

## THE INFLUENCE OF FOOD SHORTAGE ON INTERSPECIFIC NICHE OVERLAP AND FORAGING BEHAVIOR OF THREE SPECIES OF AUSTRALIAN WARBLERS (ACANTHIZIDAE)

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*Abstract.* Three species of similar-sized Australian warblers (Acanthizidae) differed markedly in their foraging behavior in eucalypt woodland in northeastern New South Wales. The Brown Thornbill (*Acanthiza pusilla*) is a shrub feeder, the Striated Thornbill (*A. lineata*) is a canopy feeder, whereas the Buff-rumped Thornbill (*A. reguloides*) forages on the ground and on foliage and bark over a range of heights. This study attempted to associate changes in their foraging behavior over three years with changes in the availability of food. Rainfall was well below average in the second and third years of the study. The energy demand of insectivorous birds did not decline during the study, although it was higher in spring and summer than in autumn each year. The abundance of arthropods declined markedly during the drought. Foraging overlaps between the species initially declined as food became scarce. They rose again in winter and spring, 1980, at the height of the drought, when food was particularly scarce. Thornbills appeared to respond to persistent food shortage by expanding their foraging niche and risking greater interspecific competition. Attempts to correlate foraging behavior of insectivorous birds with availability of food are valuable, although measuring arthropod abundance is time-consuming and results are rarely clear cut.

*Key Words:* Foraging behavior; food shortage; niche overlap; thornbills; *Acanthiza*.

Most studies comparing the foraging behavior of related bird species have made no attempt to measure changes in the abundance of food. Yet, changes in foraging behavior and overlap between species in relation to food abundance provide valuable information on the potential for interspecific competition. For instance if food is superabundant, then two species could overlap completely yet not experience competition. As food becomes scarcer, species should diverge in their foraging behavior and so use different resources to reduce the potential for competition (Lack 1947, Svårdson 1949). However, as intraspecific competition will be stronger than interspecific competition, each species should also broaden its diet (Svårdson 1949, MacArthur and Pianka 1966). As food becomes scarce, an individual should take a wider range of the foods that it encounters, regardless of what other species are doing (Krebs and Davies 1981). In extreme conditions a species may resort to unusual foraging behavior or food.

The foraging behavior of species has been compared during periods of relative abundance and scarcity in many studies (summarized by Smith et al. 1978, Schluter 1981, Schoener 1982). In all but two of these studies overlaps between the species were less when food was judged to be scarce. These studies included animals as diverse as fish (Zaret and Rand 1971), ungulates (Jarman 1971), and doves (Morel and Morel 1974). In none of the studies was foraging behavior and food compared continuously over a period of a year or more. Wiens (pers. comm.)

has suggested that as food becomes increasingly scarce one might expect species first to diverge and become more specialized and then to become more opportunistic and exploit whatever food remains. The latter could lead them to overlap more extensively with each other.

The primary objective of this paper was to describe changes in foraging behavior and niche overlap among three small, insectivorous birds through a period of severe food shortage. In particular, the following questions were asked: (1) How do the species differ in their foraging behavior? (2) How does their foraging behavior change seasonally and in successive years? (3) Are seasonal changes related to changes in food abundance? (4) Does food shortage lead to increased or decreased overlap in foraging behavior?

### *Australian warblers*

The Australian warblers (Acanthizidae) are small, insectivorous birds related to the Australian wrens (Maluridae) and honeyeaters (Meliphagidae) (Sibley and Ahlquist 1985). The main genera are *Acanthiza* (thornbills), *Gerygone* (gerygone-warblers) and *Sericornis* (scrub-wrens). *Gerygone*-warblers forage actively from the foliage of trees, whereas scrub-wrens mostly forage on or near the ground (Recher et al. 1985, Ford et al. 1986). Thornbills, the focus of this study, range from the ground to the canopy. They are found in the temperate parts of Australia or in cool montane forests in the tropics. The three main species groups are the *A. lineata-nana* group

