

Chapter 3.

Habitat selection by Regent Honeyeaters in the Bundarra-Barraba region

3.1 Introduction

The type of habitat that a bird selects is determined by, and determines, its morphology and behaviour, and its ability to obtain food and shelter successfully (Cody 1985). The proximate stimuli for the choice of habitat might be structural features of the landscape, foraging or nesting opportunities, or the presence of other species. These factors might operate independently, hierarchically as a system of sequential decisions, or synergistically in a complex fashion (Cody 1985). However, we are still far from explaining and predicting actual species or assemblages of any community by a set of rules (Bersier and Meyer 1995).

Large-scale and small-scale heterogeneities in an ecosystem are thought to influence individual species and assemblages. Traditionally, studies on the relationships between birds and their environment, to identify how they occupy their habitat, have concentrated on the habitat structure, rather than plant taxonomic composition (e.g., MacArthur and MacArthur 1961, Recher 1969). However, some Australian studies have shown that floristic diversity rather than habitat structure is an important factor affecting bird species diversity in eucalypt forests (Recher *et al.* 1980, Milledge and Recher 1985). Recher (1971) found that heath dominated by *Hakea* sp., which had low plant species diversity, supported low densities of honeyeaters, compared to other habitats. In North America, Wiens and Rotenberry (1981) found strong relationships between composition of shrub steppe bird communities and floristics of steppe vegetation.

Vegetation structural diversity may be an important determinant of avian species diversity at the continental scale, but at the regional scale floristic diversity may be more important (Rotenberry 1985). Birds may be able to distinguish between broad habitat types according to vegetation structure, and then at a smaller scale they use floristic features to identify an appropriate habitat (Recher 1985, Rotenberry 1985). Mac Nally (1990) found that both physiognomy and floristics were important predictors of the bird community in forest and woodland in southeastern Australia.

Rotenberry (1985) proposed that the underlying mechanism responsible for the association between birds and plants is related to food and foraging behaviour. He suggested that the most significant source of variation among plants to which birds are likely to respond is the provision of food. Different tree species provide different types of food at different densities, and on distinct foraging substrates (Holmes *et al.* 1979, Holmes and Robinson 1981). In other words, different tree species present discrete foraging opportunities to birds, which in turn could influence the presence and/or abundance of certain bird species and thus bird community patterns. For birds that are specialised frugivores or nectarivores, it is obvious that there would be associations with particular plant species. In the case of Regent Honeyeaters, it is believed that there is a strong association with Mugga Ironbarks, which they depend on for nectar (Franklin *et al.* 1989, Webster and Menkhorst 1992).

Landscape features may also provide important cues for birds on habitat suitability. Characteristics such as the size and connectivity of remnants or islands of vegetation may be important, as some bird species are only found in continuous habitat, or well connected habitat fragments above a certain threshold size. Barrett (1995) found that a large proportion of woodland bird species on the New England Tablelands did not occur in habitat remnants below five hectares. This may simply be the inability or avoidance of a species to fly across open spaces between small remnants, rather than birds visually selecting patches by size. It is possible that Regent Honeyeaters, too, only occupy large, or well connected remnants, rather than small patches. Other landscape characteristics that can affect avian species richness and abundance include altitude, distance to water sources, and other abiotic features (Loyn 1987, Barrett 1995, Bennett and Ford 1997). In the case of nomadic birds such as Regent Honeyeaters, rivers, mountains, and other features may provide navigational cues across a landscape. Therefore, it is important to measure many types of habitat variables, and at different scales to be able to produce statistical models which define those characteristics that influence the probability of a site being occupied by a Regent Honeyeater.

Conservation managers need to know what types of habitats need to be protected or managed for Regent Honeyeater conservation. They need to know the plant species composition of known Regent Honeyeater sites, and the distinctive physical features at the sites, and across the landscape. With the development of statistical models that can extrapolate existing location-specific information over complete regions, decisions about habitat protection and management can be made without the need for costly surveys (Nicholls 1989). The class of regression models known

as generalised linear models (McCullagh and Nelder 1983) summarise the relationships between species distributions and environmental variables. Ecologists can use these models to assess which environmental variables at the local and landscape scale best explain the presence of a species. Once the relationships between species and environmental variables have been quantified, they can be used to predict the species' presence from observed values of one or more environmental variables (Jongman *et al.* 1995). This information can efficiently focus habitat conservation towards other sites with similar habitat characteristics. Also, habitat models can be used to assess the suitability of new sites for the re-introduction of captive bred individuals as part of a recovery effort.

Logistical regression is a type of generalised linear model (McCullagh and Nelder 1983), that has previously been used to determine the important variables in habitat selection of birds (Straw *et al.* 1986, Pearce *et al.* 1995, Brigham *et al.* 1998) and mammals (Lindenmayer *et al.* 1990), and to model the occurrence of plants (Austin *et al.* 1990). In a study on the endangered Helmeted Honeyeater, Pearce *et al.* (1994) used logistical discrimination modelling to show that swamp habitat with high water cover, and trees with lots of decorticated bark were the best predictors of occupancy by Helmeted Honeyeaters. An extension of this habitat modelling approach for conservation management was made by Pearce *et al.* (1995), to look for niche overlap between Helmeted Honeyeaters and Bell Mirers *Manorina melonophrys*, which are known to displace Helmeted Honeyeaters. Regression modelling has been used effectively in studies on sedentary habitat specialists such as the Helmeted Honeyeater and Rufous Scrub-bird *Atrichornis rufescens* (Ferrier 1985). However, mobile, low density, widely dispersed, generalised bird species, such as the Regent Honeyeater, Swift Parrot and Painted Honeyeater, present a greater challenge for ecologists. In this chapter I employ logistical regression analyses to look for relationships between habitat structure and taxonomic composition of survey transects, and the presence or absence of Regent Honeyeaters.

The objective of this chapter is to construct generalised linear models that incorporate explanatory habitat variables, that best predict the probability of occurrence of Regent Honeyeaters. A large suite of habitat characteristics from the local and landscape scale were measured or derived at each

survey transect. Floristic and physiognomic microhabitat variables, derived landscape variables, and derived GIS landscape vegetation cover variables were accepted or rejected in the forward-stepping regression modelling procedure until a final model was constructed which best explained the occurrence of Regent Honeyeaters on survey transects. Habitat selection by Regent Honeyeaters involves a wide range of factors, not just the physiognomic and taxonomic attributes of the vegetation measured in my study. Factors such as food supply, competition and predators may also play a part in influencing habitat selection (Rotenberry 1985, Pearce *et al.* 1995), but it was not possible to incorporate all of these factors into the models. These aspects of the ecology of Regent Honeyeaters are dealt with in chapters 5, 6 and 8.

Habitat models for Regent Honeyeaters could be useful for predicting the occurrence of the species at unsurveyed locations in the Bundarra-Barraba region, and for identifying key habitat components that need protecting and managing. It is possible that my models may be applicable to other key Regent Honeyeater areas in New South Wales and Victoria, depending on available habitat data

3.2 Methodology

3.2.1 Bird surveys

Between January 1995 and January 1997, 93 transects were surveyed every two months (total of 13 surveys) for Regent Honeyeaters and all other birds in the Bundarra-Barraba study area (described in Chapter 2). Twelve of the transects were established at sites with historical records of Regent Honeyeaters, dating from 1984 to 1993 (H. Hines, A. Ley, B. Williams pers. comm.). Eight of these were in Box/Ironbark woodland habitat, three were in riparian gallery forest, and one was in White Box woodland. I established 51 transects in Box/Ironbark habitat that had not been previously surveyed for Regent Honeyeaters. These transects were in habitat of similar appearance and species composition to the eight historical Box/Ironbark sites. However, to test whether other habitat types such as Box/Gum, Box.Stringybark, dry plateau complex woodland and riparian gallery forest are used by Regent Honeyeaters, 31 transects were established in these other four habitat types (see Chapter 2 for details)

3.2.2 Microhabitat variables

Twenty four microhabitat variables were measured in each of the 93 one-hectare transects; a comparison of the means of variables of occupied and non-occupied transects is presented in Table 3.1. To prevent any differences due to observer bias (Gotfryd and Hansell 1985), I collected all of

the microhabitat data myself. Other researchers have shown that rapid habitat assessments are adequate for describing relationships between birds and environmental variables (Howe 1984, Arnold 1988, Austin 1991, Barrett 1991). However, I invested a large effort in counting all trees above two metres high in the one hectare area of all 93 transects, and estimating their height (to the nearest metre), and diameter at breast height (to the nearest centimetre). Trees were categorised as “canopy trees” if they were greater than eight metres in height, or “sub-canopy trees” if they were two to eight metres tall. To check the accuracy of my tree height estimates, I used a Hagameter to measure the height of trees that had previously been measured. In all cases ($n = 20$), my estimates were within one to two metres of the height recorded by the Hagameter method.

Other microhabitat variables that were measured included numbers of mistletoes, standing dead trees, and tree stumps. Transects were divided into four 50 m sectors to reduce errors when counting large numbers of trees. Subjective visual assessment was made in each of the 50 m sectors of percentage canopy cover, and percentage shrub cover (< 2 m). The four sector counts were averaged to give a mean percentage cover for the whole transect. Six derived variables representing the floristic composition of trees were measured. They were the proportion of 1. Mugga Ironbark, 2. Box species, 3. Gum species, 4. Stringybark species, 5. Riparian tree species (River Sheoak *Casuarina cunninghamiana*, Weeping Willow *Salix babylonica* and Manna Gum *E. viminalis*) and 6. Other tree species in each transect. Percentages of each category were calculated from the number of trees greater than eight metres tall in each category.

To test for the influence of nectar availability on the occurrence of Regent Honeyeaters, I measured the numbers of flowers, to the nearest 100 flowers, in each transect after each bird survey was completed (refer to Chapter 2 for methodology). The flowering abundance was recorded for all eucalypts and mistletoes and then totaled for the two years of surveys. Four flowering indices were included in the microhabitat models: total flowering abundance, Mugga Ironbark flowering abundance, number of tree species that flowered over the two year survey, and the number of surveys (possible total of 13) where flowering of eucalypts and mistletoes (*Amyema* spp.) occurred.

3.2.3 Landscape variables

Eleven landscape variables were derived from 1: 25000 topographical maps (Table 3.2). These included the altitude (m) of each transect, the area of wooded habitat around each transect (scale of 1-6, where 1 = < 5 ha, 2 = $> 5-20$ ha, 3 = $> 20-100$ ha, 4 = $> 100-500$ ha, 5 = $> 500-2000$ ha, and 6 =

Table 3.1 Mean and standard deviation of micro-habitat variables in each transect surveyed for Regent Honeyeaters. (* indicates where stepwise logistical regression analysis detected variables that could be used to discriminate between occupied and non-occupied transects * $p < 0.05$, ** $p < 0.01$).

Variable	Description	New transects (mean \pm s.d.)		Old + New transects (mean \pm s.d.)	
		occupied transects	unoccupied transects	occupied transects	unoccupied transects
fl	flowering index of all nectar plants	0.95 \pm 0.37	0.94 \pm 0.50	0.94 \pm 0.38	0.95 \pm 0.52
ib	flowering index of Mugga Ironbarks	3.54 \pm 1.59	2.81 \pm 2.51	3.25 \pm 1.99	2.84 \pm 2.54
flsp	no. of nectar-producing plant species	3.00 \pm 1.10	2.99 \pm 1.30	2.92 \pm 1.16	3.04 \pm 1.31
flfq	number of survey periods with flowering	4.67 \pm 1.36	4.93 \pm 2.16	4.78 \pm 1.87	4.91 \pm 2.21
pib	% Mugga Ironbark	45.88 \pm 28.09	35.55 \pm 33.07	40.56 \pm 28.68	36.74 \pm 34.15
pbox	% Boxes	15.54 \pm 13.41	19.57 \pm 21.90	19.14 \pm 17.33	18.14 \pm 21.76
pgum	% Gums	16.00 \pm 14.45	16.23 \pm 18.91	13.75 \pm 13.73	17.70 \pm 19.90
pstr	% Stringybarks	21.13 \pm 19.52	14.09 \pm 18.46	18.75 \pm 18.66	14.11 \pm 18.98
prip	% Riparian plants	0.00 \pm 0.00	3.33 \pm 16.84	6.14 \pm 23.07 **	0.16 \pm 1.07
poth	% Other plant types in transect	4.25 \pm 7.51	11.22 \pm 23.32	3.47 \pm 6.51	13.18 \pm 25.22
tspp	No. of tree species	5.67 \pm 1.09	5.80 \pm 1.43	5.78 \pm 1.27	5.75 \pm 1.41
ncan	No. of trees >8m tall	184.63 \pm 82.79	209.41 \pm 110.33	186.03 \pm 81.19	213.74 \pm 115.63
cht	Mean height (m) of trees > 8m tall	14.51 \pm 0.37	14.11 \pm 1.86	14.66 \pm 1.38	13.94 \pm 1.90
cdbh	Mean DBH (cm) of trees > 8m tall	28.70 \pm 1.20	29.06 \pm 7.85	29.14 \pm 3.79	28.85 \pm 8.37
pcan	% canopy cover	27.33 \pm 9.11 *	23.33 \pm 8.62	25.69 \pm 8.49	23.53 \pm 9.09
nsc	No. of trees 2-8m tall	140.67 \pm 100.30	171.59 \pm 172.93	127.47 \pm 85.95	186.44 \pm 186.45
scht	Mean height of trees 2-8m tall	5.28 \pm 0.45	5.28 \pm 0.63	5.18 \pm 0.68	5.34 \pm 0.51
scdb	Mean DBH of trees 2-8m tall	7.49 \pm 1.53	7.92 \pm 2.07	7.66 \pm 2.10	7.91 \pm 1.89
sspp	No. of shrub species	5.79 \pm 3.11	5.77 \pm 2.36	5.47 \pm 2.87	5.96 \pm 2.34
ps	% shrub cover	12.29 \pm 19.97	12.28 \pm 12.28	10.19 \pm 24.71	13.60 \pm 12.88
s2	No. of shrubs >2m tall	5.5 \pm 7.28 *	34.23 \pm 76.02	6.83 \pm 15.75 **	39.44 \pm 82.03
mt	No. of mistletoes	142.96 \pm 136.46 **	71.39 \pm 65.59	126.22 \pm 120.14 *	66.89 \pm 63.98
dt	No. of dead standing trees	31.13 \pm 32.61	39.36 \pm 41.94	26.92 \pm 28.82	43.75 \pm 44.30
st	No. of tree stumps	47.16 \pm 31.16	41.51 \pm 37.38	41.97 \pm 23.31	43.60 \pm 39.37

>2000 ha), the distance from the centre of the transect to the edge of the habitat (m), and the connectivity of the transect patch to other vegetation. An index of connectivity was developed on a scale of one (poorly connected) to four (highly connected to many patches) based on a system similar to Barrett (1995). However, the variegated landscape (McIntyre and Barrett 1992) in the Bundarra-Barraba study area made it difficult to assess patch size and degree of connectivity. The distance from each transect to the nearest Regent Honeyeater transect was measured to see whether sites were clustered or distributed randomly across the region.

The distance of transects to nearest water point, creek and river (m) was also recorded, as water appears to be important to Regent Honeyeaters for bathing and drinking (Chapter 5). Creeks were a more permanent water source than the ephemeral water points such as dams, rock pools and surface water. However, because some of the creeks may have been dry during the survey period, proximity to rivers was also considered. The slope of the transect was categorised as zero if flat, one if gentle, two if moderately sloping, three if steep and undulating and four if very steep (from Barrett 1995). The effect of the aspect of each transect (1 = 0°-90°, 2 = 91°-180°, 3 = 181°-270°, 4 = 271°- 360°) on the presence or absence of Regent Honeyeaters was also tested, as Lindenmayer *et al.* (1990) found that arboreal marsupials were more likely to be found in trees with certain aspects.

3.2.4 GIS vegetation variables

Digitised landscape vegetation cover data was extracted from the Northern Tablelands and North West Slopes database of the New South Wales National Parks and Wildlife Service. Vegetation cover data was based on air photo interpretation information that was digitised onto a GIS database. Using the ERMS (NSW NPWS 1995) program, I was able to produce a “zone of proximity” around each transect at specified radii (in this case 1 km, 2 km, 5 km, 10 km, 20 km). Zones of proximity are circular areas created around each transect for the specified radius. For example, a zone of proximity with a radius of 1 km has a circular area of 3,142 hectares. The ERMS database contains the estimated ground cover, in hectares, of different habitat types within the zone of proximity. For the NSW NPWS North Western Slopes database, five vegetation types have been defined and quantified: 1. Mugga Ironbark patches (ib), 2. Dry open forest (do), 3. Dry plateau complex (dp), 4. Disturbed remnant vegetation (dr), and 5. Treeless (tl).

Table 3.2 Mean and standard deviation of landscape variables around each transect surveyed for Regent Honeyeaters. (* indicates where stepwise logistical regression analysis detected variables that could be used to discriminate between occupied and non-occupied transects * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Variable	Description	New transects (mean \pm s.d.)		Old + New transects (mean \pm s.d.)	
		occupied transects	unoccupied transects	occupied transects	unoccupied transects
psi	size of patch (scale of 1-6)	3.67 \pm 1.01	4.33 \pm 1.30	3.64 \pm 1.17	4.49 \pm 1.21
np	distance to nearest patch (m)	812.5 \pm 119.1	1214.5 \pm 796.4	777.8 \pm 330.9	1321.1 \pm 824.1
ped	distance to patch edge (m)	191.7 \pm 51.7 *	318.1 \pm 294.9	194.4 \pm 116.4 **	343.0 \pm 311.4
con	connectivity (scale of 1-5)	2.67 \pm 0.36	2.80 \pm 1.16	2.67 \pm 0.89	2.82 \pm 1.20
slo	slope of transect (scale of 1-5)	1.96 \pm 0.52	2.11 \pm 0.86	1.89 \pm 0.62	2.18 \pm 0.89
alt	altitude of transect (m)	704.6 \pm 118.9 **	707.2 \pm 108.6	706.9 \pm 69.5	706.2 \pm 115.1
asp	aspect of transect (scale of 1-4)	3.04 \pm 0.36	3.17 \pm 0.92	3.08 \pm 0.84	3.18 \pm 0.95
nrh	distance to nearest RHE transect (m)	556.3 \pm 170.7 ***	3084.8 \pm 3843.9	1205.6 \pm 1948.4 **	3207.0 \pm 4019.6
wp	distance to nearest water point (m)	522.9 \pm 138.2	501.0 \pm 285.2	499.2 \pm 295.6	511.4 \pm 260.0
crk	distance to nearest creek (m)	1447.9 \pm 1092.4	935.8 \pm 838.9	1326.9 \pm 1049.6	904.4 \pm 818.1
riv	distance to nearest river (m)	2508.3 \pm 1728.3 *	2707.5 \pm 2022.2	2592.2 \pm 2288.4	2696.5 \pm 1711.1

A “report” is produced by the ERMS program for the five zones of proximity (1 km, 2 km, 5 km, 10 km and 20 km) around each transect. Each report gives the number of hectares of each vegetation type. By importing these data into an Excel spreadsheet, I was then able to calculate the proportion of each vegetation type in each zone of each transect. In total, 25 variables were calculated for each transect and fitted to the GIS landscape models. The descriptions of abbreviations of all GIS variables, and a comparison of their mean values for occupied and non-occupied transects, are presented in Table 3.3.

3.2.5 Modelling procedure

Logistical regression analyses (McCullagh and Nelder 1983) were performed using the forward-stepping stepwise logistical regression program of GLIM (Crawley 1993). Logistical regression belongs to the class of generalised linear models that allow for error distributions different from normal for the dependent variable. The dependent or response variable is binomial and takes the form of presence/absence data. Logistical regression assumes that the distribution of a species in the study area is obtained experimentally (Pearce *et al.* 1994, 1995). In this study data on Regent Honeyeaters are obtained both experimentally (my two-year survey) and from historical observations (A. Ley, B. Williams, H. Fines pers. comm.). Therefore, two groups of models were developed, one group based on transects that were selected by Regent Honeyeaters during my study, and the other group based on transects occupied during my study and historically. The models used in my study take the form of the equation

$$\text{logit}(p) = \log(p/1-p) = \beta_0 + \beta_1x_1 + \beta_2x_2 + \dots + \beta_px_p$$

The right hand side of the equation is termed the linear predictor, and the x s are the significant explanatory variables in the model. Variables were logit-transformed by the logit link function (**Link G**) of the GLIM (Crawley 1993) program, which assumes a binomial distribution for variables in a logistical regression. Variables were deleted in turn from multiple regression models, commencing with the least significant terms until the minimum acceptable model, containing only significant terms, was achieved. In order to minimise the likelihood of rejecting significant terms, the $p \leq 0.05$ significance value was used as a criterion to retain terms to develop models. Selection of significant individual variables in the minimum acceptable models was facilitated by calculating the χ^2 statistic for each variable.

