

Is the uncommon Black-chinned Honeyeater a more specialised forager than the co-occurring and common Fuscous Honeyeater?

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Abstract. In New South Wales (NSW), Australia, the Black-chinned Honeyeater (*Melithreptus gularis*) is uncommon in comparison with the co-occurring Fuscous Honeyeater (*Lichenostomus fuscus*), which is common. The relative rarity of the former may be because it specialises on a narrow range of resources that are not abundant. Alternatively, it may be excluded from more abundant food resources by other bird species, such as the Fuscous Honeyeater. We thus compared the foraging ecologies of these two species on the New England Tableland of NSW. Broad-scale quantitative analysis of foraging, using tree species, foraging height, height of tree species, and conventional categories of foraging manoeuvres (glean, probe, snatch, hawk and pounce) revealed only slight differences between the foraging ecology of the two species. However, when foraging was investigated using finer scale analysis of gleaning techniques, Black-chinned Honeyeaters were found to spend a greater proportion of effort probing between leaves that were bound together than did Fuscous Honeyeaters. This supports the hypothesis that Black-chinned Honeyeaters are less common than Fuscous Honeyeaters because they are more specialised in foraging and their food supply is uncommon. Aggression did not seem to inhibit foraging for either species.

Introduction

Why some species are rare while others are abundant is not necessarily easily determined (Gaston 1997). However, some species are rare because they use a narrow range of resources that are themselves not abundant. These species are often characterised as relatively specialised in their resource use compared with other species. In contrast, a species may be abundant owing to its ability to utilise a wide range of common resources. Such species are often called generalists (Gaston 1997). If there is little overlap between the generalist and specialist, then it is likely that both species can coexist (Hassel 1976). If the overlap of resources used by both species is considerable, competition through exploitation or interference can act to reduce the abundance of one or both species. Competition is, however, only important when resources are limited (Newton 1998). One way in which a species can cope with competition from other species is to shrink its niche breadth, thereby reducing the extent of niche overlap with its likely competitors. Alatalo *et al.* (1986) provided a good example of the influence of competition and the co-existence of species. They found that tit species (*Parus* spp.) undergo niche divergence in areas of sympatry by reducing niche breadth, compared to areas of allopatry. Other potential environmental factors were discounted in changing the species' niche.

Rarity can often be understood better by studying foraging ecology. Our knowledge of how a species fits into a community and the relationship it has with its resources and competitors is vital for its survival (Recher *et al.* 1985). In an effort to understand Australian avifaunal communities, comprehensive analyses of foraging behaviour have been undertaken. For example, Recher *et al.* (1985) and Ford *et al.* (1986) documented foraging of bird communities in eucalypt woodland and open forest by recording data on foraging substrate, foraging method and for-

aging height. Other Australian studies (for example, Cale 1994; Mac Nally 1994; Antos and Bennett 2006; Hodgson *et al.* 2006) have also looked at the foraging ecology of bird communities. There has also been a focus on the utilisation of resources by Australian honeyeaters. This is because honeyeaters (Meliphagidae) are a common avian group in Australian ecosystems (Ford and Paton 1977), with many species co-occurring and often exploiting similar foods. Because certain honeyeaters forage mainly on nectar resources, niche utilisation, resource depletion and competition can be comprehensively studied resulting in a greater understanding of community ecology. For example, Ford (1979) found that nectar was common in winter and spring in South Australia, but less abundant in summer and autumn. He hypothesised that honeyeaters could coexist during resource shortages by small honeyeaters foraging on poor nectar resources and large honeyeaters defending and foraging on richer resource patches. Evidence in support of this hypothesis was produced by Ford and Paton (1982). Mac Nally and Timewell (2005) also found that the large aggressive honeyeater, the Red Wattlebird (*Anthochaera carunculata*), dominated rich nectar patches by aggressively excluding smaller honeyeaters, which were most common in sites with moderate levels of flowering. Armstrong (1991) found that two species of territorial honeyeaters were most aggressive when nectar was least abundant. Feeding on resources such as insects and alternative carbohydrates also may reduce competition among honeyeaters (Ford 1979; Paton 1980).

By comparing the ecology of rare and common co-occurring species, the factors that determine rarity can often be better understood (Gaston 1997). Symonds and Johnson (2006) found that body mass and latitude were the only strong predictors of

the abundance of Australian honeyeaters and related insectivorous groups. The Black-chinned Honeyeater (*Melithreptus gularis*) is an uncommon species (Barrett *et al.* 2003) and is listed as threatened in New South Wales (NSW Scientific Committee 2001) and South Australia (*National Parks and Wildlife Act 1972* (South Australia)), and near threatened nationally (Garnett and Crowley 2000). Further, it has also been listed as a declining species in the NSW sheep–wheat belt (Reid 1999) and Barrett *et al.* (2003) provided evidence for a decline on the New England Tableland. The Fuscous Honeyeater (*Lichenostomus fuscus*) can be an abundant honeyeater that co-occurs with the Black-chinned Honeyeater and is of similar weight. Therefore, factors other than latitude and weight must determine the difference in their abundance. Our focus was to collect data on the foraging of the Black-chinned Honeyeater to gain knowledge of its ecology and to compare it with the Fuscous Honeyeater on the New England Tableland, NSW. We predicted that the Black-chinned Honeyeater should be a more specialised forager than the Fuscous Honeyeater. We also collected information on the density of other honeyeaters in Black-chinned Honeyeater territories and quantified aggression towards Black-chinned Honeyeaters to judge whether the species might be excluded from certain areas through aggression or suffer frequent interspecific aggression, which may interfere with other activities.

