rapidly increase its numbers. Certainly the data for arthropod abundance show that numbers remained fairly constant throughout that summer.

332. Despite the evidence for a rise in overlap during the latter part of periods of scarcity the evidence generally supports Prediction j.(1), that overlaps are low when food is scarce.

Prediction j. (2): (overlaps should increase when food is scarce)

333. This prediction is a contradiction of the preceding one. Nevertheless the data in Figures 61, 62 and 63 give some support for it. The 'mysterious' rise in overlap well before a period of scarce food supply starts to show signs of improvement, suggests that other factors are counteracting with the need to specialise when food becomes scarce. Jarman (1971), working with large ungulates in Africa, found a situation similar to mine. In Jarman's study dietary overlap was greatest during the abundance of the wet season, was least during the reversion to food staples in the early dry season, and increased again in the late dry season when herbivores turned to the few evergreen and early-leafing plant species for food i.e. overlap increased at the worst time of year, when food was most scarce, and when animals were denied access to traditional dry-season habitats. Perhaps when food is reduced to a very low level then a species may have to search for whatever is available, even at the price of energy-costly foraging habits to which it may not be specially adapted or with the risk of increased interspecific competition. This seemed the case with the Brown Thornbill in the winter of 1980. Its overlap with the ground-feeding Buff-rumped Thornbill rose during the autumn and winter, but most of this increase in overlap was caused by the Brown switching to ground-feeding, an abnormal habit (less than 1% of observations at other periods involved feeding on the ground). Specialised for feeding in dense under-shrubs (see Chapter 7) the Brown Thornbill may have had to abandon this specialisation, not only because insects were scarce relative to the amount of foliage but also because there had been massive defoliation of the understorey (see Chapter 2). This possibly resulted in increased overlap, and competition with, its congener.

334. Lack (1947) and Svårdson (1949) postulated that although overlaps should decrease in times of scarcity, intra-specific competition may compel a widening of niche, i.e. having 'retreated' to its specialised niche in lean times, exhaustion of that niche by the species may force a return to less-specialised foraging.

335. My conclusions are: (a) that when food is abundant there is less need for the three species to specialise; (b) the resource exceeds the capacity of the birds to consume it (see Otvos 1979); that when food is scarce the species specialise and overlap decreases; and (c) if the scarcity is prolonged and severe then the species become opportunistic feeders, broaden or even radically change their foraging niches and inevitably overlap more, and perhaps only then, suffer competition. I consider that Prediction j. (2) is supported by the evidence, in times of severe shortage. Thus my data supports Predictions j (1) and j (2) as well showing reasons why, in certain circumstances both could be correct.

Prediction k: (overlap should be higher when species in MSF, and MSF should be more frequent in times of scarcity)

336. Table 35 shows that in general overlaps are increased by 30% when species associate in MSF. In some cases the degree of overlap is apparently affected by the numbers of individuals involved i.e. overlaps tend to be greater when a small party of one species is associated with a large party of another. Apart from the advantages discussed in Chapter 6, of protection from predation and efficiency of foraging, joining an MSF appears to exempt the joiner from interference competition should the MSF find a clumped food resource. Shifts in foraging behaviour (see Figures 38, 45 and 52) certainly appear to offer joiners access to foraging sites they otherwise would not visit. However I believe that the most important reason for joining is the reduced risk of failure (Thompson *et al.* 1974) i.e. to avoid wasting energy, and time (surely critical in short winter days), looking for food in areas which may already have been swept clean by a flock of some gregarious species.

337. However, the findings of Morse (1970), that MSF are more frequent at times of scarcity, do not match the evidence at Wollomombi. Morse's studies were in North America where MSF, composed chiefly of migratory species, formed MSF after breeding had finished and before migrants left, in the autumn when food was becoming rapidly less abundant. At Wollomombi, the incidence of MSF, as shown in Figure 27, Chapter 6, was unrelated to the abundance of food (Figure 7, Chapter 3). MSF at Wollomombi occurred at much the same frequency throughout the non-breeding season (about August to December). MSF were as frequent in mid-summer, the time of greatest abundance of food, as they were in mid-winter, the time of greatest scarcity. Indeed they started breaking up in August/September when food was still scarce. I believe that joining MSF is the 'normal' pattern of behaviour at Wollomombi, and is only interrupted by breeding. Breeding birds are somewhat inhibited from wandering too far, but more importantly the nuclear species of MSF, those that other species join, are themselves split up into much smaller groups in the breeding season (Chapter 5) and offer less attraction (i.e. the protection of large flocks) to join. I would not deny that MSF must be very important at times of scarcity, but maintain that the advantages they bestow apply to all conditions of abundance. I therefore consider that the second part of Prediction k. does not apply, at least in my study area.