TABLE 1. RAINFALL (MM) EACH MONTH OF THE STUDY, COMPARED WITH 40-YEAR MEAN

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1978	209	34	137	43	73	42	33	36	30	62	54	176	929
1979	128	14	90	12	63	36	14	9	12	46	81	6	511
1980	63	36	16	0	123	13	9	2	0	56	8	45	371
1981	3	86	16	56	63	8	22	12	53	87	76	92	574
Mean	118	95	68	34	31	45	36	53	38	66	80	95	759

of arboreal feeders, the *pusilla* group of shrub feeders, and the *reguloides* group, which tends toward ground feeding. One member of each group was common in the study area: Striated Thornbill (*A. lineata*), Brown Thornbill (*A. pusilla*) and Buff-rumped Thornbill (*A. reguloides*). General information on habitat, foraging and breeding behavior is summarized in McGill (1970), Frith (1969, 1976) and MacDonald (1973). Recher et al. (1985), Woinarski (1985), Ford et al. (1986) and Recher et al. (1987) have presented data on foraging behavior. Details of the social organization have been published in Bell and Ford (1986). Basically, *lineata* and *reguloides* are cooperative breeders that occur in pairs, trios, or quartets in the breeding season and in clans of up to 20 birds in the nonbreeding season. In contrast, *pusilla* holds territories as pairs throughout the year. All three species are sedentary and of similar size (7 g). Full details of breeding and foraging behavior of the populations studied are presented in Bell (1983) and a summary is provided in Bell (1985a).

#### STUDY AREA AND METHODS

The work was carried out at Wollomombi Falls Recreation Reserve (30°32'S, 152°02'E, now part of the Oxley Wild Rivers National Park), 40 km east of Armidale in northeastern New South Wales. The site was on the edge of an undulating plateau (920 m) above the gorges of the Macleay River. Steep escarpments provided boundaries to the study area on three sides and cleared land bounded the fourth.

Mean temperatures in Armidale range from 26°C (mean maximum) and 12°C (mean minimum) in January to 12°C (mean maximum) and 1°C (mean minimum) in July. The annual rainfall at Wollomombi averages 759 mm, with a peak in summer. The study coincided with a period of increasing drought (Table 1), which had a severe effect on the vegetation and arthropods.

The vegetation is eucalypt woodland merging in places into open forest. The tree canopy covered 36.7% of the area, with shrubs covering 13.6% (line-transect interception technique, McIntyre 1953). We estimated 84 trees and 316 shrubs per hectare (point-centered quarter sampling method, Cottam et al. 1953). The main trees were stringybarks (*Eucalyptus caliginosa* and *E. laevopinea*—52%), boxes (undescribed species related to *E. cypellocarpa*, *E. conica*, *E. melliodora* and *E.*

*bridgesiana*—28%) and gums (*E. viminalis*, *E. amplifolia* and *E. blakelyi*—19%). The main shrubs were bipinnate *Acacia* (17% of plants, 45% of canopy volume of shrubs), *Cassinia* (18% of plants and volume), *Olearia* (44% and 21%), *Jacksonia* (16% and 9%), and *Exocarpos* (1% of each). Most trees were about 15 m tall, with a few to 30 m. Shrubs were mostly about 2 m high, except for the acacias (typically 5 m). About 3% of the trees and 21% of the shrubs died during the drought. One third of the trees and 40% of surviving shrubs lost most or all of their leaves. Canopy cover of the remainder was thinned.

Arthropods were sampled at monthly intervals from the foliage of *Eucalyptus*, *Acacia*, *Olearia*, *Jacksonia*, *Cassinia* and *Exocarpos*. Samples of insects from ground vegetation were also taken each month. The details of methods and the results are presented in Bell (1985b) and in Ford, Huddy, and Bell (this volume).

Arthropods were also counted monthly from March 1978 to February 1979 on the surface of eucalypt trunks (by Noske 1982). A square 50 cm on each side was checked on eight trees of each of four species and all arthropods seen in a 3-minute period were recorded.

