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# SEASONAL CHANGES IN FORAGING BEHAVIOR OF THREE PASSERINES IN AUSTRALIAN EUCALYPTUS WOODLAND

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*Abstract.* The foraging behavior of the Fuscous Honeyeater (*Lichenostomus fuscus*), Scarlet Robin (*Petroica multicolor*), and Buff-rumped Thornbill (*Acanthiza reguloides*) was compared in different seasons in evergreen eucalypt woodland. Fuscous Honeyeaters mostly gleaned from leaves (52–85% of observations), an activity that tended to increase slightly in autumn and winter. Flowers of eucalypts and mistletoes were visited for nectar when available. Bark and aerial foraging did not change consistently between seasons, but all categories changed between years. Scarlet Robins foraged by hawking, snatching and pouncing, and changed from leaf, bark, and aerial foraging to mostly ground foraging in winter. This change reflected the abundance of arthropods on the different substrates and perhaps the influence of temperature on the activity of arthropods and birds. Buff-rumped Thornbills also fed on the ground most in winter, moving onto foliage and bark in spring and summer. They also occurred in larger groups in winter. Seasonal changes in foraging may also be influenced by vulnerability to predation.

*Key Words:* Foraging; seasonal changes; eucalypt woodland; Fuscous Honeyeater; *Lichenostomus fuscus*; Scarlet Robin; *Petroica multicolor*; Buff-rumped Thornbill; *Acanthiza reguloides.*

There have been numerous studies of the foraging behavior of birds, principally during the breeding season. Several studies have compared behavior in different seasons, in particular foraging of birds in winter with that during the breeding season (e.g., Ulfstrand 1976, Morrison and With 1987). Most of these studies have been in seasonal habitats in the Northern Hemisphere. Birds in deciduous woodland frequently change their behavior through the year, because a major foraging substrate, foliage, is absent or scarce for part of the year (Hartley 1953, Gibb 1954, Willson 1970). Birds in coniferous forests also may show marked seasonal changes (Ulfstrand 1976, Alatalo 1980), although foliage is not shed in winter, as days are short, substrates may be snow-covered, and food is scarce. In addition, many potentially competing species have left the area. Migratory species themselves may alter their foraging behavior between breeding, migratory and winter areas (Greenberg 1987b; Martin and Karr, this volume). In addition, birds may show marked changes in foraging behavior among years (Szaro et al., this volume).

Fewer studies have been conducted at low latitudes, where changes in the weather and bird community may be less drastic than in cool temperate regions. A notable exception is the series of studies on Darwin's finches (*Geospiza* spp.) on the Galapagos Islands (Smith et al. 1978, summarized in Grant 1986). Here, a dry season, severe in some years, led to food shortage and a divergence in the diet of congeners.

Our objective is to contrast seasonal changes in the foraging behavior of three species of passerines in eucalypt woodland in Australia. We also examine changes in foraging between years in two of the species. This habitat is evergreen and not strongly seasonal in climate or food abundance (Bell 1985a); therefore, we might not expect to find substantial seasonal changes in foraging. Alternatively, such seasonal changes as do occur may still affect the foraging behavior of birds, or it may be influenced by other factors such as predation and competition.

The Fuscous Honeyeater (*Lichenostomus fuscus,* Meliphagidae) is a dull-colored, small (18 g), insectivore-nectarivore. It is active, loosely social, and aggressive. The Scarlet Robin (*Petroica multicolor,* Eopsaltriidae) is sexually dimorphic with a brilliant red, black, and white male and pink, brown, and gray female. It weighs 13 grams and resembles in appearance and behavior the small Palearctic muscicapines. The Buff-rumped Thornbill (*Acanthiza reguloides,* Acanthizidae) is a tiny (7 g) brown, actively gleaning Australian warbler. All three species, as well as most other common species, are sedentary.

## STUDY SITES AND METHODS

Fuscous Honeyeaters were studied at Eastwood State Forest, 12 km southeast of Armidale (30°30'S, 151°30'E), whereas the other two species were studied at Wollomombi Falls Reserve, 40 km east of Armidale. Both sites were at about 1000 m elevation in the Northern Tablelands of New South Wales and have already been described in detail (Noske 1979, Ford et al. 1985, Bell 1985a, Bell and Ford 1986). The habitat is eucalypt woodland with trees fairly well spaced and a deep canopy up to about 20 m. Virtually all trees belong to the genus *Eucalyptus* with four common species at each site (*E. caliginosa* and *E. melliodora* at both sites, *E. laevopinea* and *E. conica* at Wollomombi, and *E. viminalis* and *E. blakelyi* at Eastwood). These eucalypts differ principally in their type of bark. Eucalypts have sclerophyllous, evergreen leaves that tend to hang down and show less variation between species than do those of trees in northern deciduous forests. A tall shrub layer of *Acacia* was present along with smaller shrubs of *Olearia, Exocarpos, Cassinia,* and *Jacksonia.* These were more common at Wollomombi. Armidale has a cool winter (mean minimum 1°C, maximum 12°C in July) and warm summer (mean minimum 12°C, maximum 26°C in January) with an annual rainfall of 790 mm peaking in summer. The period from early 1980 to middle 1982 was very dry with some defoliation and death of trees and shrubs and a marked scarcity of insects (Bell 1985a).