#### CONCLUSION

338. Predictions, that in time of scarcity, b. (mortality is higher), d. (no breeding occurs) e. (foraging rates are highest), g. (morphology is related to specialised foraging), h. (specialisation is related to diet), i. (specialised foraging more frequent), j. (1) (overlaps decrease) and j. (2) (overlaps increase) are generally upheld by the data from this study. Predictions a. (birds leave or eat other food), c. (interference competition greater) and f. (smaller prey taken), are not wholly supported by the data but evidence for them was found.

Prediction k. (increase in MSF) is partly upheld and partly refuted by the evidence. Overall the data shown supports the suggestion that thornbills are at times limited by the supply of food. Therefore it is reasonable to suggest the differences in foraging behaviour between them as being the result of interspecific competition.

## CHAPTER 14

## GENERAL SUMMARY

339. This chapter will be presented as answers to the questions proposed in the introduction (paragraph 14, Chapter 1). These questions outlined the aims of the study.

How do the three species of thornbills differ in foraging ecology?  
(Chapters 7-10)

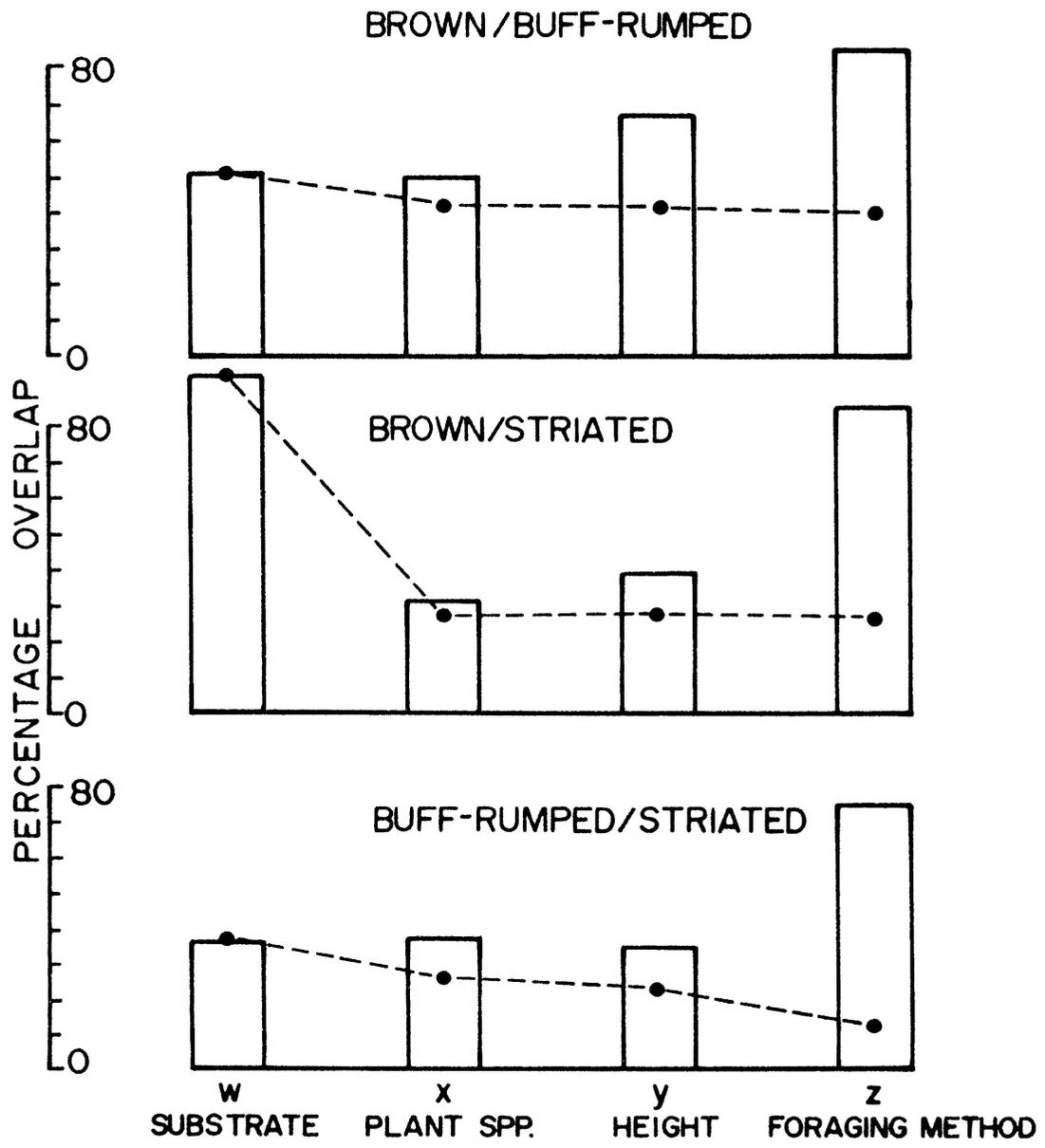
340. Basically, the three thornbills differ in that the Brown forages on foliage of the understorey, the Buff-rumped forages on bark or on the ground, and the Striated forages on the foliage of the tree canopy. These generalisations mask many diurnal and seasonal variations and the effects of flocking with their own or different species.