Methods

Study site

The study was conducted on the western edge of the Northern Tablelands bioregion of NSW, in the area bounded by the towns and hamlets of Bundarra (30°10'S, 151°04'E), Kingstown (30°30'S, 151°06'E), Uralla (30°38'S, 151°30'E) and Armidale (30°30'S, 151°39'E). This region is also known as the Bundarra Downs and is described in NSW National Parks and Wildlife Service (2003). Study sites were located mainly on travelling stock routes (TSRs), with some occurring on private land.

The vegetation is predominantly dry sclerophyll woodland dominated by eucalypts and with a sparse understory. Study sites comprised four vegetation types, with most in box–gum eucalypt woodland (Table 1). The second most common habitat

was box–ironbark eucalypt woodland, the third most common habitat was box–stringybark eucalypt woodland and the fourth habitat, cypress pine woodland. Common shrub species found across the habitat types included *Cassinia quinquifaria*, *Olearia viscidula*, *Bursaria spinosa*, *Acacia ulicifolia*, *A. implexa* and *A. filicifolia*.

Species

The Black-chinned Honeyeater has a mean weight of 21 g (range 18–22.5 g, $n = 7$ males, 2 females), a total length of 15.5 cm, and a short, slightly down-curved bill (Higgins *et al.* 2001). It is a gregarious species that forms tight social groups that range from a pair to five individuals, and is sedentary (defends territories during the breeding season and stays within the study area over the study period) within the study area.

The Fuscous Honeyeater weighs ~17 g (range 12–24 g, mean of males = 18.4 g, $n = 38$, mean of females = 16.9 g, $n = 60$) and has a total length of ~15.5 cm. It has a moderately long bill that is slightly down-curved. It is an abundant, aggressive, and gregarious species that usually socialises in pairs or small flocks (Higgins *et al.* 2001) and appears to be sedentary throughout the year within the study area.

Study design

Groups of Black-chinned Honeyeaters were initially located by using systematically placed playback points (400 m apart) during late August and September of 2003 and August and September 2004. On arrival at a point, 3 min of playback began. This was followed by 2 min of listening, followed by a further 3 min of playback. If a Black-chinned Honeyeater was heard at any time during this sequence, playback stopped. Reaction to playback was strong in the breeding season, with all individuals of a group approaching the tape recorder and calling loudly. Groups were then followed to determine the size of groups. No foraging data were collected during the first 10 minutes after initial detection to avoid any influence of playback on foraging. Fuscous Honeyeaters were abundant in all Black-chinned Honeyeater territories, hence, no playback was used to locate them.

Foraging data were initially collected from spring (September) 2003 to winter (August) 2004. Birds were located

Table 1. The four vegetation types in the study sites and the tree species found within them

Tree species are grouped in the analyses: B, boxes; G, smooth-barked gums; A, angophora; S, stringybarks; I, ironbarks; and O, other

Species	Grouping	Box–gum woodland	Box–ironbark woodland	Box–stringybark woodland	Cypress pine woodland
<i>Eucalyptus albens</i>	B	x	x		
<i>E. andrewsii</i>	S				x
<i>E. blakelyi</i>	G	x	x	x	
<i>E. caleyi</i>	I		x		x
<i>E. caliginosa</i>	S			x	
<i>E. dealbata</i>	G				x
<i>E. melliodora</i>	B	x	x	x	
<i>E. moluccana</i>	B	x	x	x	
<i>E. prava</i>	G	x			x
<i>E. sideroxylon</i>	I		x		
<i>Angophora floribunda</i>	A	x	x		x
<i>Callitris endlicheri</i>	O				x

by searching areas where they had been previously found. About the same number of foraging observations were made for each species at each site to reduce bias associated with the different vegetation types. Each foraging event was cross-classified on the basis of foraging manoeuvre, foraging substrate, foraging height, substrate species and height of foraging substrate species (except in spring 2003, when height of substrate species was not recorded). Foraging manoeuvres included glean, probe, snatch, hawk and pounce, as defined in Ford *et al.* (1986). Foraging substrates were foliage, under bark of branches and trunk, flower, ground and air. Substrate species was the plant species on which the bird was foraging. For the analysis, plant species were grouped into seven categories: angophora (*Angophora floribunda*), boxes (*Eucalyptus albens*, *E. moluccana*, *E. melliodora*), ironbarks (*E. caleyi*, *E. sideroxylon*), smooth-barked gums (*E. blakelyi*, *E. prava*, *E. dealbata*, *E. viminalis*), stringybarks (*E. caliginosa*, *E. andrewsii*), mistletoes (*Amyema* sp.), and other species (shrubs and *Casuarina cunninghamiana*). Foraging height and height of tree species were measured to the nearest metre by visually estimating heights <17 m, and using a Bushnell Yardage Pro 500® laser range-finder (Bushnell Performance Optics Australia, Heatherton, Vic.) for heights >17 m. Up to five sequential foraging events (an individual foraging manoeuvre) were recorded per individual. To ensure independence of data, this was then followed by a gap of at least 10 min until the next recording episode of foraging events by any focal bird (Porter *et al.* 1985).

