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THE IMPORTANCE OF EUCALYPT NECTAR IN THE DIET OF LARGE HONEYEATERS

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In a study comparing the densities of Noisy Friarbirds *Philemon corniculatus*, Red Wattlebirds *Anthochaera carunculata* and flowering eucalypts, between 1992 and 1996 in central eastern New South Wales, the flowering of trees was found to be a very highly significant explanatory variable accounting for changes in honeyeater numbers at both regional and local scales. Correlations between counts of honeyeaters and flowering trees and the proportion of time spent in aggression and foraging at flowering trees were significant. At sites on the western slopes, flowering trees are more significant in determining the density of these two honeyeaters than sites on the coast and tablelands. While eucalypt nectar is important at some sites and for some seasons, it is suggested that other factors, such as patch size and other foods, may determine the whereabouts of these two honeyeaters. The correlations suggest that both honeyeaters seek higher yielding flowering patches, and that defence of nectar sources is more worthwhile when resources are more concentrated and localized. This study indicates that remnant forests on the western slopes provide important foraging habitat in winter and spring, particularly for *P. corniculatus*.

INTRODUCTION

Several studies have revealed a positive correlation between honeyeater numbers and flower or nectar abundance over both spatial and temporal scales (e.g. Ford 1983; Collins, Briffa and Newland 1984; McFarland 1985; Newland and Wooller 1985), with the correlation being stronger for larger honeyeaters in some studies (e.g. Collins and Newland 1986). In studies comparing patches within a site at any one time, positive correlations were found between nectar availablity and honeyeater numbers (Collins 1985; Ford and Paton 1985; Collins and Newland 1986; Paton 1986). Over time, honeyeater numbers diminished as nectar became scarce in patches that were initially nectar rich (Collins 1985). Patchy and asynchronous flowering of eucalypts is thought to drive nomadism in many honeyeaters (McGoldrick and Mac Nally 1998) and dispersal patterns are in the order of hundreds, rather than the thousands of kilometres for pronounced seasonal migrants (Mac Nally 1996). Thus nectar probably exerts considerable force on the dynamics of honeyeater communities.

In open forest, honeyeater density was positively correlated with nectar both seasonally and spatially; however, these correlations were weak (Pyke 1985). In heathlands, no correlation was found between honeyeaters and nectar (Pyke 1983; Pyke and Recher 1988; Armstrong 1992; Pyke *et al.* 1993), although these studies involved resident honeyeaters and correlations would not be expected.

Honeyeaters are not exclusively nectarivorous and other foods may affect their densities over both spatial and temporal scales. Their diet includes insects and fruit (Brown *et al.* 1978). A seasonal shift in diet has also been observed when nectar is in short supply (Craig and MacMillen 1985). Alternative carbohydrates such as lerp, manna and honeydew become important components of the diet when nectar is scarce (Paton 1980; Ford and Paton 1985). Invertebrates are relatively more common dietary components during warmer months than at other times of the year (Collins and Newland 1986), and are important as a source of protein which nectar does not provide (Paton 1982).

In many studies, the lack of correlation between honeyeater numbers and nectar supply could also relate to other factors. Inappropriate scales of measurement, over-abundance of nectar locally or over a broad area and other social behavioural factors may contribute (Franklin and Noske 1999). Mac Nally and McGoldrick (1997) argued that it is difficult to interpret the dynamics of honeyeater communities as scale affects most studies. Insufficient data could explain the lack of correlation in some cases.

Large honeyeaters utilize nectar mainly from *Eucalyptus* and *Banksia* species (Keast 1968; Ford and Paton 1976, 1977; Franklin 1997). Paton and Ford (1977) suggested that this was because the flowers in these two genera are clumped, which may lead to improved foraging efficiency.

Several honeyeater species may share abundant nectar sources with little interspecific aggression (Keast 1968;

Rasch and Craig 1988; Armstrong 1991). However, when nectar is less abundant, aggression may occur. Larger honeyeaters dominate such aggressive interactions (Ford 1979; McFarland 1986; Collins and Paton 1989; Ford and Debus 1994). Both *P. corniculatus* and *A. carunculata* typify this pattern as they have varied diets that consist mainly of nectar and arthropods but include some fruit and seeds (Blakers *et al.* 1984; Longmore 1991).

Nectar, when available, is an important food for both *P. corniculatus* and *A. carunculata*. In some studies, when an abundant nectar supply from *Eucalyptus* and/or *Banksia* species was available, one or both of these large honeyeaters were present at sites within their range (Keast 1968; Ford 1979, 1983; Newland and Wooller 1985; McFarland 1986). Both species are described as 'blossom nomads' whose appearance at many sites is tied to the flowering of appropriate nectar sources (Keast 1968). Between 36 per cent and 65 per cent of foraging observations for these species were spent at nectar sources (Pyke 1980; Recher and Holmes 1985). Ford *et al.* (1986) found that *P. corniculatus* and *A. carunculata* spent 53 per cent and 47 per cent of their foraging time at nectar respectively. Both species will exploit and defend rich patches of nectar (Ford 1981; Ford and Paton 1982; Collins 1985; Ford and Debus 1994).

Alternative carbohydrates have been recognized as important for *A. carunculata* when nectar is not available (Paton 1980). They will forage at manna, lerp and honeydew in the field (Recher and Holmes 1985) and have been shown experimentally to take lerp (Woinarski *et al.* 1989).

Few studies (e.g. Mac Nally and McGoldrick 1997; McGoldrick and Mac Nally 1998) have investigated honeyeater dynamics over broad spatial scales in forests. Most have attempted to correlate honeyeaters with their nectar sources at small spatial and temporal scales and mostly in heathlands. This study examined correlations at larger spatial and temporal scales in eucalypt forests over two years and at seven sites along a 350 kilometre