Table 3.3 Mean and standard deviation of GIS vegetation cover variables around each transects surveyed for Regent Honeyeaters. (* indicates where stepwise logistical regression analysis detected variables that could be used to discriminate between occupied and non-occupied transects ** $p < 0.01$, *** $p < 0.001$).

Variable	Description of zone of proximity	New transects (mean \pm s.d.)		Old + New transects (mean \pm s.d.)	
		Occupied transects	Unoccupied transects	Occupied transects	Unoccupied transects
ib1	1 km % Ironbark cover	25.29 \pm 15.61	22.10 \pm 17.23	23.36 \pm 16.38	22.65 \pm 17.20
do1	1 km % Dry open forest cover	1.79 \pm 4.35	1.22 \pm 1.37	3.33 \pm 7.14 ***	13.37 \pm 14.21
dp1	1 km % Dry plateau complex	0.00 \pm 0.00	6.99 \pm 23.10	0.00 \pm 0.00	8.46 \pm 25.21
dr1	1 km % Disturbed remnant cover	20.67 \pm 5.85	24.57 \pm 14.60	22.94 \pm 15.57	23.95 \pm 14.67
tl1	1 km %treeless cover	52.38 \pm 5.82	34.45 \pm 24.25	50.58 \pm 17.80	31.81 \pm 24.13
ib2	2 km % Ironbark cover	13.00 \pm 7.40	12.72 \pm 8.55	12.39 \pm 7.56	13.05 \pm 8.68
do2	2 km % Dry open forest cover	1.83 \pm 2.75	7.22 \pm 7.44	2.47 \pm 4.25	7.95 \pm 7.51
dp2	2 km % Dry plateau complex	0.00 \pm 0.00 ***	6.09 \pm 19.05	0.00 \pm 0.00	7.37 \pm 20.76
dr2	2 km % Disturbed remnant cover	21.08 \pm 4.91	24.97 \pm 11.28	23.67 \pm 14.01	24.16 \pm 11.31
tl2	2 km %treeless cover	64.33 \pm 5.07	49.20 \pm 19.01	61.72 \pm 13.97	47.67 \pm 20.13
ib5	5 km % Ironbark cover	4.38 \pm 2.04	4.25 \pm 2.48	4.33 \pm 2.14	4.25 \pm 2.52
do5	5 km % Dry open forest cover	1.79 \pm 3.08	3.88 \pm 4.83	1.86 \pm 2.86	4.28 \pm 5.12
dp5	5 km % Dry plateau complex	0.25 \pm 1.22	4.38 \pm 11.68	0.17 \pm 1.00 **	5.30 \pm 12.67
dr5	5 km % Disturbed remnant cover	17.42 \pm 9.74 **	23.49 \pm 8.53	20.14 \pm 10.10	23.05 \pm 8.48
tl5	5 km %treeless cover	76.50 \pm 2.40	64.26 \pm 16.89	73.81 \pm 11.85	63.39 \pm 18.08
ib10	10 km % Ironbark cover	2.33 \pm 0.96 **	2.10 \pm 1.09	2.36 \pm 0.99	2.04 \pm 1.09
do10	10 km % Dry open forest cover	4.88 \pm 6.26	4.97 \pm 4.78	4.19 \pm 5.49	5.42 \pm 4.94
dp10	10 km % Dry plateau complex	3.04 \pm 5.96 ***	5.86 \pm 7.84	2.75 \pm 5.37	6.63 \pm 8.23
dr10	10 km % Disturbed remnant cover	18.96 \pm 4.55 ***	25.77 \pm 7.54	21.22 \pm 6.16	25.77 \pm 7.78
tl10	10 km %treeless cover	71.13 \pm 12.27 ***	61.51 \pm 15.34	69.75 \pm 12.04	60.35 \pm 15.86
ib20	20 km % Ironbark cover	1.17 \pm 0.38	1.12 \pm 0.32	1.17 \pm 0.38	1.11 \pm 0.31
do20	20 km % Dry open forest cover	7.04 \pm 4.87 ***	6.49 \pm 4.23	6.33 \pm 4.51	6.82 \pm 4.33
dp20	20 km % Dry plateau complex	4.83 \pm 4.95 ***	8.65 \pm 5.92	5.36 \pm 5.03	9.12 \pm 5.99
dr20	20 km % Disturbed remnant cover	24.92 \pm 1.74 **	26.38 \pm 2.97	25.39 \pm 2.18	26.39 \pm 3.04
tl20	20 km %treeless cover	62.17 \pm 7.30	57.64 \pm 8.41	61.97 \pm 7.07	56.81 \pm 8.52

Six models were constructed, three different categories of independent habitat variables (microhabitat, landscape, GIS), against two different dependent (or response) variables: 1) Regent Honeyeater records from this study only, 2) all Regent Honeyeater records (from this study, and historically). Following this, I constructed two overall models (two different response variables), which incorporated all of the significant response variables from the six original models, to determine whether microhabitat, landscape or GIS variables, or all, were important predictors of Regent Honeyeater occurrence.

3.3 Results

In the two-year survey period, I found Regent Honeyeaters at 24 of the 93 transects (see Chapter 2 for details). A further 12 transects had historical records of Regent Honeyeaters (H. Hines, A. Ley, B. Williams pers. comm.), giving a total of 36 occupied transects. Regent Honeyeater sites were clustered in the Bundarra-Barraba region, especially in the scarce Mugga Ironbark habitat (see Figure 2.1, Chapter 2). Many of the Regent Honeyeater transects were in roadside travelling stock reserves, 200-400 m wide, rather than in large continuous blocks of habitat. Regent Honeyeaters were never found on transects within large continuous areas of habitat, particularly Linton Nature Reserve and Warrabah National Park which are over 1000 ha in area. The size of the habitat patch surrounding occupied transects was smaller, on average, than unoccupied patches, but not significantly so. However, Regent Honeyeater transects were better connected to other habitat, and closer to other habitat patches (Table 3.2). All occupied transects were on crown or leasehold land. The only transect used by Regent Honeyeaters within reserve land was an historic site (H. Hines pers. comm.), and no birds were recorded at that site during my surveys, between 1995 and 1997.

Regent Honeyeaters were only seen in transects in the four types of woodland habitat, and not in the riparian gallery forest transects (see Chapter 2). However, three historic riparian vegetation sites were known to have been occupied by Regent Honeyeaters several years before my study began in 1994.

3.3.1 Microhabitat models

Records from this study

The first microhabitat model explained 17.8% of variance; three factors significantly influenced the probability that a transect would be occupied by a Regent Honeyeater (Table 3.4). Transects used

by Regent Honeyeaters had significantly greater tree canopy cover, greater numbers of mistletoes, and lower numbers of shrubs above 2 m tall than transects not selected. There were no significant interaction terms between the three significant variables. The modes of action of the independent variables were linear rather than of the form of a step function. In the case of canopy cover, the probability of a transect being occupied by a Regent Honeyeater rose steadily from 0% at 10% cover, to 50% at 50% canopy cover (Appendix 1.1). For mistletoes, the probability rose from 25% at 100 mistletoes per transect, to almost 100% at 300 mistletoes (Appendix 1.2). In contrast, the probability decreased sharply from 50% to zero when shrubs above 2 m tall numbered more than 50 per transect (Appendix 1.3).

All records

The second microhabitat model incorporated three significant variables explaining the occurrence of Regent Honeyeaters, and accounted for 19.2% of variance in the data (Table 3.5). As shown in the first model, transects occupied both recently and historically by Regent Honeyeaters had high numbers of mistletoes and low numbers of shrubs taller than 2 m compared to unoccupied transect. However, in this second model tree canopy density was not a significant factor. Instead, the proportion of riparian tree species was an important predictor. Occupied transects had a higher proportion of riparian tree species than unoccupied ones. There were no significant interaction terms between the significant independent factors. The response curves for mistletoes and shrubs (Appendices 2.1 and 2.2) were similar to those in the first model. For riparian habitat, there was a steady increase in probability from 25% to nearly 100% as proportion of riparian tree species rose from 0% to about 25% (Appendix 2.3).

3.3.2 Landscape models

Records from this study

Of the 11 original variables, four were identified as significant using logistical modelling (Table 3.6). This first landscape model accounted for 30.5% of variance. Regent Honeyeater transects were closer to the edge of the habitat patch, closer to the nearest Regent Honeyeater site and were located at lower altitudes than non-Regent Honeyeater transects. Occupied transects were closer to rivers than unoccupied sites. I tested for interaction terms for distance to river x distance to creek, distance to river x distance to patch edge, and distance to river x distance to nearest Regent Honeyeater site. None of these was significant when fitted and then removed from the model. The modes of action were linear for the variables distance to nearest Regent

Table 3.4 A model of the significant microhabitat variables explaining the recent occupancy of Regent Honeyeaters at transects in the Bundarra-Barraba region from logistical regression analyses. Model explains 17.8% of variance. χ^2 values for significant values are presented (* $p < 0.05$, ** $p < 0.01$).

estimate	s.e.	parameter	χ^2	p
-3.080	0.9909	constant		
6.088	3.153	% canopy cover	4.17	*
0.007574	0.002021	no. of mistletoes	8.04	**
-0.02730	0.02059	no. of shrubs >2 m	4.30	*

Table 3.5 A model of the significant microhabitat variables explaining the recent and historical occupancy of Regent Honeyeaters at transects in the Bundarra-Barraba region from logistical regression analyses. Model explains 19.2% of variance. χ^2 values for significant values are presented (* $p < 0.05$, ** $p < 0.01$).

estimate	s.e.	parameter	χ^2	p
-0.7636	0.4128	constant		
-0.04286	0.02276	no. of shrubs >2 m	9.19	**
23.98	11.50	% of riparian tree	7.87	**
0.006988	0.003120	no. of mistletoes	6.49	*

Table 3.6 A model of the significant landscape variables explaining the recent occupancy of Regent Honeyeaters at transects in the Bundarra-Barraba region from logistical regression analyses. Model explains 30.5% of variance. χ^2 values for significant values are presented (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

estimate	s.e.	parameter	χ^2	p
10.15	3.709	constant		
-0.003732	0.002117	distance to patch edge	4.81	*
-0.01406	0.005405	altitude	7.91	**
0.0004534	0.000149	distance to river	4.66	*
-0.001329	0.0001337	distance to nearest RHE	26.19	***

Table 3.7 A model of the significant landscape variables explaining the recent and historical occupancy of Regent Honeyeaters at transects in the Bundarra-Barraba region from logistical regression analyses. Model explains 14.6% of variance. χ^2 values for significant values are presented (** $p < 0.01$).

estimate	s.e.	parameter	χ^2	p
1.025	0.4728	constant		
-0.0002626	0.0001036	distance to nearest RHE	9.16	**
-0.003996	0.001573	distance to patch edge	9.56	**

Honeyeater site (nrh), distance to patch edge (ped) and altitude (alt). For distance to nearest Regent Honeyeater site, the probability of a transect being occupied by a Regent Honeyeater rapidly decreased from 50% to zero, from a distance of 0 m to just over 2500 m (Appendix 3.1), while for distance to patch edge, there was a steady decrease in probability of occupancy from 50% to zero if the distance to patch edge increased from zero to 750 m (Appendix 3.2). The mode of action for distance to river (riv) was more difficult to interpret, and appeared to take the form of a step function (Appendix 3.3). The probability of occupancy remained steady at about 30% between 0 m and 7500 m, and then dropped to about 15% at 10000 m. For altitude, there was no apparent change in probability (about 25%) of occupancy between 500 m and 850 m altitude (Appendix 3.4).

All records

Two significant variables were identified for the second landscape model that explained 14.6% of variance (Table 3.7). Occupied transects were closer to the edge of the habitat patch (ped), and closer to the nearest Regent Honeyeater transect (nrh) than non-occupied transects. The interaction term of distance to patch edge (ped) x distance to nearest Regent Honeyeater site (nrh) was not significant when fitted and removed from the model. The modes of action for the significant independent variables were linear, and similar to those for the same variables in the first landscape model. However, the decrease in probability of occurrence for distance to nearest Regent Honeyeater site decreased less rapidly, from 50% at 0 m to 0% at about 11000 m (Appendix 4.1). For distance to patch edge, probability decreased steadily from about 60% at 0 m towards 0% at about 800 m from patch edge (Appendix 4.2).

3.3.3 GIS models

Records from this study

The first GIS model incorporated eight significant variables and one significant interaction term of dr10 x dr20 (refer to Table 3.3 for full description of variable) from the original 25 independent variables (Table 3.8). The model accounted for 53.2% of variance. I tested the significance of the interaction terms dp2 x dp10, dp2 x cp20, dp10 x dp20, dr5 x dr10, dr5 x dr20 and dr10 x dr20. Only the dr10 x dr20 interaction term was significant. Modes of action were linear for the variables dp2, dr5, tl10, dp20 and dr10 x dr20, while the other variables showed response curves in the form of step functions. An almost vertical decrease from 100% towards zero probability of occupancy was shown for dp2, if the percentage cover rose above zero (Appendix 5.1). In this

case the occupied sites had no dry plateau complex habitat in the 2 km zone, while the unoccupied transects had a mean of 6% dry plateau complex cover (see Table 3.3). There was steady decrease in probability of occurrence for dr5 (Appendix 5.2). At 5% cover of disturbed remnant vegetation, the probability of occupancy was about 60%, but decreased towards zero at 30% cover. For ib10 the probability of occupancy was about 20% at zero Ironbark cover, but increased to about 25% probability at 1% cover (Appendix 5.3), remaining there between 1% and 3% Ironbark cover, and then increasing to about 30% probability at 4% Ironbark cover.

The response curve for dp10 is a steady decrease in estimated probability of occurrence of 40% at 1% cover, towards zero probability at 25% cover (Appendix 5.4). As the proportion of treeless habitat at 10 km zone (tl10) increased from 30% treeless cover to about 75% treeless cover, the probability of occupancy increased from zero to 50% (Appendix 5.5). For do20, the probability of occupancy remained at 25% between 0% and 8% dry open forest cover, and then jumped to about 35% at 10% cover (Appendix 5.6). The chance of a site being used by a Regent Honeyeater on the basis of cover of dry plateau complex in the 20 km zone (dp20) decreased from 50% at 0% cover towards zero at about 15% cover (Appendix 5.7). A similar trend in decreasing probability was shown for % cover of disturbed remnant in the 20 km zone (Appendix 5.8). At 22% cover the probability was nearly 50%, but decreased to zero at about 30% cover. The mode of action for the significant interaction term dr10 x dr20 was in the form of a linear decrease from 60% probability of occurrence at 3% disturbed remnant cover towards a zero probability at 9% cover (Appendix 5.9).

All records

The second GIS model comprised two significant variables; percentage cover of dry open forest at 1km zone, and percentage cover of dry plateau complex at 5 km zone (Table 3.9). The model explained 20.5% of variance. The interaction term of the two significant variables was not significant. The modes of action of both variables were linear. For do1, the probability of a Regent Honeyeater occupying a transect decreased from 50% at zero cover, towards zero probability at about 22% cover (Appendix 6.1). A very steep decrease in probability from 50% towards zero was exhibited when the cover of dry plateau complex in the 5km zone increased from zero to 10% (Appendix 6.2).

Table 3.8 A model of the significant GIS variables explaining the recent occupancy of Regent Honeyeaters at transects in the Bundarra-Barraba region from logistical regression analyses. Model explains 53.2% of variance. χ^2 values for significant values are presented (** $p < 0.01$, *** $p < 0.001$).

estimate	s.e.	parameter	χ^2	p
58.23	31.82	constant		
-114.0	112.1	% dry plateau complex 2 km	27.19	***
-49.72	19.11	% disturbed remnant 5 km	10.38	**
305.4	127.1	% Ironbark 10 km	7.86	**
121.1	39.74	% dry plateau complex 10 km	12.82	***
-102.1	41.1	% treeless 10 km	14.79	***
-142.1	56.59	% dry open forest 20 km	15.92	***
-167.5	50.50	% dry plateau complex 20 km	23.38	***
218.8	73.2	% disturbed remnant 20 km	17.72	***
-491.1	173.4	interaction term: % disturbed remnant 10 km x % disturbed remnant 20 km	17.94	***

Table 3.9 A model of the significant GIS variables explaining the recent and historical occupancy of Regent Honeyeaters at transects in the Bundarra-Barraba region from logistical regression analyses. Model explains 20.5% of variance. χ^2 values for significant values are presented (** $p < 0.01$, *** $p < 0.001$).

estimate	s.e.	parameter	χ^2	p
04148	0.2873	constant		
-9.469	2.94	% dry open forest 1 km	14.66	***
-13.49	10.7	% dry plateau complex 5 km	8.76	**

3.3.4 Overall models

Records from this study

Of the 17 significant variables, and one significant interaction term identified in the above six models, only two, proportion of dry open forest in 1 km zone (do1), and distance to nearest Regent Honeyeater transect (nrh), were significant predictors in the first overall model which accounted for 37.5% of total variance (Table 3.10). The interaction term of do1 x nrh was not significant. The estimated probability of occupancy decreased from 50% at zero dry open forest cover in the 1km zone, towards zero probability at 15% cover (Appendix 7.1). A similar trend was found for distance to nearest Regent Honeyeater transect. The probability dropped from 50% at zero metres distance towards zero probability at about 2000 m (Appendix 7.2).

All records

The second overall model comprised four significant predictors: distance to nearest Regent Honeyeater transect (nrh), proportion of riparian tree species (prip), proportion of dry open forest in 1km zone (do1), and number of shrubs > 2 m tall (s2), and explained 35.4% of total variance (Table 3.11). None of the interaction terms was significant. The probability of Regent Honeyeater occurrence decreased from 50%, when the number of shrubs above 2m was zero, to zero, when the number of shrubs reached 100 (Appendix 8.1). A similar decrease from 50% to zero probability is seen in Appendix 8.2, where the % cover of dry open forest in the 1 km zone increases from zero to 20%, and in Appendix 8.3, where the distance to the nearest Regent Honeyeater transect increases from 0 m to about 7000 m. In contrast, an increase in the proportion of riparian tree species from zero to 20% results in an increase in probability of occurrence of 40% to 80% (Appendix 8.4).

Table 3.12 provides a general summary of the relationships between significant habitat variables of all models and the presence of Regent Honeyeaters in the Bundarra-Barraba study area. GIS models were the most robust models produced, while the microhabitat models explained the least amount of variance in the data.

3.4 Discussion

The habitat models I have developed allow the suitability of potential new Regent Honeyeater sites to be assessed in the Bundarra-Barraba region. However, the models can only be successfully applied to the conservation and management of Regent Honeyeater habitat, with a sound

Table 3.10 An overall model of the significant variables, from a total of 18 significant microhabitat, landscape, and GIS variables identified in previous models (see Tables 3.4 to 3.8, inclusive), that explain the recent occupancy of Regent Honeyeaters at transects in the Bundarra-Barraba region from logistical regression analyses. The overall model explains 37.5% of variance. χ^2 values for significant values are presented (***) $p < 0.001$).

estimate	s.e.	parameter	χ^2	p
0.958	0.4728	constant		
-17.01	5.19	do1	22.80	***
-0.001	0.00045	nrh	22.23	***

Table 3.11 An overall model of the significant variables, from a total of 18 significant microhabitat, landscape, and GIS variables identified in previous models (see Tables 3.4 to 3.8, inclusive), that explain the recent and historical occupancy of Regent Honeyeaters at transects in the Bundarra-Barraba region from logistical regression analyses. The overall model explains 35.4% of variance. χ^2 values for significant values are presented (* $p < 0.05$, *** $p < 0.0001$).

estimate	s.e.	parameter	χ^2	p
1.264	0.4098	constant		
34.06	12.19	prip	11.04	***
-0.0004032	0.0001341	nrh	17.49	***
-0.03037	0.01003	s2	4.90	*
-11.01	3.47	do1	15.36	***

appreciation of the microhabitat and landscape attributes of the region. The small regional population size of Regent Honeyeaters (ca. 100 birds, Chapter 2) means it was inevitable that some “suitable” sites were unpopulated, and because the species is nomadic, birds sometimes occurred in “unsuitable” habitat. Moreover, because Regent Honeyeaters are so rare, and their habitat cleared or degraded, it is difficult to obtain data on habitat selection. With these limitations in mind, I have been able to produce six predictive habitat models, that can be used to protect and manage unsurveyed “suitable” Regent Honeyeater habitats. These habitats could be used as release sites for captive-reared birds in the future, if necessary (Menkhorst 1997).

