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TEMPORAL VARIATION IN FLOCK SIZE AND HABITAT USE OF PARROTS IN NEW CALEDONIA

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Abstract. We examined daily activity patterns, flock-size variations, use of vertical space, and small-scale habitat selection of the New Caledonian Parakeet (*Cyanoramphus saisseti*), Horned Parakeet (*Eunymphicus cornutus*), and New Caledonian Rainbow Lorikeet (*Trichoglossus haematodus deplanchii*) on mainland New Caledonia. All three species had bimodal patterns of activity, with most encounters occurring in the morning and a second smaller peak of encounters in the late afternoon. The parakeets were usually seen singly or in twos, and most flocks contained fewer than four individuals. Parakeet flocks remained relatively consistent in size through the day and through the year. Most Rainbow Lorikeet flocks contained only a few individuals, though some reached up to 40 birds. Rainbow Lorikeets were encountered mainly in small flocks during the breeding season from September to January, and their average flock size was higher and more variable for the rest of the year. Rainbow Lorikeets selected valley forest and urban areas, where they were most common in parks and gardens. New Caledonian Parakeets favored slope forest over valley forest, and they foraged low, either at the edge of forest, in slope forest, or in maquis (shrubland). Horned Parakeets generally fed at greater heights than did New Caledonian Parakeets, preferred valley forest to slope forest, and avoided maquis. We suggest that the observed difference in habitat use between the New Caledonian Parakeet and Horned Parakeet is the result of spatial resource partitioning, which allows these closely related species to coexist.

Key words: *conservation, ecology, forest edge, New Caledonia, parrot.*

Variación Temporal en el Tamaño de la Bandada y Uso de Hábitat por Loros en Nueva Caledonia

Resumen. Examinamos los patrones de actividad diaria, las variaciones del tamaño de la bandada, el uso del espacio vertical y la selección de hábitat de pequeña escala de *Cyanoramphus saisseti*, *Eunymphicus cornutus* y *Trichoglossus haematodus deplanchii* en Nueva Caledonia. Las tres especies tuvieron patrones bimodales de actividad, con la mayoría de los encuentros ocurriendo en la mañana y un segundo pico más pequeño de encuentros a finales de la tarde. *C. saisseti* y *E. cornutus* fueron vistos usualmente solas o en dúo, y la mayoría de las bandadas contuvo menos de cuatro individuos. El tamaño de las bandadas de estas dos especies permaneció relativamente consistente durante el día y a lo largo del año. La mayoría de las bandadas de *T. h. deplanchii* contuvieron sólo unos pocos individuos, aunque algunas alcanzaron las 40 aves. *T. h. deplanchii* fue encontrada principalmente en pequeñas bandadas durante la estación reproductiva, de septiembre a enero, y su tamaño promedio de bandada fue más grande y más variable para el resto del año. *T. h. deplanchii* seleccionó valles con bosque y áreas urbanas, donde fueron más comunes en parques y jardines. *C. saisseti* prefirió las laderas boscosas por sobre los valles con bosque y forrajeó bajo, ya sea en el borde del bosque, en laderas boscosas o en maquis (arbustales). *E. cornutus* usualmente se alimentó a mayor altura que *C. saisseti*, prefirió los valles con bosque más que las laderas con bosque y evitó el maquis. Sugerimos que las diferencias observadas en el uso de hábitat entre *C. saisseti* y *E. cornutus* es son el resultado de la partición espacial de los recursos, lo que permite que coexistan estas especies estrechamente relacionadas.

INTRODUCTION

Parrots (Psittacidae) have a higher proportion of threatened species than most groups of birds, yet the vast majority of parrots have never been thoroughly studied in the wild (Snyder et al. 2000). In New Caledonia, only the endangered Ouvéa Parakeet (*Eunymphicus uvaeensis*) has been given much attention in the literature (e.g., Robinet et al. 1995, 1996, 1998, 2003). Very little is known about the ecology of the New Caledonian Parakeet (*Cyanoramphus saisseti*) or Horned Parakeet (*Eunymphicus cornutus*) (e.g., Theuerkauf et al. 2009a, Legault et al. 2011), despite their relative scarcity

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and apparent historical decline (Layard and Layard 1882, Bregulla 1993, Hahn 1993). Although the Rainbow Lorikeet (*Trichoglossus haematodus*) has been researched in other parts of the world (e.g., Bell 1966, Cannon 1979, 1984a, Utschick and Brandl 1989, Brooker et al. 1990), the ecology of the endemic New Caledonian subspecies (*T. h. deplanchii*) remains largely unstudied (Legault et al. 2011).