### INVERTEBRATE SAMPLING

Arthropods were sampled from foliage and the ground at Wollomombi from September 1978 and March 1979, respectively, to August 1981 (details in Bell 1985a). Samples were taken at 09:00, mid-monthly on calm, sunny days, from six plant genera (*Eucalyptus, Acacia, Olearia, Jacksonia, Exocarpos* and *Cassinia*). From 1–2 kg of leafy branches were collected from at least 20 plants of each genus. Where there was more than one species per genus, each was sampled in proportion to its relative abundance. Foliage was placed into plastic bags before removal and sprayed with Baygon household insecticide. It was then vigorously beaten to dislodge invertebrates, which were later identified, mostly to order, and measured. Measurements were converted to dry weight using the formulae of Zug and Zug (1979).

One hundred sweep-net samples were made each month at 11:00 over the ground vegetation. Arthropods were killed, identified, counted, and measured as for the foliage samples.

Also at Wollomombi, litter samples were taken from February to July 1979 (Huddy 1979). Six 30 cm × 30 cm samples of plant and loose material were collected each month; arthropods were sorted from it and identified. In addition, 120 sweeps each covering 5 m were made just above ground level each month. Arthropods were killed and later identified. Arthropods on bark were estimated by counting them on 50 cm × 50 cm grids on 32 trees each month (method described in Noske 1985).

### AVIAN FORAGING

As the studies were independent, different methods were used for each species, and several methods were used for the Fuscous Honeyeater. Fuscous Honeyeaters were studied from January 1981 to December 1982 and from February 1984 to March 1986. In the first period a single foraging observation was recorded for each individual bird at each encounter. The foraging method, substrate, plant species, and height were recorded for the first attempt at prey capture after the bird was seen (details in Ford et al. 1986). In this paper only six categories have been analyzed: aerial hawking, bark foraging, ground foraging, probing flowers, gleaning leaves, and hovering at leaves. For the second period individual birds were followed for at least 20 s and up to 10 min, during which each activity was timed and accumulated into different categories. Major activities were perched (inactive but including preening and incubating), flying, and foraging. Foraging behavior was subdivided into six categories as for the first period of study. Discrete records were taken whenever an individual changed method or substrate or moved to a new tree. The comparisons between the two periods included methods as well as years and in the second period the methods of time-budgeting and discrete sampling were compared.

Scarlet Robins were studied from February to July 1979. Foraging was recorded in the same way as for Fuscous Honeyeaters in the first period except that sequential records were taken. The four categories of ground, bark, leaves, and air were compared by month. Most individuals were color-banded and were resident and territorial in the area (Huddy 1979).

For Buff-rumped Thornbills five consecutive foraging moves were recorded for each individual encountered from September 1978 to August 1981. Again most birds were color-banded and consisted of a resident clan made up of several breeding pairs or groups (Bell and Ford 1986).

Observations between different periods were compared using contingency tests. Comparisons made and sample sizes are outlined in Appendix 1. Where tests indicated significant differences, cells were examined to identify categories and periods with higher values. In some cases rows or columns were combined and further tests applied. For all except honeyeaters in the first period there is a risk of non-independence due to sequential sampling. This is alleviated by the large sample sizes and setting significance levels at $P < 0.01$. For thornbills all frequencies were divided by 5 to make the contingency test more rigorous (virtually all sequences were of five observations). Niche breadth was calculated from the formula $B = -\Sigma P_i \log_e P_i$, where $p_i$ = proportion of observations in the $i$th category. Ten categories were used for niche breadth in Fuscous Honeyeaters (hawking, hover and gleaning leaves, gleaning twig, branch, trunk and ground, probing branch, and probing flowers of mistletoe and eucalypt). Five substrate categories were used for the other two species.