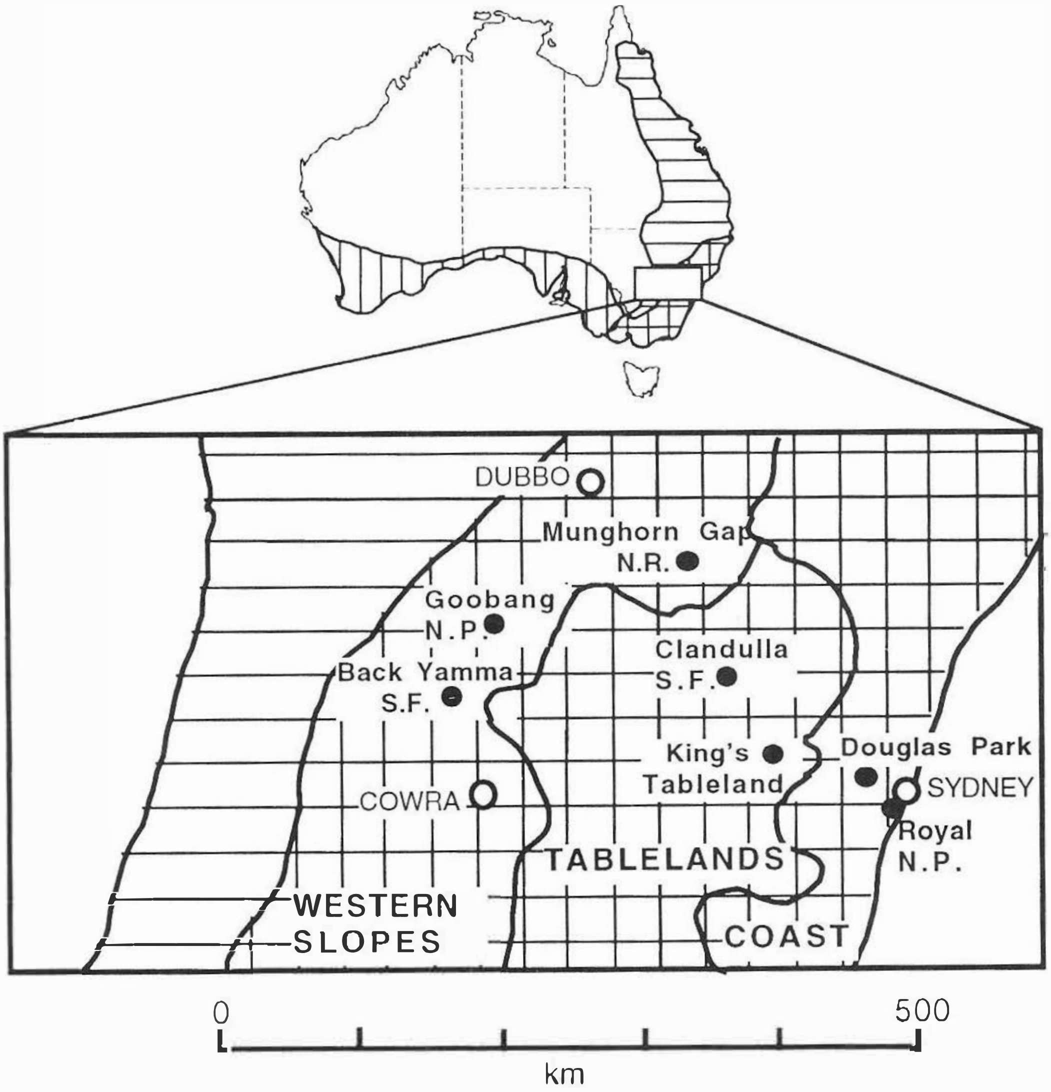

Figure 1. *Location of sites, topographical regions and range of* A. carunculata *(vertical stripes), and* P. corniculatus *(horizontal stripes). (N.P. = National Park, N.R. = Nature Reserve, S.F. = State Forest).*

east-west transect. In particular, we investigated whether there were correlations between honeyeater density and flowering tree density at local and regional scales, and whether these densities correlated with the proportions of time spent foraging at flowering trees and in aggression.

METHODS

Study sites

Two sites were selected in three regions within the sympatric range of *P. corniculatus* and *A. carunculata* in central eastern New South Wales (see Fig. 1). Sites were selected in open eucalypt forest as this habitat is frequented by both species (Saunders 1993).

Goobang National Park, on the western slopes, was selected in order to investigate correlation between flowering trees and large honeyeaters at a smaller spatial scale in *Eucalyptus sideroxylon* forest. *Eucalyptus sideroxylon* was an important source of nectar for honeyeaters in winter and spring on the western slopes. Although *E. sideroxylon* was present at Back Yamma State Forest, the patch was too small for setting-up independent, replicated plots.

Within each site, two transects (length given in Table 1) were established. These were along tracks and fire trails because some sites had dense leaf litter or a dense shrub layer. At such sites the noise created while conducting trial counts along randomly placed transects through the bush resulted in displacement of birds and reduced detectability, and hence an under-estimation of bird density. At other sites bird counts were not so affected. Off-track transects were considered to introduce unequal bias between sites. Sites were to be compared and relative densities were considered important. Using tracks also meant that a steady pace could be maintained and birds could be detected by call as far as 80 metres from the transect line. Hanowski and Niemi (1995) observed that counts of bird species that forage in canopy that is continuous over tracks, did not differ significantly between transects placed on tracks and off tracks. Hence the use of tracks is unlikely to affect counts as both *P. corniculatus* and *A. carunculata* are mainly canopy foragers (Higgins *et al.* 2001). The availability of tracks at most of the sites was limited and the distribution of both honeyeaters appeared patchy, hence long transects were established to compensate. In a simulation of transect counts of randomly distributed birds, Engel-Wilson *et al.* (1981) found that more accurate estimates were achieved for longer transects.

Trees counts and species composition

In general, all trees along a transect within a 20 metre wide band, with a diameter at breast height of 30 centimetres or more and at least eight metres high, were counted and identified. This ensured that only mature trees were sampled and avoided bias towards species that produced prolific saplings. Because of small patch size and the need to avoid ecotones between habitat types, shorter transects were necessary at some sites (see Table 1). At Royal National Park and Back Yamma State Forest, where the transects were restricted in length, the band width was increased to 50 metres. These initial tree counts were then used to calculate the tree species density per hectare.

During each visit, the number of trees with flowers were counted for each species. These counts were made at the same transect width as the initial tree species composition surveys. In addition, in spring 1994 at Goobang National Park, counts were made along 41 fixed width transects 500 metres long by 100 metres wide, each separated by 50 metres. The density of flowering trees was determined for each visit. Only those flowering tree species that were flower-probed by either species of honeyeater during the study are included in the analyses, and henceforth, counts of flowering trees refer only to those species.