Without adequate ecological data for these species, it is difficult to assess and monitor their populations. Information about activity patterns is essential to ensure that densities are estimated at appropriate times (Blake 1992, Pizo et al. 1997), and knowledge of flock-size variability can help to determine the most appropriate method for estimating density (Pizo et al. 1995, 1997). Understanding the foraging behavior of threatened species may also be important to their conservation (Butler 2006), and information on habitat use can help with the identification and preservation of critical habitats (Marsden and Fielding 1999, Robinet et al. 2003, Evans et al. 2005).

As part of a broader investigation into the spatial ecology of parrots in New Caledonia, we examined the activity patterns and flock sizes of the New Caledonian Parakeet, Horned Parakeet, and Rainbow Lorikeet. We also studied each species' use of particular vegetation types, vertical strata, and forest edges at a small scale, in order to complement existing data on the broad-scale habitat associations of these species (Legault et al. 2011). Although the New Caledonian Parakeet and Horned Parakeet are sympatric and have similar requirements for rainforest (Legault et al. 2011), we have not observed any signs of interspecific competition over resources, such as food or nests. We hypothesised that these closely related species are able to coexist by partitioning spatial resources, which is likely to be reflected in their use of habitat at a small scale.

METHODS

STUDY AREA

Our primary study sites were located in the Parc Provincial de la Rivière Bleue (PPRB; 22° 07′ S, 166° 40′ E) and Parc des Grandes Fougères (PGF; 21° 37′ S, 165° 46′ E) on mainland New Caledonia (Fig. 1). We also recorded data in a variety of other locations on the island (Legault et al. 2011), including the greater Nouméa metropolitan area (22° 15′ S, 166° 28′ E), which contains approximately 160 000 inhabitants, or two-thirds of the population of New Caledonia.

PPRB (140–1230 m above sea level) is a 90-km² reserve located in the south of New Caledonia and forms part of the 159-km² Réserve Spéciale de Faune de la Haute Yaté. The park was created in 1980, after logging of kauri (*Agathis lanceolata*) ceased. It currently functions as a reserve for conservation, recreation, and research and is home to most of New Caledonia's endemic bird species (Ekstrom et al. 2000). The region comprises part of the southern massif, a large expanse of ultramafic rock, and most soils in the area are highly weathered and very poor in nutrients. In the valley of the Rivière Bleue, richer alluvial soils support lowland rainforest with a dense canopy approximately 20 to 25 m high. We focused our research around this region, which contained a mixture of low- to medium-altitude rainforest, and maquis (shrubland). The mean annual temperature in forest is 18 °C, and the mean annual rainfall is 3200 mm (Bonnet de Larbogne et al. 1991).

PGF (300–860 m above sea level) is a 45-km² reserve located in Province Sud, New Caledonia. The park was established in 2008 with the aim of merging conservation and recreation with existing hunting practices. The park supports a rich and diverse flora and fauna, especially avifauna. Its vegetation consists mainly of medium-altitude rainforest, but secondary forest, scrub, savanna, and pine plantations are also present. At the Col d'Amieu forestry station (450 m above sea level), approximately 2 km east of the reserve, the mean annual temperature is 20 °C, and the mean annual rainfall is 1800 mm (Jaffré and Veillon 1995).

Black rats (*Rattus rattus*), feral cats (*Felis catus*), and goshawks (*Accipiter haplochrous* and *A. fasciatus*) inhabit the study areas (Rouys and Theuerkauf 2003) and are predators of parrots (Robinet et al. 1998, 2003, Gula et al. 2010). Until recently, poaching posed a considerable threat to the Ouvéa Parakeet (Robinet et al. 1996, Barré et al. 2010), but it is not suspected of having a substantial effect on parrot populations on the mainland (Pain et al. 2006).

FIELD WORK

From 2002 to 2011, we recorded encounters with New Caledonian Parakeets, Horned Parakeets, and Rainbow Lorikeets on the main island of New Caledonia. We detected parrots both visually and aurally, and used both morphological and vocal cues to distinguish the species. During encounters with parrots, we recorded the following information: species, flock size, time, date, GPS coordinates, and type of detection (visual or aural). Whenever we observed parrots, we estimated their height above the ground (to the nearest meter) and recorded their behavior (e.g., flying, perching, or feeding). We used a *G*-test of independence to assess the significance of differences between species with respect to flock size and to determine whether the species flew, perched, or fed at heights significantly different from one another. We used encounter data to assess patterns of activity, flock size, foraging, and habitat use. We expressed activity with encounter rates because active parrots are more likely to be detected. Parrots typically chatter while foraging and socializing, so they are likely to have been inactive during the times when detections were low.

