

Activity patterns, habitat use, foraging behaviour and food selection of the Ouvéa Parakeet (*Eunymphicus cornutus uvaeensis*)

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Abstract. Habitat use, activity pattern, foraging behaviour and habitat selection of the Ouvéa Parakeet (*Eunymphicus cornutus uvaeensis*) were studied from July 1994 to December 1996 on the island of Ouvéa (New Caledonia, south-west Pacific), using line transects, quadrats, and radio-telemetry techniques. Home ranges of juveniles were small (mean 2.3 ha), and no dispersal from the natal area was observed up to nine weeks post-fledging. Parents spent 80% of their time during the breeding season within the home range of the juveniles and were seen near the nest site throughout the year. Parakeet densities on two study quadrats were higher (0.31 and 0.42 birds ha⁻¹) than the average density found in a previous transect census (0.22 ± 0.09 birds ha⁻¹). More than 20 plant species were foraged, seven of which represented 70% of the diet (31% for the single *Ficus* sp.). The phenology of the plants foraged on by the parakeet was marked by a long fruiting season, leading to a relative abundance of food throughout the year, especially during the breeding season. Observations on behaviour (time spent on foraging, absence of inter- or intra-specific competition for food) suggest that food is not a factor limiting the population size of the parakeets. The parakeet's habitat is tall forest, including Melanesian fields, where its distribution is remarkably patchy. The possibility of nest-site limitation is assessed in the context of the conservation of this endangered parakeet.

Introduction

Habitat loss has been identified as one of the main factors affecting the survival of the 1025 bird species currently threatened (Collar and Andrew 1988; Collar *et al.* 1994), especially forest and island birds (King 1985; Rands 1991). Parrots (Psittaciformes) have suffered particularly from habitat destruction, with no less than 90 (27%) of the world's 330 parrot species being threatened with extinction (IUCN 1996; Snyder *et al.* 2000). Since most parrot species live in tropical rain forests, are mainly sedentary fruit and/or seed-eaters, and require hollow trees for nesting, they have been greatly affected by the massive destruction of tropical forests throughout the world (Forshaw and Cooper 1989; Collar and Juniper 1992). Although parrot biology has been studied extensively in captivity, the basic ecology of most species in the wild remains very little known, especially with regard to foraging and feeding ecology (Forshaw and Cooper 1989). However, these aspects are critical, as food shortage can act globally by limiting the level of a population, and the reproductive success of a number of tropical birds have been found to be limited by food (e.g. Martin 1987; Thiollay 1991). In parrots, food has been recognised as a key factor in the reproductive success of the Kakapo (*Strigops habroptilus*) (Powlesland *et al.* 1992), the Kaka (*Nestor*

meridionalis) (Moorhouse 1991; Moorhouse *et al.* 1999), Black Cockatoos (*Calyptorhynchus* spp.) (Saunders 1986, 1991), Australian parrots of the genera *Neophema* and *Psephotus* (Forshaw and Cooper 1989) and the Bahama Parrot (*Amazona leucocephala bahamensis*) (Gnam 1991).

The endangered Ouvéa Parakeet (*Eunymphicus cornutus uvaeensis*) is endemic to New Caledonia, south-west Pacific. Its population, estimated at about 100–120 breeding pairs, and its range have decreased continuously since the beginning of the century, due to destruction of its habitat and captures for the pet trade (Macmillan 1939; Hannecart 1988; Robinet *et al.* 1995). It is now restricted mainly to the northern part of Ouvéa, where it inhabits patches of native forest. The species currently has a low reproductive rate, due to capture of nestlings by islanders combined with an apparently high mortality of fledglings caused by natural predation (Robinet *et al.* 1996; Robinet and Salas 1999). The long-term survival of the Ouvéa Parakeet depends on knowledge of the availability and quality of its habitat. Our aims were therefore to study the distribution, home range and foraging behaviour of the species with respect to habitat quality (availability of food and nest-site cavities) in order to identify potential limiting components of the population size of the Ouvéa Parakeet.

Material and Methods

Study area and species

The study was conducted in different parts of the north of Ouvéa Island (Fig. 1; see also Robinet *et al.* 1995, 1996 for complete descriptions) from July to December 1994, and from July 1995 to December 1996. We also used data collected during a line transect census in November and December 1993 (Robinet *et al.* 1996). Almost all Ouvéa Parakeets are restricted to the north of Ouvéa (4600 ha), separated from the rest of the island by a narrow isthmus (Fig. 1). Nine habitat classes have been recognised and described, that follow roughly a north-east-south-west succession, and include reef banks, tall, medium and low forests, recent and old Melanesian fields (i.e. small clearings in native forest), coconut plantations, domestic gardens and mangrove (see Robinet *et al.* 1996 and Fig. 1).

The Ouvéa Parakeet (body weight 130 g), living on Ouvéa Island, Loyalty Islands, with the Horned Parakeet (*Eunymphicus cornutus cornutus*), which lives on the main island of New Caledonia, constitute an endemic genus belonging to the Australasian platycercine group (Forshaw and Cooper 1989).

Radio-telemetry

Adult parakeets were captured in a net set at the entrance of the nest while an adult was inside, one or two weeks before the fledging of the young, to avoid the risk of nest abandonment. Three adults were captured using this technique, were given a metal band on one leg and a plastic coloured band on the other, and were radio-tagged. Additionally, 16 pre-fledging chicks were caught in the nest and also banded and fitted with radio-transmitters. Single-stage transmitters were attached via a harness to the back of the birds with a weak link designed to break after a few months (Karl and Clout 1987). The package weighed 5 g, representing 4–5% of the fledglings' body weight. The birds were then radio-tracked two or three times per week until the transmitters failed, fell off or the bird died. The location of birds was determined by homing on signal strength and was recorded on a 10 m × 10 m grid map.

We were also able to collect data on four non-radio-tagged birds that were nonetheless of known identity. These were all banded adults, and mates of radio-tagged birds or parents of radio-tagged fledglings. These data were analysed as 'associated' records instead of direct fixes.

Data were collected and recorded using the method described by O'Donnell and Dilks (1988), on a one-minute time-lag basis, including date, time, bird identification, location and perch type (tree species, height and situation within the vegetation strata). Observations ceased when the bird flew away, showed signs of disturbance by observers or after 30 min had passed without any change in activity. To maintain independence of the data and to avoid bias due to interaction with the observer, we did not pursue birds after they were flushed by our presence and we waited at least two hours before continuing observations of the same bird.