Birds counts

Data were collected at all sites in each year (1992 and 1993) during mid-season over a period of two to three weeks in January, April, July and October. Bird counts were started approximately one hour after sunrise, during still and sunny weather. Birds, when seen or heard, were recorded in each ten-metre band either side of the transect up to the 70–80 metre band width. Only counts up to 50 metres from the transect were used in the analysis as few data were collected beyond this range. In spring 1994 at Goobang National Park, counts of *A. carunculata* and *P. corniculatus* were made along the 41 fixed width transects.

Time budgets for individual honeyeaters were collected as follows. When a bird was located it was observed through binoculars. If the bird's behaviour changed when it became aware of the recorder's presence (i.e. it stopped feeding, preening or calling and watched the researcher) observations were not recorded until the bird resumed its previous behaviour or started another activity. Every 10 seconds, the behaviour that occupied the majority of the time unit was recorded. Observations were terminated after 5 minutes, or when the bird was lost from sight. Hence up to 30 observations may have been recorded for an individual. When both species were present, observations alternated between species. Generally, it was possible to keep track of the birds in a patch, so there was little risk of reselecting an individual.

The two behaviours of concern here are aggression and flower-probing. Aggression is defined as an approach of a bird which disrupts the behaviour of the bird under observation or when the observed bird disrupts another bird's behaviour. No attempt was made to distinguish types of disruptive behaviour. The direction of aggression was not considered here. Flower-probing was used to describe the time spent at flowers. Birds at flowers may be taking nectar, insects or both, but the actual food is difficult to identify (McFarland 1984).

Analysis of bird count data

Count data are Poisson distributed rather than normally distributed, hence Generalized Linear Models were used to model bird counts with a Poisson distribution specified for the error term (McCullagh and Nelder 1989). Estimation of the regression coefficients was by maximum likelihood, using iteratively reweighted least-squares. All models were initially assessed by comparing the residual deviances of competing models and further validated by examining plots of regression diagnostics.

Counts of honeyeaters from different locations were often made over differing transect lengths so an adjustment was made by including an offset in the Poisson regression models for the logarithm of the area surveyed (Venables and Ripley 1997).

TABLE 1

Location of study sites, transect length and sampling period for each site.

Region	Central Western Slopes			Central Tablelands		Central Coast	
Site	Back Yamma State Forest	Goobang National Park	Munghorn Gap Nature Reserve	Clandulla State Forest	Kings Tableland	Douglas Park	Royal National Park
Location	33°19'S 148°14'E	32°49'S 148°21'E	32°24'S 149°50'E	32°54'S 149°55'E	33°49'S 150°25'E	34°12'S 150°42'E	34°04'S 151°06'E
Altitude (m)	340	500	600	720	670	130	50
Transect T1 length (m) T2	600 700	2 000 2 000	2 000 2 000	2 000 2 000	2 000 1 000	1 250 625	540 630
Sampling period	1992 to 1993	1993 to 1996	1992 to 1993	1992 to 1993	1992 to 1993	1992 to 1993	1992 to 1993

The deviance from a Generalized Linear Model is a measure of the variability in the data. A large reduction in the deviance of a model, achieved by fitting an additional term, indicates that the term is important in explaining the variability of the bird counts (McCullagh and Nelder 1989).

Poisson variables often exhibit over-dispersion which is indicated when the residual deviance exceeds the number of degrees of freedom for the model. The variance of a Poisson distributed variable Y is Var $(Y) = \phi\mu$ where μ represents the mean of Y and the dispersion parameter ϕ is fixed at 1 (i.e. a Poisson distribution assumes the variance equals the sample mean). Moderate over-dispersion can be accounted for by relaxing this constraint and estimating the value of ϕ via quasi-likelihood estimation. This produces more realistic estimates of the standard errors of the regression coefficients (McCullagh and Nelder 1989).

As *P. corniculatus* was absent from Royal National Park, this site was not incorporated in the analysis for this bird species. Similarly only a single *A. carunculata* was counted on only one survey at Douglas Park and at Kings Tableland, so these sites were not included in the analysis for this bird species. Counts were pooled over transects for each season within each site as we were interested in site, season, year and counts of flowering trees as explanatory variables for bird counts.

Analyses of time budget data

Variables were tested for normality using a Shapiro-Wilk W Test (Shapiro *et al.* 1968). All correlations were calculated as Spearman Rank Correlations as only time spent in aggression was normally distributed.

Time budgets were collected on a per site visit basis. Transect counts were treated as sub-samples and were summed for correlations with other variables for each site visit. Across all sites there was the potential to collect 64 time budget samples for each species. However, one or both species were often absent from some sites and during some seasons, or in such low densities that collecting time budget data was impractical. Only 22 samples were collected for *P. corniculatus* and 35 samples for *A. carunculata*. The means of percent time spent in aggression during each survey for each honeyeater were compared using a student's t-test.

RESULTS

Flowering trees

The tree densities of the canopy species for each site are presented in Figure 2. The potential importance of sites for honeyeaters is reflected in the density of those tree species used as a nectar source. The three most frequently flower-probed coastal and tableland species were *Eucalyptus gummifera, E. crebra* and *Banksia serrata*, while on the western slopes *E. sideroxylon, E. albens* and *E. melliodora* were most frequently visited. On the western slopes, flower-probed species represent an average of 43 per cent of the forests' trees, while they averaged 20 per cent of the forests' trees at all other sites to the east. Goobang National Park and Back Yamma State Forest (both on the western slopes) have the highest densities of flower-probed trees and *E. sideroxylon* was a dominant species at these sites. Flower probing consumed most of the birds' time on the western slopes sites, often more than 85 per cent and as much as 100 per cent of foraging time (details of time budgets will be considered elsewhere). Both flora and fauna of Munghorn Gap Nature Reserve have similarities with Clandulla State Forest and Goobang National Park, and this site is probably best considered as an intergrade between the tablelands and the western slopes, having properties of both (unpubl. data).

Honeyeater counts at the regional scale

Densities of *P. corniculatus* and *A. carunculata* varied considerably between sites, years and seasons (Figs 3 and 4, Table 2). Their relationship to flowering trees also varied between sites. Flowering trees did not appear to determine the presence of either honeyeater at coastal and tableland sites, whereas they did appear to be important at sites on the western slopes.