Relative densities of birds were estimated during fine weather each month on transects 600 m long. Distance from the center line of the transect was recorded and the density of insectivorous species estimated by the method of Balph et al. (1977). These data were used mainly to identify changes in relative abundance over the 3 years of the study. Weights for each species were taken from our own banding data. Daily energy requirements were calculated from the formula of King (1974) ( $\log_{10} \text{DER} = \log_{10} 317.7 + 0.7052 \log_{10} W$ , in which  $W$  = weight in kg, DER multiplied by 4 to convert into kJ). Values were weighted by season, 1.5 × in winter and spring, 1.1 × in summer and autumn to allow for thermoregulation in cold weather and increased demands due to breeding and molt. Energy demand was calculated from the sum of DER for each species, multiplied by its estimated density.

Foraging data were collected each month from September 1978 to April 1981. For each of the three species, 750 foraging moves were recorded each month, consisting of five successive moves from 150 encounters. A foraging move was one move, in the course of foraging, from one perch to another. In the last year only 450 moves from 90 individuals were recorded monthly. Observations were distributed evenly among morning, the middle of the day and afternoon, and were made in fine weather with no more than light to moderate winds. For each move the following were recorded: substrate, plant species, height and foraging method. For each bird, its identity, location, identity of any

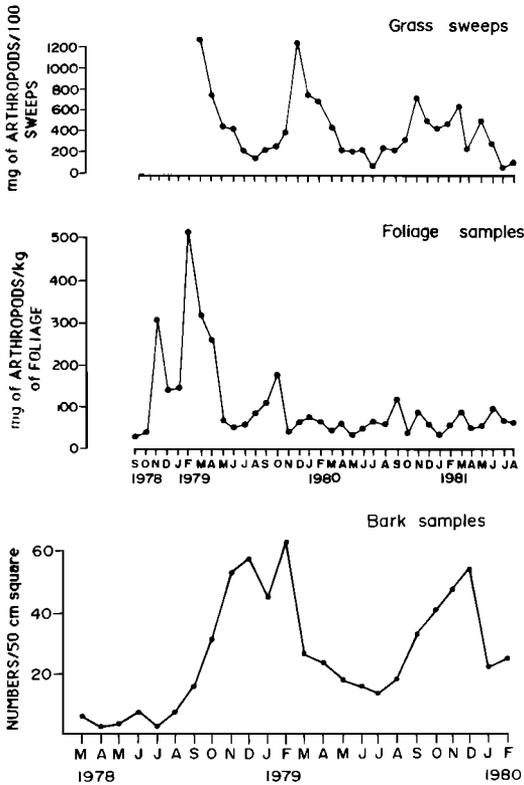


FIGURE 1. Monthly biomass of arthropods from surface vegetation (March 1979 to August 1981), foliage (September 1978 to August 1981), and bark (March 1978 to February 1980).

birds with which it was associated, date, and time of day were recorded. Substrates used were ground (including grass-tussocks, logs, stumps, stones, and cow dung), bark (including trunks, limbs, branches, hollows, lichen, and strips of hanging bark); leaves (including mistletoe clumps, insect nests, and flowers) and air. Plant species included the shrubs mentioned previously; eucalypts were separated into three groups by bark type, though initially the types were not separated (eucalypts grouped). Heights were recorded in the following categories: ground, 0–1 m, 1–2 m, 2–5 m, 5–10 m, 10–15 m, and >15 m. The following foraging methods were used: hawking (bird and prey in air), snatching (bird flying, prey on a substrate), hovering (similar to snatching but bird hovering), gleaning (bird and prey on substrate), and hanging (bird gleaning from substrate upside down).