We used 'Ranges V' software to analyse the radio-tracking data (Institute of Terrestrial Ecology, Wareham, UK), and estimated the home range of each individual (defined with 95% of the fixes) using minimum convex polygon, harmonic mean and kernel methods (Kenward 1987; Worton 1989). Incremental area plots were used to check the minimum number of fixes necessary to reach an asymptote in the size of home range and thus exclude birds for which insufficient data were available. The interval of two hours between successive fixes of an individual was also tested using autocorrelation to determine whether this was sufficient to assure independence of the data (Kenward 1987). Territoriality was analysed by measuring the overlap between home ranges (static territorial interaction: White and Garrott 1990).

Time budgets and foraging behaviour

Behavioural data were collected on the 19 radio-tracked birds and by occasional observations of other individuals encountered while walking transects. Additional observations came from unbanded individuals, pairs or families, detected opportunistically while walking on transects for vegetation monitoring (see below). Approximately 40% of observations came from radio-tracked individuals.

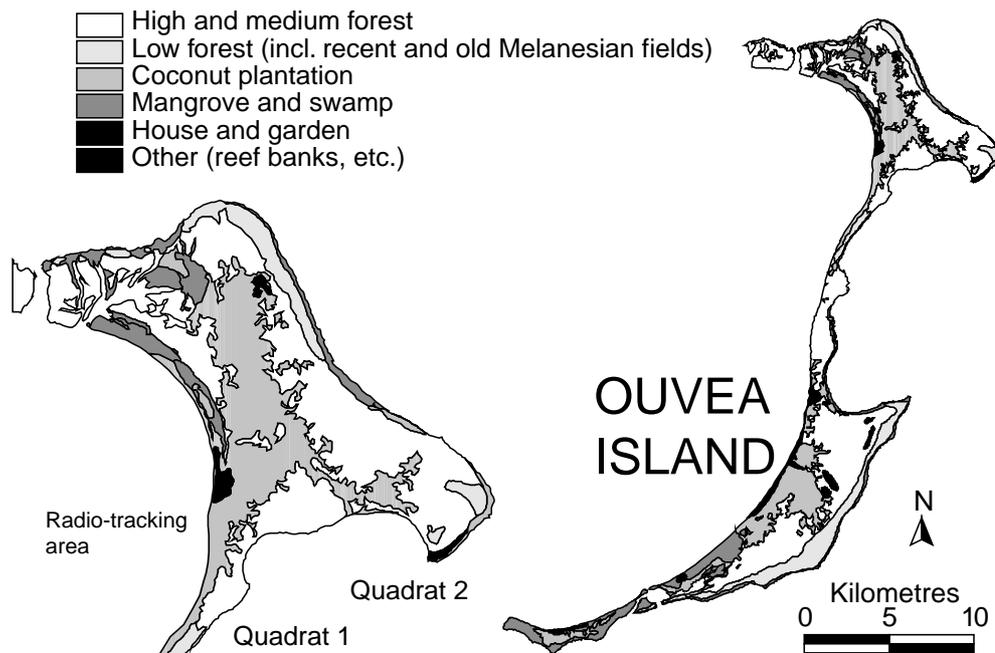


Fig. 1. Map of Ouvéa Island showing vegetation types (see also text), and a closer view of the main study areas (radio-tracking area, where birds were caught and monitored) and the two quadrats. Note that Melanesian fields are not distinguished on the map because they are too small.

Focal observations were stopped if a given behaviour (see below) was performed continuously during >15 min, or was otherwise prolonged for a maximum of 1 hour. If birds moved, they were not pursued. A total of 1623 hours of observations were made, most of this during the breeding period (July–February). Behaviours were categorised as follows: breeding activities (i.e. incubation, chick-, fledgling- and mate-feeding, etc.), roosting, calling, preening, moving (i.e. flying), and foraging. Foraging records included direct feeding observations and also, because the birds frequently flew away soon after they were seen, the presence of a parakeet on a plant bearing edible fruits or seeds, associated with food remains in the vicinity of the plant (see also Wermundsen 1997). These data were then analysed on an hourly basis, and are presented as the percentage of time spent in a given activity per hourly interval.

Habitat use

The distribution of parakeets within their primary habitat was studied using two combined sets of methods, i.e. quadrats and transects. First, habitat availability and habitat use by parakeets were assessed by a total mapping of each habitat type within two quadrats (Q1 and Q2) as well as the radio-tracking area, representing a total of 74 ha (Fig. 1). The two quadrats were chosen randomly in the forest habitat of the north of Ouvéa, and were separated by *c.* 3 km, and *c.* 7 km to the radio-tracking area. This forest was known to be the main habitat of the parakeets (Robinet *et al.* 1996). Each quadrat was 30 ha (600 × 500 m) traversed by transects spaced at 50-m intervals (assumed to be narrow enough to count all the birds within transects). Transects were subdivided by coordinate plots every 50 m, defining 50 m × 50 m wide grid cells. Each transect line of the quadrat (6.5 km in total) was walked during the same session from 07:00 to 11:00 hours, when the birds are the most active. Four sessions (from September) in Q2 and two sessions (from November) in Q1 were repeated every month in 1994, and three more sessions (from October) were conducted on both quadrats in 1995, each time walking the transects in a different order. The locations of the birds were recorded on maps with 50 m × 25 m grid cells (each side of transects). Behaviour and movements of the birds were noted; birds moving in the same direction as the observer along the line transect or toward following transects were excluded from subsequent counts. The distribution of parakeets within each quadrat (see above) was analysed with a generalised linear model by comparison with a Poisson distribution. The repeatability of sightings within each cell during the sessions (site attachment) was assessed by comparison with a binomial distribution.

Second, habitat selection was also analysed from line transect censuses conducted once for each transect in the north of Ouvéa in November and December 1993. A total of 134.5 km (500 m long, 30 m wide) of transects (*n* = 269 transects, *c.* 4.7% of the total area covered) were walked in the morning (07:00–11:00 hours) and evening (15:00–17:00 hours) along tracks or in a predetermined direction, recording the length of the track in each habitat. The number of birds seen or heard along each transect was recorded (see Robinet *et al.* 1996 for additional details on methodology). The availability of each of the nine habitat types was assessed by using an IGN 1 : 50000 map (Institut Géographique National, Paris 1992), digitised and analysed with a GIS (ARCCinfo, ESRI), with calibration in the field. Habitat selection was investigated by comparing the proportion of birds observed in each habitat type during the line transect survey with the proportion of each habitat (expected habitat use) using a non-parametric Kendall correlation coefficient (i.e. a significant association means no selectivity). For each habitat category, Chi-square tests and Bonferroni simultaneous confidence intervals were calculated to determine whether habitat type was significantly preferred or avoided (Neu *et al.* 1974; Byers *et al.* 1984).