For *P. corniculatus* coastal sites did not appear to be important, as this species was absent from Royal National Park and was seen in very low numbers at Douglas Park. Counts of *P. corniculatus* were higher on the tableland sites of Kings Tableland and Clandulla State Forest in spring and summer, but at these sites flowering trees were not important during these seasons. Goobang National Park and Back Yamma State Forest, on the western slopes, appeared to be more important for the winter to spring period, and *P. corniculatus* was only present when flowering trees were present. At Munghorn Gap, *P. corniculatus* was not present in winter unless trees were flowering, but it was present in other seasons when trees were not flowering. In terms of patterns in counts of honeyeaters and flowering trees, Munghorn Gap exhibits characteristics of both tablelands and western slopes.

At the coastal site of Royal National Park counts of *A. carunculata* were high but these high counts did not coincide with the flowering periods of trees. At Clandulla State Forest there was little seasonal variation and no relationship with flowering trees. At sites on the western slopes *A. carunculata* often persisted all year-round even when no trees were in flower, but were more common when numbers of flowering trees increased.

For both species of honeyeater site, year, season, flowering trees and the site × year, site × season and year × season interactions were all highly significant in explaining the variation in bird counts (Table 3). For *A. carunculata* the site × year interaction could not be fitted to the model as there were insufficient degrees of freedom. The change in deviance was very large for the number of flowering trees (log-transformed) and indicates that flowering trees was still a very important explanatory variable after adjusting for temporal and spatial variability in honeyeater numbers.

Honeyeater counts at the local scale

In spring 1994 at Goobang National Park bird counts were strongly correlated with counts of flowering trees (log scale) for both species of honeyeater (Fig. 5). Poisson regression models of counts against log(flowering trees + 1) produced a better fit than models of flowering trees on an untransformed scale as indicated by the smaller residual deviance for the former model (Table 4). *P. corniculatus* was absent on plots without flowering trees and from many plots where the density of flowering trees was as high as 19 trees per plot, whereas *A. carunculata* was occasionally present when no trees were in flower. The maximum density of flowering trees on a plot without *A. carunculata* was seven trees per plot.

Correlations of bird behaviour with densities of flowering trees

All correlations were significant except for the proportion of time spent foraging versus time spent in aggression for *A. carunculata* (Table 5). The correlations do not appear to produce clusters based on sites (Fig. 6) and sample size per site was too small to do separate site analyses.

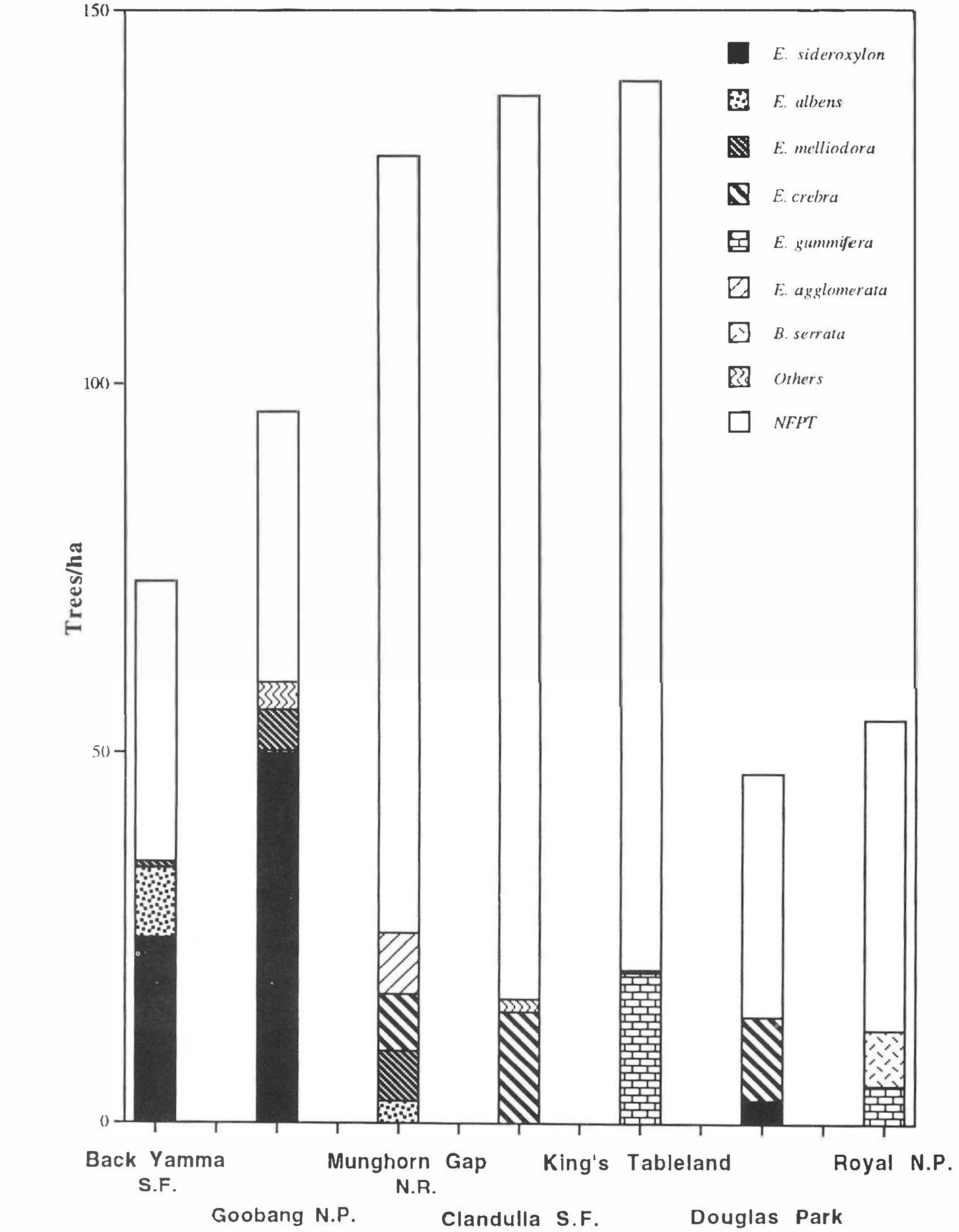

Figure 2. *Density of trees at each site. (NFPT = trees not flower-probed by either* P. Corniculatus *or* A. carunculata*).*