341. Figure 64 shows the overlaps between species in use of substrate, plant species, height and foraging method. Figure 64 also shows the degree of overlap when the variables are combined i.e. substrate by plant species, substrate by plant species by height, and substrate by plant species by height by foraging method. In all cases overlaps drop markedly when substrate and plant species are combined but change little when height is added. This is probably because plant species and height are dependent (all trees are eucalypts while there are few eucalypts in the understorey). Addition of foraging method causes little further reduction in overlaps except with the Buff-rumped/Striated combination, because, unlike the other two species, the Buff-rumped virtually never hangs.

342. Only the Brown and Striated overlap substantially in the use of substrate (> 50%) both feeding off leaves, but this overlap is substantially reduced when substrate by plant species is considered i.e. they forage on different plant species. Only the Brown and Buff-rumped overlap substantially in plant species but their use of substrate (leaves by Browns, bark by Buff-rumpeds) reduces overlap. The Brown and Buff-rumped overlap substantially in foraging height, both mainly

## Figure 64

Percentage overlap in foraging between thornbill species, by the four variables (histogram) and degrees of overlap when variables are combined (graph)



occurring close to the ground. All three, being mainly gleaners, overlap substantially in foraging method, the Buff-rumped/Striated combination least so. Overall the main separating mechanism appears to be differential selection for a combination of substrate and plant species.

How do the three species differ in the food they eat? (Chapter 11)

343. Except for the possible selection of smaller prey by the Striated Thornbill the three species appear to eat much the same things, and diets overlapped strongly (72-83%) during periods of abundance. However divergence occurs during times of scarcity. This divergence is caused by Brown and Buff-rumped Thornbills taking more ants and possibly seeds in such periods, an option less open to the obligatorily arboreal Striated Thornbill.

344. Do the birds change to other foods in times of scarcity or do they merely change foods as a result of change of foraging station? I believe that the dietary change results from the switch by the birds in foraging station, for two reasons. Firstly Buff-rumped Thornbills feed close to or on the ground (sites from where they would obtain most ants and seeds) according to their social grouping (Chapter 9), regardless of scarcity of food. Secondly the Brown and Buff-rumped Thornbills appear to be morphologically adapted (Chapter 12) to foraging at lower levels (i.e. not in tree canopies). However, adaptation to a switch to lower levels of vegetation at times of scarcity could have originally arisen from such foraging stations offering foods not readily available to competitors (e.g. Striated Thornbills).

How are ecological differences related to morphological ones? (Chapter 12)

345. The three species are very similar in morphology and virtually identical in weight. Even the significant differences are quite small. However, these differences are related to differences in foraging ecology, the important point being that they are most strongly manifested, by the emphasis on specialised foraging habits, in times of scarcity.

Brown Thornbills are adapted to foraging off and manoeuvring through the dense vegetation of the understorey, which they do more frequently in times of scarcity. Buff-rumped Thornbills are adapted to cling to bark which they also do more in time of scarcity. They also feed more on the ground in lean periods and their legs are not ill-adapted (i.e. too short) for such a role. As discussed earlier, the fact that their legs are not longer, as expected for a ground-feeder, results from a compromise between the demands of ground and bark feeding. Striated Thornbills are adapted to feed on the leaves of eucalypts and their specialised roles of hanging and hovering are more frequently used in times of scarcity. These facts support the contention of Schoener (1982) that 'during lean times, strong directional selection resulting from interspecific competition produces in each species adaptations most suitable for resources used relatively exclusively'.

Did the species differ more in feeding ecology when food was scarce?  
(Chapters 11 and 13)

346. Overlaps in both foraging and diets decreased in times of scarcity. However in times of prolonged scarcity overlaps rose before food increased in abundance. This suggests that either intra-specific competition within a species' specialised niche forces it to revert to a broader niche; or, when food becomes acutely scarce, specialisation is abandoned and each species searches for food wherever it can find it and consequently directly competes with the others.