Availability of nest-sites and food

To assess the availability of potential nesting sites, we counted the number, and measured the diameter at breast height (DBH), of each of the five species of trees (*Syzygium pseudopinnatum*, *Mimusops elengii*, *Dysoxylum rufescens*, *Intsia bijuga* and *Ficus* sp.) used for nesting (see Robinet and Salas 1999). We used a sampling band 10 m wide along the transect lines in both quadrats. The area sampled thus covered 20% of each 50 m × 25 m cell, and was assumed to be representative of the cell.

A list of 30 plant species eaten by the parakeets was compiled from earlier observations and from the results of a questionnaire completed by local people (Robinet *et al.* 1995). The occurrence and availability of these plants within the study area was investigated along a 1400-m line transect covering the whole of this area and recording within 5 m each side of the transect the number and species of each plant (with a diameter of more than 7 cm for tree species). This allowed an estimate of the relative abundance of each of the 30 plant species to be produced. The phenology and amount of food provided by the 30 plant species was then estimated by identifying four individuals of each species within the study area, and recording each month the presence and number of fruits on each individual (F_i , in a ten-power scale) from July 1995 to July 1996. A monthly index of abundance (IA) was thus constructed for each plant species (*x*) and each month (*m*), using the formula:

$$IA_{x,m} = P_x * 1/n(\sum_{i=1,n} \log_{10}(F_i)),$$

where P_x is the proportion of the species found in the transect, F_i is the number of fruits counted on specimen *i*, and *n* is the number of specimens of each species (four in this study).

Food availability was analysed in the form of cumulative IA over the complete year (i.e. a yearly index of abundance), and then compared statistically to the relative frequency of foraging locations of the parakeets. The correlation between food availability (IA) and observations of foraging parakeets was tested using Spearman's Rank test. The preference (or avoidance) of each plant species was then determined using Bonferroni's simultaneous confidence intervals analysis. Data are expressed as mean ± s.d. except when specified. Analyses were performed with SAS 6.11.

Results

Home ranges size during breeding season

Of the 19 birds equipped with radio-transmitters, only eight could be followed for more than ten days. Four adults with associated records were also added, so 11 birds were analysed further (as one adult provided both direct and associated fixes; Table 1). The main causes of failure included predation by Brown Goshawks (*Accipiter fasciatus*), transmitter loss (due mainly to destruction by the adult parakeets), or restricted access for the authors to one study site.

Incremental area plots showed that home range reached an asymptote for 8 of the 11 parakeets (see Table 1), with those ranges that were still increasing being excluded from the remainder of the study. The four juvenile parakeets for which direct fixes were obtained had an average home range of 2.34 ha (±0.47, s.e.), with no significant difference being found between the minimum convex polygon, harmonic mean and kernel methods (Kruskal–Wallis test, $H = 0.346$, $n = 3$, n.s.). Home ranges of adults could be estimated only from associated records, and ranged between 1.21 and 2.8 ha, with mean home ranges of males (2.27 ha) being

larger than those of females (1.41 ha). The home ranges of Ouvéa parakeets largely overlapped with each other in the study area: 69.2% ($\pm 14.1\%$, s.e.) within pairs ($n = 2$ pairs), 63.3% ($\pm 7.5\%$, s.e.) within families ($n = 8$ pairs, parent/fledgling), and 25.7% ($\pm 6.0\%$, s.e.) between adults of different pairs ($n = 4$ birds). The parents were found close to their offspring in $>80\%$ of the observations of radio-tagged juveniles ($n = 193$ fixes).

Bird density, distribution and habitat use.

The distribution of birds within the quadrats was significantly different from that expected under a Poisson distribution, in both quadrats (Q1: $\chi^2_2 = 134.9$; Q2: $\chi^2_2 = 76.8$; $P < 0.001$ in both cases.). Parakeets also had a patchy distribution on the quadrats, as indicated by the coefficient of dispersion (CD, σ^2/μ) (CD = 2.74 for Q1; CD = 2.19 for Q2; F test, both $P < 0.01$; see also Fig. 2). The site attachment between the sessions was significantly higher than expected under a binomial distribution ($\chi^2_4 = 1066$ for Q1; $\chi^2_6 = 697.1$ for Q2; both $P < 0.001$).

During the line transect census, 43 different parakeets were seen in the north of the island along the 134.5 km of transects. When data from only those parts of the transects that were forested (i.e. 73 km) are considered, the average

density of parakeets was 0.22 ± 0.09 birds ha^{-1} (Robinet *et al.* 1996). For comparison, the densities in the two quadrats were 0.31 ± 0.08 and 0.42 ± 0.03 birds ha^{-1} respectively, whereas the density was 0.71 ± 0.14 birds ha^{-1} in the radio-tracking area. This suggested that we chose the quadrats and the radio-tracking area within more favorable habitat. The mean number of birds seen per kilometre of transect ranged from 4.2 for Melanesian and recently fallow fields, 1.5 for domestic gardens, 0.9 for old fallow fields, 0.8 for high forest, 0.4 for medium forests, to 0 for the remaining habitats (see also Table 2 for frequencies of occurrence). Parakeets were not randomly distributed between the different habitats, as indicated by the absence of a relationship between available and used habitats (Kendall correlation coefficient, $\tau = 0.012$, $P = 0.74$). High forest, fields and recent fallow fields were significantly preferred while the parakeets were absent from other non-forest habitats (Table 2).

The parakeets were seen most of the time in the shaded canopy (71.5%, $n = 187432$ 1-min parakeet observations), sometimes in the unshaded canopy (17.7%) and understorey (10.6%), but only exceptionally on the ground (0.2%). Similarly, most records were obtained for parakeets in the stratum 5–7 m above the ground (55.7% of the observations), while strata >7 m (24.1%) and 3–5 m (14.3%) were less used.