## RESULTS

### ARTHROPODS

The abundance of arthropods on foliage from all plant genera combined in the proportion to which they contribute to the foliage are shown in Bell and Ford (this volume:Fig. 1). The first year showed a marked spring and summer peak in abundance, with lower numbers in autumn and winter. Spring and summer peaks were much less noticeable in the last two years, which were exceptionally dry. Indeed, numbers throughout the last 20 months were similar to those in winter 1979. As trees had lost many of their leaves by mid-1980, this indicates a period of relative and probably absolute shortage of food for leaf-gleaning birds. Arthropods from the ground showed a summer peak in 1979 and 1980, with less marked peaks in spring 1980 and summer 1981 (Bell and Ford [this volume:Fig. 1]). Levels in

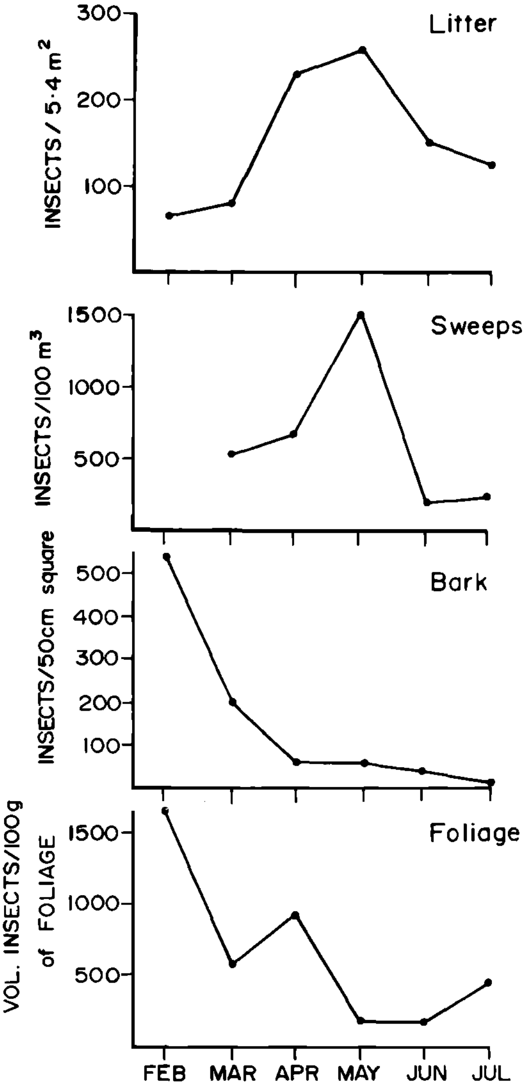

FIGURE 1. Estimated abundance of arthropods from litter, air, bark and eucalypt foliage at Wollomombi (from Huddy 1979, Noske 1982, Bell 1985a).

winter were very low. Arthropods in litter and the air peaked in autumn; those from bark and foliage declined from summer to winter (Fig. 1).

## FUSCOUS HONEYEATER

Fuscous Honeyeaters spent a greater proportion of the day foraging in autumn and winter than in spring and summer, though this was never above 80% (Fig. 2). The proportion of time perched and flying peaked in spring when territorial vigilance and defense were highest and activities such as nest-building and incubation were observed. The breeding season lasts from September to January (Dunkerley, unpubl. data).

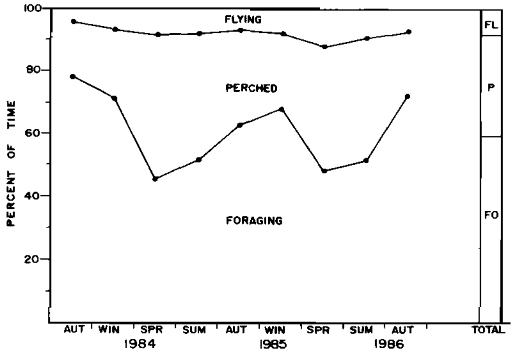

FIGURE 2. Seasonal changes in proportion of time spent foraging, perched, and flying by Fuscous Honeyeaters, at Eastwood, based on time budgets. (AUT = autumn, WIN = winter, SPR = spring, SUM = summer.)

Use of the six foraging categories differed significantly between seasons in both 1981 and 1982 ($\chi^2 = 76.6$, df = 15 for 1981; $\chi^2 = 147.9$, df = 20 for 1982; both $P < 0.001$; Fig. 3). The categories that contributed most to these values differed between years, however. In 1981, hawking was more frequent in autumn yet less frequent in winter, and hovering at leaves was less frequent in winter and more frequent in spring. Leaf gleaning was higher than expected in winter. In 1982 seasonal changes in leaf gleaning and flower probing contributed most to the significant value, with the former high in winter and low in both summers and the latter showing the reverse pattern. Bark feeding was high in spring.

Data from 1981 and 1982 also differed ($\chi^2 = 28.1$, df = 5, $P < 0.001$; Fig. 4), mostly because hovering at leaves was more frequent in 1981 than in 1982. There were also differences between discrete data from 1984 and 1985 ($\chi^2 = 24.5$, df = 5, $P < 0.001$; Fig. 4), with less bark foraging but more flower foraging in 1984 than 1985. The first and second periods also differed ($\chi^2 = 197$, df = 5, $P < 0.001$), with high residuals in all but bark foraging. The different recording methods employed in the two periods probably contributed to these substantial differences.