Because foliage gleaning was found to be important for both species, a closer examination was made of how birds fed from foliage during spring (September–October) of 2005 and summer (December–February) of 2005–2006. As with the initial foraging data, foraging events were recorded. Foraging on foliage was classified into two categories: foliage gleaning or prying between a pair of leaves that were dorso-ventrally bound together. Each foraging record was spaced at least 10 min apart per individual, to assure independence of data (Hejl *et al.* 1990). Again, samples were evenly dispersed between species and among territories.

For the purpose of quantifying aggression, we recorded time-budget data for both species in 11 Black-chinned Honeyeater territories from September 2004 to February 2005. The 11 territories were randomly selected from 20 available territories. Bird movements and territorial boundaries had been monitored since 2003. All but one of the sites had low levels of flowering of eucalypts. We endeavoured to sample each species equally within each territory to reduce inter-site bias. The activity states recorded included: foraging, sitting (including preening), calling, chasing other birds, being chased by other birds, socialising with a conspecific and flying. No non-aggressive socialising occurred between all species. If a bird was lost for more than 10 s during recording the time budget, recording was stopped at that point. If an individual was lost before 1 min of sampling had been completed, the sample was not included in the dataset in order to avoid bias towards conspicuous behaviours (Recher and Gebiski 1990). Each activity of the focal bird was classified and timed to the nearest second. Because playback can influence aggression among honeyeaters, it was not used to find birds when recording time budgets.

In conjunction with time budgeting, estimates of density of all honeyeater species, excluding Black-chinned Honeyeaters, were determined for the same 11 territories during the same season. We used distance sampling (Buckland *et al.* 2001), so that a relationship between honeyeater density and aggression could be investigated. Distance sampling requires the modelling of a detection function based upon the distances of detected objects from the centre of a point or line transect. The required horizontal distances were determined using a Bushnell Yardage Pro 500® laser range-finder. Sampling began by taking a 'snapshot' 2 min after arriving at a survey point. Although this allowed any disturbed honeyeaters to settle, it was unlikely that birds were disturbed because they typically stay high in the canopy. Covariates measured at each point were wind-speed (0, no wind; 1, slight breeze; 2, moderate wind that moved minor tree branches); and cloud cover (0, no cloud; 1, 25% cloud cover; 2, 50% cloud cover; 3, 75% cloud cover; and 4, overcast). Sampling began at sunrise and was completed within 2 hours. Total length of each bird species was taken from Higgins *et al.* (2001) and was included as a covariate. Using pilot data (September 2004, unpublished data) to explore trade-offs between sample size and spatial coverage, a sampling regime of eight points per territory, sampled four times each, was selected. The distribution of survey points was selected using the survey design engine of Distance 4.1, Release 2 (Thomas *et al.* 2004). All field data were collected by G. W. Lollback.

Data analysis

The cross-classified foraging data were analysed by fitting various generalised linear models with a Poisson error term. These models were nested and selected *a priori* (Burnham and Anderson 2002). Akaike's information criterion (AIC) was used to determine which foraging model fitted the data best (Johnson and Omland 2004). Because the data were overdispersed, QAIC values (quasi-AIC) (Burnham and Anderson 2002) were used for the foraging analyses. The larger the value of Δ_i (the QAIC value for model i , minus the lowest QAIC value from the suite of models), the less plausible it was that a particular model was the best out of the suite of models considered in an analysis. Akaike weights (w_i) provide a relative weight of evidence for each model as part of the model assessment process. The relative importance for each variable was also calculated by summing the weights ($\sum w_{\text{model containing variable } i}$) of each model in which the variable was included. For an explanation of the QAIC equation, AIC difference (Δ_i) and Akaike weight (w_i), see Burnham and Anderson (2002).

For the analysis, the foraging manoeuvre and foraging substrate categories were merged under a foraging variable to provide more ecological relevance. The sub-categories under this variable were gleaning from foliage, gleaning from ground, gleaning from branch, probing under bark of branch or trunk, probing a flower, hawking in air, hover-gleaning from foliage and snatching from branch. Foraging height was grouped into the following classes to reflect actual habitat vegetation structure: ground; 1–2 m; 3–5 m; 6–10 m; 11–15 m; 16–20 m and 21–30 m. Foraging below 1 m was grouped into the 1–2 m category and other foraging heights were measured to the nearest 0.5 m. Height of trees was grouped in the same categories, excluding the ground category.