Table 1. Fate of the 19 Ouvéa Parakeets equipped with radio-transmitters, with number of fixes and estimates of home-range size

Only birds with >10 fixes were considered for home-range estimates (see text). Birds without transmitters, but for which associated records were available, are also shown. Home ranges calculated using associated records are shown within parentheses. See Methods for details of estimates of home-range size. 'Transmitter failed' indicates that the bird was seen still alive with the transmitter still attached; 'transmitter destroyed' indicates that the bird destroyed its transmitter (but still wore the harness); 'harness destroyed' indicates that the harness was found on the ground, the fate of the bird being unknown

Site ^A	Age (sex) ^B	Season	Tracking period (days)	Reason for cessation of tracking	Nest no.	No. of fixes		Home range (ha) ^C		
						Direct	Associated	MCP	HM	KER
RT	J	1994/95	8	Killed by goshawk	1	–	–			
RT	J	1994/95	9	Killed by goshawk	1	–	–			
RT	A (M)	1995/96	–	–	1	0	87	(2.11)	(4.09)	(2.08)
RT	A (F)	1995/96	1	Harness destroyed	1	0	73	(0.97)	(1.3)	(1.38)
RT	J	1995/96	30	Transmitter failed	1	8	9	1.13	0.33 (0.41)	2.49 (3.22)
RT	J	1995/96	28	Dead (unknown reason)	1	27	0	0.21	0.09	0.14
RT	J	1995/96	9	Transmitter destroyed	1	19	0	0.16	0.11	0.22
RT	J	1995/96	6	Signal lost	1	–	–			
RT	J	1996/97	38	Killed by goshawk	1	54	0	2.99	2.71	4.05
RT	J	1996/97	45	Signal lost	1	62	0	3.27	4.2	4.33
RT	A (M)	1995/96	–	–	2	0	37	(2.16)	(1.77)	(2.42)
RT	A (F)	1995/96	18	Transmitter destroyed	2	7	31	0.56 (1.48)	0.03 (1.38)	0.67 (2.01)
RT	J	1995/96	60	Signal lost	2	50	0	2.3	1.69	2.11
RT	A (F)	1996/97	8	Transmitter destroyed	3	14	0	0.2	0.03	0.08
RT	J	1995/96	8	Killed by goshawk	3	–	–			
RT	J	1995/96	8	Killed by goshawk	3	–	–			
Q2 ^D	J	1995/96	8	Signal lost	4	–	–			

^ART = Radio-tracking area, Q2 = second quadrat

^BA = adult, J = juvenile, M = male, F = female.

^CMCP = minimum convex polygon (95%), HM = harmonic mean (95%), KER = kernel method (95%).

^DNo data were available from four additional birds from Q2 (see text); these are thus not included in the table.

In order to investigate whether the suitability of breeding sites may constitute a limiting factor for this population, we used data from quadrats (Q1, Q2 and the radio-tracking area), and compared the density of breeding parakeets (0.03, 0.07 and 0.20 breeding pairs per hectare, respectively) and the density of trees suitable for breeding (0.9 ± 0.14 , 1.7 ± 0.19 and 9.78 ± 1.76 , respectively). These two parameters were positively related, although the very limited sample size did not allow statistical testing.

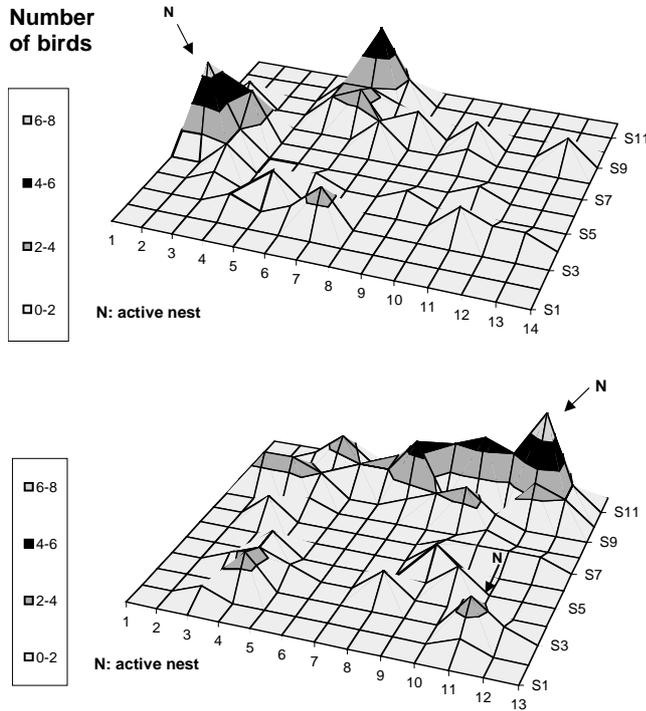


Fig. 2. Habitat use by the parakeets on the two quadrats. Each quadrat has been divided into $50 \times 50 \text{ m}^2$ grid cells (see Methods). Frequency of use is expressed by the total number of birds seen after five passages (first quadrat, Q1) or seven passages (Q2).

Food availability

The plant phenology of the 30 plant species foraged by the Ouvéa Parakeet follows a typical tropical pattern, i.e. extended and asynchronous fruiting season (mean 6.3 ± 3.3 months), suggesting no apparent food shortage. The average proportion of species presenting fruits was $70.9 \pm 9.9\%$ (range 52–80%). Some plants (e.g. *Carica papaya*, *Ficus* sp. and the vines *Maesa novocaledonica*, *Rhamnella vitiensis* and *Passiflora suberosa*) bear fruit almost all year while some others (e.g. *Elattostachys apetala*) show great variation in their fruiting season between years and between individuals. However, most plants have a fruiting season from October to March, i.e. during the hot season, leading to a greater abundance of food during this period, followed by a decrease in April. Breeding by the parakeets, i.e. August to January (Robinet and Salas 1999), coincided with peak fruit availability (Fig. 3). Only four species of plants had fruit in all months: *Carica papaya*, *Ficus* sp., *Rhamnella vitiensis* and *Elattostachys apetala* (Fig. 3).

Daily activity patterns, foraging behaviour and food selection

On average, 47% of the time was spent on foraging activities (Fig. 4). However, the daily pattern of foraging was not evenly distributed, as two peaks of foraging were obvious, in late morning (9:00–11:00 hours) and then mid-afternoon (14:00–16:00 hours). During mid-day most of the time was spent on roosting, preening and breeding activities (incubation and allo-feeding) while during the last hour of the day, vocalisation was the main activity, although the reduced sample size means that infrequent activities could have been missed.