In total, we documented 1691 encounters with parrots, including 588 with the New Caledonian Parakeet, 671 with the Horned Parakeet, and 432 with the Rainbow Lorikeet. The majority of these records were from PPRB (1155) and PGF (272), where we spent the most time making detailed observations. For the analysis of activity patterns, we incorporated an additional 1040 records from point counts

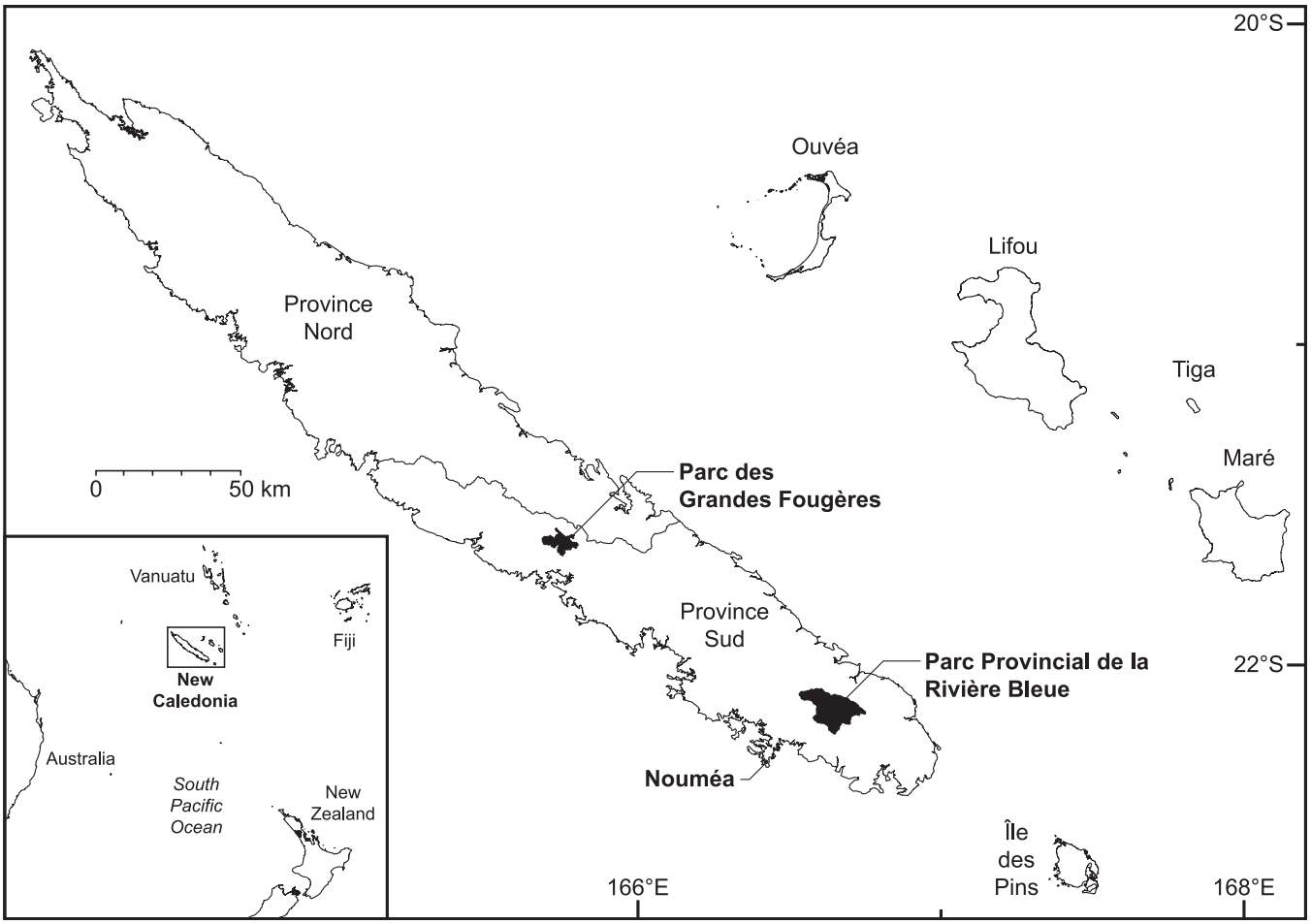

FIGURE 1. New Caledonia, including the location of Nouméa and the main study areas (in black).

taken during a larger bird survey (Chartendrault and Barré 2005, 2006). We analyzed these records separately, as point counts involved listening for calls from dawn until 09:30 and from 15:30 until dusk. Through the year, sunrise varies from 05:00 to 06:30, sunset from 17:15 to 18:45.

ANALYSIS OF HABITAT SELECTION

We based our study of habitat selection on encounters recorded in PPRB, PGF, and in urban areas. For the PPRB analysis, we used a 1:10 000-scale vegetation map (Institut Géographique National, France) vectorized from SPOT (Système Pour l'Observation de la Terre) satellite photographs of the park. The vegetation map originally distinguished only forest and maquis, but we modified it with GIS to include also slope forest and valley forest. We defined slope forest as forest above 170 m, generally on slopes of 10–70°, valley forest as forest below 170 m, generally on slopes <10° and located predominantly along the lower alluvial sections of the Rivière Bleue.