The two different model types (records from this study only, and all records) often incorporated the same predictors. However, there were several important exceptions. For example, only after the historical data were added, was the importance of riparian habitat to Regent Honeyeater identified. I took a similar approach to that of Pearce *et al.* (1995), and incorporated a broad range of occupied habitats into the models.

Microhabitat models

My models did not show obvious relationships between food abundance, floristic composition or structural complexity and occurrence of Regent Honeyeaters, which may have been useful for habitat conservation. There were no key microhabitat characteristics that could be targeted for management, as was the case for the Helmeted Honeyeater study (Pearce *et al.* 1994, 1995). Flowering indices, tree species composition and size and number of trees exerted little influence on the likelihood of Regent Honeyeaters being present. This could be due to the generalised habitat (see Chapter 2) and resource selection (see Chapters 5 and 6) of Regent Honeyeaters, compared to the relatively specialised Helmeted Honeyeater (Wykes 1982).

Because Regent Honeyeaters prefer tall trees with wide trunks (see Chapter 5), I would have expected tree size to be a significant predictor in the microhabitat models. Perhaps Regent Honeyeaters select large trees within a transect rather than transects with many large trees. In the future, microhabitat models should include categorical data for tree height and DBH, which has been used in other modelling studies (Lindenmayer *et al.* 1990, Pearce *et al.* 1994, Barrett 1995).

The proportion of riparian tree species at the microhabitat scale is a good predictor of the presence of Regent Honeyeaters. Three riparian gallery forest transects had historic Regent Honeyeater

Table 3.12 Habitat variables identified as making a significant contribution to one or more microhabitat, landscape, GIS and overall models for sites in which Regent Honeyeaters were recorded during surveys only (survey) and during surveys and historically (all). + indicates positive relationship, - indicates negative relationship. Significance of relationship indicated by: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Variable	Microhabitat		Landscape		GIS		Overall	
	This study	All records	This study	All records	This study	All records	This study	All records
% canopy cover	+ *							
no. of mistletoes	+ **	- *						
no. of shrubs >2 m	- *	- **						- *
% riparian tree spp.		+ **						+ **
distance to patch edge			- *	- **				
altitude			- **					
distance to river			- *					
distance to nearest RHE site			- ***	- **			- ***	- ***
% dry open forest 1 km						- ***	- ***	- ***
% dry plateau complex 2 km					- ***			
% dry plateau complex 5 km						- **		
% disturbed remnant 5 km					- **			
% Mugga Ironbark 10 km					+ **			
% dry plateau complex 10 km					- ***			
% treeless 10 km					+ ***			
% dry open forest 20 km					+ ***			
% dry plateau complex 20 km					- ***			
% disturbed remnant 20 km					- ***			

records, although no birds were recorded in them during my study. Regent Honeyeaters were, however, found breeding at two riparian gallery forest locations within 200 metres of two of my survey transects (see Chapters 6, 7 and 8). Other floristic variables, in particular the proportion of Mugga Ironbark, was not significant. This is because Regent Honeyeaters use a range of tree species, and not just Mugga Ironbarks (see Chapters 5, 6 and 8).

Regent Honeyeaters preferred sites with dense tree canopies, which could be related to their arboreal foraging on flowers, lerp and insects. These sites were typified by a low cover of shrubs, perhaps from the shading effect of the dense tree canopy above. However, I found no significant collinearity between canopy and shrub cover. An alternative explanation for the low shrub cover, is that many of the occupied transects were in travelling stock reserves, where grazing pressure was intermittently high, directly reducing shrub cover. The indirect effects of stock on shrubs include compaction of soils, and the erosion of topsoil on hillsides that have been grazed, which reduces the chance of shrub establishment.

Shrubs, particularly Sifton Bush, are used for nesting material by Regent Honeyeater (Ley and Williams 1994). However, I found a negative relationship between the occurrence of birds, and the number of shrubs above 2 m. The shrub cover below 2 m was the same between occupied and control sites. Webster and Menkhurst (1992) also found that the shrub layer did not play an important role in determining habitat utilised by Regent Honeyeaters, although their occupied sites tended to have a taller shrub layer than the control sites, which is in contrast to what I found.

Regent Honeyeaters selected habitat with high densities of mistletoes. Although mistletoes are sometimes used for food and nesting sites, they are not a key component in the habitat and resource requirements of Regent Honeyeaters. One could argue that there were more mistletoes at occupied sites because they had more tree canopy available for mistletoe parasitism. However, the interaction term of mistletoes and canopy cover was not significant in the models. The most likely explanation for the high mistletoe densities at occupied sites, was that most of the sites were in close proximity to the edge of linear roadside reserves or remnant woodland patches on pastoral land that are prone to infestation (Reid *et al.* 1994).

It is important that the microhabitat predictors are not misinterpreted when applying them to the management of Regent Honeyeater habitat. For example, the microhabitat predictors of high mistletoe numbers and low numbers of large shrubs does not mean that we should provide more habitat with those types of attributes in order to save Regent Honeyeaters. It would also be premature to physically remove mistletoes from key Regent Honeyeater habitat as a possible management strategy, because this may have serious consequences for other fauna such as rare Painted Honeyeaters, which rely on mistletoes for food. If anything, the microhabitat predictors are a warning sign that sites occupied by Regent Honeyeaters, which are often in small roadside Box/Ironbark woodland patches, are threatened by degradation, due to being reduced in size, and being fragmented. Mistletoes are known to have an impact on the vigour of eucalypts in the New England Region (Heatwole and Lowman 1986, Reid *et al.* 1994). Microhabitat modelling has heightened the awareness about monitoring Regent Honeyeater sites, so that they are not further degraded in the future from mistletoe infestation and other agencies, as a result of ecologically insensitive land management.

Landscape models

The landscape models were more powerful at explaining Regent Honeyeater occurrence than the microhabitat models, despite being comprised of variables derived from outdated and inaccurate topographical maps. Therefore, one must be cautious with the predictions of these models. I found that Regent Honeyeaters are likely to be found near rivers, at the edge of habitat patches, and near known Regent Honeyeater sites. The close proximity between Regent Honeyeater sites may be an artefact of my survey design, which aggregated many of the transects in Box/Ironbark woodland. These transects were clustered, because of the small proportion of remaining Box/Ironbark woodland in the study area (4% of Bundarra-Barraba region), and the fact that this is localised. Mugga Ironbarks now mainly occur on nutrient-poor granite hills and slopes below 900 m altitude (B. Williams pers. comm.). A random selection of survey sites across the region would have alleviated such effects, but may have detected far fewer Regent Honeyeaters.

The results from the landscape models can be applied to protecting and managing unsurveyed habitat close to rivers, edges and places where Regent Honeyeaters have been recorded. A second application could be identifying suitable locations for the release of captive-reared birds, if this becomes necessary. Releasing Regent Honeyeaters close to where others occur is a sensible strategy to augment a local population.

My landscape models show that patch size is not an important factor in predicting the presence of Regent Honeyeaters. This may be due to the strong influence from Regent Honeyeater not occupying any of the 22 transects located in the two largest patches of the study area; Linton Nature Reserve (ca. 750 ha) and Warrabah National Park (>3000 ha). It is worthy of note that both of these large “islands” supported very low bird species richness and individual abundance, compared to much smaller “islands”. This adds to the conflicting evidence about the applicability of island biogeography theory (MacArthur and Wilson 1967, Diamond 1975b) to complex natural systems.

GIS models

The GIS landscape models were the most robust of all the models developed, because they explained the highest proportion of variance in the data. The GIS model predictors can only be effectively applied to Regent Honeyeater habitat identification and management, by someone with a sound knowledge of the GIS database for the Bundarra-Barraba region, and surrounding regions. This will allow the extrapolation of the models to predict the occurrence of Regent Honeyeaters at new sites, provided they are within the GIS database region. This would allow a quick assessment of site suitability without the need to survey for Regent Honeyeaters, nor to measure microhabitat characteristics, which takes a great deal of time and effort.

Regent Honeyeater sites are surrounded by more Box/Ironbark woodland and treeless habitat, and less dry open forest, dry plateau complex woodland, and disturbed remnant woodland, than unoccupied sites. The complex relationships between the presence of Regent Honeyeaters, and the percentage cover of different habitat categories, is probably influenced by the broad habitat (Chapter 2) and resource (Chapter 5) requirements of the species. However, it was sometimes difficult to explain the ambiguities of vegetation cover correlations for the different zones of proximity, because the actual plant species composition was not known, and habitat classification was open to individual interpretation from aerial photographs. The major tree species in Mugga Ironbark patches were recorded from ground surveys by Beth Williams. However, similar data on the floristic composition of other GIS categories were not available. Quantitative ground-based floristic data for all habitat categories may allow more meaningful models to be produced, but this was beyond the scope of my project.

The GIS models show that Regent Honeyeater transects are surrounded by a low proportion of dry plateau complex woodland, from the 2 km zone right out to the 20 km zone. Regent Honeyeaters may avoid this infertile woodland, because nectar production is generally low. My observation of four birds using dry plateau complex woodland (Chapter 2), however, shows that they will use it, when resources in their preferred Box/Mugga Ironbark habitat are low.

The relationship between Regent Honeyeater occupancy and dry open forest cover differed at different scales. At the 1 km scale, there was a negative correlation, but at the 20 km scale there was a positive relationship. The positive association at 20 km is difficult to explain without knowing the actual floristic composition of the dry open forest category. The negative correlation at the 1 km scale, which was also significant in the overall models, may be due to the preference of Regent Honeyeater for other habitats, such as Mugga Ironbark woodland and riparian gallery forest, at the local scale.

There was a significant positive relationship between Mugga Ironbark cover and occurrence of Regent Honeyeaters at the 10 km scale. There was also a positive relationship at the 2 km and 5 km scale, which came close to being significant. The positive association between Mugga Ironbark habitat and Regent Honeyeaters in the GIS models adds further support to the contention that such habitat is a vital food and nesting resource.

The negative relationship between Regent Honeyeater sites and disturbed remnant vegetation possibly relates to their preference for habitat with high canopy cover. However, this conflicts with the results of the micro-habitat modelling, which shows that Regent Honeyeater sites have high densities of mistletoes and low understorey cover, both signs of disturbance. The high proportion of treeless habitat surrounding Regent Honeyeater sites is associated with the clearance of productive Box/Gum woodland on the most fertile soils, for agriculture. Box/Ironbark woodland has, itself, been reduced to small remnants from timber extraction (see Figure 2.1 in Chapter 2). The landscape surrounding Regent Honeyeater sites contrasts with that around unoccupied transects in dry plateau complex woodland, which has virtually been uncleared. One could argue that habitat selection by Regent Honeyeaters is not influenced by landscape variables, that have been derived from a human perspective. It is possible that I was using too large a scale but, nevertheless, seven of the ten significant GIS variables were in the 10 km and 20 km zone.

Overall models

The significant landscape-scale variables in both overall models were the close proximity to other Regent Honeyeater transects, and a low proportion of dry open forest in the 1 km zone. The significance and application of these has been discussed in the more restrictive models. Incorporating historical data proved to be effective for identifying microhabitat predictors. A high proportion of riparian tree species and low number of shrubs taller than 2 m were good indicators of Regent Honeyeater occupancy.

Application of the models to Regent Honeyeater management

Habitat selection modelling has helped to identify areas where Regent Honeyeater may occur, to suggest the highest priority of habitats for protection and rehabilitation, and to identify sites for re-introduction of captive-reared birds. In contrast to my study, most habitat selection models for birds have been developed for sedentary species such as Helmeted Honeyeaters (Pearce *et al.* 1994, 1995), and Rufous Scrub-birds (Feirier 1985), which have specific habitat and resource requirements within a restricted range. Clearly, my models are less robust, and have lower predictive power than other models, and the generality of my habitat modelling procedure to other studies on widely-dispersed and mobile species (e.g., Swift Parrot, Painted Honeyeater) is limited. Even if a similar survey and habitat assessment effort can be achieved, the microhabitat and landscape models would probably share similar shortcomings to mine. However, the predictive ability of GIS models may be useful in the study of other nomadic and endangered species.

My models show that new Regent Honeyeater sites in the Bundarra-Barraba region are likely to be in Box/Ironbark woodland close to where Regent Honeyeaters have been previously recorded, or in habitat close to rivers with a high proportion of riparian tree species. New sites are also likely to be found near the edges of small to medium-sized remnants on rural properties, or along roadsides and streamsides. This means that habitat conservation for Regent Honeyeaters must focus on proper management of the relatively scarce Mugga Ironbark and riparian habitat types, which are vulnerable to further loss and degradation. For example, the illegal removal of Mugga Ironbarks from roadside reserves must be addressed by Rural Lands Protection Boards in Armidale, Tamworth, and other key Regent Honeyeater regions. Also, River Sheoaks and other riparian tree species, which now occur in narrow fragmented bands along rivers and creeks in the Gwydir and Namoi catchments in the Bundarra-Barraba region, need to be better protected from impacts such as stock grazing and sand mining. The reduction of grazing along waterways will assist the natural

regeneration of Sheoaks, and replanting of riparian eucalypts in severely degraded locations will also improve riparian ecosystem health providing hydrological benefits to water users, as well as benefiting wildlife.

Most of the Mugga Ironbark and riparian gallery forest remnants used by Regent Honeyeaters are too small to be viable National Park reserves. Therefore, it is essential to provide incentives for landholders, shire councils and rural lands protection boards to become involved in the conservation and management of non-reserve land. Because Regent Honeyeater sites are surrounded by large amounts of cleared land, and are showing signs of localised degradation, landholders and shire councils should be encouraged and remunerated for fencing and reducing grazing of vegetation, which has significant conservation value for Regent Honeyeaters and other woodland biota. Controlled grazing should allow understorey species to recover which may provide important resources such as nesting material and abundant insects for food. Smaller remnants should be increased in size by replanting endemic plant species to reduce the impacts of edge effects, such as mistletoe infestation (Norton *et al.* 1995). It may also be necessary in some situations to reduce the number of mistletoes which reduce the vigour of important roosting (Oliver 1998), feeding, and nesting trees. The rehabilitation and restoration of degraded lands and waterways in the Bundarra-Barraba region requires integrated action among land managers and water users, which will provide substantial environmental and economic benefits (Recher 1998).

If the Bundarra-Barraba Regent Honeyeater population appears to be heading towards extinction, and re-introduction of captive-reared birds was a realistic option, my models may help to optimise where to release them. Historically-occupied sites, or sites close to known Regent Honeyeater habitat would be the best option, provided that these have not become further degraded. In regions where Regent Honeyeaters are known to occur, but where there are no available habitat data (e.g., Inverell region), the best places for release would be in Box/Ironbark woodland close to waterways, or in riparian gallery forest preferably with a dense canopy cover. Areas with a high proportion of dry open plateau complex woodland, dry open woodland, or disturbed remnant woodland would be less suitable habitat for re-introduction.

Survey transects were established in relatively healthy woodland and forest, because I assumed that Regent Honeyeaters would not be found at sites that were cleared, or highly degraded. Hence, my models explain the occurrence of Regent Honeyeaters in relatively good quality habitat. However,

in the last three years, Regent Honeyeaters have been recorded using paddock trees for food and nesting (pers. obs, Geering and French 1998). Considering that my microhabitat models showed that there are signs of declining ecosystems health at occupied sites, it might be relevant to further investigate the relationships between the distribution of Regent Honeyeaters and degree of habitat degradation.

In conclusion, the modelling of habitat selection by Regent Honeyeaters has provided a series of predictive tools at different habitat scales, that could be used to assess the suitability of unsurveyed sites in northern New South Wales. Secondly, the models developed in this research do have some application for habitat conservation and management. By knowing that Regent Honeyeater habitat is potentially threatened from the edge effects of habitat fragmentation, we can address this problem in the future by mistletoe removal, enlargement of habitat remnants by tree planting, and a change in attitude towards land management by landholders and shire councils.

Chapter 4.

Activity budgets of the behaviour of Regent Honeyeaters in northern New South Wales

4.1 Introduction

The behavioural strategies used by an animal will, ultimately, determine its chances of survival and reproduction (Moreno and Hillstrom 1982). If the animal manages its time and energy efficiently, it will have sufficient time to perform other activities (Pyke *et al.* 1977). However, when other factors such as vigilance against predators, aggressive interactions, or fluctuations in resource availability in an unpredictable environment are considered, then an animal will not always meet its energy requirements efficiently, and may not adequately perform other behaviours such as breeding (Wiens 1984).

The clearance, fragmentation, and degradation of woodlands and associated habitats used by Regent Honeyeaters, has reduced the amount of food and other resources available to them, and other members of their guild, nectarivores. One possible reason for the decline of the Regent Honeyeater is a decrease in foraging efficiency, due to this resource diminution. Alternatively, increased competition for scarce resources may have reduced the time in which they can gather enough food. Put another way, Regent Honeyeaters may now be spending more time than they did historically to gather their energy requirements. This reduces the amount of time available for other activities such as predator surveillance, personal maintenance, and breeding, which are essential for the fitness of an individual and hence survival of the species.

Effects of habitat clearance and fragmentation on Regent Honeyeater behaviour

The clearance of eucalypt woodland and forest in southern Australia (Robinson and Traill 1996) has, undoubtedly, reduced the availability of resources (food, nesting sites etc.) to Regent Honeyeaters. The subsequent fragmentation of habitat isolates these resources, which can affect the activity and foraging behaviour of animals (Redpath 1995). The discontinuous distribution of resources makes it difficult for some animals to properly exploit them (e.g., Saunders 1977, 1980). Nomadic honeyeaters such as Regent Honeyeaters and Painted Honeyeaters have movements that

are believed to be based on the phenological patterns of resources in a succession of different habitats (Keast 1968). In a fragmented landscape, Regent Honeyeaters have to increase their search effort for fragmented resources, which may impact on their survival.

Effects of habitat degradation on Regent Honeyeater behaviour

The clearance of woodlands within the range of Regent Honeyeaters has primarily taken place on the most accessible and productive land leaving habitat remnants on nutrient-poor soils (Ford *et al.* 1993). The resource availability in these remnants is, therefore, likely to be much lower than the average productivity of the original continuous habitat prior to clearance, and to cover only a limited range of those originally available. The productivity of remnant habitat in agricultural landscapes is affected by a multitude of factors that affect the health of those systems (Heatwole and Lowman 1986). Logging, altered fire regimes, and grazing by exotic herbivores has changed and degraded the structure and floristic composition within the majority of remnants (Majer *et al.* in prep.). Symptoms of habitat degradation include soil salinisation, dieback from insect attack and fungal root infection by *Phytophthora cinnamomi* (Heatwole and Lowman 1986), and infestation of mistletoes. These factors can all affect the vigour of plants, which in turn may affect their ability to produce resources such as nectar used by Regent Honeyeaters. The addition of nutrients (stock excreta, artificial fertilisers) to degraded ecosystems may also have adverse affects on the health of trees (Landsberg *et al.* 1990). In some cases, the level of foliar nutrients in trees may increase, attracting phytophagous insects such as psyllids, which seek nitrogen in leaves (Moore 1972, White 1969). Alternatively, plants that have adapted to growing on infertile soils can be killed by the application of phosphate-rich fertilisers (Heatwole and Lowman 1986).

The degradation of habitat after clearance and fragmentation has probably further reduced the abundance and range (i.e., variety) of foods used by Regent Honeyeaters, and other nectarivores, in the Bundarra-Barraba region, and elsewhere in southeastern Australia. The Regent Honeyeater is neither a large dominant, nor a small efficient honeyeater, and potentially faces difficulties in securing food, due to both interference and exploitation competition. Franklin and Robinson (1989) found numerous records of Regent Honeyeaters being attacked by other honeyeaters, while Davis and Recher (1993) raised the possibility that aggressive competition for nectar and nesting sites with larger honeyeaters could be affecting the survival of the species. If Regent Honeyeaters are now spending most of their time acquiring necessary energy, they are at greater risk from

predation, poor physical condition, or even death from starvation, and are unlikely to produce many offspring (Bryant and Tattner 1988).

4.2 Aims

There are two major components to my research on Regent Honeyeater behaviour. The first component, presented in this chapter, seeks to quantify the proportion of time that adult Regent Honeyeaters spend in their repertoire of behaviours. The second behavioural component, presented in the following chapter (Chapter 5), investigates the resource selection by adult Regent Honeyeaters, where I measured the proportion of foraging time birds spent feeding on different foods, and the plant species from which they were gathered.

In this chapter, I measured the proportion of time Regent Honeyeaters spent foraging, and in aggressive interactions (intra- and interspecific), to determine whether they were spending excessive amounts of time in those activities, to the extent that time remaining for other activities, such as predator vigilance, personal maintenance and breeding activities was limited. I compared my results for Regent Honeyeaters with other studies on Australian honeyeaters to elucidate possible behavioural differences, which may be responsible for the decline of the species. In particular, I was interested to know whether Regent Honeyeaters spent more time foraging and fighting than the average honeyeater, which is about 34% (n = 28 studies, Table 4.20) and 3.6% (n = 14 studies, Table 4.20), respectively.