In total, 770 foraging observations were made during the study; these involved 23 different plant species from the 30 plants previously thought to be eaten by Ouvéa Parakeets. The other seven species were never seen to be foraged on and

Table 2. Total and relative area of each habitat type in the north of Ouvéa, compared with the proportion of Ouvéa Parakeets seen in each of these habitats, according to line-transect data

Differences between expected and observed proportions of usage by parakeets were tested using a Bonferoni simultaneous confidence interval analysis. *, $P < 0.05$; **, $P < 0.01$; significance levels in parentheses indicate negative selection

Vegetation type		Total area (ha)	Relative area (%)	Frequency of observations	Observed proportion of usage (%)	Significance
Forest	1A High forest	988	21	17	40	*
	1B Medium forest	675	15	6	14	
	1C Low forest	163	4	0	0	(*)
Clearings	2A Melanesian fields and recent fallow	184	4	17	40	**
	2B Old fallow	51	1	1	2	
Coconut plantations	3 Coconut plantations	1401	30	0	0	(*)
Coastal vegetation	4A On reef banks	494	11	0	0	(*)
	4B Mangrove and marsh	550	12	0	0	(*)
	5 Domestic gardens	100	2	2	4	
Total		4606	100	43	100	

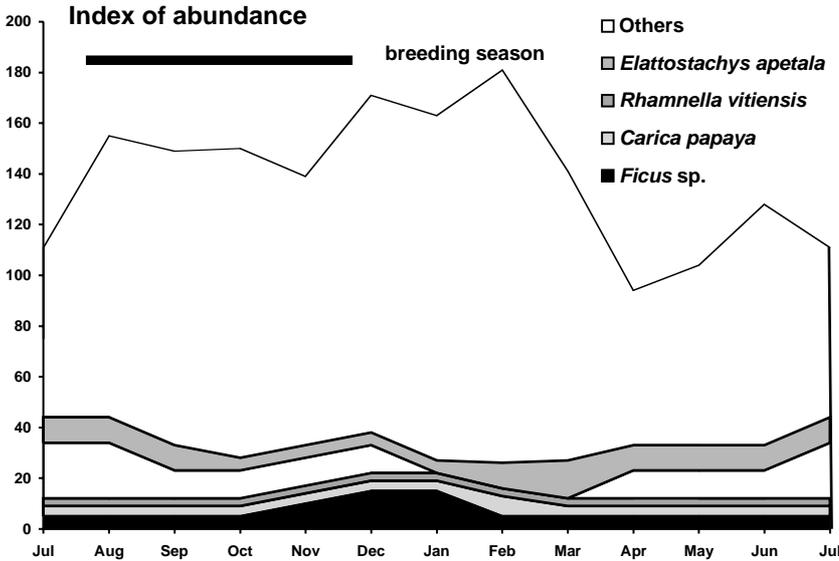


Fig. 3. Food abundance of the plant species foraged by the Ouvéa Parakeet, from the start of the breeding season. A index of fruit abundance (see Methods) was computed for each month for each of 30 plant species. Plant species shown in black and gray (bottom) are species positively selected by the Ouvéa Parakeet. Note that their fruit abundance is relatively constant all year round. The breeding season is also shown at the top of the figure.

can therefore be discounted as being part of the regular diet of the parakeets. Seven species were involved in more than two-thirds of the observations, with *Ficus sp.* alone representing >30% of all sightings (Table 3). Comparison of the proportion of foraging observations with the availability of food for each species (measured from the food abundance index accumulated over the complete year) shows that the foraging pattern is significantly different from what might be expected simply on the basis of the availability of some species (Spearman Rank test, $r_s = 0.18, P = 0.46$; values from Table 3). *Ficus sp.*, *Carica papaya*, *Rhamnella vitiensis*,

Polyalthia nitidissima, *Baloghia inophylla* and *Malaisia scandens* were significantly preferred by parakeets, while others appeared less attractive (Table 3). It should be noted that the most strongly selected plant species were plants with fruit all year round (Table 3, Fig. 5).

Comparison of foraging observations with the abundance of food during the year for the three most selected species (Fig. 4) showed that *Ficus sp.* constitutes a major food in all months, with a maximum from May to October, before and at the beginning of the breeding season while it produces more fruits from November to January. On the other hand, *Carica papaya*, which produces fruit all year, is mostly consumed from November to January (the second half of the breeding season). *Malaisia scandens*, *Baloghia inophylla* and *Harpullia neocaledonica* are then eaten successively, from January to July (Fig. 4). Seeds of various sizes (range 1.5–45 mm), were almost exclusively eaten, with the exception of the pawpaw fruits, the flesh of which was also consumed. We found no evidence of foraging on insects during this study although an exceptional incursion near the ground may be related to this behaviour.

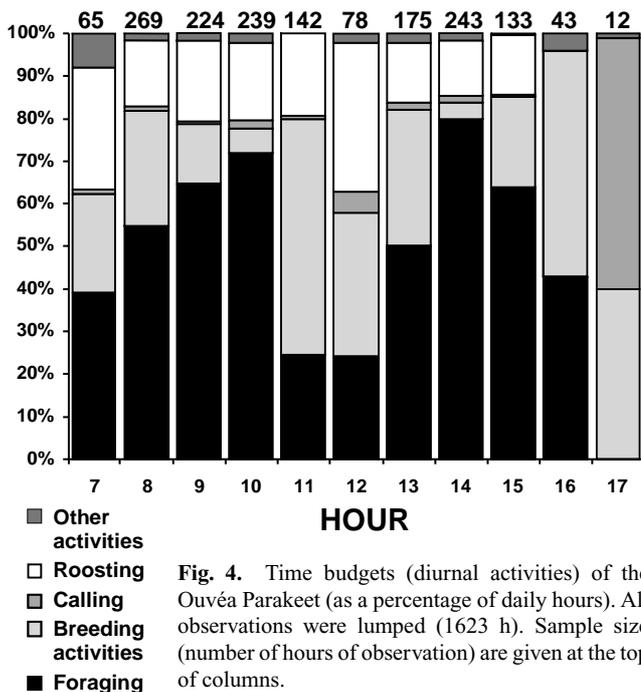


Fig. 4. Time budgets (diurnal activities) of the Ouvéa Parakeet (as a percentage of daily hours). All observations were lumped (1623 h). Sample size (number of hours of observation) are given at the top of columns.

Discussion

Distribution and home range

As has been observed for other rainforest parrot species (Gilardi and Munn 1998), the Ouvéa Parakeets showed distinct preference for, or avoidance of, particular habitats. The parakeets were mainly found in the high forest, which includes the forest *per se*, and in Melanesian fields. These two habitats were significantly preferred, whilst coconut plantations and coastal vegetation were avoided. The distribution of birds within their habitat was patchy during the breeding season, with large areas of forest in the quadrats and on the transect area apparently never being used. This clus-

tered distribution was largely repeated during each visit, suggesting a high site attachment during the breeding season. Similarly, the three pairs followed in the radio-tracking area nested in the same site during three breeding seasons (two of them twice a year) and were observed within their small territories every month during two consecutive years, during both the breeding and the non-breeding periods.