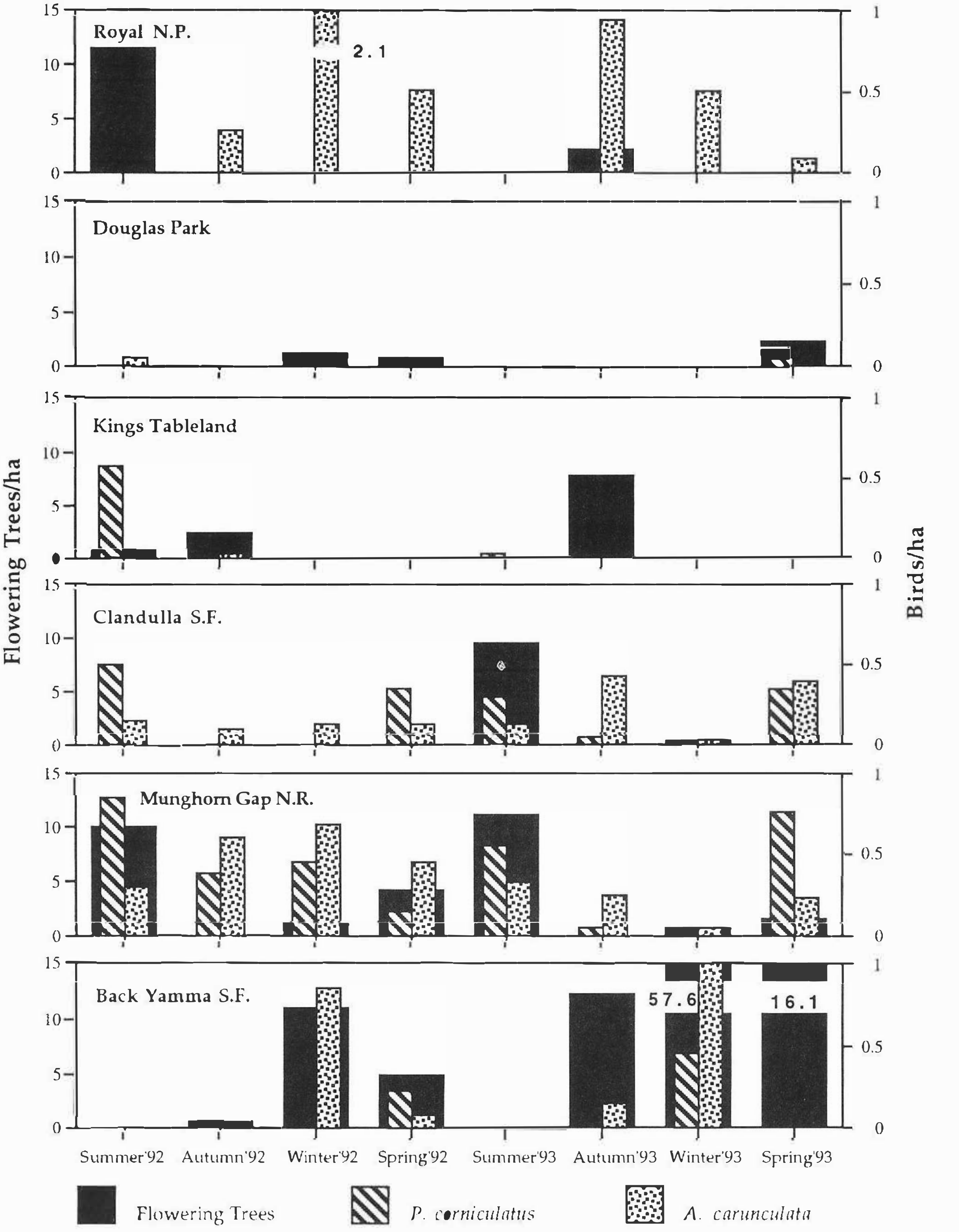

Figure 3. *Seasonal densities of flowering trees,* P. corniculatus *and* A. carunculata *at sites from 1992 to 1993. (N.P. = national park, N.R. = nature reserve, S.F. = state forest).*

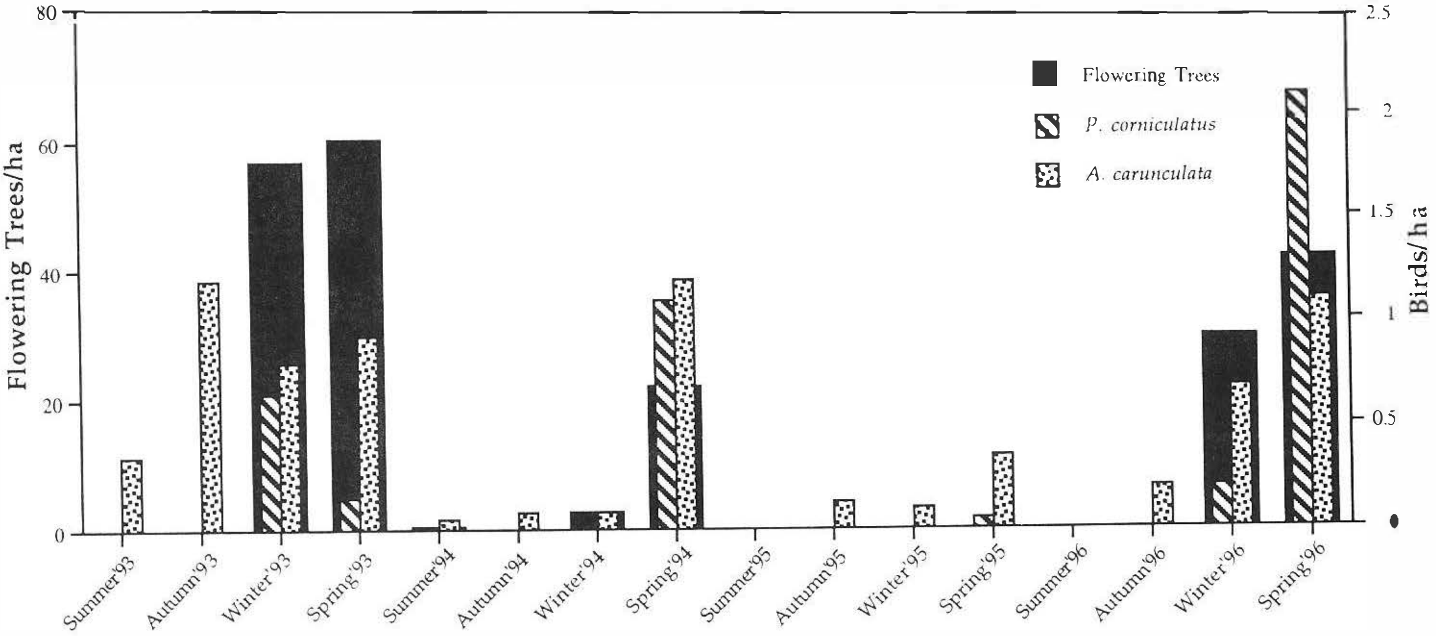

Figure 4. *Densities of flowering trees,* P. corniculatus *and* A. carunculata *for each season at Goobang National Park for 1993 to 1996.*

TABLE 2

Total counts of *P. corniculatus* and *A. carunculata* by site and season (years and transects pooled).