Behavioural comparisons were also made between Regent Honeyeaters using different diets to determine which type of food met the birds' energy requirements best, by testing for differences in the proportion of time spent foraging, as well as the time left for resting. The level of aggression of birds using different diets was also compared, as there may be a trade-off between time spent feeding and time spent on intra- and interspecific aggression. The effect of time of day, year and breeding status on behaviour was also addressed.

4.3 Methodology

From May 1994 to February 1997 the activity budgets of breeding and non-breeding Regent Honeyeaters were measured in the Bundarra-Barraba region, and at two other locations in northern New South Wales; the Warrumbungle National Park and Howes Valley. Regent Honeyeaters were found during regular censusing (Chapter 2), or opportunistically at other times and locations in the

Bundarra-Barraba region. From May to December 1994, behavioural studies were conducted on Regent Honeyeaters in large non-breeding flocks at Howes Valley (32°52'15"S, 150°48'00"E) and the Warrumbungle National Park (31°16'30"S, 148°59'00"E), as few birds could be found in the Bundarra-Barraba region. Behavioural data for birds at the Warrumbungle National Park were collected using a focal-animal "scan-sample" method (Altmann 1974). This involved instantaneously recording the activity of the focal bird every 15 seconds until the bird was lost. By recording the number of times each activity was performed during an observation bout, the overall proportion of time spent in each activity was calculated. This method was later replaced by a more accurate focal-animal method involving continuously recording every activity performed by the focal bird. This method allowed behaviours of short duration to be measured, removing the bias towards recording only conspicuous and longer activities. When the focal bird was located, sequential observation data on its behaviour were collected.

It was not possible to distinguish the sexes during the non-breeding season, as there is a lack of distinctive plumage dimorphism. During the breeding season however, females were distinguished from males by observing their behaviour in the nesting territory prior to collecting activity budgets (Chapter 7). It has been assumed that female Regent Honeyeaters are entirely responsible for nest construction, incubation and brooding (Longmore 1991, Ley and Williams 1994), and colour-banding of at least one member of 18 out of 40 breeding pairs confirmed this (Chapter 7). Colour-banding also helped me to distinguish between the sexes when collecting behavioural data, particularly when birds were away from the nest. I was able to distinguish between the sexes of unbanded pairs based on morphometric differences (Schodde *et al.* 1992, Ley *et al.* 1996), and sometimes on small plumage differences; males were often much blacker, and had larger warty eye patches, than females.

Before commencing this time-budget study, behavioural activities were based on similar criteria from Recher *et al.* (1985), and Webster and Menkhorst (1992) (see Table 4.1 for descriptions). Birds were observed using 10 x 50 binoculars from a distance that did not affect the behaviour of the subjects - 15 to 20 metres. In general, Regent Honeyeaters are not easily disturbed by human presence. A 15 second delay between locating the subject and commencement of recording its activities was imposed, to avoid any bias towards recording the most conspicuous behaviour at the beginning of each observation bout (Recher and Gebski 1990). A continuous account of all activities was recorded onto audio micro-cassette tapes until the bird was lost, and only bouts

Table 4.1 Description of activities recorded during behavioural observations of Regent Honeyeaters.

Activity category	Activity name	Activity description
resting	perching unalert	bird perched and asleep, or unalert
“	perching alert	bird perched and resting, but alert
“	perching calling	bird perched, resting but calling
“	preening	bird grooming its feathers
“	scratching	bird scratching itself during preen
“	stretch/shake	bird shakes or stretch its body during preening/resting
“	bill wiping	bird wipes its bill on a substrate during preening or after foraging
flying/other activities	flying	bird flies between activities
“	defaecate	bird defaecates (typically during or after foraging)
“	bath	bird bathes at water source
“	hopping on ground	bird hopping on ground, but not foraging
aggression	chasing	bird chases another bird(s)
“	chased	bird is chased by another bird(s)
foraging	perching searching	bird perched but looking for food resources
“	hopping searching	bird hopping between food sources
“	drinking	bird drinking from water source (river, dam or surface water)
“	hawking	bird flies from a perch to capture a flying insect
“	insect	bird captures an insect from a substrate
“	snatch	bird flies or jumps up to take a prey item from a substrate
“	glean	bird perches or hops to collect prey from substrate (typically lerp)
“	probe nectar	bird feeds on the nectar from flowers
“	manna	bird collects manna from substrate (under bark or on leaves)
“	sap	bird collects sap from substrate
“	probing bark	bird collects undefined prey from under bark
breeding activities	collecting nest materia	female gathering nest material
“	building nest	female constructing nest
“	display	mating display/copulation between breeding pair
“	at nest	bird checks nest but does not sit on nest
“	on nest	female incubating eggs/brooding nestlings
“	feed chicks	bird feeding nestlings/fledglings

lasting more than 60 seconds were considered for analysis using the *Activity* (Evans 1996) computer program. *Activity* measured the number of times each behaviour was performed, and the cumulative time, of each behaviour within an observation bout. The percentage of total time for each behaviour within an observation period was also calculated. Later, all behaviours were grouped into one of five categories: foraging, resting, flying/other activities, breeding activities, and aggression. Activity budgets of Regent Honeyeaters were compared with those of other Australian honeyeaters and insectivorous birds, and some non-Australian birds to interpret whether they spent unusually high amounts of time foraging or in aggressive interactions with other birds.

Behavioural comparisons

Behavioural data from the three study areas were analysed separately. Foraging, resting and aggression were grouped into categories according to which year, and what time of day they were collected, as well as the bird's diet. The three daytime categories were "morning": the first three hours after sunrise; "middle": the hours between the morning and afternoon periods, and "afternoon": the last three hours of daylight. The two dietary categories were birds feeding mostly on nectar, and birds feeding primarily on lerp and insects. The duration of an observation bout potentially affected the number of times, or proportion of time, spent on a behaviour. That is, a behaviour is likely to be displayed more often in a longer bout, than a shorter bout. It was, therefore, necessary to test for the effect of bout length, as a co-variate, by employing analyses of co-variance (ANCOVA) to comparisons of behavioural data. An unbalanced sample design from Howes Valley, with inadequate replication of the time category for nectar feeding birds, meant effects of diet and time of day on behaviour were tested using one-way ANCOVA. Dietary and diurnal comparisons of the behaviour of birds at the Warrumbungle National Park were analysed using two-way ANCOVA. Data from birds from the Bundarra-Barraba region were analysed using either one-way or two-way ANCOVA to test for behavioural differences between years, time of the day, and between birds eating different foods. Each observation bout of non-breeding Regent Honeyeaters was treated as an independent data point. However, in the case of breeding birds, the means of data collected for the female and male from each nest were used to avoid pseudoreplication (Hurlbert 1984). The proportions of time spent foraging, resting and in aggression were arcsin-transformed, to meet the assumption of normality for analysis of co-variance (Zar 1984). Two other measures of aggression level were tested: the number of aggressive acts per observation bout and the number per minute, and being count data, they were square-root-transformed before attempting an analysis of co-variance.

4.4 Results

4.4.1 Activity budgets

The Warrumbungle National Park

Fifteen hours (53,790 seconds) of observation data were collected from three separate sampling periods in June and July 1994. A total of 3,664 activities were recorded in 146 observation bouts. Regent Honeyeaters spent an average of 52.0% of their time feeding, 39.6% resting, 6.0% flying and other activities, and 2.4% in aggressive interactions (Figure 4.1).

Howes Valley

A total of 32 hours (115,718 seconds) of sequential behavioural data were collected on non-breeding Regent Honeyeaters in August, October and December 1994. Overall, Howes Valley birds spent 43.4% of time in foraging, 43.4% resting, 10.3% flying and in other activities, and 2.9% in aggression (Figure 4.2).

Bundarra-Barraba region

Between January 1995 and February 1997, 215 hours (775,764 seconds) of activity budgets of breeding and non-breeding birds were collected from 1,202 observation bouts. On average, Regent Honeyeaters spent 43.2% of total time feeding, 22.7% resting, 23.6% in breeding activities, 8.7% flying and in other activities, and 1.8% in aggressive interactions (Figure 4.3). A summary of the activity budgets of breeding and non-breeding birds over two years is presented in Table 4.2, and the activity budgets of breeding birds at, or near, their nests are presented in Chapter 7.

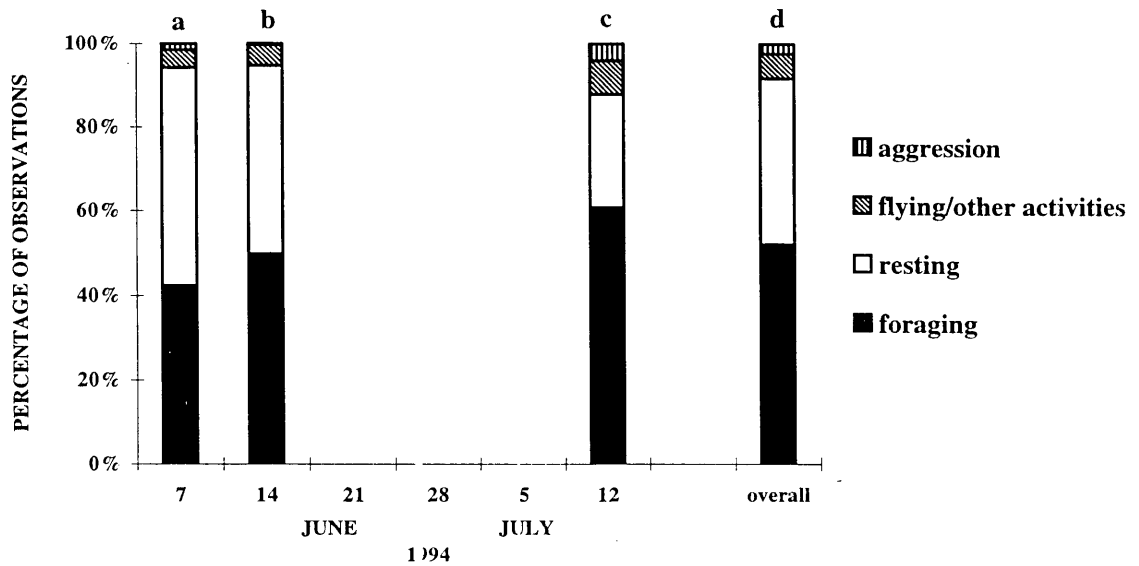
4.4.2 Dietary effects on behaviour

Warrumbungle National Park

Nectar-feeding birds tended to spend more time foraging, though not significantly so, and less time resting, than birds that foraged on lerp and honeydew (Figure 4.4). Birds that ate mostly nectar spent significantly more time in aggressive activities (Figure 4.4), and were involved in more aggressive acts per observation bout, and per minute, than birds feeding on other carbohydrates (Figure 4.5).

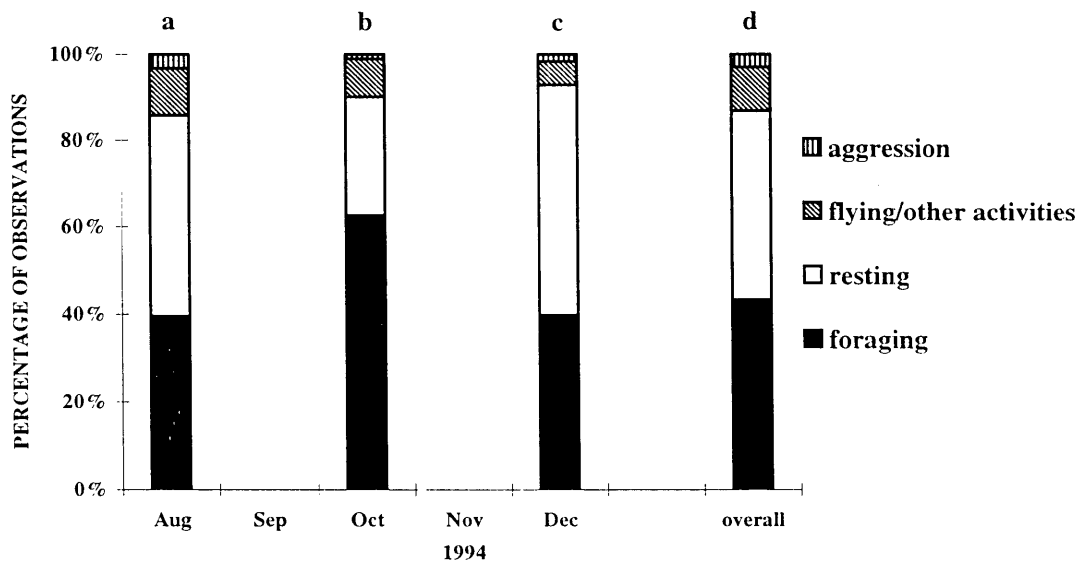
Howes Valley

There was no difference in proportion of time spent foraging, resting, or in aggression (Figure 4.6), or in aggression rates (Figure 4.7), between birds feeding on nectar and those on lerp.



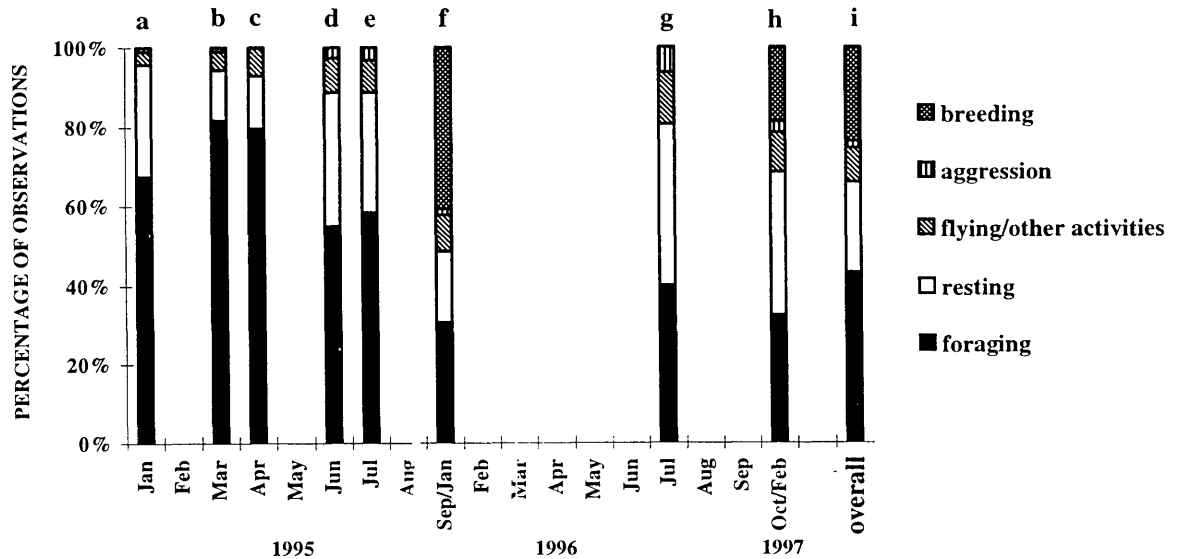
[a = 40⁺, 53, 17,415; b = 47, 25, 12,780; c = 30⁺, 68, 23,595; d (overall mean) = 47, 146, 53,790]

Figure 4.1 Activity budgets of non-breeding Regent Honeyeaters at the Warrumbungle National Park in 1994 [legend letter = number of birds, number of observation bouts, total observation time].



[a = 115⁺, 323, 82,795; b = 50⁺, 66, 19,008; c = 30⁺, 18, 13,854; d(overall) = 115⁺, 407, 115,718]

Figure 4.2 Activity budgets of non-breeding Regent Honeyeaters at Howes Valley in 1994 [legend letter = number of birds, number of observation bouts, total observation time (s)].



[a(N): (Howell, 2, 8, 14,627); b(N): (Linton, 8, 54, 12,748); c(N): (Coonoor, 24⁺, 187, 37,163); d(N): (Torryburn, 2, 75, 30,877); e(N): (Bundarra, 2, 33, 8,619); f(B): (Coonoor/Torryburn, 73, 637, 555,322); g(N): (Nangahrah Ck., 15⁺, 68, 19,985); h(B): (Torryburn/Linton, 64, 140, 96,387); (overall): (190⁺, 1,202, 775,764)]

Figure 4.3 Activity budgets of breeding (b) and non-breeding (n) Regent Honeyeaters in the Bundarra-Barraba region. [legend letter = (breeding status): (location, number of birds, number of observation bouts, total observation time (s)).]

Table 4.2 Summary of activity budgets of breeding and non-breeding Regent Honeyeaters in the Bundarra-Barraba region (n = number of observation bouts).

Breeding status/year	n	% foraging	% resting	% flying/other	% breeding	% aggression
Breeding 1995	637	30.7%	18.0%	9.1%	40.8%	1.5%
1996	140	32.5%	36.0%	10.1%	18.8%	2.7%
Non-breeding 1995	357	72.9%	19.4%	6.6%	0%	1.1%
1996	68	40.0%	40.6%	13.1%	0%	6.2%

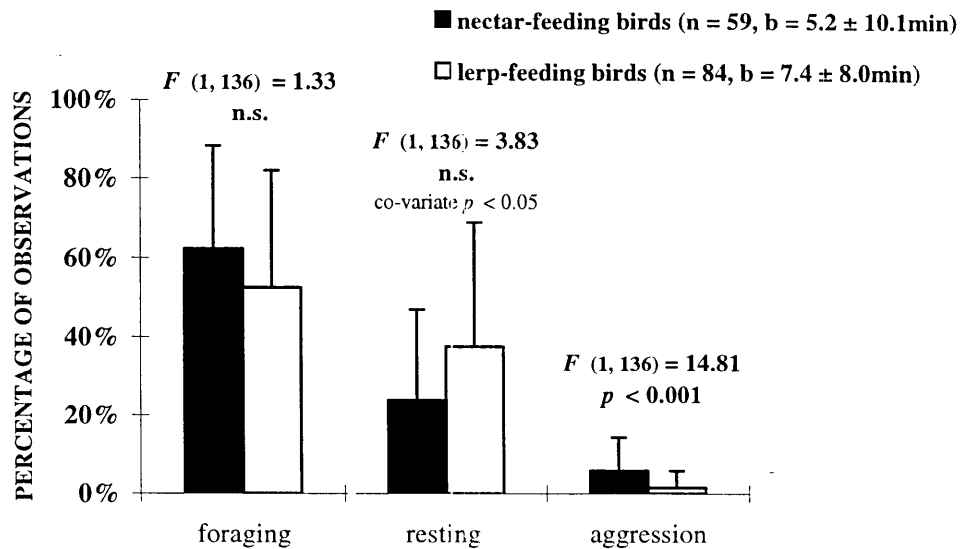


Figure 4.4 Dietary comparisons of the proportion of observation time spent in foraging, resting, and aggressive activities (+ s.d.) by non-breeding Regent Honeyeaters in the Warrumbungle National Park, using two-way ANCOVAs. (n = observation bouts, b = average observation bout length (\pm s.d.)).