Time-budget data were used to calculate expected values for the discrete observations. This indicated that the two methods, although carried out simultaneously, yielded different results ($\chi^2 = 372$, df = 5, $P < 0.001$; Fig. 4). In particular, time-budgeting underestimates aerial feeding compared with discrete data. The time-budget data indicate that flower probing and leaf gleaning changed seasonally in 1984–1985, but this was not tested statistically (Fig. 3).

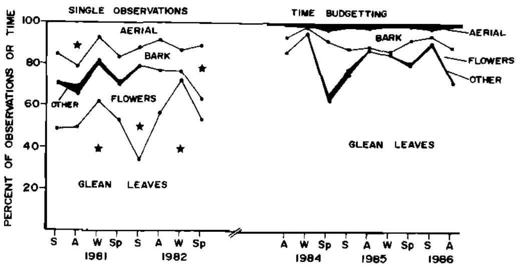

FIGURE 3. Percentage of observations (1981–1982) and percentage of time (1984–1986) spent foraging in each category in each season for Fuscous Honeyeaters at Eastwood. A star indicates significantly more foraging in this category in this season than average (S = summer, A = autumn, W = winter, SP = spring.)

There were marked seasonal changes in the incidence of foraging on the two main genera producing nectar ($\chi^2 = 161$, df = 8, $P < 0.001$ for 1981–1982; Fig. 5). Mistletoes (*Amyema pendulum* and *A. miquelii*) tended to flower regularly from late summer to winter, at which time honeyeaters visited them. This pattern was less clear for the second than the first period (Fig. 5). *Eucalyptus melliodora* flowered fairly regularly in spring and *E. blakelyi* irregularly in summer. Feeding on eucalypt flowers tended to peak in spring or summer, but there were differences between years.

The foraging niche breadth tended to be lowest in winter (Fig. 6), the season when more time was spent foraging and leaf gleaning. Niche breadth tended to be highest in spring and summer, though summer 1985–1986 was an exception. Niche breadths were consistently lower in 1984–1986 than in 1981–1982.

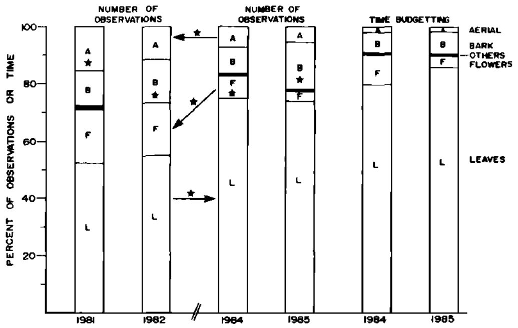

FIGURE 4. Percentage of observations by foraging substrate by Fuscous Honeyeaters in each of 4 years, and percentage of time in each category in 1984 and 1985. A star indicates significantly ($P < 0.05$) more foraging in this category than in other years in the same period. Arrows indicate significantly ($P < 0.05$) more foraging in the category in one 2-year period than the other.

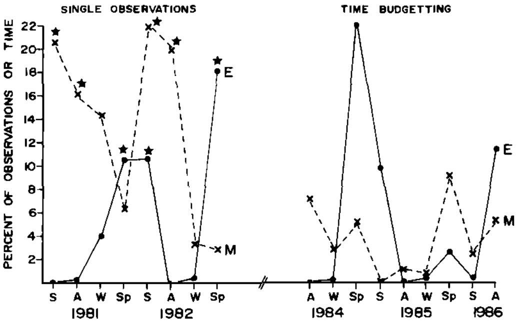

FIGURE 5. Percentage of observations or time spent foraging on flowers of mistletoes (M, *Amyema*) and eucalypts (E) each season by Fuscous Honeyeaters at Eastwood. A star indicates significantly ($P < 0.05$) more foraging on the genus in a season within each year for 1981 and 1982 (seasons as in Fig. 3).

## Scarlet Robin

Scarlet Robins are sit-and-wait foragers, which typically snatch insects from bark, pounce on them on the ground, or hawk for them in the air (Huddy 1979, Recher et al. 1985, Ford et al. 1986). However, they showed marked seasonal changes in method and particularly substrate ($\chi^2 = 2360$, df = 15, $P < 0.001$). Hawking and snatching from bark and leaves declined from summer through to winter ($r_s = -0.83, -1.0, -0.94$ for air, bark, and leaves, respectively, against month; all $P < 0.05$; Fig. 7). Ground foraging, mostly by pouncing, progressively increased during this period ($r_s = 1.0$, $P < 0.005$).