Contingency tests were used to compare categories among seasons within a year and among years for each species and each foraging dimension. As five sequential moves were recorded the data were not entirely independent. For this reason a level of  $P < 0.001$ , for the appropriate degrees of freedom, was taken as denoting significance. In fact, all seasonal and yearly comparisons were significant at this level. Cells were examined to determine which contributed most to the large  $\chi^2$

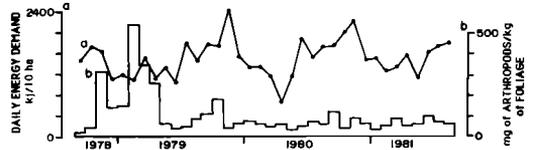


FIGURE 2. Mean daily energy demand of insectivorous birds each month (a) and arthropod biomass (b).

value and categories that were greater than expected in one or more seasons or years identified. Overlaps were calculated from Schoener's (1968) equation:

$$O = 1 - \sum |P_{xi} - P_{yi}|$$

in which  $O$  = overlap, and  $P_{xi}$  and  $P_{yi}$  were the frequencies of observations of species  $x$  and  $y$  in category  $i$ . A Spearman's Rank Correlation was used to determine whether overlap was correlated with insect abundance.

## RESULTS

Biomass of arthropods on foliage tended to peak in spring and early summer (Fig. 1), as found in other studies in southeastern Australia (e.g., Woinarski and Cullen 1984). Arthropod abundance declined as the drought worsened and in the last year it remained at levels more typical of winter in a normal year. As the amount of foliage declined through the drought, declines of arthropods would have been even greater than indicated in Figure 1. Biomass of arthropods from the ground also peaked in spring and summer and declined during the drought, although not as markedly as those from foliage. Arthropods on the bark surface showed marked peaks in both summers, but counts were terminated early in the drought.

The daily energy demand of insectivorous birds did not appear to decline during the study, despite the drought (Fig. 2). As the density of arthropods on foliage was lower in the last two years than in the first year, the potential for competition would have been higher then. This would have been particularly so in the third year when the amount of foliage had also declined. All three thornbills were sedentary and, as they had high adult survival rates but low breeding success (Bell and Ford 1986), their densities did not change markedly through the study (though Buff-rumped and Striated thornbills declined slightly).

## SUBSTRATE

Brown and Striated thornbills mostly foraged from foliage and to some extent on branches (Fig. 3). Buff-rumped Thornbills used a variety of substrates, with about equal amounts of time on branches and the ground and somewhat less time on foliage. Brown Thornbills foraged on the

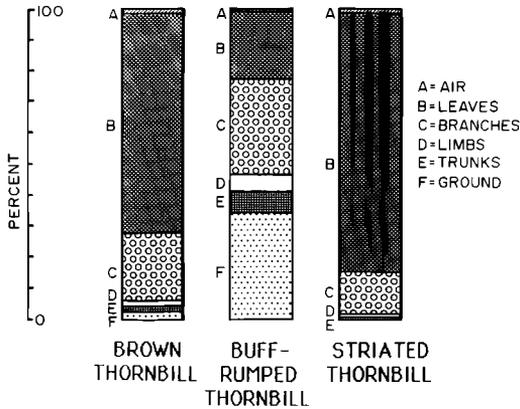


FIGURE 3. Percentage of foraging observations of each thornbill species from each substrate (data for whole study combined, sample sizes 22,222–24,369 moves per species).

ground far more in autumn and winter than in other seasons in 1980 and more in 1980 than in other years. Buff-rumped Thornbills showed the most regular seasonal change in foraging substrate (Table 2; see Fig. 8 of Ford, Huddy, and Bell, this volume). Leaves were used more in spring and summer than in autumn and winter. Bark was also visited more in the warmer months. The ground was used most in winter, and in autumn in 1980. Ground foraging was not a response to increasing abundance of arthropods on ground vegetation. The amount of ground feeding by Buff-rumped Thornbills was negatively