Foraging niche-breadth was calculated using the Shannon–Wiener index (H') (Krebs 1989) and was then standardised to a 0–1 scale, thereby creating an evenness measure (J') (Krebs 1989):

$$J' = \frac{H'}{\log n}$$

where J' = evenness measure of the Shannon–Wiener index, H' = Shannon–Wiener index and n = total number of possible resource states.

If $J' \leq 0.4$ then the species is regarded as a specialist in relation to the respective niche dimension. If $J' \geq 0.6$, the species is regarded as a generalist in relation to the respective niche dimension (Antos and Bennett 2006). Foraging niche overlap was calculated using Morisita's measure (C), a measure regarded as the least biased overlap index relative to sample size, evenness of resource categories and the number of resource categories (Krebs 1989).

The subsequent foraging data on foliage feeding (i.e. either foliage gleaning or leaf prying) between species, formed a two-by-two contingency table and were analysed using a Pearson's χ^2 -statistic. The P value was computed by a Monte Carlo test with 1000 replicates to guard against type I error associated with low expected values.

Distance sampling data were analysed in Distance 4.1, Release 2 (Thomas *et al.* 2003). Six detection-function models were considered. These were: a uniform key function, with or without a simple polynomial or cosine key adjustment; a half-normal key function with or without a cosine or hermite polynomial key adjustment; and a hazard-rate key function, with or without a cosine or simple polynomial adjustment. The model with the lowest AIC value was selected as the detection function. The multiple covariates distance sampling analysis engine (MCDS) was generally used to estimate honeyeater density. There were, however, major model fitting problems when estimating Fuscous Honeyeater density using the MCDS. Hence, the conventional distance sampling analysis engine was used to estimate Fuscous Honeyeater density.

The time-budget data were analysed using backward stepwise multiple linear regressions. The basic model for the regression equation is $Y = \alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_m X_m + \epsilon$, where X_1 to X_m are explanatory variables, β_1 to β_m are parameters, α is the intercept, ϵ is the error, and Y is the response variable. Data were initially plotted to assess if any transformations were needed to achieve a linear relationship between the data. Rate of aggression is the number of aggressive acts per minute, and was the response variable in the analysis. The proportion of time spent sitting, calling, flying, and honeyeater density and Fuscous Honeyeater density were used as explanatory variables. Conspicuous behaviour such as calling and flying may increase aggression, whereas sitting is relatively inconspicuous and might result in reduced aggression towards a bird. The null hypothesis tested were $\beta_i = 0$, where i is an explanatory variable.

Results

Foraging behaviour

A total of 1205 Black-chinned Honeyeater foraging events (from 71 individuals and 32 groups) and 1140 Fuscous

Honeyeater foraging events (from at least 100 individuals) were recorded from spring 2003 to winter 2004 (Fig. 1). Foliage gleaning was the main foraging method for both species in all seasons, with bark foraging (gleaning and probing) and probing flowers also being important for both species in some seasons. Fuscous Honeyeaters had a greater overall range of foraging manoeuvres on different substrates than did Black-chinned Honeyeaters. The latter species never gleaned on the ground, hawked or hover-gleaned. Black-chinned Honeyeaters had a smaller variety of manoeuvres in spring compared to the Fuscous Honeyeater, while diversity of foraging method was similar between species for autumn, summer and to a lesser extent, winter (Fig. 1; Table 2). Overall overlap between the two species for manoeuvre/substrate was $C = 0.97$, with a seasonal overlap range of $C = 0.86$ – 0.99 .

The distribution of foraging height and selection of trees of certain heights were similar for each species (Fig. 2). This was reflected by the overall high proportion of foliage gleaning undertaken by both species. However, Fuscous Honeyeaters foraged more often at lower heights (<5 m) and in shrubs, saplings and smaller canopy trees than did Black-chinned Honeyeaters, which foraged more in the taller trees (>16 m; Fig. 2).

Diversity of foraging height and tree-height selection for both Black-chinned Honeyeaters ($J' = 0.70$ and 0.81 respectively) and Fuscous Honeyeaters ($J' = 0.76$ and 0.83 respectively) were both similarly high. Selection of tree types was similar between the two species, as reflected in the high overlap value ($C = 0.99$) (Fig. 3). Both species selected a diverse range of tree species, hence the same diversity measure of $J' = 0.79$. The foraging height overlap and tree height selection overlap values were also high, with values of $C = 0.97$ and $C = 0.95$ respectively.

The comparison of *a priori* ecological foraging models using an information-theoretic approach to model selection (Burnham and Anderson 2002) reflected the high degree of overlap between the two species. Models considered included the explanatory variables and interactions among these variables of species (Black-chinned Honeyeater and Fuscous Honeyeater), foraging height, season, foraging manoeuvre/substrate, and tree type. Some of the models considered and the relationship among them are given in Table 3. Of the models listed, all but one had a $\Delta_i > 2$ in relation to the model with the smallest AIC, indicating reduced support for the likelihood that they best explained the data. On this basis, there were 12 models (not listed in Table 3) that were found to be inconsequential. No single model best explained the data, although based upon the distribution of Akaike weights among the models considered, two models could be considered as possible representations of the data. Both of these models included the variable tree height, indicating that both species foraged in trees of different heights disproportionately. The second best model included a tree height by species interaction term, which can be interpreted as implying that the two species differ in the size of the trees in which they forage (Fig. 2). In terms of Akaike weights, the most parsimonious model, the one that included only the explanatory variable of tree height, had a weight of 62%, while the next most parsimonious model, that including honeyeater species and a tree height by honeyeater species interaction term, had a weight of 26%.