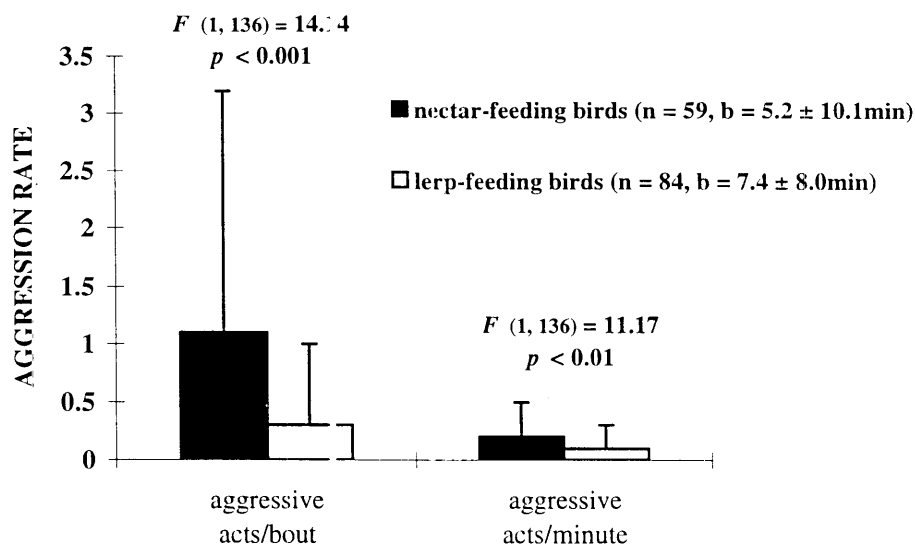


Figure 4.5 Dietary comparisons of aggression rates per observation bout, and per minute (+ s.d.), of non-breeding Regent Honeyeaters in the Warrumbungle National Park, using two-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

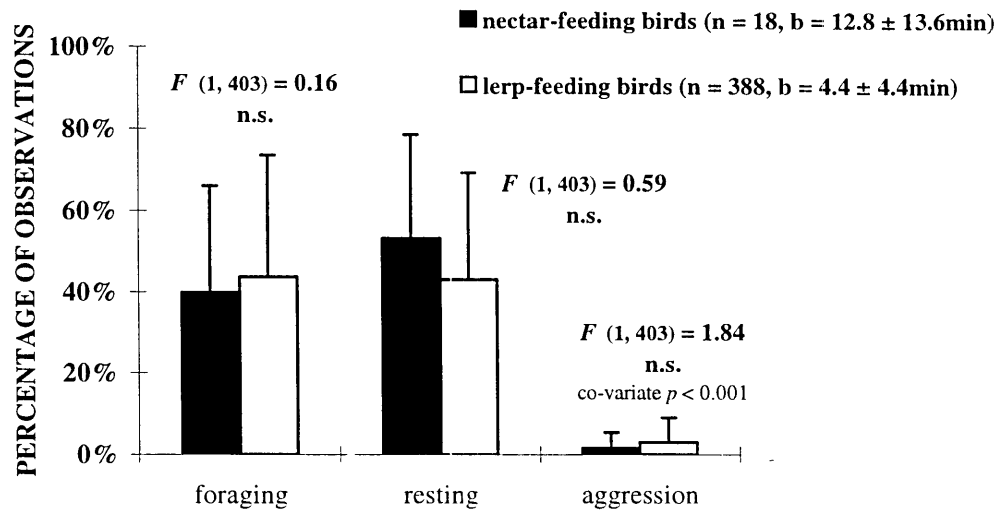


Figure 4.6 Dietary comparisons of the proportion of observation time spent in foraging, resting, and aggressive activities (+ s.d.) by non-breeding Regent Honeyeaters at Howes Valley, using one-way ANCOVAs. (n = observation bouts, b = average observation bout length (\pm s.d.)).

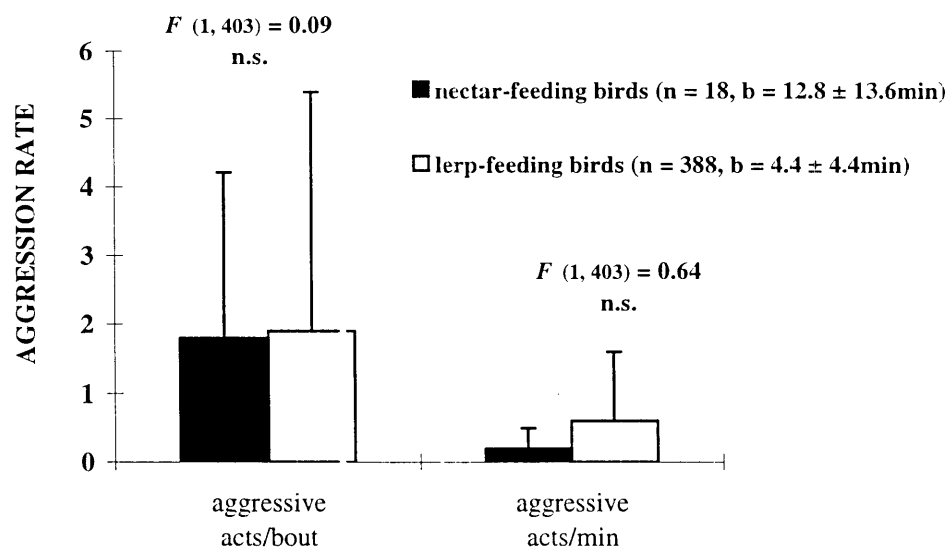


Figure 4.7 Dietary comparisons of aggression rates per observation bout, and per minute (+ s.d.), of non-breeding Regent Honeyeaters at Howes Valley, using one-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

Bundarra-Barraba region

Non-breeding birds

In 1995, non-breeding Regent Honeyeaters were observed feeding either primarily on nectar, or on lerp. Nectar-feeding birds spent significantly less time foraging, and more time in aggression than birds feeding on lerp (Figure 4.8). However, birds on both diets rested for similar amounts of time (Figure 4.8). Birds feeding on nectar had more aggressive encounters per observation bout, and per minute, than lerp-feeding birds (Figure 4.9). In 1996, non-breeding Regent Honeyeaters fed primarily on nectar and, hence, no dietary behavioural comparison could be attempted. When data were pooled for both years, nectar-feeding birds spent less time foraging, more time resting, and more time in aggression than lerp-feeding birds (Figure 4.10). The aggression rate per observation bout, and minute, was significantly higher for nectar-feeding birds (Figure 4.11).

Breeding birds

In 1995, breeding birds in the Bundarra-Barraba region fed either mostly on nectar, or lerp. Nectar-feeding females were involved in significantly more aggressive interactions per minute, but spent about the same amount of time in foraging and resting, as lerp-feeding females (Table 4.3). In the same year, nectar-feeding males spent a similar amount of time foraging, and slightly more time resting and fighting other birds, than males eating lerp (Table 4.4). It was not possible to make a similar dietary behavioural comparison in 1996, as all breeding birds fed primarily on nectar.

4.4.3 Diurnal effects on behaviour

The Warrumbungle National Park

Regent Honeyeaters spent similar proportions of time feeding throughout the day (Figure 4.12). Aggressive behaviour (proportion, number of acts per observation bout, and rate per minute) (Figure 4.13), and proportion of time spent resting (Figure 4.12), was also similar throughout the day. There was significant variation in the co-variate of observation bout length for resting data. Bouts were longer in the middle of the day than the other two periods (Figure 4.12).

Howes Valley

Regent Honeyeaters spent almost the same amount of time foraging and resting in the morning and middle of the day, but spent significantly less time foraging and more time resting in the afternoon

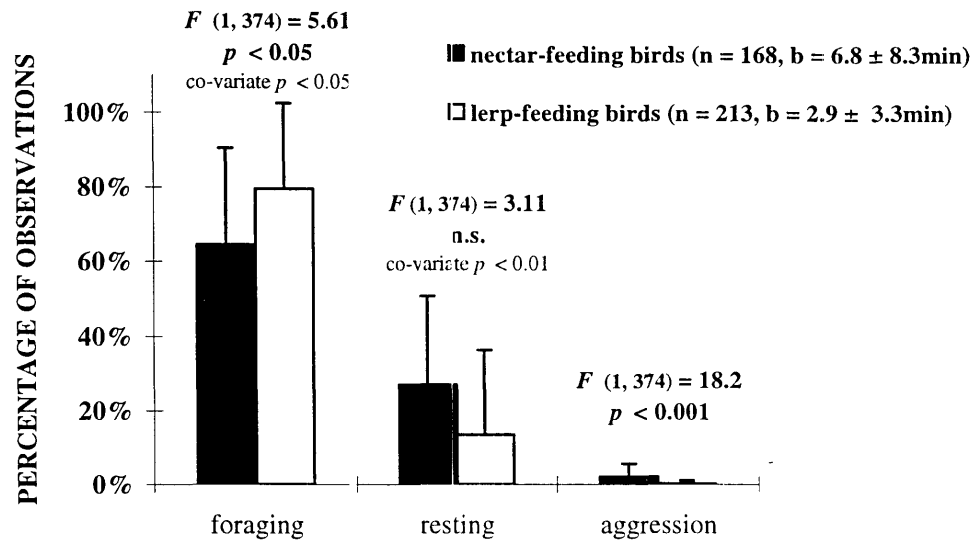


Figure 4.8 Dietary comparisons of the proportion of observation time spent foraging, resting, and in aggressive activities (+ s.d.), by non-breeding Regent Honeyeaters in the Bundarra-Barraba region in 1995, using two-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

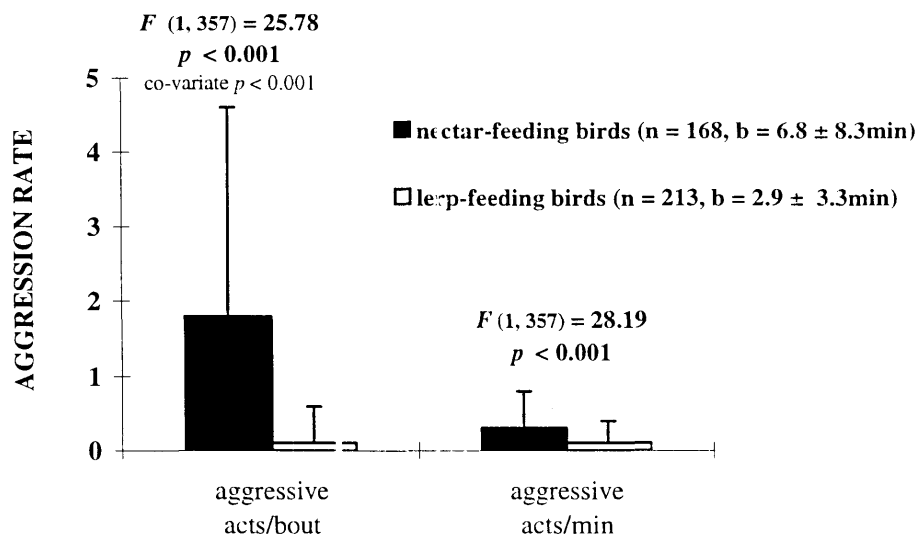


Figure 4.9 Dietary comparisons of aggression rates per observation bout, and per minute (+ s.d.), of non-breeding Regent Honeyeaters in the Bundarra-Barraba region in 1995, using two-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

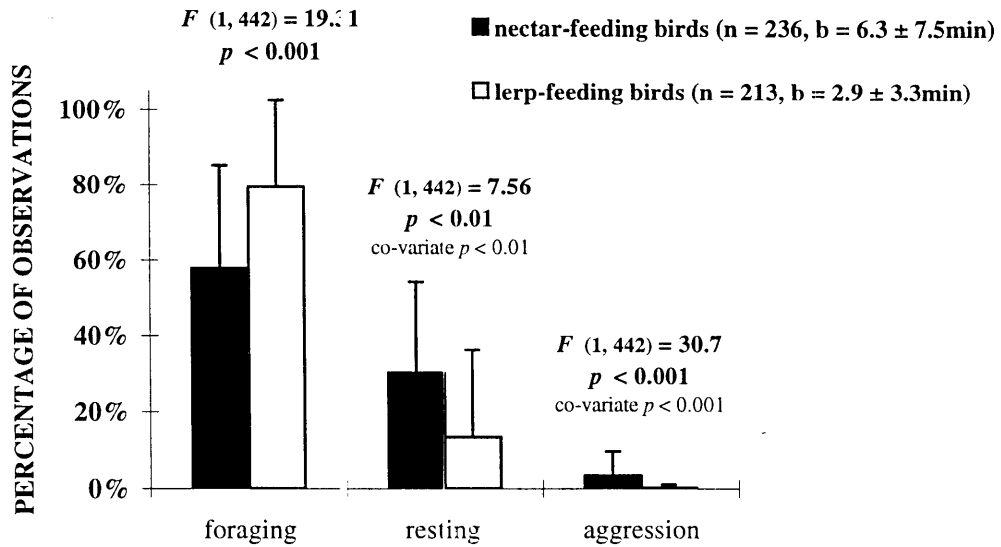


Figure 4.10 Dietary comparisons of the proportion of observation time spent in foraging, resting, and aggressive activities (+ s.d.), by non-breeding Regent Honeyeaters in the Bundarra-Barraba region (data pooled from 1995 and 1996), using two-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

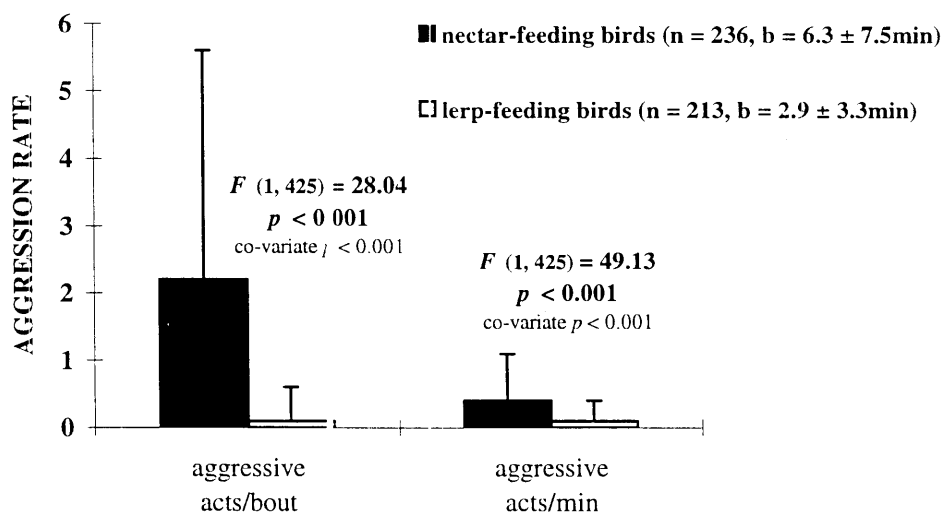


Figure 4.11 Dietary comparisons of aggression rates per observation bout, and per minute (+ s.d.), of non-breeding Regent Honeyeaters in the Bundarra-Barraba region (data pooled from 1995 and 1996), using two-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

Table 4.3 Dietary behavioural comparison of the proportion of time spent in foraging, resting, and aggressive activities, by breeding female Regent Honeyeaters in the Bundarra-Barraba region in 1995, using two-way ANCOVAs.

Behaviour (mean \pm s.d.)	nectar (n = 4)	lerp (n = 3)	d.f.	MS	F	p	co-variate
% foraging	24.0 \pm 10.2	21.3 \pm 10.9	1, 14	0.00	3.01	n.s.	n.s.
% resting	4.7 \pm 6.5	10.7 \pm 13.3	1, 14	0.02	3.81	n.s.	n.s.
% aggression	1.1 \pm 2.1	0.5 \pm 1.2	1, 14	0.00	2.22	n.s.	n.s.
aggressive acts/obs. bout	1.0 \pm 1.4	0.6 \pm 1.1	1, 14	1.39	3.05	n.s.	n.s.
aggressive acts/minute	0.4 \pm 0.6	0.2 \pm 0.5	1, 14	0.28	7.51	*	n.s.
observation duration (m)	3.3 \pm 1.9	4.5 \pm 7.7	-	-	-	-	-

Table 4.4 Dietary behavioural comparison of the proportion of time spent in foraging, resting and aggressive activities by breeding male Regent Honeyeaters in the Bundarra-Barraba region in 1995, using two-way ANCOVAs.

Behaviour (mean \pm s.d.)	nectar (n = 6)	lerp (n = 2)	d.f.	MS	F	p	co-variate
% foraging	43.8 \pm 17.3	43.5 \pm 19.8	1, 12	0.07	2.95	n.s.	n.s.
% resting	38.7 \pm 20.7	27.7 \pm 20.9	1, 12	0.121	2.88	n.s.	n.s.
% aggression	3.4 \pm 3.6	2.8 \pm 4.2	1, 12	0.000	0.74	n.s.	n.s.
aggressive acts/obs. bout	9.5 \pm 13.3	2.2 \pm 2.9	1, 12	1.70	1.56	n.s.	n.s.
aggressive acts/minute	0.4 \pm 0.4	0.2 \pm 0.3	1, 12	0.065	1.80	n.s.	n.s.
observation duration (m)	20.9 \pm 17.2	12.4 \pm 14.5	-	-	-	-	-

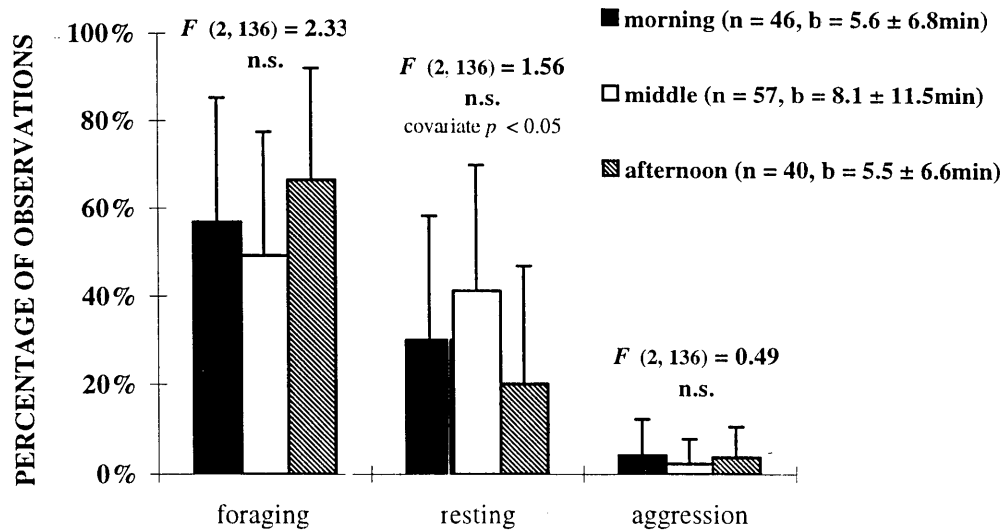


Figure 4.12 Diurnal comparisons of the percentage of observation time spent in foraging, resting and aggressive activities (+ s.d.), by non-breeding Regent Honeyeaters at the Warrumbungle National Park, using two-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

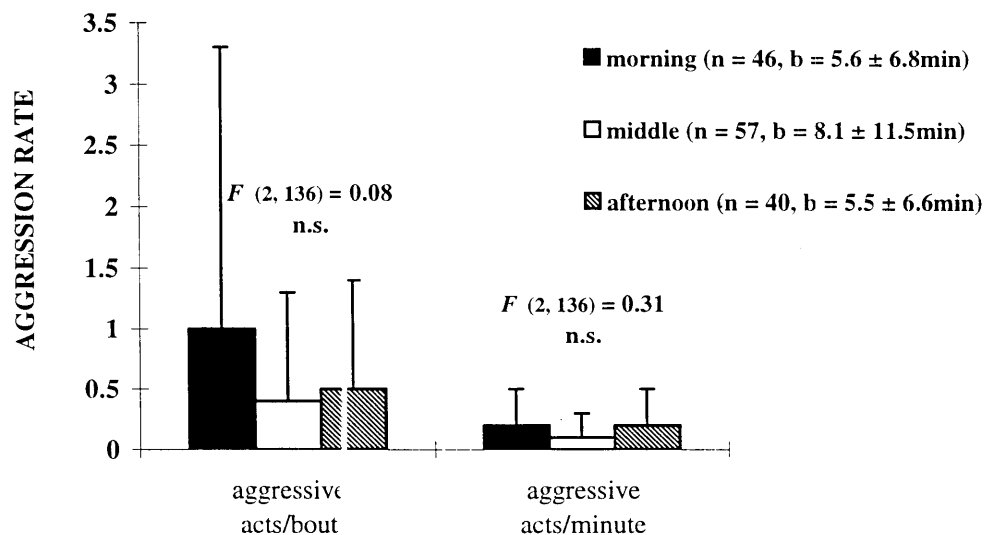


Figure 4.13 Diurnal comparisons of aggression rates per observation bout, and per minute (+ s.d.), of non-breeding Regent Honeyeaters at the Warrumbungle National Park, using two-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

than the other two periods (Figure 4.14). Aggression was highest in the morning and lowest in the afternoon, and the difference between the three daytime periods was significant for all three measurements of aggression level (Figure 4.14). The proportion of time spent in aggression (Figure 4.14), and the rate of aggressive acts per minute (Figure 4.15), were much higher in the morning than the middle, and afternoon periods. The number of aggressive interactions per observation bout, however, was similar in the morning and afternoon periods, and significantly lower in the middle period, but this was strongly influenced by the length of observation bouts (Figure 4.15).