Site	Summer	Autumn	Winter	Spring
P. Corniculatus				
Royal National Park	0	0	0	0
Douglas Park	0	0	0	1
Kings Tableland	24	0	0	0
Clandulla State Forest	32	2	0	28
Munghorn Gap Nature Reserve	56	17	18	36
Goobang National Park	0	0	34	136
Back Yamma State Forest	0	0	6	3
A. carunculata				
Royal National Park	0	14	31	7
Douglas Park	1	0	0	0
Kings Tableland	0	1	0	0
Clandulla State Forest	11	21	6	21
Munghorn Gap Nature Reserve	25	34	29	27
Goobang National Park	16	64	66	143
Back Yamma State Forest	0	2	24	1

TABLE 3

Analysis of deviance summary for counts of *P. corniculatus* and of *A. carunculata* for all sites, times and seasons. (Terms were added sequentially from first to last as a series of nested models, P = Peason Chi-square probability).

Term	Change in d.f.	Change in deviance	Residual d.f.	Residual deviance	$P(>\chi^2)$
P. Corniculatus					
null			43	482.1	
site	5	139.3	38	342.8	<0.001
year	1	8.3	37	334.4	<0.01
season	3	78.0	34	256.4	<0.001
log (flowering trees + 1)	1	23.2	33	233.2	<0.001
site × year	4	20.5	29	212.7	<0.001
site × season	15	151.2	14	61.6	<0.001
year × season	3	17.9	11	43.7	<0.001
A. carunculata					
null			47	545.1	
site	4	58.8	43	486.4	<0.001
year	4	95.5	39	390.8	<0.001
season	3	96.3	36	294.5	<0.001
log (flowering trees + 1)	1	26.7	35	267.8	<0.001
site × season	12	110.8	23	157.0	<0.001
year × season	12	118.3	11	38.7	<0.001

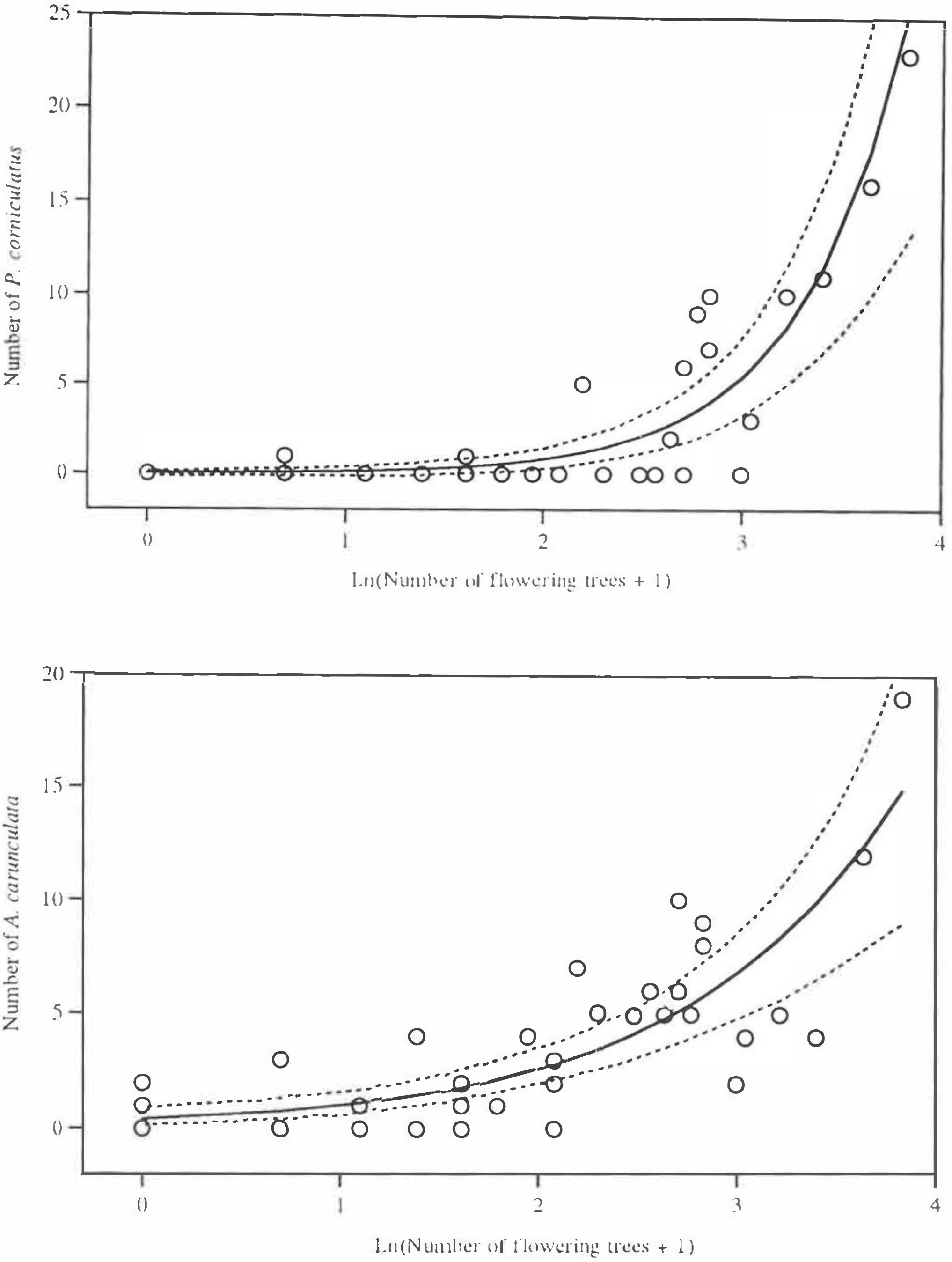

Figure 5. *Poisson regression models for counts of* P. corniculatus *(Y_1) and* A. carunculata *(Y_2) against flowering trees (X) at Goobang National Park in spring 1994 (n = 41) with 95% confidence limits.*

$Log (Y_1) = -3.85(0.709) + 1.85(0.220) \log [X + 1]$, $\phi = 2.01$, $P < 0.001$, and

$Log (Y_2) = -0.93(0.359) + 0.95(0.127) \log [X + 1]$, $\phi = 1.59$, $P < 0.001$, (Standard errors are as given in parentheses).