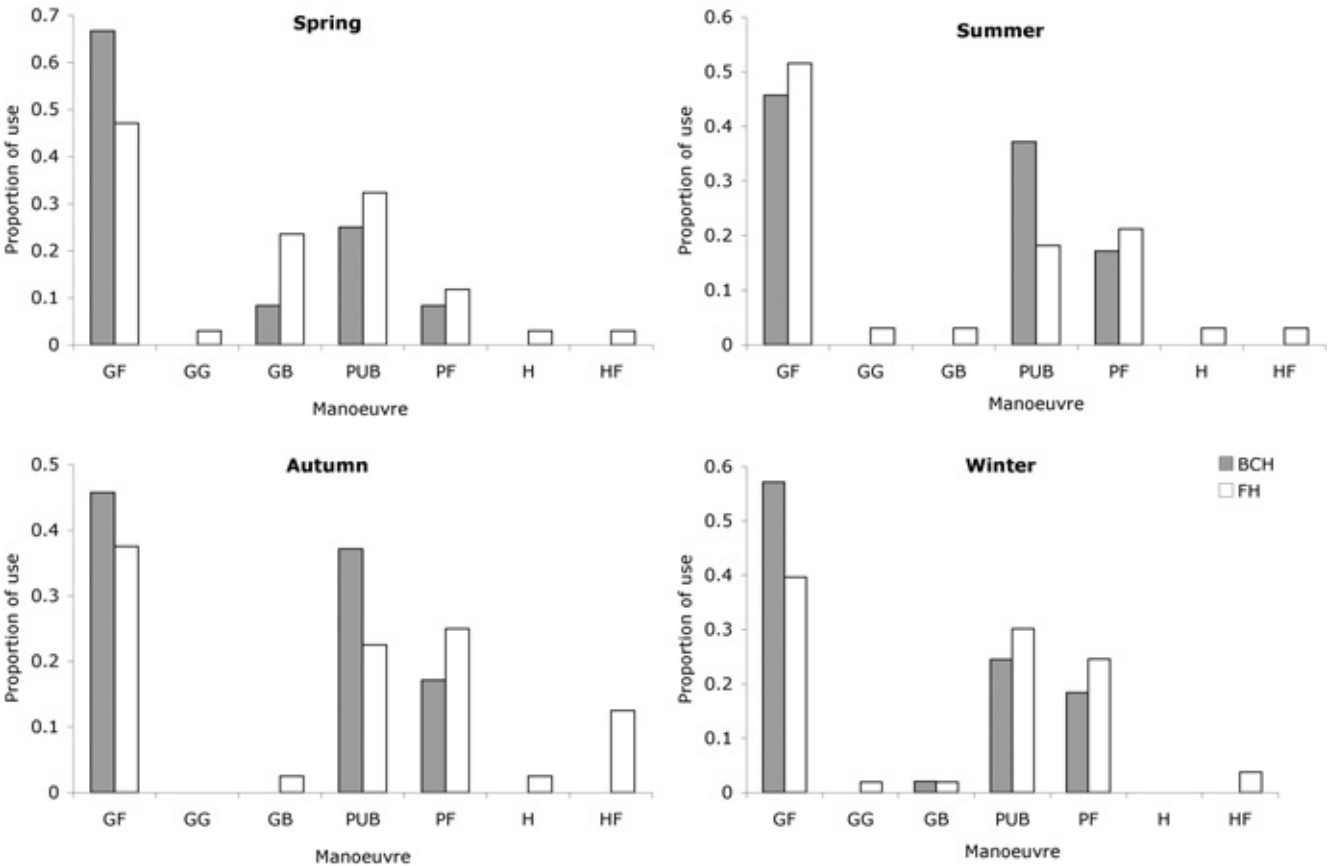


Fig. 1. Foraging manoeuvres of the Black-chinned Honeyeater (BCH; $n = 1205$ observations) and Fuscous Honeyeater (FH; $n = 1140$) for different seasons. Key: GF, glean foliage; GG, glean ground; GB, glean off branch; PUB, probe under bark on branch or trunk; PF, probe flower; H, hawk in air; HF, hover-glean from foliage.

The subsequent foraging analysis involved a closer examination at foliage foraging. The samples were derived from observations of 20 Black-chinned Honeyeaters (from the 12 groups used in the time budgets) and at least 30 Fuscous Honeyeaters from these Black-chinned Honeyeater territories. There were 138 Black-chinned Honeyeater samples and 110 Fuscous Honeyeater samples. Black-chinned Honeyeaters gleaned off leaves 38 times and pried between leaves 100 times. In contrast, Fuscous Honeyeaters gleaned off the surface of leaves 100 times and pried between leaves only 10 times. Hence, Black-chinned Honeyeaters foraged by prying between leaves much more often than did Fuscous Honeyeaters ($\chi^2_1 = 99.60$, $P = 0.001$, Monte Carlo test with 1000 replicates).