Niche breadths declined from autumn to winter. Robins also showed changes in foraging within the day ($\chi^2 > 26.2$, df = 12, $P < 0.01$ for all months except May), which were similar in all months (Fig. 8). Aerial foraging peaked around

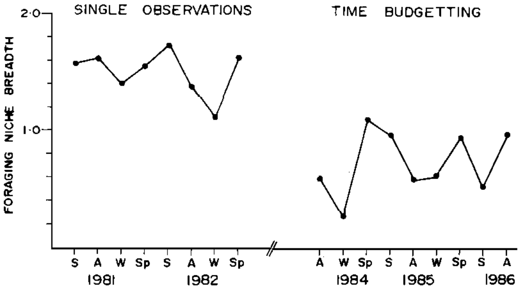

FIGURE 6. Foraging niche breadth of Fuscous Honeyeaters in each season at Eastwood (seasons as in Fig. 3).

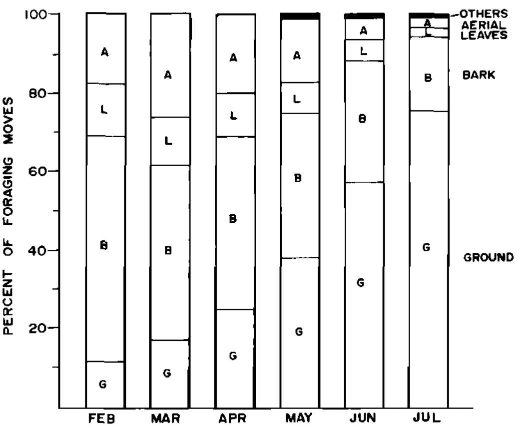

FIGURE 7. Percentage of observations of foraging on four substrates each month by Scarlet Robins at Wollomombi in 1979.

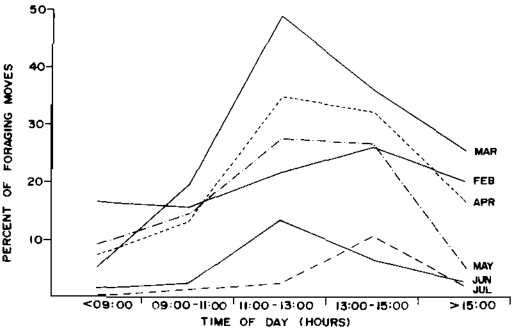

FIGURE 8. Changes in the proportion of aerial foraging in each period through the day by Scarlet Robins at Wollomombi in 1979.

midday and early afternoon, while ground foraging was lowest during these periods. Bark and foliage feeding did not change consistently during the day.

Data were separated according to the maximum temperature on the day that they were collected. Overall, ground foraging was the predominant activity at low temperatures, whereas bark and aerial foraging were more common at higher temperatures ($\chi^2 = 1660$, df = 9, $P < 0.001$). Leaf foraging increased slightly with an increase in temperature (Table 1). Differences in foraging at different temperatures were shown in data collected within the months of April, May, and June, but not in February and March (Table 1). There were data from only one temperature range in July, so no within-month between-temperature comparisons were possible. Within the lower temperature ranges there were increases in ground foraging over successive months, whereas at the highest temperature range there were declines in bark foraging and increases in aerial foraging from February to April.

### BUFF-RUMPED THORNBILL

Buff-rumped Thornbills are typically gleaners (Bell 1985b). Their use of different substrates varied consistently through the year ($\chi^2 > 108$, df = 9, $P < 0.001$ each year; Fig. 9). Leaf gleaning reached a peak in spring, at which time bark foraging predominated. From late summer to late winter use of the gound increased so that in winter it was the most frequently used substrate.

Superimposed on the regular seasonal changes in foraging were some changes between years ($\chi^2 = 40.5$, df = 6, $P < 0.001$). Ground feeding was more frequent in autumn 1980 than in 1979 or 1981. At this time leaf gleaning was particularly infrequent. The drought was severe in autumn 1980, when many trees and shrubs were defoliated.

Niche breadth fluctuated sharply between months but there was a tendency to decline towards the winter of 1980, when the drought was at its worst, and rise thereafter.

## DISCUSSION

The small, though consistent, changes shown by the Fuscous Honeyeater are perhaps not surprising in a leaf-gleaner that lives in an evergreen habitat where the abundance of insects does not vary greatly between summer and winter (Woinarski and Cullen 1984; Bell 1985a; Lowman, unpubl. data). The ratios of high to low abundance estimates of arthropod biomass on leaves are 10:1 or less, even in years with a marked spring or summer peak (Bell and Ford, this volume:Fig. 1; see also Woinarski and Cullen 1984). Deciduous and coniferous forests of the Northern Hemisphere display much more marked seasonal changes in abundance of arthropods (e.g., Gibb 1950, Perrins 1979:Fig. 58). Even in the latter habitats some species do not show marked seasonal changes in foraging. For instance the rather generalized Willow Tit (*Parus montanus*) did not show marked seasonal changes in foraging in coniferous forests in Scandinavia (Ulfstrand 1976, Alatalo 1980). Titmice (Paridae), whose seasonal changes in foraging have been extensively studied in Europe, may show broader (Ulfstrand 1976) or narrower (Alatalo 1980) niches in winter. In deciduous woodland, Gibb (1954) found that niches were broadest in autumn and early winter, but narrowest in early summer. We found that our species showed a narrower foraging niche when food was least abundant.