Was breeding and mortality related to abundance of food? (Chapters 3, 4 and 5)

347. Breeding of insectivorous birds at Wollomombi appeared to be timed so that most young fledged at the period of peak abundance of food. However the amount of breeding did not relate to the greatly reduced availability of food during the drought period of 1979/80. Thus, the proximate factor which initiates breeding, increasing day-length, appears to over-ride local variations in the supply of food. Thornbills showed the same pattern as for other insectivores, except that the Buff-rumped Thornbill bred later than the other two species. Being

mainly foliage-gleaners, Brown and Striated Thornbills would be expected to coincide breeding with the spring flush of leaf-growth and attendant insects. Perhaps insects on bark, the substrate favoured by Buff-rumped Thornbills, take longer to increase, though the data in Chapter 3 suggest otherwise. Breeding success at Wollomombi seems unrelated to food, though the drought year of 1980 was disastrous for breeding. There is strong evidence that predation accounts for most nest-failure rather than shortage of food. Predation, however, may have been drought-related, because the massive defoliation (see Chapter 3) could have made nests easier to detect by predators.

348. Mortality appears directly related to scarcity of food (Chapter 4). The climatic conditions during periods of high mortality (i.e. winter) no doubt also play a part in mortality but it was noteworthy that in the winter (1981) when food was least scarce, following drought-breaking autumn rains, there were few deaths.

Could differences in foraging ecology explain the differences in social organisation? (Chapters 5, 6, 7 and 9)

349. The non-gregarious species, the Brown Thornbill, occurs throughout its range in dense vegetation; rain forests, the denser heaths, the understorey of sclerophyll forest and the denser parts, (usually drainage lines) of woodlands. In patchy environments, where dense undergrowth is in clumps, a species that occurs only in pairs could more easily find a viable territory than another that occurs only in groups bigger than two birds. A more highly social species, particularly one with a two-tiered permanent organisation such as the Buff-rumped and Striated Thornbills, would have difficulty in maintaining group/flock cohesion in dense undergrowth and I know of few such species in rainforest understoreys, as opposed to the tree canopies.

350. The habit of the Brown Thornbill of evicting young in autumn is in contrast to the other two species, which retain theirs until the following spring. This habit would allow a small territory, in times of scarcity, to support a breeding unit (pair) because only two birds would have to be sustained during the winter.

351. The ground-foraging of the Buff-rumped Thornbill would make it more vulnerable to predation, against which a flocking habit would afford it protection (see Chapters 5 and 6). With the Striated Thornbill, its partiality for the top of the tree canopy (Chapter 9) could also make it vulnerable to predation (possibly by falcons and currawongs) and flocking for it would also be an advantage.

352. The greatly differing size of territories of the two gregarious species is related to their foraging habits. Buff-rumped Thornbills, including young of the year, numbered at most *ca.* 14/10 ha, whereas Striated Thornbills without young numbered as many as 40/10 ha. The Striated Thornbill, almost entirely a leaf-forager had probably much more substrate on which to feed, in any given area, than a species restricted to the ground or to bark substrates (the Buff-rumped Thornbill).

353. The selective advantages to the individuals in the two types of social organisation is open to question. Breeders in the two gregarious species have advantages of helpers in the breeding group and, later within the clan (but not too many to attract attention to the nest). Once breeding is over all individuals have the advantages of group-living (alertness) to predators, finding clumped food etc (Chapter 5). Young birds are advantaged in that the following spring they may take up a territory in a familiar area. Against these advantages, their opportunities to spread, and colonise 'new' or ephemeral habitat could be inhibited by their social organisation. A young Brown Thornbill only needs a very small territory and one bird of the opposite sex in order to found a new breeding unit. Having been evicted from its parental territory in autumn it has had five months in which to look for a mate and a territory. The young of Buff-rumped Thornbills do not leave until the breeding season is under way, the sex ratios of emigrant young are strongly skewed to females, but vacancies for females are much fewer than for males. Also the larger territories required for Buff-rumped Thornbills, and the absence of advantages conferred by the gregarious habits of the species, would seem to

make establishment of new breeding units more difficult than in the case of the Brown Thornbill. It is perhaps noteworthy that whereas Brown Thornbills have re-colonised Tasmania (Keast 1961), neither the Buff-rumped nor the Striated, both present on the nearby Australian mainland, have failed to do so.

354. As is often the case when discussing communal breeding it is almost impossible to suggest which of several adaptations came first and provided the conditions necessary for the other adaptations (e.g. did the Buff-rumped Thornbill start feeding on the ground because it lived in groups or did it evolve group-living because it fed on the ground?).

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