Table 2. Evenness measure for foraging in different seasons for Fuscous (FH; $n = 1140$ observations) and Black-chinned (BCH; $n = 1205$) Honeyeaters

	BCH	FH
Overall	0.54	0.66
Spring	0.41	0.54
Summer	0.54	0.52
Autumn	0.54	0.62
Winter	0.52	0.61

Aggression

In estimating honeyeater abundance using distance sampling, data were truncated at 50 m for the honeyeater abundance in general and 40 m for the Fuscous Honeyeater analysis in particular (Fig. 4). Doing this ensured the fitting of robust detection

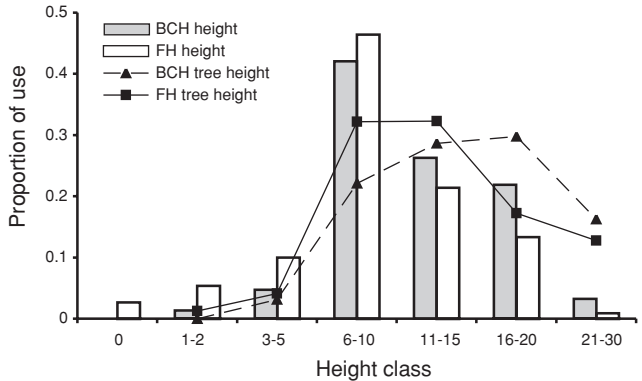


Fig. 2. Distribution of foraging heights (columns) and the height of the trees in which foraging occurred (lines) for Black-chinned Honeyeaters (BCH; $n = 1205$ for foraging height, 890 for tree height) and Fuscous Honeyeaters (FH; $n = 1140$, 845).

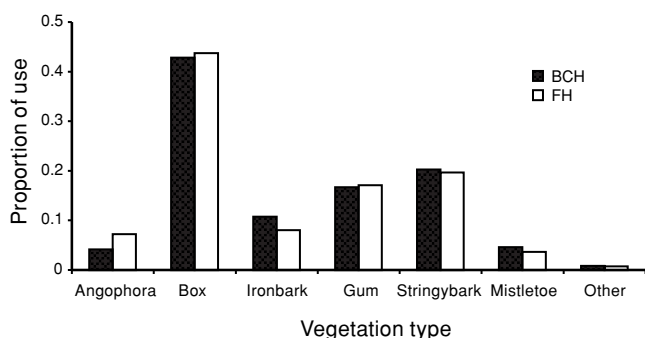


Fig. 3. Selection of vegetation type by Black-chinned Honeyeaters (BCH; $n = 1205$ observations) and Fuscous Honeyeaters (FH; $n = 1140$).

functions (Buckland *et al.* 2001). Estimated honeyeater density and Fuscous Honeyeater density ranged from 2.3–6.9 birds ha^{-1} and 2.7–7.1 birds ha^{-1} respectively (Table 4).

Just over 720 min of Black-chinned Honeyeater activity and just over 706 min of Fuscous Honeyeater activity were recorded. Fuscous Honeyeaters spent: 78.4% of their time foraging; 14.8% of their time sitting; 2.3% of their time calling; 2.9% of their time in flight; 1.5% of their time occupied with aggression; and <1% of time socialising. Black-chinned Honeyeaters spent: 66.4% of their time foraging; 23.1% of their time sitting; 4.0% of their time calling; 4.0% of their time in flight; 2.2% of their time occupied with aggressive acts; and <0.3% of time socialising.

In terms of aggression towards Black-chinned Honeyeaters, no explanatory variable predicted aggression, hence, $\beta_{\text{sit}} = \beta_{\text{call}} = \beta_{\text{flight}} = \beta_{\text{honeyeater density}} = \beta_{\text{Fuscous Honeyeater density}} = 0$. Most importantly, density of all honeyeaters, and Fuscous Honeyeaters, were not related to the number of aggressive acts experienced by Black-chinned Honeyeaters. Likewise, no explanatory variable suitably explained aggression towards Fuscous Honeyeaters.