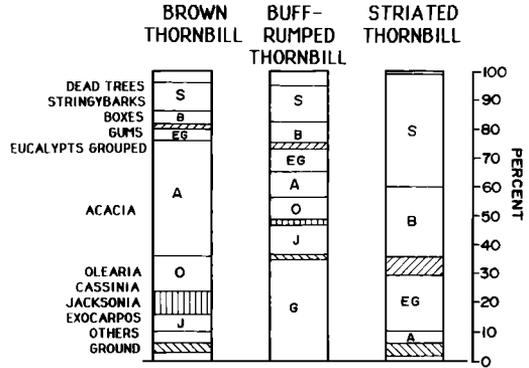


FIGURE 4. Percentage of foraging observations of each thornbill species from each plant species (sample sizes as in Fig. 3). (Eucalypts were not separated by type before April 1979.)

correlated with the abundance of arthropods on the ground ( $r_s = -0.707$ ,  $P < 0.05$ ), and the peak of ground feeding in Brown Thornbills coincided with very low levels of arthropods on the ground. Striated Thornbills did not show consistent seasonal changes in the substrate on which they foraged (Table 2).

PLANT SPECIES

Brown Thornbills fed mostly from shrubs, Buff-rumped Thornbills almost equally on eucalypts, shrubs and the ground, and Striated Thornbills foraged almost exclusively on eucalypts (Fig. 4). Brown Thornbills fed proportionally more on acacias in summer than in other seasons, and

TABLE 2. SUBSTRATES USED MORE THAN EXPECTED EACH SEASON WITHIN YEARS AND BETWEEN YEARS BY THE THREE THORNBILLS (CONTINGENCY TESTS, ALL  $P < 0.001$ )

Thornbill species	Spring	Summer*	Autumn	Winter
Brown	Ground (1978) Leaves (1979)	Leaves (1979/80)	Ground (1980)	Ground (1980)
Buff-rumped	Leaves (1978) (1980) Bark (1978)	Bark (all years) Leaves (1978/79) (1980/81)	Leaves (1979) (1981) Ground (1980)	Ground (all years)
Striated	Bark (1978)		Bark (1980)	Bark (1980)
	1978/79	1979/80	1980/81	
Brown		Ground		
Buff-rumped	Leaves, bark	Ground	Leaves	
Striated		Bark		

\* As summer spans the months December–February, the year is denoted 1979/80, etc.

TABLE 3. PLANT SPECIES USED MORE IN A SEASON WITHIN A YEAR, OR IN ONE YEAR COMPARED WITH OTHER YEARS BY THREE THORNBILL SPECIES (CONTINGENCY TESTS, ALL  $P < 0.001$ )

Thornbill species	Spring	Summer	Autumn	Winter
Brown	<i>Olearia</i> (1979)	<i>Acacia</i> (all years)	<i>Eucalyptus</i> (1979)	<i>Olearia</i> (1979)
	<i>Exocarpos</i> (1979) (1980)		Ground (1980)	<i>Eucalyptus</i> (1980) (1981) Ground (1980) <i>Cassinia</i> (1981)
Buff-rumped	<i>Eucalyptus</i> (1978)	<i>Acacia</i> (all years) <i>Jacksonia</i> (1979/80)	Ground (1980)	Ground (all years)
	<i>Acacia</i> (1979)			
	<i>Jacksonia</i> (1978) (1979)			
Striated	<i>Acacia</i> (1979) (1980)	<i>Acacia</i> (1978/79)	<i>Eucalyptus</i> (1979)	Low shrubs (1979)
	Low shrubs* (all years)			
	1978/79	1979/80	1980/81	
Brown	<i>Olearia</i>	<i>Olearia</i>	<i>Eucalyptus</i> , <i>Cassinia</i> , <i>Exocarpos</i>	
Buff-rumped	<i>Eucalyptus</i> , <i>Acacia</i>	Ground <i>Jacksonia</i> <i>Exocarpos</i>	<i>Eucalyptus</i>	
Striated	<i>Acacia</i> Low shrub	<i>Eucalyptus</i>	<i>Acacia</i> Low shrub	

\* All shrubs combined, except *Acacia*.

tended to visit eucalypts more in autumn and winter and other shrubs more in spring (Table 3). Buff-rumped Thornbills consistently visited acacias in summer and *Jacksonia* in spring and summer more than in other seasons, whereas Striated Thornbills visited acacias and other shrubs most in spring. There was no correlation between the proportion of observations of foraging by Brown Thornbills on each plant species and the abundance of arthropods each month (Spearman Rank Correlations, all  $P > 0.1$ ). Buff-rumped Thornbills, however, fed more on acacias and *Olearia* when arthropods were more abundant on these shrubs ( $P < 0.05$ ).