The radio-tracking data were too few and for too restricted a period (the few weeks after fledging) to provide a complete view of juvenile dispersal and adult movements. However, this study showed that the home ranges of radio-tracked fledglings were small and no juvenile dispersal was observed for up to nine weeks after fledging: during this period the parents (some of them identified with colour bands) were found close to the juveniles in 80% of observations. We therefore assume that, during the breeding season, adults spend at least the same proportion of their time within the home range of the juveniles. These data reflect those of the neotropical Green-rumped Parrotlet (*Forpus passerinus*), which has a strong site fidelity (Sandercock *et al.* 2000).

It is not possible to assess whether the radio-tracking equipment had any impact on mortality rate. However, the high mortality during the few weeks after fledging due to predation by raptors is similar to that observed for juvenile Puerto Rican parrots (Lindsey *et al.* 1994). Furthermore, we observed several juvenile parakeets killed by raptors outside

the study area (i.e. not carrying transmitters), thus confirming the importance of predation on survival of fledglings.

Foraging activities and food selection

Ouvéa Parakeets showed the typical pattern of activity of diurnal tropical birds, with peaks of activity in the morning and the afternoon, avoiding high-metabolic activities (flight and foraging) when the temperature is greatest. The last hour of the day, as well as the first, are spent on social activities, such as vocalisations and a few agonistic interactions. Foraging, although the main behaviour recorded, accounted for less than half of the total activity of the birds.

The 30 species potentially foraged by the Ouvéa Parakeets represent half of the 60 most common forest plants species of Ouvéa (J. M. Veillon, unpublished). Among these, only a few plant species are of particular importance in terms of their contribution to the total diet, being available at key periods (i.e. breeding), and being significantly preferred by the parakeets. This is especially the case for *Ficus* sp., to which a third of the foraging observations related, and which thus can be considered a key food source, especially during May–October. This plant may play a critical role during a period that corresponds to the preparation and beginning of the breeding season, when the food of the other most preferred plants is less abundant. However, from November, while *Ficus* sp. is still common, *Carica papaya* is preferred.

Table 3. Index of abundance of fruit on various plant species foraged by Ouvéa Parakeets, and number and proportion of foraging observations

Plant species were sampled on a 1400-m transect (see Methods for details). IA, Index of Abundance (see text for definition). *, $P < 0.05$; **, $P < 0.01$; significance levels in parentheses indicate negative selection

	Food availability		Foraging observations		
	Accumulated IA	%	No.	%	
<i>Ficus</i> sp.	70	4.60	239	31.04	**
<i>Carica papaya</i>	48	3.15	73	9.48	**
<i>Rhamnella vitiensis</i>	33	2.17	51	6.62	**
<i>Harpullia neo-caledonica</i>	121	7.94	50	6.49	
<i>Elattostachys apetala</i>	100	6.57	41	5.32	
<i>Polyalthia nitidissima</i>	28	1.84	39	5.06	**
<i>Passiflora suberosa</i>	64	4.20	39	5.06	
<i>Baloghia inophylla</i>	6	0.39	27	3.51	**
<i>Diospiros fasciculosa</i>	27	1.77	26	3.38	
<i>Malaisia scandens</i>	9	0.59	25	3.25	**
<i>Mimusops elengi</i>	28	1.84	22	2.86	
<i>Olea paniculata</i>	40	2.63	20	2.60	
<i>Intsia bijuga</i>	160	10.51	17	2.21	(**)
<i>Zieridium pseudobtusifolium</i>	36	2.36	16	2.08	
<i>Syzygium pseudopinnatum</i>	9	0.59	16	2.08	*
<i>Garcinia pedicelata</i>	56	3.68	13	1.69	(**)
<i>Podonophelium homer</i>	22	1.44	12	1.56	
<i>Maesa novocaledonica</i>	76	4.99	9	1.17	(**)
<i>Flagellaria indica</i>	50	3.28	5	0.65	(**)
Others	540	35.46	30	3.90	(**)
Total	1523	100.00	770	100.00	

This shift to the high-energy pawpaw fruits during the second half of the breeding season is likely to be linked to the growing needs of the clutch from hatching to fledging. As noted in a previous paper (Robinnet *et al.* 1995), Ouvéa Parakeets largely benefit from *Carica papaya*, an introduced plant that grows in traditional Melanesian fields. A similar pattern of food selection and its variation according to availability and season has also been documented for the Pacific Parakeet (*Aratinga strenua*) (Wemundsen 1997).

Food abundance or nest cavities as limiting factors?

Although we did not specifically address the relationship between the distribution of feeding trees and the distribution and abundance of the parakeets, we found evidence that the availability of food on Ouvéa Island is high throughout the year, especially during the breeding season of the parakeets.

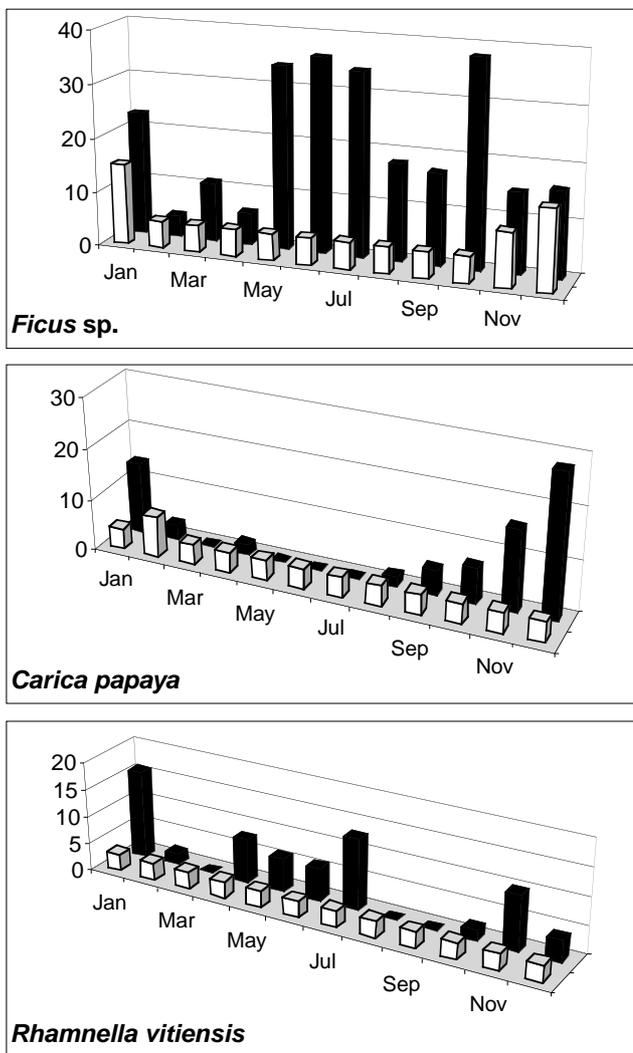


Fig. 5. Comparison between foraging observations (in black) and availability of food (in white) for three plants significantly selected by the Ouvéa Parakeets (from Table 1). Data are shown for each month.