Bundarra-Barraba region

Non-breeding birds

In 1995, Regent Honeyeaters spent a similar amount of time foraging and fighting throughout the three daytime periods (Table 4.5). However, there was a diurnal difference in the amount of time spent resting (Table 4.5). Resting was highest in the middle part of the day and lowest in the morning, though there were no significant pairwise differences between the daytime periods using a Bonferroni test. In 1996, birds fed and rested for a similar amount of time throughout the day, but there was a diurnal difference in aggression level (Table 4.5). In particular, they spent a significantly higher proportion of time in aggression, and performed a greater number of aggressive acts per observation bout in the morning than in the afternoon (both $p < 0.05$ using Bonferroni pairwise comparisons). When data were pooled for the two years, the amount of time spent foraging was similar in all three daytime periods, but there was a significant difference in proportion of time spent resting, and in proportion of time in aggression (Figure 4.16). Resting was lowest in the morning and highest in the middle of the day, though there were no significant pairwise differences between daytime periods using Bonferroni tests. The highest proportion of time spent fighting was in the morning, and lowest in the middle of the day. Time spent in aggression was significantly higher in the morning than the middle part of the day (Bonferroni pairwise comparison $p < 0.01$), but was similar in the afternoon to the other two periods. The aggression rate per observation bout, and per minute, did not differ significantly throughout the day (Figure 4.17)

Breeding birds

Breeding female (Table 4.6) and male (Table 4.7) Regent Honeyeaters spent similar amounts of time feeding, resting and in aggression throughout the day in both 1995 and 1996.

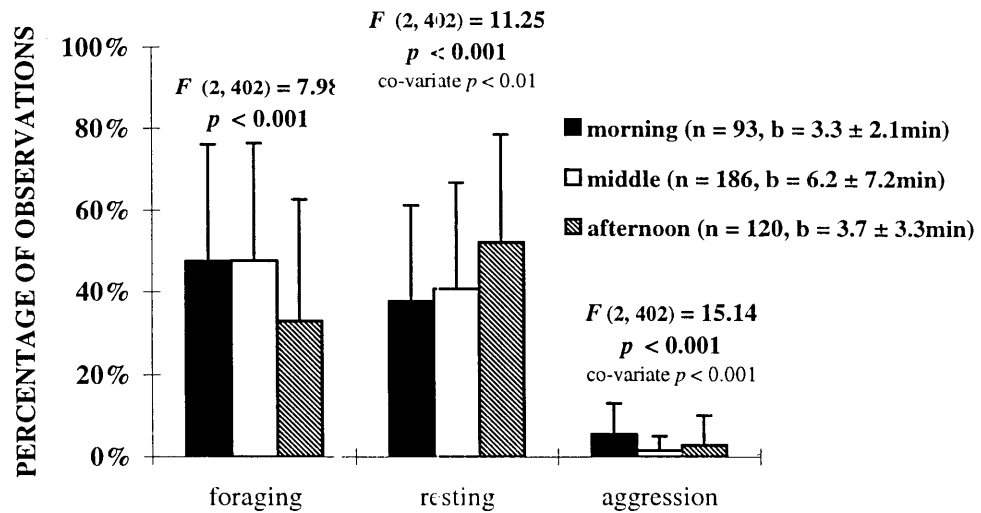


Figure 4.14 Diurnal comparisons of the percentage of observation time spent in foraging, resting and aggressive activities (+ s.d.), by non-breeding Regent Honeyeaters at Howes Valley, using one-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

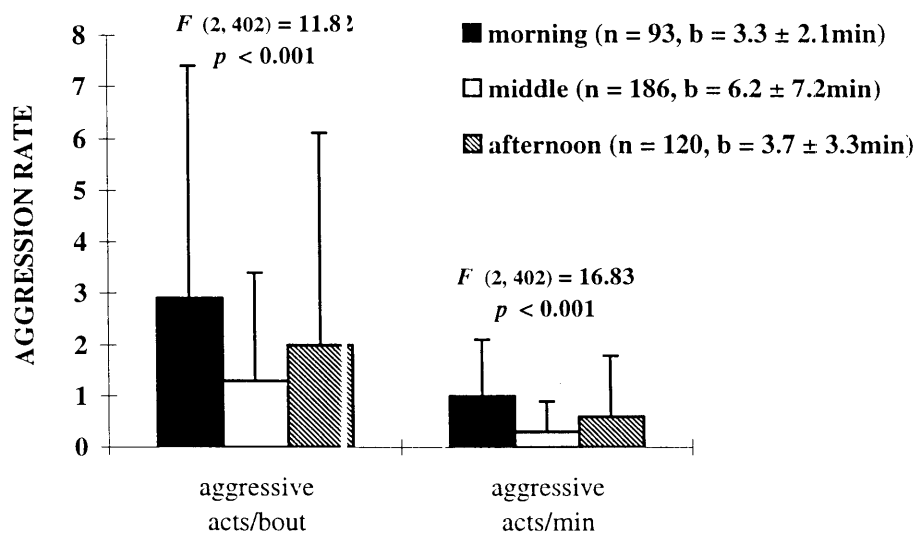


Figure 4.15 Diurnal comparisons of aggression rates per observation bout, and per minute (+ s.d.), of non-breeding Regent Honeyeaters at Howes Valley, using one-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

Table 4.5 Diurnal behavioural comparisons of the percentage of observation time spent in foraging, resting, and aggressive activities, by non-breeding Regent Honeyeaters in the Bundarra-Barraba region in 1995 (two-way ANCOVAs), and 1996 (one-way ANCOVAs).

Behaviour (mean \pm s.d.)	morning (n = 31)	middle (n = 279)	afternoon (n = 71)	d.f.	MS	F	p	co- variate
1995								
% foraging	76.8 \pm 18.2	72.2 \pm 27.2	74.4 \pm 20.2	2, 374	0.165	1.39	n.s.	*
% resting	14.9 \pm 19.7	20.5 \pm 26.1	17.2 \pm 17.3	2, 374	0.229	3.41	*	**
% aggression	0.6 \pm 1.3	0.6 \pm 1.6	3.0 \pm 4.2	2, 374	0.000	0.88	n.s.	n.s.
aggressive acts/obs. bout	1.7 \pm 3.1	0.6 \pm 1.7	1.4 \pm 2.3	2, 357	0.197	0.48	n.s.	***
aggressive acts/minute	0.13 \pm 0.27	0.14 \pm 0.37	0.31 \pm 0.51	2, 357	0.013	0.11	n.s.	n.s.
observation duration	8.94 \pm 13.26	4.05 \pm 5.38	4.91 \pm 4.17	-	-	-	-	-
1996	morning (n = 13)	middle (n = 50)	afternoon (n = 5)					
% foraging	42.0 \pm 22.6	35.6 \pm 24.3	53.8 \pm 7.4	2, 64	0.05	0.71	n.s.	n.s.
% resting	31.7 \pm 15.0	40.8 \pm 24.4	31.8 \pm 14.6	2, 64	0.085	1.20	n.s.	n.s.
% aggression	13.1 \pm 13.8	5.3 \pm 8.5	3.3 \pm 3.8	2, 64	0.038	4.15	*	n.s.
aggressive acts/obs. bout	5.7 \pm 7.2	2.6 \pm 3.5	1.0 \pm 0.7	2, 64	2.83	3.83	*	***
aggressive acts/minute	1.2 \pm 1.1	0.7 \pm 0.9	0.6 \pm 0.6	2, 64	0.64	2.42	n.s.	n.s.
observation duration (m)	5.3 \pm 6.1	4.8 \pm 4.8	4.4 \pm 3.8	-	-	-	-	-

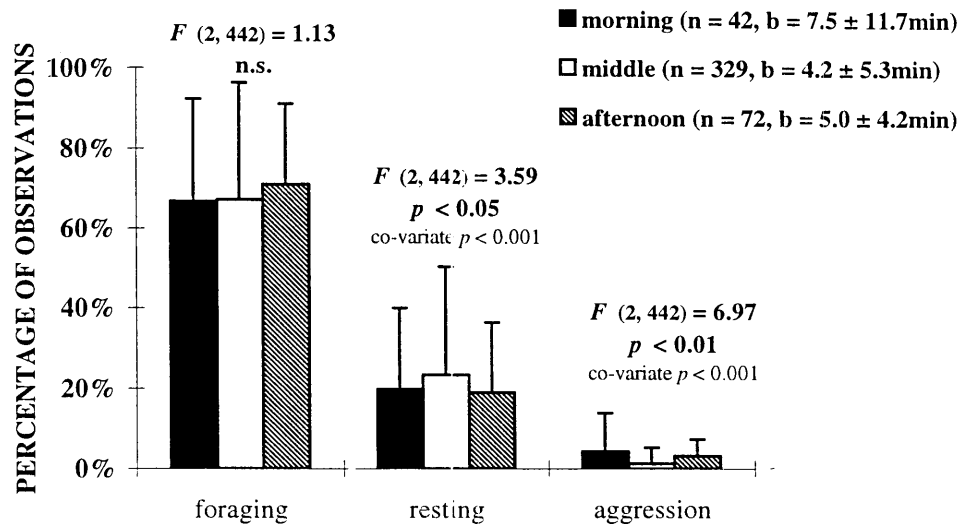


Figure 4.16 Diurnal comparisons of the percentage of observation time spent in foraging, resting and aggressive activities (+ s.d.), by non-breeding Regent Honeyeaters in the Bundarra-Barraba region (data pooled from 1995 and 1996), using two-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

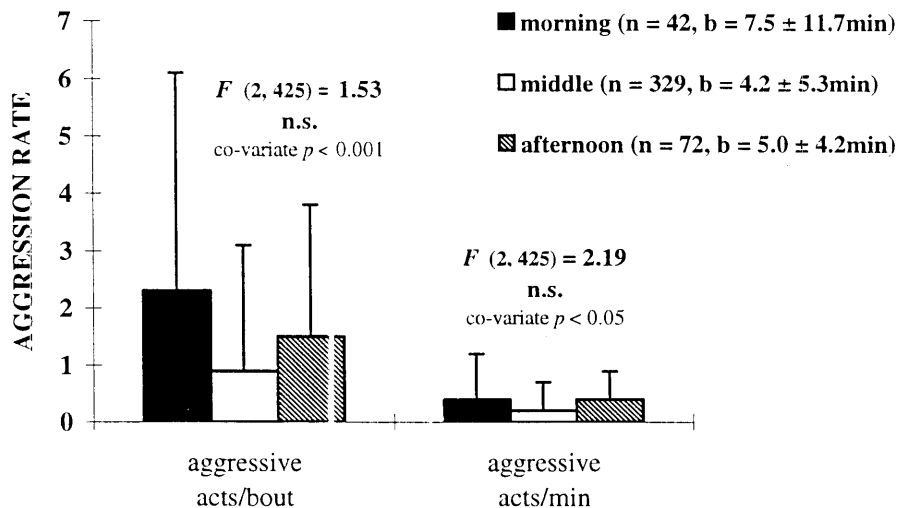


Figure 4.17 Diurnal comparisons of the aggression rates per observation bout, and per minute (+ s.d.), of non-breeding Regent Honeyeaters in the Bundarra-Barraba region (data pooled from 1995 and 1996), using two-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

Table 4.6 Diurnal behavioural comparisons of the proportion of observation time spent in foraging, resting, and aggressive activities, by breeding female Regent Honeyeaters in the Bundarra-Barraba region in 1995 (two-way ANCOVAs), and 1996 (one-way ANCOVAs).

Behaviour (mean \pm s.d.)	morning (n = 7)	middle (n = 7)	afternoon (n = 7)	d.f.	MS	F	p	co- variate
1995								
% foraging	22.2 \pm 12.3	23.6 \pm 11.0	21.8 \pm 9.0	2, 14	0.001	1.17	n.s.	n.s.
% resting	8.9 \pm 11.3	7.5 \pm 11.4	6.3 \pm 8.1	2, 14	0.001	0.09	n.s.	n.s.
% aggression	1.3 \pm 2.3	0.7 \pm 1.7	0.9 \pm 1.7	2, 14	0.000	1.05	n.s.	n.s.
aggressive acts/obs. bout	1.3 \pm 2.1	0.8 \pm 1.1	0.8 \pm 1.0	2, 14	0.402	0.88	n.s.	n.s.
aggressive acts/minute	0.4 \pm 0.7	0.3 \pm 0.5	0.32 \pm 0.58	2, 14	0.022	0.57	n.s.	n.s.
observation duration (m)	4.6 \pm 8.3	3.9 \pm 5.2	3.4 \pm 3.3	-	-	-	-	-
1996	morning (n = 2)	middle (n = 3)	afternoon (n = 2)					
% foraging	16.7 \pm 12.6	31.3 \pm 17.9	28.1 \pm 14.9	2, 3	0.006	0.26	n.s.	n.s.
% resting	12.5 \pm 6.2	28.3 \pm 18.7	19.9 \pm 19.9	2, 3	0.021	4.12	n.s.	*
% aggression	1.1 \pm 1.1	1.9 \pm 3.8	0.9 \pm 1.5	2, 3	0.000	4.54	n.s.	*
aggressive acts/obs. bout	2.9 \pm 2.9	2.7 \pm 3.1	3.7 \pm 6.5	2, 3	0.216	0.8	n.s.	*
aggressive acts/minute	0.2 \pm 0.2	0.3 \pm 0.5	0.2 \pm 0.3	2, 3	0.029	1.02	n.s.	*
observation duration (m)	15.6 \pm 11.5	11.3 \pm 9.5	10.7 \pm 13.2	-	-	-	-	-

Table 4.7 Diurnal behavioural comparisons of the percentage of observation time spent in foraging, resting, and aggressive activities, by breeding male Regent Honeyeaters in the Bundarra-Barraba region in 1995 (two-way ANCOVAs), and 1996 (one-way ANCOVAs).

Behaviour (mean \pm s.d.)	morning (n = 5)	middle (n = 8)	afternoon (n = 6)	d.f.	MS	F	p	co- variate
1995								
% foraging	33.4 \pm 12.6	45.5 \pm 19.5	48.0 \pm 14.0	2, 12	0.024	1.01	n.s.	n.s.
% resting	48.0 \pm 15.4	36.2 \pm 22.8	30.9 \pm 18.4	2, 12	0.002	0.05	n.s.	n.s.
% aggression	5.7 \pm 3.9	2.6 \pm 3.1	2.9 \pm 3.9	2, 12	0.000	0.17	n.s.	n.s.
aggressive acts/obs. bout	18.5 \pm 21.5	5.8 \pm 7.1	6.1 \pm 7.3	2, 12	0.067	0.06	n.s.	n.s.
aggressive acts/minute	0.7 \pm 0.4	0.3 \pm 0.3	0.3 \pm 0.3	2, 12	0.006	0.17	n.s.	n.s.
observation duration (m)	24.7 \pm 20.8	18.9 \pm 16.9	17.3 \pm 13.7	-	-	-	-	-
1996	morning (n = 3)	middle (n = 3)	afternoon (n = 1)					
% foraging	30.5 \pm 20.0	34.4 \pm 24.4	21.0 \pm 0.0	2, 3	0.015	2.00	n.s.	n.s.
% resting	55.4 \pm 21.4	51.3 \pm 26.3	64.3 \pm 0.0	2, 3	0.015	1.70	n.s.	n.s.
% aggression	3.6 \pm 3.1	4.9 \pm 3.3	3.8 \pm 0.0	2, 3	0.000	0.02	n.s.	n.s.
aggressive acts/obs. bout	9.9 \pm 13.2	7.3 \pm 7.4	4.0 \pm 0.0	2, 3	0.005	0.01	n.s.	**
aggressive acts/minute	0.5 \pm 0.4	0.7 \pm 0.5	0.6 \pm 0.0	2, 3	0.004	0.16	n.s.	n.s.
observation duration (m)	17.6 \pm 13.5	12.4 \pm 12.6	6.5 \pm 0.0	-	-	-	-	-

4.4.4 Inter-year differences in behaviour

Bundarra-Barraba region

Non-breeding Regent Honeyeaters spent significantly more time foraging, less time resting, and less time in aggression in 1995, than in 1996 (Figure 4.18). There were no inter-year differences in the proportion of time that breeding females spent in these activities (Table 4.8). Breeding males however, spent more time feeding (Figure 4.19), and were involved in fewer aggressive interactions per minute (Figure 4.20) in 1995, than 1996. There was no annual differences in amount of time breeding males spent in resting and aggression (Figure 4.19), nor the number of aggressive acts per observation bout (Figure 4.20).

4.4.5 Aggressive behaviour of breeding and non-breeding Regent Honeyeaters

Non-breeding birds

Non-breeding Regent Honeyeaters from all three study areas were involved in aggressive acts, on average, 16 times per hour (Table 4.9). A total of 1,309 interactions were recorded between Regent Honeyeaters and 16 other bird species (Figure 4.21). Sixty-one percent of aggressive acts comprised Regent Honeyeaters chasing other birds ($n = 800$), and the other 39% involved Regent Honeyeaters being chased by other birds ($n = 509$). Non-breeding Regent Honeyeaters primarily interacted with conspecifics (67.5% of all interactions) (Figure 4.21). Over 94% of aggressive acts recorded were between Regent Honeyeaters and birds of similar size or smaller. Fuscous Honeyeaters (16.4%), White-plumbed Honeyeaters *Lichenostomus penicillatus* (1.1%), Noisy Miners (1.6%) and Musk Lorikeets (1.0%) were the species most often involved in aggression with Regent Honeyeaters.

Comparisons between breeding, and non-breeding birds

The proportion of time spent in, and the rate of, aggression by breeding and non-breeding Regent Honeyeaters was higher in 1996, than 1995, in the Bundarra-Barraba region (Figures 4.22, 4.23, 4.24), although I could not test this statistically. Non-breeding birds in the region spent an average of 1.9% of time in aggression, and made 12.5 aggressive manoeuvres per hour. In comparison, breeding birds spent an average of 1.7% of time in aggression, with an aggression rate of about 20 acts per hour. A detailed description of aggressive behaviour of breeding birds close to the nest is presented in Chapter 7 (Tables 7.5, 7.6 and 7.7). Non-breeding birds spent significantly more time fighting (6.7%), than breeders (2.5%) in 1996 (Figure 4.22). However, there were no differences

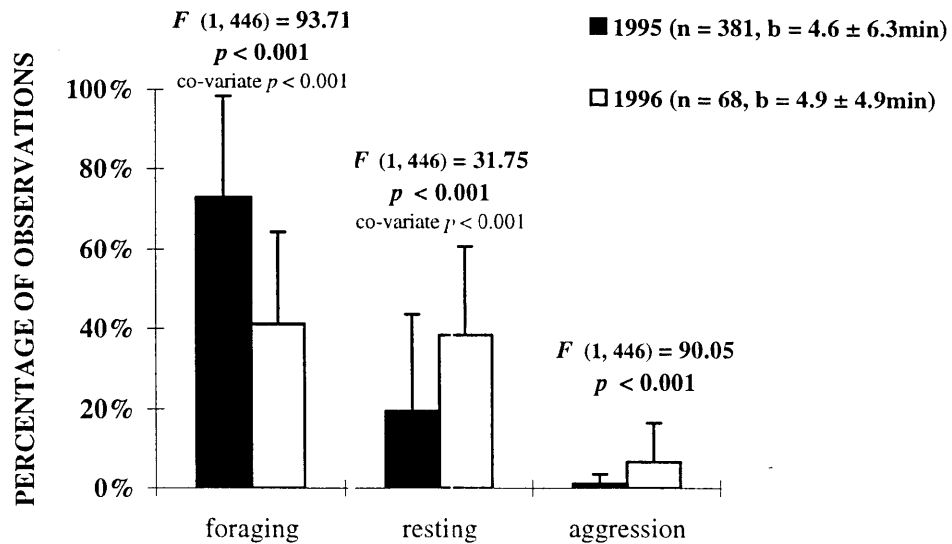


Figure 4.18 Inter-year comparisons of the percentage of observation time spent in foraging, resting, and aggressive activities by non-breeding Regent Honeyeaters in the Bundarra-Barraba region in 1995 and 1996, using one-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

Table 4.8 Inter-year behavioural comparisons of the percentage of observation time spent in foraging, resting, and aggressive activities, by breeding female Regent Honeyeaters in the Bundarra-Barraba region in 1995 and 1996, using one-way ANCOVAs.