All species showed differences between years in the amount of foraging on each plant species (Table 4), although these were not consistent in the three species.

HEIGHT

Brown Thornbills foraged at intermediate levels, as expected from their preference for

shrubs (Fig. 5). Buff-rumped Thornbills foraged on the ground and at a wide range of other heights. Striated Thornbills mostly foraged high, on eucalypts. Brown Thornbills fed most often on the ground in the autumn and winter of 1980 and more often above 5 m in autumn and winter of 1981 (based on contingency tests between seasons within years and between years). Buff-rumped Thornbills fed more on the ground in winter each year and in autumn in 1980 and higher in spring and summer in all years. Striated Thornbills tended to forage low during the first year but high in autumn to spring 1980.

FORAGING METHOD

All three species foraged principally by gleaning (Fig. 6). Brown Thornbills snatched and hung more than the Buff-rumped Thornbills. Buff-rumped Thornbills sallied least and gleaned most and Striated Thornbills hung more than the other two species (contingency tests, all  $P < 0.01$ ). There was a tendency for Brown and Buff-rumped

TABLE 4. SEASONS WITHIN YEARS AND YEARS IN WHICH THE THREE THORNBILLS USED LESS COMMON FORAGING METHODS MORE THAN EXPECTED (CONTINGENCY TESTS, ALL  $P < 0.001$ )

Thornbill species	Spring	Summer	Autumn	Winter
Brown	Hang (1979, 1980) Snatch (1979)	Hang (1979/80)	Snatch (1979) Hang (1979)	Hover (1979) Hang (1981) Sally (1980) Snatch (1979, 1980)
Buff-rumped	Nonglean* (1978)			Nonglean (1981)
Striated		Snatch (1979/80) Hang (1979/80)	Hang (1979) Snatch (1979)	Hover (1979) (1980) Hang (1981)
	1978/79	1979/80	1980/81	
Brown	Hover Hang		Snatch	
Buff-rumped	Nonglean			
Striated	Sally Hover Hang	Snatch		

\* Sally, hover, snatch and hang combined.

thornbills to glean most in summer and use the more active methods more in winter (Table 4). These methods were used by all species most in 1978/79.

#### OVERLAPS

All three species showed moderate to substantial differences along each of the foraging dimensions (Table 5). Cody (1974) proposed that overlaps along different niche dimensions could be combined in two ways. Where the dimensions were totally independent then overlaps should be multiplied (product  $\alpha$ ), but where they were totally dependent they should be averaged (sum  $\alpha$ ). We found some cases in which the different dimensions were highly interdependent and others in which they were independent to at least some degree. Therefore, a matrix of 2310 categories (6 substrates by 11 plant species by 7 heights by 5 methods) was constructed. In fact many of these categories, (e.g., ground and all but one plant species and height) did not exist and only about 50 ever occurred at frequencies of greater than 1%. Overlaps were then calculated from all categories for which data were available.

The interspecific overlaps in this unidimensional combination are also shown in Table 5. Plant species and either height or substrate were

the best separators between species. Combined overall overlaps were not much less than overlaps from plant species alone. Combined overlaps were calculated for each month and compared with the abundance of arthropods from foliage, corrected for relative abundance of different plant species (Fig. 7). Positive correlations existed between some overlaps and arthropod abundance on some substrates (Table 6). When food was more abundant, the thornbills tended to be more similar to each other in their foraging. However only a small proportion of the variance was accounted for by this correlation ( $r^2 = 0.08-0.23$ ). Certainly part of the reason for this was the small sample size and inherent variability in the monthly arthropod samples. When overlaps were compared with the abundance of arthropods on a seasonal basis, the correlation coefficients were higher ( $r^2 = 0.50, 0.53, \text{ and } 0.42$  for Brown/Buff-rumped, Brown/Striated, and Buff-rumped/Striated, respectively, against arthropods on foliage).