There were no major seasonal changes in the abundance of leaf-foraging birds at Eastwood

TABLE 1. PERCENTAGE OF FORAGING MOVES BY SCARLET ROBIN BETWEEN 11:00 AND 15:00 ON EACH SUBSTRATE AT DIFFERENT DAILY MAXIMUM TEMPERATURES EACH MONTH. NOTE THAT SOME TEMPERATURE RANGES WERE NOT ENCOUNTERED IN SOME MONTHS

| Temp. | Substrate | February | March | April | May | June | July | N[a] | P |
|---|---|---|---|---|---|---|---|---|---|
| 0–15°C | Ground | | | | 49.7 | 54.4 | 69.9 | 781 | * |
| | Bark | | | | 30.4 | 37.8 | 23.2 | 341 | |
| | Air | | | | 16.1 | 4.4 | 5.8 | 84 | * |
| | Leaves | | | | 3.7 | 2.0 | 1.0 | 20 | |
| 15–20°C | Ground | 0 | | 21.5 | 22.5 | 45.5 | | 508 | * |
| | Bark | 69.0 | | 42.2 | 49.6 | 34.6 | | 615 | |
| | Air | 28.6 | | 29.1 | 20.8 | 11.6 | | 274 | * |
| | Leaves | 2.4 | | 7.3 | 5.8 | 6.6 | | 97 | |
| 20–25°C | Ground | 13.5 | 6.5 | 25.6 | 11.1 | | | 110 | |
| | Bark | 51.4 | 41.8 | 34.4 | 42.9 | | | 362 | |
| | Air | 25.7 | 44.0 | 30.0 | 37.5 | | | 326 | |
| | Leaves | 9.5 | 7.7 | 10.0 | 8.4 | | | 75 | |
| >25°C | Ground | 0 | 8.1 | 3.1 | | | | 11 | |
| | Bark | 86.5 | 45.0 | 38.5 | | | | 120 | * |
| | Air | 11.5 | 41.4 | 50.8 | | | | 85 | * |
| | Leaves | 1.9 | 5.4 | 7.7 | | | | 12 | |

[a] N = number of foraging moves on each substrate at different temperatures.

[b] Significant ($P < 0.01$, based on cell values from contingency tests) trend in foraging site at same temperature level over months.

(Ford et al. 1985), so the potential for competition between Fuscous Honeyeaters and other species probably does not change seasonally. Indeed, Fuscous Honeyeaters aggressively dominate all other foliage gleaners and may drive them from the most productive areas (Dunkerley, pers. comm.). This is in contrast to the situation in Scandinavia where, for instance, an abundant summer visitor, the Willow Warbler (*Phylloscopus trochilus*), may exclude resident species from deciduous trees (Ulfstrand 1976).

Flowers provided a resource whose abundance and use showed some seasonal patterns, but where abundance can be very high when, for instance, some eucalypts flower prolifically. At such times larger honeyeaters like Red Wattlebirds (*Anthochaera carunculata*) and Noisy Friarbirds (*Philemon corniculatus*) and lorikeets (*Glossopsitta*) feed on nectar (Ford et al. 1986). Fuscous Honeyeaters may be aggressively excluded from flowering trees or their foraging efficiency may be reduced by exploitation of nectar by other species. Smaller honeyeaters (Eastern Spinebill [*Acanthorhynchus tenuirostris*] and Scarlet Honeyeater [*Myzomela sanguinolenta*]) also feed on the less productive but more regular mistletoe flowers, but these can be driven away by Fuscous Honeyeaters (Ford et al. 1986; Ford, pers. obs.; Dunkerley, pers. comm.).

Differences in foraging behavior and niche breadth between the two periods and within the second period between discrete observations and time budgets indicate that the observational method can greatly influence the results. Time budgets relative to discrete observations apparently overestimated activities that continue for long periods, but underestimated those that were brief, though more conspicuous, such as hawking.

Scarlet Robins showed a change from leaf, bark, and aerial foraging to ground feeding from midsummer to mid-winter (Fig. 7). This was partly because food did not decline seasonally as much on the ground as on bark and foliage (Fig. 1). Indeed, arthropods may be more common on the ground surface in winter than in summer. It is also partly because aerial and bark foraging increased with increasing temperature, whereas ground feeding declined (Table 1). This may be because insect activity on most substrates, and hence conspicuousness, is greater when it is warmer (e.g., Taylor 1963). In addition, when ground temperature becomes elevated, insects may leave the ground surface to travel to other substrates or burrow deep into the litter.