More specifically, we found a large number of tree species with extended fruiting seasons, and these plants were particularly selected by Ouvéa Parakeets. The *Ficus* spp. are very common in Ouvéa and provide food throughout the year. Pawpaw trees, an introduced species, grow in most of the Melanesian and fallow fields of Ouvéa; this is also an important source of food during most of the year. High food availability, both temporal and spatial, associated with a wide range of plant species in the diet of the Ouvéa Parakeets, may explain the small home ranges of juveniles and adults during the breeding season.

As observed in other studies (e.g. Gilardi and Munn 1998), the limited time spent foraging is also consistent with an abundant food supply, which allows the birds to stop feeding for several hours in the middle of the day. In contrast, parrots that feed on seeds in temperate or dry habitats (e.g. Cannon 1981; Beggs and Wilson 1987) spend longer foraging each day. The absence of interactions with other potential competitors for food during this study suggests that food resources are not limited. The results of this study thus strongly suggest that, currently, habitat quality in terms of food supply may not be limiting the population size, compared with the availability of nest sites.

The carrying capacity of parrot habitat may decrease through a reduction of its area and/or quality (e.g. food and nest site availability), but also through habitat fragmentation, which increases edge effects and may render part of the potential habitat inaccessible or insecure for the species (Mace and Lande 1991; Lambert *et al.* 1992). The availability of suitable nest sites has been recognised as a factor limiting productivity of many cavity nesters (see review in Newton 1994), including New World parrots (Snyder 1977b; Wiley 1985; Beissinger and Waltman 1991; Munn 1992) and cockatoos (Saunders *et al.* 1982). Besides the density of potential nest sites, several other factors can result in limitation, including behavioural limitations (a strong site selectivity and fidelity, and the ability of the bird to locate nest sites) and ecological factors (the accessibility of nest sites, predation and competition: Snyder 1977a). In our study, the density of breeding parakeets was positively related to the distribution of suitable trees (i.e. the five tree species used for nesting). These results, although they would benefit from larger sample sizes in different areas, suggest that the number of suitable trees for nesting may limit the proportion of breeders, in some parts of the Ouvéa Parakeet's range. Ecological features such as the fragmentation of the forest in Ouvéa, and the number of nest sites that have been destroyed by local people for collecting the chicks as pets, may contribute to a limitation of nest sites (Robinnet *et al.* 1995; Robinnet and Salas 1999). In two cases (outside the intensive study areas), we observed successful nesting a few weeks after the restoration (by patching of holes) of former nest sites that had been destroyed, further suggesting the possibility of nest-site limitation.

Suitable habitat seems to be highly patchy and isolated, mainly as a consequence of the presence of coconut plantations. The latter provide no food and limited shelter against predation by Brown Goshawks and may thus represent an important barrier against dispersal. In the three years of this study, parakeets were not seen venturing more than a few metres into coconut plantations surrounding the forest. The quality of habitat in terms of protection against predators, and especially Brown Goshawks, which killed more than 50% of the fledglings studied (Robinet and Salas 1999), may be an important factor in the present distribution of the Ouvéa Parakeets. The goshawk mainly undertakes surprise attacks from the edges of forest and clearings, and does not venture very far into dense forest (Aumann 1988; Thiollay 1993). This may explain the presumed inability of Ouvéa Parakeets to recolonise apparently suitable habitat in the south of the island (Robinet *et al.* 1995, 1996).

The results of this study strongly suggest that habitat quality is important for the conservation of the Ouvéa Parakeet. Recovery measures should include a habitat-quality assessment, including nest sites and shelter against predation in different parts of its former range. It would also be important to confirm experimentally the role of nest sites as a factor limiting reproductive success, by provisioning artificial nest sites. Preventive measures to avoid damage to the trees suitable for nesting, nest-site provision and restoration, protection of the understorey, and also the key feeding trees could be implemented by involving the local community. Finally, a translocation of birds to the south of the island, where there are large areas of suitable habitat, could also be undertaken to lower the risks of extinction due to stochastic events.

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References

- Aumann, T. (1988). The diet of the Brown Goshawk, *Accipiter fasciatus*, in south-eastern Australia. *Australian Wildlife Research* **15**, 587–594.
- Beggs, J. R., and Wilson, P. R. (1987). Energetics of the south island Kaka (*Nestor meridionalis meridionalis*) feeding on the larvae of kanuka longhorn beetles (*Ochrocidus huttoni*). *New Zealand Journal of Ecology* **10**, 143–147.
- Beissinger, S. R., and Waltman, J. R. (1991). Extraordinary clutch size and hatching asynchrony of a neotropical parrot. *Auk* **108**, 863–871.
- Byers, R. C., Steinhorst, R. K., and Krausman, P. R. (1984). Clarification of a technique for utilization–availability data. *Journal of Wildlife Management* **48**, 1050–1053.
- Cannon, C. E. (1981). The diet of the Eastern Pale-headed Rosellas. *Emu* **81**, 101–110.
- Collar, N. J., and Andrew, P. (1988). 'Birds to Watch: a Checklist of the World's Threatened Birds.' (ICBP: Cambridge, UK.)
- Collar, N. J. and Juniper, A. T. (1992). Dimensions and causes of the parrot conservation crisis. In 'New World Parrot in Crisis: Solutions from Conservation Biology'. (Eds S. R. Beissinger and F. R. Snyder.) (Smithsonian Institution Press: Washington.)
- Collar, N. J., Crosby, M. J., and Stattersfield, A. (1994). 'Birds to Watch 2.' Birdlife Conservation Series N°4. (Birdlife International: Cambridge, UK.)
- Forshaw, J. M., and Cooper, W. T. (1989). 'Parrots of the World.' (Lansdowne Editions: Sydney.)
- Gilardi, J. D., and Munn, C. A. (1998). Patterns of activity, flocking and habitat use in parrots of the Peruvian Amazon. *Condor* **100**, 641–653.
- Gnam, R. S. (1991). Nesting behaviour of the Bahama Parrot *Amazona leucocephala bahamensis* on Abaco Island, Bahamas. In 'Acta XX Congressus Internationalis Ornithologici 1'. pp. 673–680.
- Hannecart, F. (1988). Les oiseaux menacés de la Nouvelle Calédonie et des îles proches. In 'Livre Rouge des Oiseaux Menacés des Régions Françaises d'Outre-mer'. (Eds J. C. Thibault and I. Guyot.) pp. 143–165. (ICBP: Cambridge, UK.)
- IUCN (1996). 'IUCN Redlist of Threatened Animals.' (IUCN: Gland, Switzerland.)
- Karl, B. J., and Clout, M. N. (1987). An improved radio transmitter harness and a weak link to prevent snagging. *Journal of Field Ornithology* **58**, 73–77.
- Kenward, R. (1987). 'Wildlife Radio Tagging. Equipment, Field Techniques and Data Analysis.' (Academic Press: London.)
- King, W. B. (1985). Island birds: will the future repeat the past? In 'Conservation of Island Birds'. (Ed. P. J. Moor.) pp. 3–16. Technical Publication No. 3. (ICBP: Cambridge, UK.)
- Lambert, F., Wirth, R., Ulysses, S. S., Thomsen, J. B., and Ellis-Joseph, S. (1992). 'Parrots: an Action Plan for their Conservation 1993–1998.' (Birdlife International–IUCN: Cambridge, UK.)
- Lindsey, G. D., Arendt, W. J., and Kalina, J. (1994). Survival and causes of mortality in juvenile Puerto Rican parrots. *Journal of Field Ornithology* **65**, 76–82.
- Mace, G. M., and Lande, R. (1991). Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conservation Biology* **5**, 148–157.
- Macmillan, L. (1939). Note sur les oiseaux des Iles Loyauté 2. *Etudes Mélanésiennes* **1939**, 30–41.
- Martin, T. E. (1987). Food as a limit on breeding birds: a life history perspective. *Annual Review of Ecology and Systematics* **18**, 453–487.
- Moorhouse, R. J. (1991). Annual variation in productivity of North Island Kaka on Kapiti Island, New Zealand. In 'Acta XX Congressus Internationalis Ornithologici 1'. pp. 690–696.