This correlation overshadowed a secondary effect, in that overlaps may also have been relatively high when food was still scarce. For instance, in the autumn and winter of 1980, Brown and Buff-rumped thornbills became more similar to each other. Not only were arthropods on

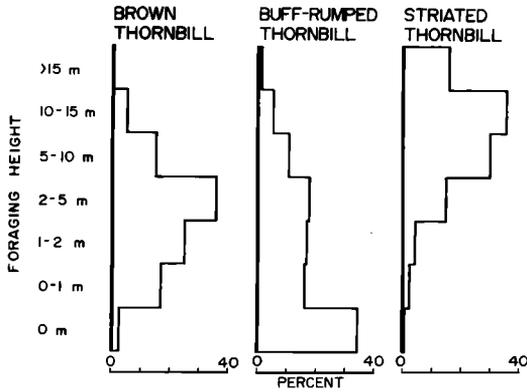


FIGURE 5. Percentage of foraging observations of each thornbill species at each height (sample sizes as in Fig. 3).

foliage and the ground scarce at this time, but the drought was at its height and many trees and shrubs were defoliated. The reason for the increased overlap was that Brown Thornbills started feeding extensively on the ground.

DISCUSSION

This study represents the first attempt to relate the foraging behavior of related and syntopic species of birds to the abundance of their food continuously over such a long period. The worst drought of the century was obviously not anticipated, but it did provide a unique opportunity to relate interspecific overlap to increasing and persistent scarcity of food. Despite the large body of data and the abundance of significant seasonal and year-to-year changes in foraging, we found few relationships between foraging behavior and food abundance. The main reason for this was that arthropod biomass tended to change in parallel on different substrates or plant species. In addition, biomass measures involved large errors and arthropods were highly variable in size and attractiveness to particular bird species. Basically, arthropod biomass was a very crude measure of the availability of food for birds such as thornbills. Except in the case of specialized insectivores where the food is known, attempts to relate behavior to food abundance are unlikely to be highly successful (see Ford, Huddy, and Bell, this volume, for discussion of examples).

The attempt to relate overlap in foraging between species to abundance of food was more successful. The similar trends in biomass of arthropods, on different substrates and plant species, meant that periods of relative overall shortage could be identified. Pooling of data from 3 months each season reduced the error in estimating biomass and allowed reasonable corre-

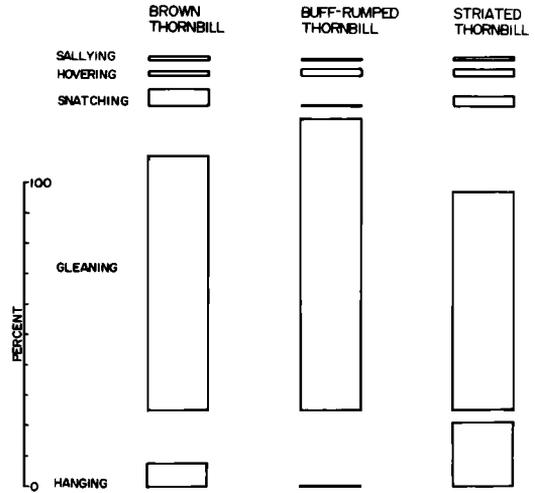


FIGURE 6. Percentage of foraging observations of each thornbill species by each method (sample size as in Fig. 3).