A similar change was shown by the distantly related European Robin (*Erithacus rubecula*), which changed from ground gleaning to pouncing at higher temperatures (East 1980). Bark feeding (in females), leaf gleaning and aerial foraging (in both sexes) also increased, though these activities were still fairly infrequent. This was perhaps because the temperature range in that study was only 0–10°C. Grubb (1975) noted temperature-related changes in foraging behavior of North American birds. Birds tended to move lower and more to the center of trees at low temperatures. This was most obvious below 0°C, lower than is usually experienced in daytime in our study sites.

Sit-and-wait predators among passerines in the Northern Hemisphere (e.g., Muscicapidae, Tyrannidae, Laniidae) are almost without exception migratory, as indeed are some Australian species, so there is little scope for studying seasonal changes in foraging within a site. Several studies have found temperature-related changes in foraging during the day (e.g., Spotted Flycatcher [*Muscicapa striata*], Davies 1977b; American Redstart [*Setophaga ruticilla*], Holmes et al. 1978; Eastern Kingbird [*Tyrannus tyrannus*], Murphy 1987). Also, Sakai and Noon (this volume) found changes in foraging behavior in *Empidonax* flycatchers through the breeding season. The seasonal change in foraging by Scarlet Robins is not due to changes in interspecific competition, as many aerial foragers leave Wollomombi in winter (Bell, unpubl.). Also, all the data that we collected were outside the breeding season.

Buff-rumped Thornbills showed a marked and consistent change in foraging substrate from bark and leaves to the ground from late summer onwards. This change to ground foraging was early in 1980 when insects on foliage were scarce. A change to ground feeding in autumn and winter was shown in European titmice (Gibb 1954, Alatalo 1980) and some finches (Newton 1975). These birds changed from feeding predominantly on arthropods in the breeding season to taking more seeds in autumn and winter. Thornbills fed mostly on arthropods throughout the year, though some seeds were taken in winter (Bell 1983).

The ground may be a more profitable place to forage than bark or leaves in winter. As shown in Figure 1, arthropods may actually be more common on the ground in winter than in summer, although Bell (1985a) showed a decline in arthropods on surface vegetation from summer to winter (see Bell and Ford, this volume:Fig. 1).

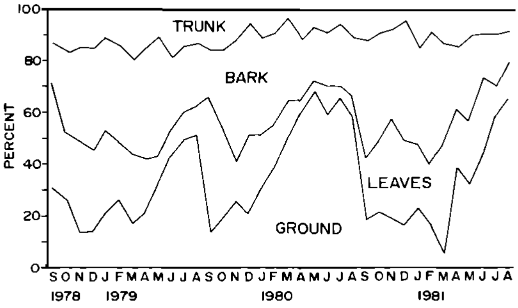

FIGURE 9. Changes in use of different substrates by Buff-rumped Thornbills each month from September 1978 to August 1981 at Wollomombi.

Buff-rumped Thornbills show a marked seasonal change in social behavior (Bell and Ford 1986). Pairs or trios defend small territories in spring to which any young reared are added. During the summer, breeding pairs or groups combine so that by January or February most birds occur in a clan of 7–15 birds. In August the clan breaks up and breeding pairs or groups are formed. Thus the high incidence of ground feeding coincides with large group size. Indeed, at such times other species join Buff-rumped Thornbills, which are nuclear species in mixed species feeding flocks (Bell 1980). These flocks probably provide benefits such as increased vigilance to predators (Morse 1980a). Some ground predators, such as snakes, are also less active in winter. Individuals or pairs in the breeding season should avoid conspicuous foraging not only for their own safety, but to avoid disclosing the position of their eggs and young.

To summarize, the three species we studied displayed three patterns of change. Fuscous Honeyeaters displayed some seasonal changes which were to some extent consistent from year to year. Scarlet Robins showed seasonal changes in foraging that resulted in part from seasonal changes in the availability of arthropods, and at least partly from short-term changes in weather. Buff-rumped Thornbills showed substantial and consistent seasonal changes in substrate, along with a change in social behaviour.

Our studies have indicated that it is easy to find statistically significant seasonal changes in foraging behavior of birds, provided that sample sizes are large. This suggests that birds usually show seasonal changes in foraging (see also Sakai and Noon, this volume: Hejl and Verner, this volume; Martin and Karr, this volume). However, the methods employed in any study may influence the results. Comparisons of different methods for collecting data on Fuscous Honeyeaters show that a consistent method must be adopted within a study and indeed between studies carried out by different observers or at different sites. Time budgets or many sequential observations may overestimate common activities, whereas single discrete observations may overestimate less common but conspicuous activities. A corollary to this is that even a rigidly consistent method may yield spurious results where the conspicuousness of an activity varies seasonally. For instance, in deciduous woodland gleaning on twigs will be more conspicuous in winter than in summer.