- Moorhouse, R. J., Sibley, M. J., Lloyd, B. D., and Green, T. C. (1999). Sexual dimorphism in the north island Kaka *Nestor meridionalis septentrionalis*: selection for male enhanced provisioning ability? *Ibis* **141**, 644–651.
- Munn, C. A. (1992). Macaw biology and ecotourism, or “when a bird in the bush is worth two in the hand”. In ‘New World Parrots in Crisis’. (Eds S. R. Beissinger and N. F. R. Snyder.) pp. 47–72. (Smithsonian Institution Press, Washington, DC.)
- Neu, C. W., Byers, C. R., and Peek, J. M. (1974). A technique for analysis of utilization–availability data. *Journal of Wildlife Management* **38**, 541–545.
- Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation* **70**, 265–276.
- O’Donnell, C. F. J., and Dilks, P. J. (1988). A method for quantifying habitat use of forest birds. Science and Research Series No. 4. Department of Conservation, Wellington.
- Powlesland, R. G., Lloyd, B. D., Best, H. A., and Merton D. V. (1992). Breeding biology of the Kakapo *Strigops habroptilus* on Stewart Island, New Zealand. *Ibis* **134**, 361–373.
- Rands, M. R. W. (1991). Conserving threatened birds: an overview of the species and the threats. In ‘Bird Population Studies: Relevance to Conservation and Management’. (Eds J. D. Perrins, J.-D. Lebreton and G. J. M. Hirons.) pp. 594–633. (Oxford University Press: Oxford.)
- Robinet, O., and Salas, M. (1999). The reproductive biology of the endangered Ouvéa Parakeet. *Ibis* **141**, 660–669.
- Robinet, O., Beugnet, F., Dulieu, D., and Chardonnet, P. (1995). The Ouvéa Parakeet – state of knowledge and conservation status. *Oryx* **29**, 143–150.
- Robinet, O., Barré, N., and Salas M. (1996). Population estimate for the Ouvéa Parakeet *Eunymphicus cornutus uvaensis*: its present range and implications for conservation. *Emu* **96**, 151–157.
- Sandercock, B. K., Beissinger, S. R., Stoleson, S. H., Melland, R. R., and Hughes, C. R. (2000). Survival rates of a neotropical parrot: implications for latitudinal comparisons of avian demography. *Ecology* **81**, 1351–1370.
- Saunders, D. A. (1986). Breeding season, nesting success and nestling growth in Carnaby’s Cockatoo, *Calyptorhynchus funereus latirostris*, over 16 years at Coomallo Creek, and a method for assessing the viability of population in other areas. *Australian Wildlife Research* **13**, 261–273.
- Saunders, D. A. (1991). The effects of land clearing on the ecology of Carnaby’s Cockatoo and the inland Red-tailed Black Cockatoo in the wheatbelt of Western Australia. In ‘Acta XX Congressus Internationalis Ornithologici 1’. pp. 658–665.
- Saunders, D. A., Smith, G. T., and Rowley, I. (1982). The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia. *Australian Wildlife Research* **9**, 541–556.
- Snyder, N. F. R. (1977a). Increasing reproductive effort and success by reducing nest-site limitations. A review. In ‘Endangered Birds: Management Techniques for Preserving Threatened Species’. (Ed. S. A. Temple.) pp. 27–33. (University of Wisconsin Press: Wisconsin.)
- Snyder, N. F. R. (1977b). Puerto Rican parrots and nest-site scarcity. In ‘Endangered Birds: Management Techniques for Preserving Threatened Species’. (Ed. S. A. Temple.) pp. 47–53. (University of Wisconsin Press: Wisconsin.)
- Snyder, N., McGowan, P., Gillardi, J., and Grajal, A. (Eds) (2000). ‘Parrots. Status Survey and Conservation Action Plan 2000–2004.’ (IUCN: Gland, Switzerland & Cambridge, UK.)
- Thiollay, J. M. (1993). Habitat segregation and the insular syndrome in two congeneric raptors in New Caledonia, the White-bellied Goshawk *Accipiter haplochrous* and the Brown Goshawk *A. fasciatus*. *Ibis* **135**, 237–246. Thiollay, J. M. (1991). Food limitation in tropical bird populations. In ‘Acta XX Congressus Internationalis Ornithologici 3’. pp. 1577–1583.
- Wermundsen, T. (1997). Seasonal change in the diet of the Pacific Parakeet *Aratinga strenua* in Nicaragua. *Ibis* **139**, 566–568.
- White, G. C., and Garrott, R. A. (1990). ‘Analysis of Wildlife Radio-tracking Data.’ (Academic Press: San Diego, CA.)
- Wiley, J. W. (1985). The Puerto Rican Parrot and competition for its nest sites. In ‘Conservation of Island Birds’. (Ed. P. J. Moor.) pp. 213–223. Technical Publication No. 3. (ICBP: Cambridge, UK.)
- Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168.

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