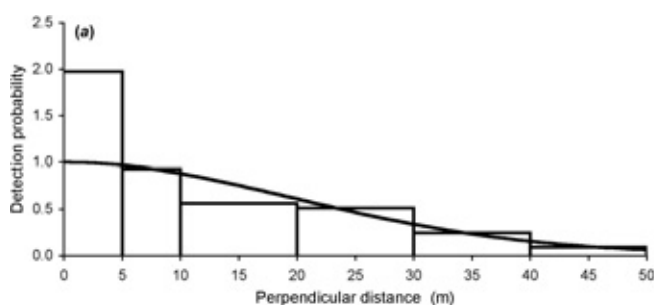


Table 3. Information theoretic analysis of foraging data
The QAIC difference (Δ_i) and Akaike weight (w_i) are shown; \times represents an interaction term

Model	QAIC	Δ_i	w_i
Tree height	364.00	0	0.62
Species \times tree height	365.74	1.74	0.26
Tree \times tree height	367.38	3.38	0.11
Species \times tree \times tree height	372.68	8.68	0.01

Discussion

When assessed using traditional and popular methods to quantify avian foraging such as those used by Recher *et al.* (1985) and Ford *et al.* (1986), the foraging ecologies of the uncommon Black-chinned Honeyeater and the common Fuscous Honeyeater were found to be similar. Although Fuscous Honeyeaters used a more diverse range of foraging manoeuvres during the breeding season and Black-chinned Honeyeaters tended to forage in taller trees, the species overlapped greatly in all foraging variables. Using these traditional methods of comparing foraging ecology, the two species had similar niche breadths, with the Black-chinned Honeyeater being slightly more specialised. Closer examination of foliage foraging, however, showed that Black-chinned Honeyeaters pried between leaves that were bound together significantly more often than did Fuscous Honeyeaters. This indicated significantly more specialisation of foraging niche by Black-chinned Honeyeaters.

Only one other study has thoroughly examined the foraging behaviour of the Black-chinned Honeyeater. Keast (1968) studied this species at two sites, near Sydney and Melbourne, during the breeding season, reporting that 59–62% of foraging manoeuvres were foliage foraging and 38–39% of foraging manoeuvres were branch and trunk foraging (most likely equivalent to probing under bark). These results are not too dissimi-

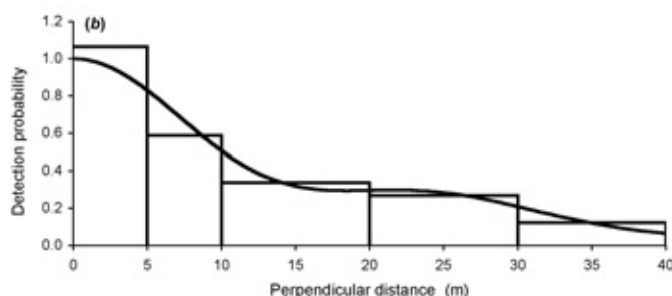


Fig. 4. Detection functions for (a) density of all honeyeaters (half-normal key function) and (b) density of Fuscous Honeyeaters (half-normal key function with two cosine adjustments) within Black-chinned Honeyeater territories. The histogram bars are scaled frequencies (counts of sightings) that correct for the increased area that is surveyed with increasing distance from the point

Table 4. Density of all honeyeaters and Fuscous Honeyeaters (birds ha^{-1}) within 11 Black-chinned Honeyeater territories
Estimated density, figures in parentheses are the standard deviation

Density	Black-chinned Honeyeater territory										
	1	2	3	4	5	6	7	8	9	10	11
All honeyeaters	4.6 (0.9)	4.6 (0.9)	6.4 (0.7)	3.3 (0.5)	2.3 (0.5)	3.8 (0.5)	6.9 (0.9)	4.4 (0.5)	6.4 (0.9)	4.8 (1.0)	6.9 (0.8)
Fuscous Honeyeaters	3.0 (0.9)	2.7 (0.8)	3.5 (0.6)	2.7 (0.5)	2.8 (1.5)	5.0 (0.9)	4.9 (1.1)	3.9 (0.8)	6.9 (1.4)	2.9 (0.9)	7.1 (1.8)

lar to the foraging results during spring and summer (breeding season) found in the present study.

Ford and Paton (1977) gathered information on foraging by Black-chinned Honeyeaters ($n = 94$) and White-plumed Honeyeaters (*Lichenostomus penicillatus*). Chan (1990) found that the White-plumed Honeyeater was found to have had a high foraging overlap with the Fuscous Honeyeater near our study area. Hence, a limited comparison of the Ford and Paton (1977) study and the results of the present study can be made. Ford and Paton (1977) found a large difference between species in the proportion of foraging manoeuvres, with hawking comprising 23% of foraging by White-plumed Honeyeaters compared with ~6% of foraging by Black-chinned Honeyeaters. The White-plumed Honeyeater in the Ford and Paton (1977) study, like the Fuscous Honeyeater in our study, spent less time foraging on bark substrates than the Black-chinned Honeyeater (~19% v. 28%) and more time foraging on the ground than did the Black-chinned Honeyeater. Proportions of other foraging behaviours were similar and overlaps were similar to those between Black-chinned and Fuscous Honeyeaters in our study.