Sequential observations and even single observations on the same bird on different occasions suffer from the problem of nonindependence. This may mean that impressive statistical differences do not reflect real biological changes. Single observations per bird at each encounter are preferable and the more individuals that are sampled the better. Seasonal changes in foraging should be consistent over several years (true for Buff-rumped Thornbills but not always for Fuscous Honeyeaters) or at least should be substantial (as in Scarlet Robin) before they should be accepted as biologically significant.

Birds may show day-to-day changes in behavior, based for example on temperature changes; they may also show changes within a day. Our data on Scarlet Robins indicate that these changes may be substantial. These changes are interesting in themselves, but may mask or exaggerate apparent seasonal changes in behavior. Studies investigating seasonal changes should cover many days each month or season, and either restrict data to one type of weather or sample all types of weather. Also, data should be collected at the same time of day in different periods, or at intervals evenly spread through the day.

We separated our data into seasons or months, which are rather arbitrary divisions. The stage of the breeding cycle (Sakai and Noon, this volume), time in relation to migration (Martin and Karr, this volume) and phenological stage of vegetation (Hejl and Verner, this volume) are more biologically realistic separators. Our species though had long, rather asynchronous breeding seasons, were residents and lived in woodland where trees may show fresh foliage from September through to May. However, comparisons of the behavior of individually marked birds at different stages of breeding could be attempted.

If there are problems in collecting data to indicate meaningful seasonal changes in foraging behavior, there are even more in explaining these changes. Our species were principally dependent on arthropods that they obtained from a variety of sites. Seasonal changes in the abundance of arthropods can be estimated in a variety of ways. Most are tedious and time-consuming, and data are hard to standardize because arthropods are heterogeneous in form and often patchily distributed. Indeed, data on arthropod abundance are far easier to criticize than to collect and interpret. Despite this, general patterns between changes in food abundance and foraging behavior can be found, but it is unlikely that these will be close.

Factors other than food influence foraging behavior. Species frequently join flocks in the nonbreeding season (Morse 1980a), which may allow them more safety from predators, particularly on exposed substrates. Predator avoidance and choosing areas where food is abundant will interact in their influence on foraging behavior and it may be hard to identify the proximate factor. For instance, in our study Buff-rumped Thornbills might feed on the ground in winter because food is available there. Because the ground is exposed to predators they consequently join flocks. Alternatively, because they only join flocks in the nonbreeding season, this may be the only time when it is safe to venture onto the ground, which could always be the more productive substrate. Identification of seasonal changes in foraging behavior of birds is clearly only the first step in opening up a whole series of interesting questions on the factors that influence a bird's behavior.

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APPENDIX 1. A SUMMARY OF THE MAIN COMPARISONS MADE IN THIS PAPER WITH SAMPLE SIZES FOR EACH TIME PERIOD AND DETAILS OF CONTINGENCY TABLE USED TO TEST FOR SIGNIFICANT DIFFERENCES. THE PROPORTION OF TIME IN EACH CATEGORY FROM TIME BUDGETS WAS USED TO CALCULATE EXPECTED VALUES FOR COMPARISON WITH SEQUENTIAL OBSERVATIONS

| | Sample sizes | Contingency table (time period by foraging category) |
|---|---|---|
| FUSCOUS HONEYEATER (6 categories) | | |
| Single foraging observations | | |
| Between seasons—1981 | 237–465 | 4 × 6 |
| Between seasons—1982 (includes 2 summers, Jan. + Feb. and Dec.) | 75–181 | 5 × 6 |
| Between years 1981 vs. 1982 | 775, 1425 | 2 × 6 |
| Sequential observations | | |
| Between years 1984 vs. 1985 | 555, 611 | 2 × 6 |
| Different periods and methods | | |
| 1981 + 1982 vs. 1984 + 1985 | 1166, 2200 | 2 × 6 |
| Different methods, same period 1984–1985 | | |
| Time-budgeting vs. sequential observations | 1166, 74,714 s | 1 × 6 |
| Feeding on mistletoes vs. eucalypts | | |
| Between seasons 1981–1982; flower-probing data only used | 9–68 | 8 × 2 |
| SCARLET ROBIN (4 substrates) | | |
| Sequential observations | | |
| Between months February–July | 856–2525 | 4 × 6 |
| Between months, same temperature | 225–1494 | 3 × 4 or 4 × 4 |
| Within day, different time | 94–1934 | 5 × 4 |
| Between temperatures, all months | 724–4655 | 4 × 4 |
| BUFF-RUMPED THORNBILL (4 substrates) | | |
| 5 sequential observations | | |
| Between seasons, each of 3 years | 1235–2445 | 4 × 4 |
| Between 3 years | 5115–9536 | 3 × 4 |