Behaviour (mean \pm s.d.)	1995 (n = 7)	1996 (n = 3)	d.f.	MS	F	p	co-variate
% foraging	22.8 \pm 10.6	28.5 \pm 17.1	1, 25	0.002	0.49	n.s.	n.s.
% resting	7.3 \pm 10.4	24.1 \pm 18.6	1, 25	0.013	1.78	n.s.	*
% aggression	0.9 \pm 1.8	1.6 \pm 3.1	1, 25	0.000	0.14	n.s.	*
aggressive acts/obs. bout	0.9 \pm 1.3	2.9 \pm 4.0	1, 25	0.268	0.55	n.s.	**
aggressive acts/minute	0.3 \pm 0.6	0.3 \pm 0.4	1, 25	0.101	2.20	n.s.	n.s.
observation duration (m)	3.8 \pm 5.3	11.3 \pm 10.7	-	-	-	-	-

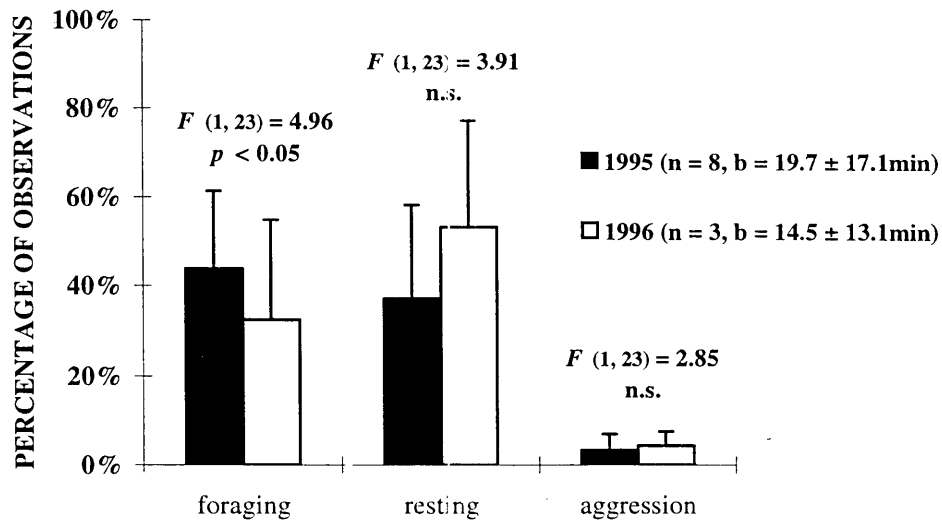


Figure 4.19 Inter-year comparisons of the proportion of observation time spent in foraging, resting, and aggressive activities, by breeding male Regent Honeyeaters in the Bundarra-Barraba region in 1995 and 1996, using one-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

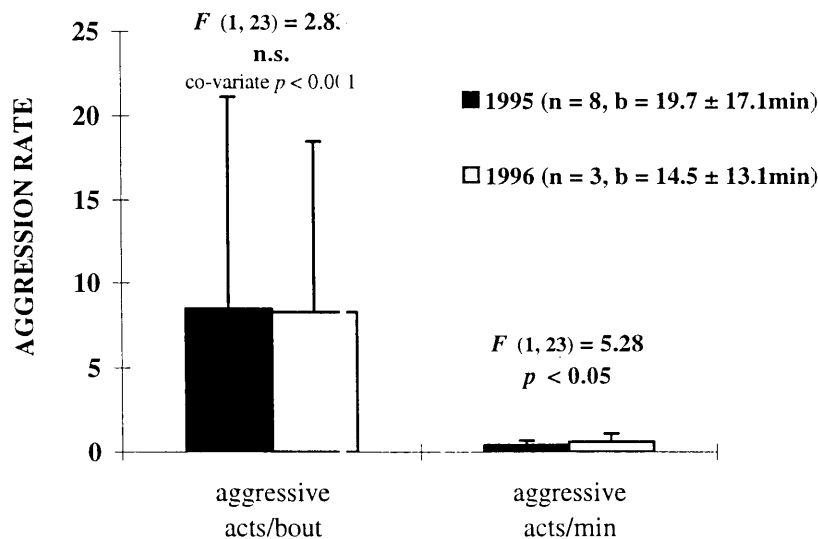


Figure 4.20 Inter-year comparisons of aggression rates per observation bout, and per minute (\pm s.d.), of breeding male Regent Honeyeaters in the Bundarra-Barraba region in 1995 and 1996, using one-way ANCOVAs. (n = number of observation bouts, b = average observation bout length (\pm s.d.)).

Table 4.9 Hourly rate of aggressive interactions, and percentage of observation time spent in aggression, by non-breeding Regent Honeyeaters (RHEs) in northern New South Wales (number of aggressive interactions in parentheses).

Location	Date	Hourly rate of RHEs chasing other birds	Hourly rate of birds chasing RHEs	Hourly rate of aggressive interactions	% total time in aggressive interactions
Warrumbungle N.P.	6,7/94	4.2 (63)	1.7 (25)	5.9 (88)	2.4%
Howes Valley	8/94	18.3 (422)	13.0 (298)	31.3 (720)	3.3%
“ “	10/94	2.8 (15)	4.3 (23)	7.2 (38)	1.1%
“ “	12/94	5.2 (20)	3.4 (13)	8.6 (33)	1.6%
Bundarra-Barraba	1/95	12.6 (51)	0.2 (1)	12.8 (52)	0.9%
“ “	3/95	4.5 (16)	3.4 (12)	7.9 (28)	1.0%
“ “	4/95	0.6 (6)	1.3 (13)	1.8 (19)	0.2%
“ “	7/95	3.3 (71)	3.6 (31)	11.9 (102)	3.1%
“ “	7/95	13.8 (33)	25.5 (61)	39.3 (94)	3.1%
“ “	7/96	18.6 (103)	5.8 (32)	24.3 (135)	6.7%
overall	-	9.8 (800)	6.2 (509)	16.1 (1309)	-

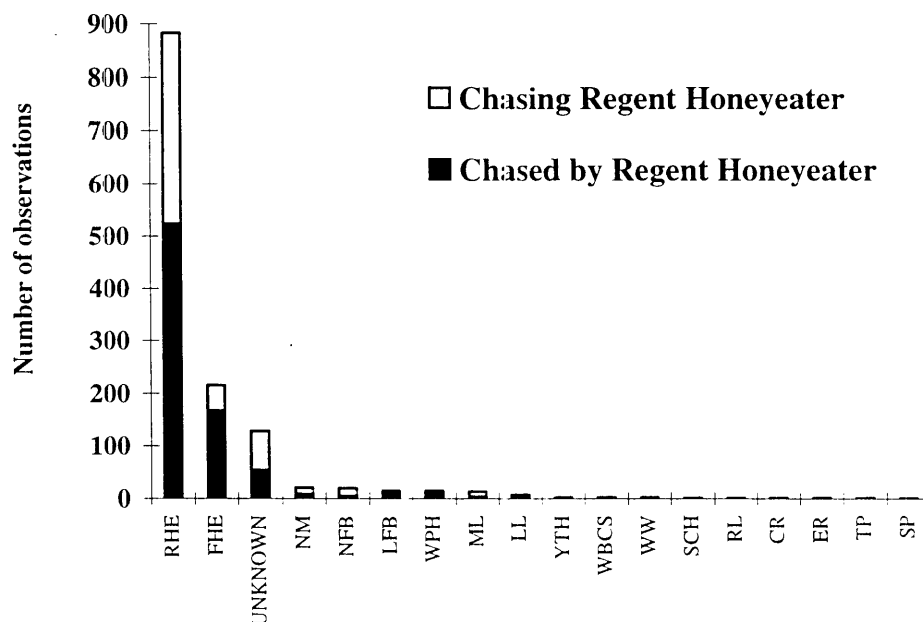


Figure 4.21 Number of aggressive interactions observed between focal non-breeding Regent Honeyeaters and other birds in northern New South Wales.
 [RHE: Regent Honeyeater (31-50 g); FHE: Fuscous Honeyeater (10-18 g); NM: Noisy Miner (70-80 g); NFB: Noisy Friarbird (75-95 g); LFB: Little Friarbird (60-80 g); WPH: White-plumed Honeyeater (14-20 g); ML: Musk Lorikeet (52-66 g); LL: Little Lorikeet (37.5 g); YTH: Yellow-tufted Honeyeater (20-24 g); WBCS: White-bellied Cuckoo-shrike (67 g); WW: Willy Wagtail (19 g); SCH: Spiny-cheeked Honeyeater (52 g); RL: Rainbow Lorikeet (139 g); CR: Crimson Rosella (129 g); ER: Eastern Rosella (104 g); TP: Turquoise Parrot (40 g); SP: Striated Pardalote (11 g).

in 1995, or when data were pooled for both years (Figure 4.22). In both years, separately, and combined, breeding birds were involved in significantly more aggressive acts per observation bout, than non-breeders (Figure 4.23). A similar trend emerged for aggressive acts per minute, although there was no difference when data were pooled for both years (Figure 4.24).

4.5 Discussion

Comparison of activity budgets of other honeyeaters

The behaviours of breeding and non-breeding Regent Honeyeaters observed in this study were similar to those of other honeyeaters, and other birds (Table 4.10 - references in table), although it is difficult to truly compare my results with other studies, because there is intraspecific variability from within and between other studies, as well as interspecific variability. It is also difficult to compare my results with most other honeyeater studies, with the exception of Paton's (1979, 1982), as they did not comparably measure the behaviours of both breeding and non-breeding birds.

My findings are similar, in some aspects, to previous small-scale behavioural studies on Regent Honeyeaters (Webster and Menkhorst 1992, Ford *et al.* 1993). Foraging time for birds in my study was similar to that of Ford *et al.* (1993), but higher than that of Webster and Menkhorst (1992). However, both previous studies did not measure the behaviours of both nesting and non-breeding individuals, which this study has achieved.

Regent Honeyeaters spent more time foraging than the average for honeyeaters in other studies (mean of $34.3 \pm 21.7\%$, $n = 28$, see Table 4.10). The amount of time Regent Honeyeaters spent feeding varied with resource availability, which was not properly measured in this, or many other honeyeater studies. However, the diurnal, seasonal and annual foraging variability of Regent Honeyeaters (25 - 90% of total time foraging) is similar to that found by Paton (1982) for New Holland Honeyeaters *Phylidonyris novaehollandiae* (33 - 90% foraging), and to that between different studies on the Red Wattlebird (6.3 - 71%) (McFarland 1986a, Paton 1980).

In this study, I regarded movement between resource patches (i.e., trees, mistletoes), and stationary searching for resources within a patch, as part of an individual's foraging effort. Resting was judged to be when a bird spent more than 10 seconds without obviously searching for food. It would appear that many previous honeyeater behavioural studies did not consider movements

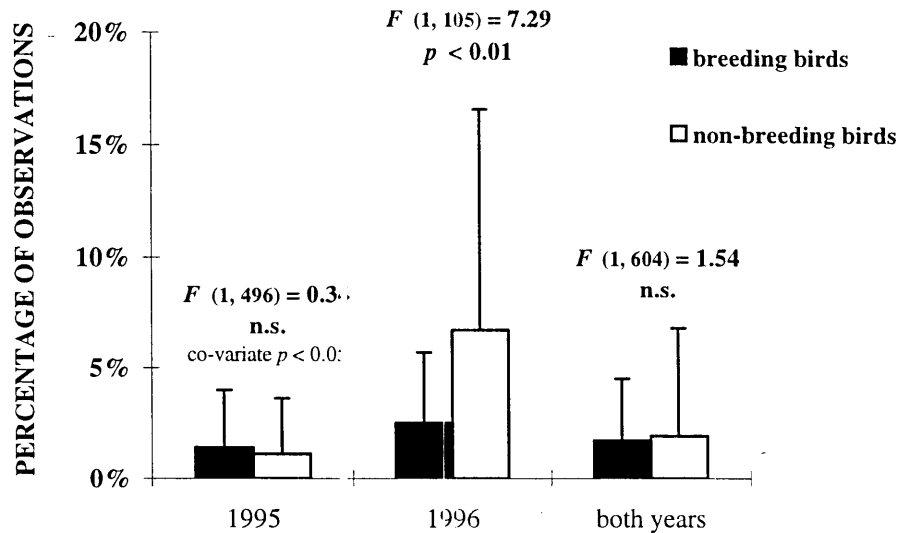


Figure 4.22 Comparisons of the proportion of time spent in aggression, between breeding and non-breeding Regent Honeyeaters in the Bundarra-Barraba region in 1995 and 1996, using one-way ANCOVAs. (1995: breeding birds: $n = 15$, $b = 7.7 \pm 11.6$ min; non-breeding birds: $n = 381$, $b = 4.6 \pm 6.3$ min; 1996: breeding birds: $n = 6$, $b = 11.5 \pm 11.2$ min; non-breeding birds: $n = 68$, $b = 4.9 \pm 4.9$ min; both years: breeding birds: $n = 21$, $b = 8.3 \pm 11.6$ min; non-breeding birds: $n = 449$, $b = 4.7 \pm 6.1$ min. (n = number of observation bouts, and b = average observation bout length (\pm s.d.)).

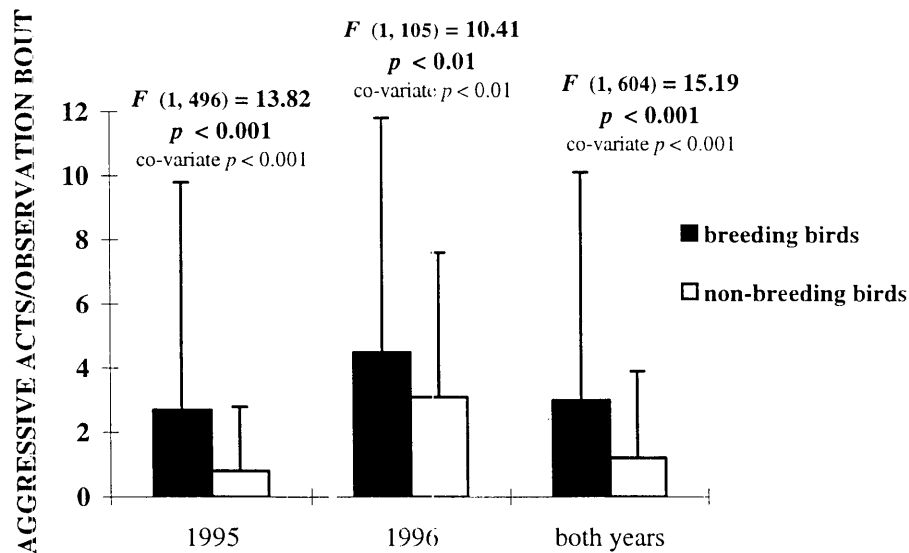


Figure 4.23 Comparisons of aggression rate per observation bout, between breeding and non-breeding Regent Honeyeaters in the Bundarra-Barraba region in 1995 and 1996, using one-way ANCOVAs. (1995: breeding birds: $n = 15$, $b = 7.7 \pm 11.6$ min; non-breeding birds: $n = 381$, $b = 4.6 \pm 6.3$ min; 1996: breeding birds: $n = 6$, $b = 11.5 \pm 11.2$ min; non-breeding birds: $n = 68$, $b = 4.9 \pm 4.9$ min; both years: breeding birds: $n = 21$, $b = 8.3 \pm 11.6$ min; non-breeding birds: $n = 449$, $b = 4.7 \pm 6.1$ min. (n = number of observation bouts, and b = average observation bout length (\pm s.d.)).

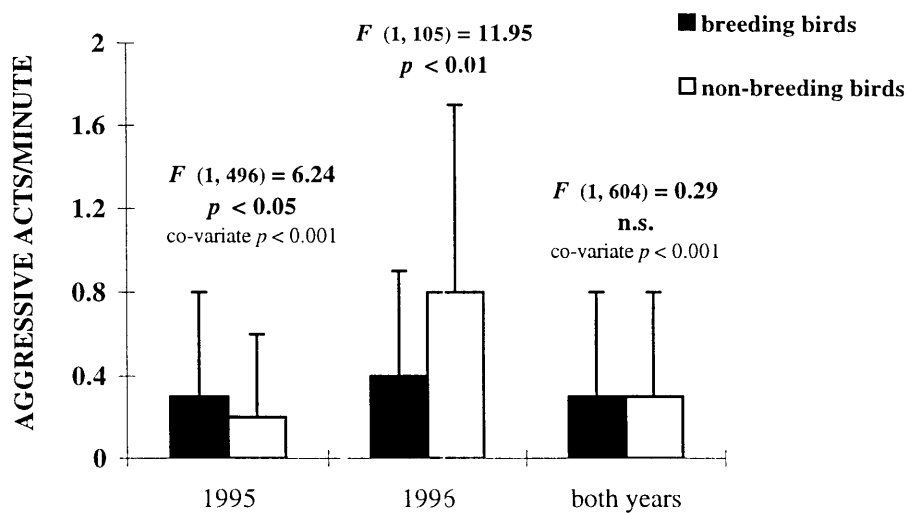


Figure 4.24 Comparisons of aggression rate per minute, between breeding and non-breeding Regent Honey eaters in the Bundarra-Barraba region in 1995 and 1996, using one-way ANCOVAs. (1995: breeding birds: $n = 15$, $b = 7.7 \pm 11.6$ min; non-breeding birds: $n = 381$, $b = 4.6 \pm 6.3$ min; 1996: breeding birds: $n = 6$, $b = 11.5 \pm 11.2$ min; non-breeding birds: $n = 68$, $b = 4.9 \pm 4.9$ min; both years: breeding birds: $n = 21$, $b = 8.3 \pm 11.6$ min; non-breeding birds: $n = 449$, $b = 4.7 \pm 6.1$ min. (n = number of observation bouts, and b = average observation bout length (\pm s.d.)).

Table 4.10 Activity budgets of Australian honeyeaters, insectivores, and selected non-Australian birds, taken from literature.

Species	foraging	resting	flying/other	aggression	Study by
Australian Honeyeaters					
Regent Honeyeater <i>Xanthomyza phrygia</i>	43.2%	22.7%	8.7%	1.8%	This study
"	20.4%	54.8%	4.2%	1.5%	Webster and Menkhorst 1992
"	38.5%	45.1%	12.7%	11.2%	Ford <i>et al.</i> 1993
Red Wattlebird <i>Anthochaera carunculata</i>	71%	-	-	-	Paton 1980
"	48%	50.8%	1.2%	-	Ford 1981
"	56.7%	-	-	-	Paton 1986a
"	6.3 - 34.3%	53.4 - 85.8%	7.9 - 12.3%	0.4 - 2.1%	McFarland 1986a
"	-	-	-	1.7%	Ford and Debus 1994
Little Wattlebird <i>Anthochaera chrysoptera</i>	8.5%	81.1%	10.4%	-	McFarland and Sale 1986
"	39.1 - 53.8%	-	-	-	Paton 1986a
Noisy Friarbird <i>Philemon corniculata</i>	-	-	-	1.8%	Ford and Debus 1994
Lewin's Honeyeater <i>Meliphaga lewinii</i>	5.6 - 11.8%	52.7 - 73.0%	8.7 - 11.0%	0.3 - 2.2%	McFarland 1986a
Yellow-faced Honeyeater <i>Lichenostomus chrysops</i>	10.6 - 17.8%	71.6 - 78.7%	10.6 - 10.7%	0.7 - 1.4%	"
Purple-gaped Honeyeater <i>Lichenostomus cratitius</i>	87.6%	-	-	-	Paton 1980
Helmeted Honeyeater <i>Lichenostomus melanops cassidix</i>	54.2%	18.7%	6.4%	20.7%	Woinarski and Wykes 1983
"	48.7%	31.9%	19.5%	-	Runciman 1996
Fuscous Honeyeater <i>Lichenostomus fuscus</i>	46 - 77%	-	-	-	Ford 1989
Brown Honeyeater <i>Lichmera indistincta</i>	34.1%	52.0%	13.9%	-	Collins <i>et al.</i> 1984
New Holland Honeyeater <i>Phylidonyris novaehollandiae</i>	32 - 90%	-	-	-	Paton 1982
"	6.6 - 37.9%	47.5 - 84.7%	8.7 - 14.6%	0.8 - 1.9%	McFarland 1986b
"	10.5%	75.8%	13.4%	-	McFarland and Sale 1986
"	11.5%	63.5%	18.5%	2.5%	Pyke 1989
"	10 - 40%	-	-	-	Armstrong 1991a
"	24.6%	73.1%	2.3%	-	Weathers <i>et al.</i> 1996
White-cheeked Honeyeater <i>Phylidonyris nigra</i>	35.9%	49.1%	15.0%	-	Collins <i>et al.</i> 1984
"	9.6%	83.7%	8.4%	0.6%	McFarland 1986a
"	10.5%	52.2%	18.0%	3.5%	Pyke 1989
"	10 - 40%	-	-	-	Armstrong 1991a
Eastern Spinebill <i>Acanthorhynchus tenuirostris</i>	7.7 - 65.2%	14.8 - 83.3%	9.1 - 20.0%	0.3 - 1.0%	McFarland 1986a
"	29.2%	68.7%	2.2%	-	Weathers <i>et al.</i> 1996
Scarlet Honeyeater <i>Myzomela sanguinolenta</i>	23.8%	66.6%	9.6%	0.8%	"
Australian Insectivorous Birds					
Brown Thornbill <i>Acanthiza pusilla</i>	88%	-	-	-	Haylock and Lill 1988
Eastern Yellow Robin <i>Eopsaltria australis</i>	12%	-	-	-	"
White-throated Treecreeper <i>Cormobates leucophaea</i>	92.4 - 97.6%	-	-	-	Stokes 1995
Red-browed Treecreeper <i>Climacteris erythroptis</i>	98.9%	-	-	-	"
Non-Australian Birds					
Long-billed Marshwren <i>Telmatodytes palustris</i>	4.0 - 74.0%	-	-	-	Verner 1965
Blue-throated Hummingbird <i>Lampornis clemenciae</i>	4.1 - 4.8%	64.4 - 82.3%	-	2.9 - 5.0%	Powers and McKee 1994
Dipper <i>Cinclus cinclus</i>	54%	43%	4%	-	Bryant and Tattner 1988
Spotted Sandpiper <i>Actitis macularia</i>	30.5 - 58.6%	6.1 - 20.4%	-	1.4 - 10.1%	Maxson and Oring 1980
Rifleman <i>Acanthisitta chloris</i>	82.5%	6.2%	9.4%	-	Lill 1991

Table 4.11 Aggression rates of Australian honeyeaters, taken from literature.