TABLE 4

Analysis of deviance summary for alternative models for honeyeater counts at Goobang National Park, spring 1994 (n = 41).

Model	d.f.	Residual deviance	
		P. corniculatus	*A. carunculata*
null	40	304.5	178.5
flowering trees	39	116.4	88.6
log (flowering trees + 1)	39	78.9	68.6

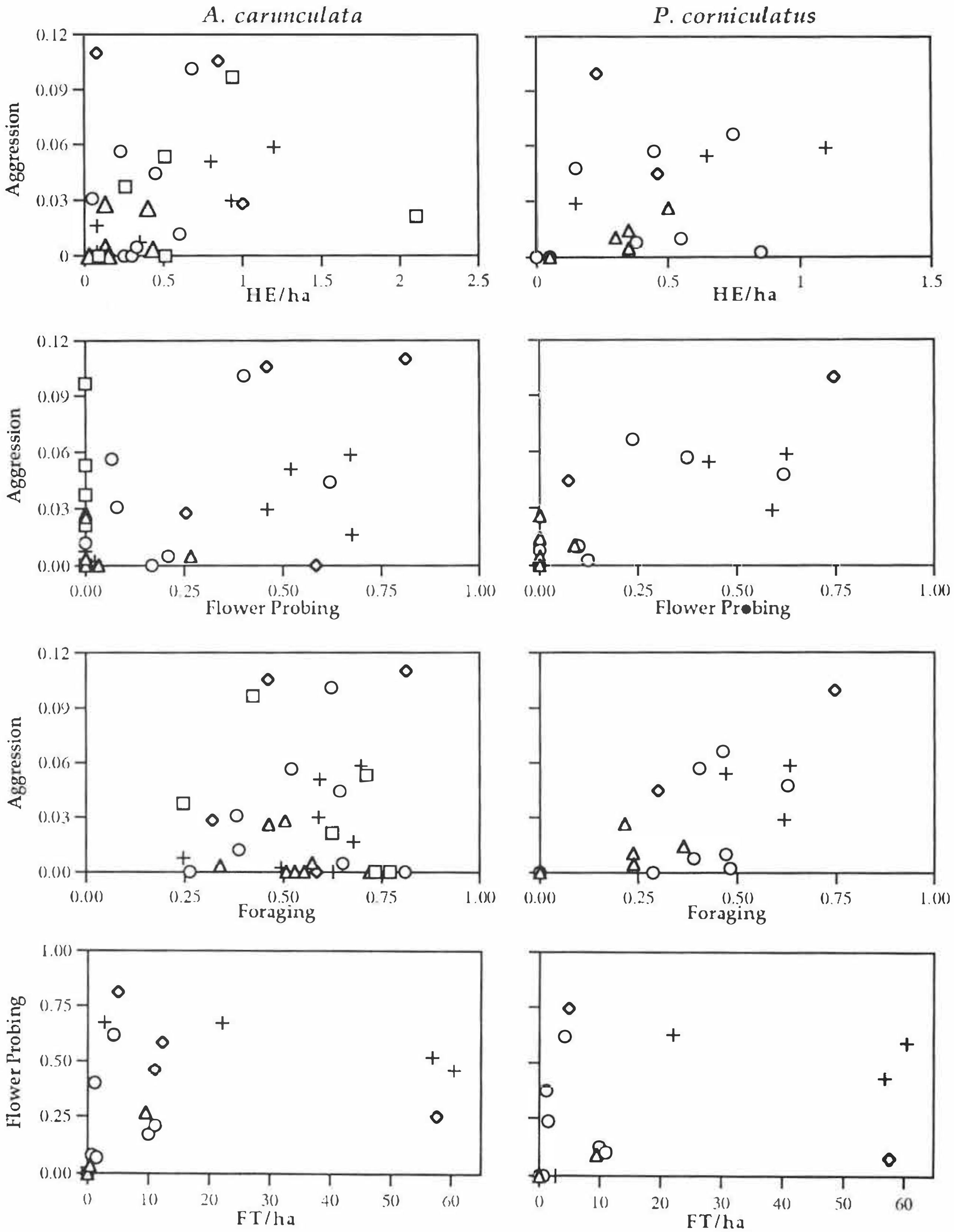

Figure 6. *Correlations between honeyeaters, flowering trees and the behaviours described in the text. (HE/ha = honeyeaters per hectare, FT/ha = flowering trees per hectare. Aggression = proportion of time spent in aggression, Flower Probing = proportion of time spent probing flowers, Foraging = proportion of time spent foraging, □ = Royal National Park, △ = Clandulla State Forest, ○ = Munghorn Gap Nature Reserve, + = Goobang National Park, ◇ = Back Yamma State Forest).*

TABLE 5

Spearman Rank correlations between honeyeaters, flowering trees and behaviours as described in the text. (*$P < 0.05$, **$P < 0.01$, *** $P < 0.001$, n.s. = not significant).

Correlation	*A. carunculata* (n = 35)	*P. corniculatus* (n = 22)
Honeyeater density × Proportion of time in aggression	0.49 **	0.55 *
Proportion of time at flowers × Proportion of time in aggression	0.46 **	0.70 **
Proportion of time foraging × Proportion of time in aggression	-0.22 n.s.	0.57 **
Flowering tree density × Proportion of time at flowers	0.87 ***	0.69 **

The means and standard errors of percent time spent in aggression during each survey by *P. corniculatus* (2.03 ± 0.486) and *A. carunculata* (1.46 ± 0.491) did not differ significantly ($t = 0.799$, $df = 70$, $P > 0.05$).