Slater (1994) also compared foraging manoeuvres, substrate and height among two *Melithreptus* species, including the Strong-billed Honeyeater (*M. validirostris*), and a *Lichenostomus* species, the Yellow-throated Honeyeater (*L. flavicollis*) in Tasmania. Of these two species, the Strong-billed Honeyeater is most like the Black-chinned Honeyeater in size and foraging behaviour, while the Yellow-throated Honeyeater is comparable to the Fuscous Honeyeater. Most foraging manoeuvres of both Strong-billed and Black-chinned Honeyeaters were gleaning off leaves and probing under bark. The smaller Fuscous Honeyeater observed in the present study gleaned much less (56% of manoeuvres) than the Yellow-throated Honeyeater (~93% of manoeuvres) (Slater 1994). Nevertheless, Slater (1994) found differences in foraging between a co-occurring *Lichenostomus* and *Melithreptus* species and which were greatest during the breeding season (spring and summer), as in our study. Slater (1994) suggested that food resources were likely to be scarcer in winter, leading to less overlap of foraging to avoid competition. Looking at the initial foraging data, it would appear that avoidance of competition owing to a lack of overlap of foraging in winter was unlikely in the present study, given the high overlap values of foraging behaviour.

When we analysed the foraging ecologies of the Black-chinned Honeyeater and the Fuscous Honeyeater in greater detail, we found a stark difference. Black-chinned Honeyeaters spent 72% of foliage foraging probing between leaves, while Fuscous Honeyeaters only probed between leaves for 9% of their gleaning events. Food sources on the surface of leaves are different from those found in leaves that are bound together dorso-ventrally. Invertebrates between bound leaves are commonly caterpillars (New 1988) or, less commonly, spiders or lerp (a honeydew protective covering exuded by the larvae of psyllid insects) (G. W. Lollback, pers. obs.). Invertebrates and carbohydrate resources (lerp and manna) that potentially constitute food for the two honeyeaters occurring on the flat surface of leaves include psyllids, and less commonly a suite of mobile invertebrates, including Arachnida, Coleoptera, Diptera, Hemiptera, Hymenoptera and Lepidoptera (Woinarski and Cullen 1984). Because a large proportion of the time was spent

foraging from foliage by both species, the implication of this result is probably ecologically profound. It was likely that the Black-chinned Honeyeater and the Fuscous Honeyeater are ecologically separated by foraging micro-site (fine-scale foraging) and most likely food type, with the Black-chinned Honeyeater likely to consume a greater proportion of caterpillars than the Fuscous Honeyeater, which selects a wider range of prey that is available on leaf and branch surfaces, the ground and in the air.

As with other *Melithreptus*, the Black-chinned Honeyeater possesses ectethmoid-mandibular articulation. Normally, birds open their bill by moving only the lower mandible. Ectethmoid-mandibular articulation permits the Black-chinned Honeyeater to move both mandibles simultaneously (Bock and Hiroyuki 1971), which allows prying between bound leaves or under bark easier and more effective. This action also facilitates lubricating the tongue with mucus, which would help capture insects (Bock and Hiroyuki 1971), especially those in hard-to-reach places. Therefore, the Black-chinned Honeyeater is likely to be more effective than the Fuscous Honeyeater at prying between leaves and under bark for prey. Within the remaining Meliphagidae, only some species of *Manorina* and *Ptiloprora* have this attribute but it is not as well developed as in *Melithreptus* (Bock and Hiroyuki 1971).

Density of honeyeaters and of the Fuscous Honeyeater specifically were poor predictors of aggression towards Black-chinned Honeyeaters. Likewise, conspicuous behaviours such as flying and calling did not predict aggression and neither did an inconspicuous behaviour, sitting. Importantly, something other than honeyeater density, including the density of Fuscous Honeyeaters, influences the rate of aggressive acts towards Black-chinned Honeyeaters. Black-chinned Honeyeaters can presumably meet their energy demands by foraging for ~66% of their diurnal activity and spend <2% of their time subject to direct interference from other birds. Additionally, time spent in aggression by Black-chinned Honeyeaters is no more than time spent by the Fuscous Honeyeater and is typical of other honeyeaters (see table 3 in Oliver 2001 for summary), suggesting interference and exclusion is not severely detrimental to Black-chinned Honeyeater existence. The species may be excluded from richer flowering patches by large aggressive honeyeaters, such as the Red Wattlebird (and possibly smaller honeyeaters also), as suggested by Ford and Paton (1982) and Mac Nally and Timewell (2005). As the Black-chinned Honeyeater may avoid rich patches, this type of exclusion will not be reflected by aggressive acts towards the species, and therefore will not be reflected in the aggression analysis in this study.

The results we obtained support our prediction that Black-chinned Honeyeaters are likely to be relatively uncommon compared with the Fuscous Honeyeater as a result of its more specialised foraging. Although we found apparently high overlaps between Black-chinned and Fuscous Honeyeaters when we used standard methods to classify foraging ecology, when we looked more closely we found substantial differences between the species. The Fuscous Honeyeater uses a wide range of foraging manoeuvres on many substrates at a wide range of heights. In contrast, the Black-chinned Honeyeater forages in the canopy predominantly by prising apart leaves that are stuck together by insects. It is unlikely that the Black-chinned Honeyeater is uncommon owing to substantial competition

from the Fuscous Honeyeater because it probably takes resources that are not often eaten by Fuscous Honeyeaters. However, these food resources are probably less common, which could explain why the Black-chinned Honeyeater is rare.

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