lations between overlap and food abundance to be obtained ( $r^2 = 0.42-0.53$ ). This supported the hypothesis that species diverge in their niches when food becomes scarce (Lack 1947, Svårdson 1949). However, we found some evidence of convergence when food was persistently scarce. This cannot be shown by correlation, but can be revealed by looking at the responses of individual species. In this study the movement of Brown Thornbills onto the ground in autumn and winter 1980 was probably a response to defoliation and scarcity of arthropods on the low shrubs where they usually foraged. Recher et al. (1985) found that ground foraging made up 7% of observations for Brown Thornbills in southern NSW in 1980, where it was also very dry. None of the other studies of foraging in the Brown Thornbill have recorded it foraging on the ground (Woinarski 1985; Ford et al. 1986; Recher et al. 1987). Inev-

TABLE 5. OVERLAPS IN ALL FOUR FORAGING DIMENSIONS AND IN THE UNIDIMENSIONAL COMBINATION BETWEEN EACH PAIR OF THE THREE THORNBILL SPECIES

Thornbill species	Substrate	Plant species	Height	Method	Combined
Brown/Buf-rumped	51	49	66	84	39
Brown/Striated	93	30	38	84	26
Buf-rumped/Striated	36	36	34	74	12

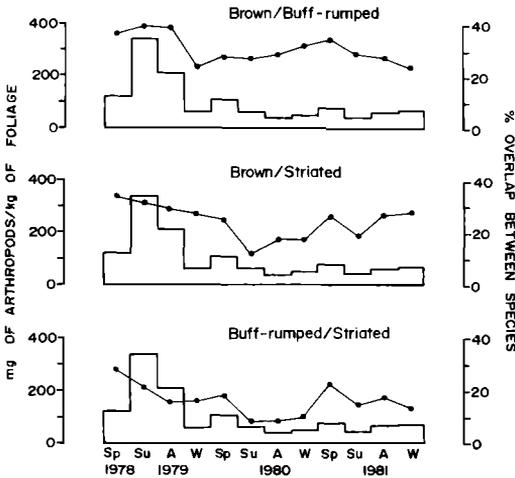


FIGURE 7. Comparison between interspecific overlap in foraging (●) and abundance of foliage arthropods in each season (histograms).

itably such extreme responses can be recorded only on an opportunistic basis.

Questions concerning interspecific overlap in foraging behavior in relation to food abundance can be answered in several other ways. These should complement rather than replace the type of study described here. Single-species studies can examine foraging method or substrate to food availability in alternative sites (Davies 1977b; Ford, Huddy, and Bell, this volume). Foraging success may be an indirect but more reliable measure of food availability from the bird's viewpoint. However, this can be affected by the level of experience and hunger of the bird. The proportion of time spent foraging from time-budget studies can also indicate the relative abundance of food.

We have attempted to infer interspecific competition from a knowledge of interspecific overlaps and food availability. This is an improvement on interpretations based on overlap alone,

TABLE 6. RELATIONSHIPS BETWEEN INTERSPECIFIC OVERLAPS AND ABUNDANCE OF ARTHROPODS ON FOLIAGE, SURFACE VEGETATION, AND BARK (SPEARMAN RANK CORRELATION)

Thornbill species	Foliage (N = 36)	Ground (N = 30)	Bark (N = 18)
Brown/Buff-rumped	0.284*	0.365*	0.399*
Brown/Striated	0.475**	-0.018	0.123
Buff-rumped/Striated	0.334*	0.128	0.401*

\* P < 0.05, \*\* P < 0.01.

or on presumed shortages of food. However, experiments either excluding birds from substrates and measuring arthropod abundance or removing birds from an area and seeking changes in foraging behavior of other species may be more profitable. Preliminary results in Armidale suggest that numbers of insects on foliage enclosed in netting increase in abundance far more than on foliage to which birds have access (Dunkerley and Bridges, unpubl.; also see Torgersen et al., this volume).

In conclusion, no single approach will provide complete answers to the questions relating foraging behavior to food abundance. Long-term monitoring of foraging behavior of insectivorous birds and the abundance of arthropods can provide a valuable overview. Carefully designed experiments may be better at answering specific questions. More studies of both types are needed to indicate the frequency and severity of food shortage experienced by birds, and the extent to which these are due to interspecific competition.

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