Species	Aggressive acts per hour	Study by
Regent Honeyeater <i>Xanthomyza phrygia</i>	12.5 - 16.0	This study
"	20	Franklin and Robinson 1989
"	10.6	Webster and Menkhorst 1992
"	32	Ford <i>et al.</i> 1993, Davis and Recher 1993
Red Wattlebird <i>Anthochaera carunculata</i>	37	Ford 1981
"	0.5 - 15	Ford and Debus 1994
Little Wattlebird <i>Anthochaera chrysoptera</i>	9.9	McFarland and Sale 1986
Noisy Friarbird <i>Philemon corniculatus</i>	1.2 - 17.7	Ford and Debus 1994
New Holland Honeyeater <i>Phylidonyris novaehollandiae</i>	2.2	Paton 1980
"	4.0	McFarland and Sale 1986
"	2.1	Armstrong 1991b
White-cheeked Honeyeater <i>Phylidonyris nigra</i>	2.1	"

between food sources, or searching for food while perching, to be part of the foraging effort of an individual, and hence may have underestimated the proportion of time spent gathering food.

Regent Honeyeaters at all three study sites met their energy demands in under 50% of their active time, with flying taking nine percent, aggression comprising less than two percent, and resting 23%. This allowed nearly 24% of their time for other behaviours, indicating that they were meeting their energy requirements sufficiently during both breeding seasons. However, resting may include important activities such as surveillance for predators and preening. Not all of it can be regarded as free time, which could be allocated to other behaviours. A major information gap of this study is the lack of behavioural data for post-breeding birds, which, typically, disappear for six months, soon after breeding. The birds observed in the autumn of 1995 spent nearly 80% of their time foraging, leaving little time for other activities, or the capacity to forage longer. It is possible that the Bundarra-Barraba Regent Honeyeaters are sometimes unable to satisfy their energy requirements in the coldest months, especially in dry years, when nectar may be scarce. Future research should focus on this period of time, if birds can be found. There is, however, no strong evidence that Regent Honeyeaters are decreasing in numbers due to difficulties in satisfying their energy requirements.

Effects of diet on behaviour

Behaviours varied significantly between Regent Honeyeaters eating different types of food. The type of food, itself, may have not been responsible for the difference in time spent on certain behaviours, but rather its abundance and energetic value. In some cases, there were obvious differences in the abundance of different food types. In the drought of 1994/95, lerp and honeydew were, typically, more abundant than nectar in all three study areas, whereas in 1996 nectar was the most abundant carbohydrate in the woodlands of the Bundarra-Barraba region.

In the Warrumbungle National Park, non-breeding Regent Honeyeaters spent a higher proportion of time foraging when eating nectar, than when they fed on lerp. Birds had access to a limited supply of nectar from a small grove (< 20 trees) of planted, non-endemic, Mugga Ironbarks, which attracted large numbers of nectarivores early in the morning. Most nectarivores, including Regent Honeyeaters, left the flowering Mugga Ironbarks within three hours of sunrise, indicating rapid depletion of nectar. The scarcity of, and high competition for, nectar would have severely increased the foraging effort need by Regent Honeyeaters to meet their energy demands. In

comparison, lerp and honeydew were distributed more evenly within the canopy of many tree species, over a much larger area, and were available throughout the day. Honeydew and lerp on the leaves of drought-stressed Rough-barked Apples *Angophora floribunda* provided four times more sugar, by mass, per leaf than the nectar in each Mugga Ironbark flower (Chapter 5). I do not know, however, whether honeydew and lerp yielded the same energy per unit weight as nectar, but Paton (1980) stated that all three carbohydrates were similar chemically. Lerp and honeydew would normally require more effort to gather than nectar, because they are usually more scattered in their distribution than nectar. The abundance of lerp and honeydew within trees in the Warrumbungle National Park, however made the gathering of these foods quite rapid.

A contrasting dietary pattern emerged for non-breeding birds in the Bundarra-Barraba region in 1995. Nectar-feeding birds foraged for less time than lerp-feeding birds. However, I did not quantitatively compare the energy value and abundance of flowering versus non-flowering sites, but I would suggest that it was higher at nectar sources, than lerp or manna sources.

There was no effect of diet or resource availability on the foraging effort of Howes Valley birds. The imbalance of behavioural data, which were mainly collected for lerp-feeding birds, may account for this. I would have expected nectar-feeding birds to spend more time foraging than lerp-feeding birds, based on my measurements of sugar, by mass, from the lerp and honeydew on the leaves of Rough-barked Apple, in comparison with the nectar from the flowers of Yellow Stringybark *E. muellerana*. There was over 200 times more sugar per leaf from lerp and honeydew than from the nectar in each flower (Chapter 5), but I couldn't quantify the energy value of the sugars in honeydew and lerp relative to nectar sugars, nor could I compare their abundance on a unit area basis.

Diet and resource availability also affected the aggressive behaviour of Regent Honeyeaters at the Warrumbungle National Park and Bundarra-Barraba region. In most cases nectar-feeding Regent Honeyeaters were involved in more aggression, than birds feeding on lerp, because they were trying to defend discrete nectar-rich patches (Pleasants and Zimmerman 1979), from other honeyeaters. In other words, the dispersion and availability of energy in a feeding territory influences the expression of resource-related defence (Wiens 1984). In contrast, it was uneconomical for Regent Honeyeaters to defend patchy resources such as lerp, honeydew and manna (Paton 1980). The

super-abundant lerp and honeydew at the Warrumbungle National Park and Howes Valley was probably not worth defending, as all birds were easily satisfying their daily energy requirements.

In this study, Regent Honeyeaters appeared to choose nectar feeding more often, because it required less time, than having to find enough lerp. The cost of nectar-feeding was higher aggression, although this was not excessive for a nectarivore. In return, nectar-feeding birds had 2-3% more time for other activities than lerp-feeders, in the breeding and non-breeding season, except for breeding males in 1995.

Diurnal variation in behaviour

In many cases, I found significant diurnal variation in the activities of Regent Honeyeaters. Other studies on the behaviour of birds have also shown diurnal differences in the proportion of time spent on certain actions (Verbeek 1964, Verner 1965, East 1982, Lill 1991). However, studies on the foraging behaviour of nectarivores have generally not found significant diurnal patterns in the amount of time spent foraging (Armstrong 1991a), although Powers and McKee (1994) did find that Blue-throated Hummingbirds *Lampornis clemenciae* spent more time away from their territories, presumably foraging elsewhere, in the afternoon when nectar was scarce. Paton (1979) found that the intake of energy was significantly higher in the morning than the afternoon for New Holland Honeyeaters, but he found no diurnal pattern in the proportion of time they spent collecting nectar from *Banksia marginata*.

At the Warrumbungle National Park, Regent Honeyeaters spent more time foraging in the morning than later in the day, and birds at Howes Valley tended to feed more in the morning and middle periods of the day than in the afternoon. This trend was also found by Lill (1991) in the foraging time of the Rifleman *Acanthisitta chloris*, and Maxson and Oring (1980) found that foraging activity was highest in the morning for the Spotted Sandpiper *Actitis macularia*, followed by a decrease in the middle part of the day with a slight increase towards the end of the day. Robbins (1981), too, found a similar diurnal behavioural pattern for a large number of bird species recorded in the North American Breeding Bird Survey. Garson and Hunter (1979) found that Wrens *Troglodytes troglodytes* and Great Tits *Parus major* sang less, and East (1982) noted that European Robins *Erithacus rubecula* fed more, in the morning, when temperatures were low. East postulated that lower invertebrate activity in low morning temperatures was the likely reason for European Robins spending more time foraging for their prey in the morning. Both Garson and

Hunter (1979) and East (1982) hypothesised that singing time was sacrificed in the morning for the need to feed after a cold night, where energy would have been expended in maintaining thermal homeostasis. It is possible that Regent Honeyeaters needed to feed more in the morning to restore their energy after roosting at temperatures as low as -10°C at the Warrumbungle National Park, and Howes Valley. The alternative strategy that Regent Honeyeaters could have taken to compensate for energy loss overnight was to forage extensively late in the afternoon, an approach taken by male Long-billed Marsh Wrens *Telmatodytes palustris* (Verner 1965), or use torpor.

The diurnal pattern of nectar-feeding by Regent Honeyeaters is different than the pattern for insect predation shown by insectivorous birds. However, Bundarra-Barraba birds exhibited a diurnal pattern for insect predation similar to that of insectivores, such as Brown Thornbills *Acanthiza pusilla*, which forage for insects significantly less at dawn and dusk, than other times of the day (Haylock and Lill 1988). Scarlet Robins *Petroica multicolor* spent most time ground foraging in the cold mornings, and most time aerial and bark foraging later in the when temperatures peaked (Ford *et al.* 1990), and American Redstarts *Setophaga ruticilla* spent more time hawking in the middle of the day than in the morning probably in response to a measured increase in arthropod abundance later in the day Holmes *et al.* (1978). Breeding Wheatears *Oenanthe oenanthe* hawked more, and gleaned less later in the day, and this was attributed to increased temperature (Moreno and Hillstrom 1992). This was supported by a previous study by Verbeek (1964) who found an inverse relationship between temperature and foraging time in Brewer Blackbirds *Euphagus cyanocephalus*.

Diurnal variation in aggression levels was observed for non-breeding Regent Honeyeaters at Howes Valley, and the Bundarra-Barraba region, with the highest levels of aggression in the morning, and the lowest in the middle of the day. This is, perhaps, due to a higher probability of encountering resource competitors early in the morning, when nectar resources are highest, or when the need to forage to replenish lost energy is greatest. At Howes Valley, aggression rates, but not time spent in aggression, rose late in the day, and this is possibly associated with the intra- and interspecific competition for roosting sites observed at dusk by Oliver (1998). Armstrong (1991b) did not find any differences in diurnal aggression level, but McFarland (1986a) found that aggression rate of five heathland honeyeater species changed according to the seasonal changes in nectar availability. Aggression was highest when nectar was moderately available, and lowest if nectar was high or scarce. Most honeyeaters reduce aggression when it becomes uneconomical to defend scarce or

super-abundant resources. When nectar is at moderate levels, larger honeyeaters can effectively defend foraging territories, while smaller energy-efficient species have to adopt secretive foraging strategies among poorer resource patches. Hawaiian Honeycreepers *Vestiaria coccinea* abandoned territory defence of their foraging patch when nectar was superabundant (Carpenter and MacMillen 1976) because it was inefficient to exclude intruders. It could be argued, then, that the typical pattern of diurnal nectar depletion (Pyke 1983, Paton 1985b, Armstrong 1991a, McFarland 1996) could also be responsible for a diurnal change in aggression of Regent Honeyeaters.

Inter-year variation in behaviour

There was significant variability between years for certain behaviours of breeding and non-breeding birds in the Bundarra-Barraba region. Few honeyeater studies have investigated or found annual variation in behaviour (Pyke 1989, Ford *et al.* 1990). Behavioural data collected in only one year, or pooled from different years, may not provide an accurate view of the flexible behaviour of the species in response to fluctuating environments (Petit *et al.* 1990). Only the general patterns of foraging ecology, and not the dynamics of those activities, will be determined (Petit *et al.* 1990). In future, it would be important to collect behavioural data of Regent Honeyeaters over different years, considering the high degree of annual variation within and between study areas.

In 1995, Regent Honeyeaters spent substantially more time foraging than in the following year, which may be attributed to differences in resource type and availability. A severe drought in 1994, and up to September 1995, suppressed the flowering of most eucalypts in the region. Nectar was scarce, and other carbohydrates such as lerp and manna were mainly eaten. Although the abundance and energy levels per unit area of these alternative carbohydrates were not measured, they are likely to have been lower, than when Mugga Ironbarks flowered prolifically. Hence, when nectar was scarce in the autumn and winter of 1995, Regent Honeyeaters foraged on lerp for up to 80% of their time, to satisfy their energy demands. There was good rain in the last few months of 1995, though flowering of eucalypts was delayed, and breeding birds primarily used lerp and insects instead of nectar at woodland breeding sites. The abundance and energy value of lerp was not measured, but was sufficiently abundant for birds to breed successfully in these sites. Other breeding birds in 1995 used riparian gallery forest along the Gwydir River as a breeding refuge. Here, they fed mainly on the nectar from Needle-leaf Mistletoes, which parasitise River Sheoaks. High nesting success and moderate foraging effort indicates that Regent Honeyeaters easily met their energy needs here, as well. The rains later in 1995, and throughout most of 1996, stimulated

flowering of woodland eucalypts in the Bundarra-Barraba region, and nectar was the food most often eaten by breeding and non-breeding birds in that year.

Breeding males spent more time foraging in 1995 than 1996, which suggests that energy was higher in the flowering woodlands of 1996, than the flowering riparian and non-flowering woodland breeding habitat of 1995. Nectar levels were higher at breeding sites in 1996 than 1995 on a per flower, and unit area basis (Chapter 5). Based on my estimations of numbers of flowers within a 0.25 hectare area within the riparian breeding site, a standing crop of 72.4 g of sugar or 1209 kJ per hectare was produced. In comparison Mugga Ironbarks in the 1996 woodland breeding site had nectar standing crops that were 5 to 10 times greater than mistletoe flowers (Chapter 5), and produced 127 g or 2120 kJ of sugar per hectare based on flower counts in a one-hectare transect. Other eucalypts, Yellow Box and Blakely's Red Gum *E. blakelyi*, were also flowering in the same area concurrently, and hence the total nectar abundance would have been higher still, but I have no measurements for these species.

Breeding male Regent Honeyeaters chased and fought other birds more frequently in 1995 than in 1996. The only explanation I can give is that males tended to make numerous, though brief, attacks on smaller birds in 1995, and made infrequent, but substantial attacks on Noisy Friarbirds in their feeding and nesting territories in 1996. In 1996, males may have avoided fighting with Noisy Friarbirds, to reduce the chance of their nests being detected, and then pirated, or predated. In 1995, however, there were very few large honeyeaters in close proximity to their nests, and Regent Honeyeaters frequently displaced smaller birds that approached the nest territory. Non-breeding birds fought more in 1996 compared to 1995, because high densities of large honeyeaters were attracted to sites that flowered in 1996, but not in 1995.

Aggressive behaviour

The levels of aggression shown by Regent Honeyeaters in this study were relatively low, compared to those recorded for two breeding pairs of Regent Honeyeaters by Davis and Recher (1993) and Ford *et al.* (1993). The best explanation I can give for the large discrepancy is that the two breeding pairs in these studies nested in heavily flowering Mugga Ironbarks, which attracted high densities of large aggressive nectarivores. The attack rates there were high, because the Regent Honeyeaters were not only defending their nests, but also their feeding territories. In contrast, breeding birds in both years of this study usually nested away from the main feeding tree(s), and

thus avoided the same problem faced by birds in the previous studies. Furthermore, H. Ford and B. Williams suggest that the flowering levels during the previous studies in 1989/90 were higher than in the 1995 and 1996 breeding season, and attracted a higher number of large honeyeaters. In this study, 1995 could be considered a “drought” year and 1996 a “recovery” year. “Boom” years, such as 1990, occur irregularly in many Australian ecosystems, including the woodlands of the Bundarra-Barraba region. It is possible that Regent Honeyeaters are not able to exploit fully the optimal conditions in these rare boom years, because they suffer high competition with larger honeyeaters such as that measured by Davis and Recher (1993).

The proportion of time Regent Honeyeaters spent in aggression, and the rates of attacks, in my study were similar to those measured for the species by Webster and Menkhorst (1992) (Table 4.10 and 4.11). A slightly higher attack rate than in this study was recorded for Regent Honeyeaters in Victoria by Franklin and Robinson (1989) (Table 4.11), who commented that the Regent Honeyeater is known to be an aggressive species. However, they are also known to co-exist amicably, at times, with other honeyeaters (Franklin *et al.* 1989). In the 1995 breeding season I observed Regent Honeyeaters nesting within the same, or neighbouring, tree to nesting Noisy Friarbirds, without any display of neighbour disputes, yet they frequently fought with Noisy Friarbirds in 1996.

The proportion of time Regent Honeyeaters spent fighting was similar to that of other honeyeaters (Table 4.11). However, the hourly rate of aggressive interactions of non-breeding Regent Honeyeaters was high, compared to some other species (Table 4.11), but lower than that of Noisy Friarbirds (17.7 attacks/hr) feeding on the nectar of a Silky Oak *Grevillea robusta* (Ford and Debus 1994). Most of the aggression recorded in my study was between conspecifics. If the species has declined, perhaps intra-specific aggression has decreased within smaller groups. Alternatively, if the species is now concentrated into just a few key sites, intra-specific aggression may have increased.

The high proportion of aggressive acts which involved Regent Honeyeaters displacing other birds, indicates that Regent Honeyeaters are able to defend their feeding and nesting territories, and are not being denied access to food. However, I have observed what might be a subtle form of resource exclusion, where Regent Honeyeaters forage in trees with lower flowering intensities than those used by larger honeyeaters such as Noisy Friarbirds. It seems that Regent Honeyeaters avoid

aggression with Noisy Friarbirds, by selecting trees with fewer flowers and low Noisy Friarbird densities.

Although non-breeding Regent Honeyeaters displayed a lower attack rate than breeders, they spent as much time fighting as breeders. The high aggression level measured for non-breeders in winter 1996 probably inflated the average for both years. I would have expected a greater time investment in aggression by breeding birds, relative to non-breeders, with the need to displace intruders from the nest territory. Based on the criteria for territoriality by Pyke *et al.* (1996), Regent Honeyeaters showed territorial behaviour around the nest and also at times in their breeding and non-breeding foraging habitat.

The rates of aggressive interactions in this chapter were measured within the feeding territory, rather than close to the nest (Chapter 7). The attack rate was twice as high within their feeding territory, than near their nest (Chapter 7). However, the proportion of time dedicated to aggression was similar in both situations, because the chases associated with nest defence, particularly between conspecifics, were often long, and sometimes involved a number of birds from neighbouring nests within a nesting aggregation. Aggressive interactions within the feeding territory were, however, of short duration.

Three times as many bird species were displaced by, or attacked Regent Honeyeaters in the breeding season (see Table 7.7, Chapter 7), than in the non-breeding season (Figure 4.4). Breeding birds are probably more likely to attack all avian intruders, nectarivorous or otherwise, which have the potential to affect nesting success through nest material kleptoparasitism (Ley *et al.* 1997), or egg and nestling predation. In contrast, non-breeding birds are unlikely to attack non-nectarivorous birds within their feeding territory. This hypothesis could be tested in future research on Regent Honeyeaters and other birds.

4.6 Conclusions

In certain years and locations, Regent Honeyeaters encounter low levels of food, which greatly elevates their time spent foraging. Conversely, when nectar levels are high, they spend a modest amount of time foraging, but are sometimes involved in relatively high aggression levels. Overall, my data indicate that Regent Honeyeaters are not consistently or frequently suffering from lack of, or problems with access, to food.

Regent Honeyeaters displays a behavioural repertoire, and proportion of time in different activities, that is typical of other honeyeaters. This repertoire appears to be adequate for their survival and reproduction. Like many other honeyeaters, they show flexibility in exploiting a range of resources (Chapter 5). The degree of dietary, diurnal, seasonal, and annual variability in behaviour is similar to other Australian birds, that also experience great environmental variability and unpredictability. Fluctuating environments, such as the woodlands of southeastern Australia, are likely to enhance a mixture of behavioural phenotypes in a population (Mangel 1991). Hence, many behavioural strategies are likely to be displayed in the Regent Honeyeater population.

Further research on Regent Honeyeater behaviour should focus on adult and juvenile birds in the six months after they leave their breeding sites. This may provide answers to whether Regent Honeyeaters are adequately meeting their energy requirements year-round, or whether there is a critical period of resource limitation that causes adult and juvenile mortality. Radio-telemetry studies to elucidate movements of post-breeding birds, will be carried out in the future to address this information gap (Menkhorst 1997). Secondly, measuring the abundance of nectar, lerp and insects at Regent Honeyeater foraging sites may explain some of the variability in their foraging behaviour.