DISCUSSION

Correlations between flowering trees and honeyeaters

Previous studies (Ford 1983; Collins, Briffa and Newland 1984; McFarland 1985; Newland and Wooller 1985; Pyke 1985) have reported a positive correlation between flowering tree density and honeyeater density. In this study we found that the numbers of *A. carunculata* and *P. corniculatus* were strongly influenced by the density of flowering trees at both regional and local scales. High density of honeyeaters and trees in flower was observed on the western slopes during winter and spring. A similar pattern was noted by Mac Nally and McGoldrick (1997) where *A. carunculata* densities were greater on the northern slopes of the Great Divide in winter and spring when *E. sideroxylon* was in flower. However, both honeyeaters were also common on tableland sites in spring but they were not feeding at flowers. On the tablelands, *P. corniculatus* were common in spring and summer when few trees were in flower. At these times other foods such as insects, seed and fruit may be important dietary components (unpubl. data, Collins and Newland 1986).

Anthochaera carunculata has been observed to persist at sites during seasons when insects, nectar, seeds and fruit were scarce and are able to switch to alternate carbohydrates when other foods are depleted (Ford and Paton 1985). This was observed at sites on the coast and tablelands where *A. carunculata* gleaned foliage in winter when *P. corniculatus* was absent. Numbers of *P. corniculatus* did not always match flowering tree density and the density of birds was often lower than expected. There are several possible explanations for the apparent lack of birds. The density of flowering trees may not be an accurate measure of the quality of the nectar supply, flowering may have been better at alternative sites (Ford and Paton 1985), patch size may have been below some minimum requirement, birds may have migrated to the tablelands to breed (pers. obs.) or honeyeater populations may be declining due to habitat degradation.

When both honeyeaters were present at sites where appropriate trees were flowering, they may spend considerable time foraging at nectar, even at sites not on the western slopes and when other foods were available e.g. Clandulla State Forest in the summer of 1993. In winter, insects and fruit may be in short supply, temperatures are relatively low and energy rich foods, such as nectar, may be required to enable birds to survive and build energy reserves for the breeding season. When nectar is available in winter, both *A. carunculata* and *P. corniculatus* appear to exploit this resource. This would explain their 'nomadic or migratory' tendencies. Comparison of the densities of each honeyeater with respect to density of flowering trees (see Fig. 5) revealed that *P. corniculatus* may be absent when appropriate trees are in flower, whereas *A. carunculata* may be present when trees are not flowering. In winter, *P. corniculatus* was only present at sites with flowering trees (see Figs 3 and 4). *P. corniculatus* possibly requires higher flowering tree density than *A. carunculata* and it may vacate a patch that falls below a certain threshold. By switching to alternative carbohydrates sources, *A. carunculata* may not experience the same pressure.

Aggression

Movement between foraging bouts involves a loss of energy and it is thus less profitable to feed at patches of low resource density (Collins 1985). Rich patches would require less movement while foraging and enable honeyeaters to acquire more energy per unit time (Collins 1985; Collins and Paton 1989). Both *A. carunculata* and *P. corniculatus* spend time defending rich nectar sources (Ford and Paton 1985; Newland and Wooller 1985; McFarland 1996). Where this occurs, the energy spent in aggression may be less than that gained when competitors are excluded.

There were highly significant positive correlations between proportion of time foraging at flowers and time spent in aggression for either honeyeater. This suggests that nectar is an important resource worth defending. When both species were spending upwards of 90 per cent of their foraging time at flowers, aggression was often relatively high (10% of time budget). However, overall time spent in aggression was low (≤2%) for both species, which was similar to the results of others (McFarland 1986; Ford and Debus 1994). Nectar from eucalypt blossom is a localized, energy-rich and replenishable resource, and hence worth defending. Establishing exclusive use of this resource through aggression, would lead to a predictable food supply that can be harvested efficiently (Gill 1978). In this study and others (e.g. Ford and Debus 1994) aggression away from flowers was much lower than at flowers, and often non-existent. This is further supported by the lack of correlation between time spent in aggression and time spent foraging in general for *A. carunculata*. *A. carunculata* could be found foraging at other food sources at sites and seasons when *P. corniculatus* was absent. Other food sources, such as fruit and insects, are not self-replenishing in the short term and may not be worth defending.

Highly significant correlations were observed between the density of flowering trees and the proportion of foraging time spent at flowers for both honeyeaters, thus when nectar was available, much of the foraging time was spent flower-probing. However, measures of nectar supply may not necessarily give a direct measure of how important the resource is to honeyeaters. With a decrease in available nectar, time spent feeding at flowers may increase because more time would have to be spent at each flower and more flowers would need to be visited in a given time to obtain sufficient nectar (Gill 1978; McFarland 1986; Armstrong 1992). Conversely, when nectar is abundant, fewer flowers need to be visited to provide an equivalent amount of nectar.

If nectar is super-abundant there would be no need to aggressively defend the supply. However, if nectar is a scarce or patchy resource, the cost of defending it may be prohibitive and it would not pay to aggressively defend the resource. For aggression to be worthwhile the nectar supply must lie somewhere between these two extremes. Several studies have found that aggression was highest at moderate nectar levels and lower when nectar was poor or very rich (Carpenter and McMillen 1976; McFarland 1986, 1996). Carpenter and McMillen (1976) proposed a model predicting that territorial exclusiveness will occur between a lower and upper threshold of nectar supply. The data presented here do not support this. However, this may reflect the scale in this study. Perhaps such relationships are only relevant at a scale matching the size of feeding territories.

Measures of bird behaviour are a good measure of nectar availability (Gill 1978). Hutto (1990) also advocated measuring bird behaviour to confirm measures of food availablity and suggested that doing so avoids the problems associated with the bird's perception of the food, scale-of-measurement, and renewal rates. Since birds spend much of their time feeding at flowers, this resource must therefore be valuable to them. Correlation between flower-probing and time spent in aggression was demonstrated in this study, suggesting that flowers are worth defending. Hence both time spent at flowers and aggressive behaviour are probably good measures of the importance of nectar as a resource.

The data presented here support the contention that nectar from specific species of eucalypt as an important resource for both *P. corniculatus* and *A. carunculata*, particularly in the winter/spring period on the western slopes. The presence of *P. corniculatus* at some sites only in winter in association with preferred eucalypts in flower suggests that this species may not be able to switch to alternative carbohydrates as readily as *A. carunculata*. The availablity of nectar in winter and early spring on the western slopes may therefore be important for the survival and reproductive success of *P. corniculatus*. Conservation of forest remnants on the western slopes may be critical to sustaining viable populations of these two honeyeaters, particularly *P. corniculatus*.

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