For the PGF analysis, we used a 1:50 000-scale vector map of vegetation from surveys carried out in 1975 by the CTFT (Centre Technique Forestier Tropicale, France) and updated to include the location of pine plantations (<1% of the area). The remaining vegetation types consisted of rainforest, secondary regrowth, and scrub. Because of an insufficient number of records ($n = 7$), we excluded the Rainbow Lorikeet from the PGF analysis.

Using GIS, we created buffers of 50 m around the GPS locations of encounters at PPRB and PGF. Buffers were required for calculation of the proportion of different habitats surrounding each location, and they provided a more robust estimate of habitat use than could be achieved by using only the locations of parrots. Buffers also helped to compensate for GPS error (usually 20 m or less, and never more than 50 m; 95% probability) and the imprecision of digital maps. As the habitat patches in our study were relatively large, there was little potential for error due to the incidence of flying birds. Additionally, the use of buffers partially compensates for the imprecision associated with the inclusion of these records.

We evaluated habitat use at PPRB and PGF with GIS by intersecting the encounter buffers with each of the vegetation maps. We calculated the proportion of each vegetation type

per buffer, then summed the proportions across all buffers to obtain an estimate of the total number of observations in each vegetation type. As the sum of all proportions within a single buffer was always one, the total number of observations for each species remained unchanged.

We also used GIS to assess habitat availability at PPRB and PGF. As we used access roads for transects and as starting points for searches in both areas, we compensated for any potential bias toward roadside habitats by considering sampling effort. First, we defined a series of 50-m-wide buffers extending outward from the main road to the edge of the park. Then, we intercepted these road buffers with the vegetation layer to determine the proportion of vegetation at 50-m intervals from the road (i.e., from 0 to 50 m, 50 to 100 m, etc.). In addition, we intercepted the road buffers with the encounter buffers to determine the proportion of encounters recorded at each interval of distance from the road. For each vegetation type, we used the following formula to calculate the weighted proportion of habitat available:

$$\text{available habitat} = \sum_{i=1}^{n} (e_i \times v_i)$$

where i represents the interval of distance from the road (i_1 = 0–50 m, i_2 = 50–100 m, etc.), n represents the interval farthest from the road, e_i represents the proportion of encounters recorded in the i^{th} distance interval, and v_i represents the proportion of vegetation in the i^{th} distance interval.

For the urban-habitat analysis, we used data from point counts in the greater Nouméa area. We pooled the habitat types at the points into the following three categories: urban land with few trees, urban parks and gardens, and woodlands (within and around urban areas). We included only the Rainbow Lorikeet in this analysis, as we heard just four New Caledonian Parakeets and four Horned Parakeets during point counts, and all were in woodlands. We evaluated habitat use in urban areas by counting the number of birds we heard or saw in each habitat type, and we assessed habitat availability by counting the number of times each habitat type was present at each point. We also conducted a 724-km survey by car (with open windows at 50 km hr^{-1} along coastal roads) to assess the Rainbow Lorikeet's habitat selection in relation to settled areas. We generated 100 random points along the road transect, then compared their average distance to the nearest settlement with that of Rainbow Lorikeet sightings (n = 24). Given the speed at which we were traveling, we may not have detected all of the birds present, though this is unlikely to have influenced selection.

We analyzed habitat selection in PPRB, PGF, and urban areas with the Savage selectivity index, as described by Ursúa et al. (2005):

$$w_i = U_i/\pi_i$$

where U_i is the proportion of encounters recorded for a particular species in a specific habitat, and π_i is the proportion of encounters expected for the same habitat (on the basis of the proportion of habitat available). Values of the Savage selectivity index range from 0 (maximum negative selection) to ∞ (maximum positive selection), with 1 representing neutral selection. We calculated the standard error (SE) of the index by following Manly et al. (2002):

$$\text{SE}(w_i) = \sqrt{(1-\pi_i)/(u_+ \times \pi_i)}$$

where u_+ is the total number of encounters recorded.

We also assessed the statistical significance of our results with Bonferroni simultaneous confidence intervals (Manly et al. 2002):

$$w_i \pm z_{\alpha/2k}\,\text{SE}(w_i)$$

where k is the number of categories (i.e., habitats) and α = 0.05. Selection is significant if confidence intervals do not contain the value 1. We use the term "selected" to indicate when a habitat is used more than expected (i.e., confidence intervals above 1), "avoided" when it is used less than expected (i.e., confidence intervals below 1).

ANALYSIS OF EDGE SELECTION

We used GIS to assess selection of forest edges in PPRB. In this analysis, we did not treat trails and dirt roads as edges because they were unlikely to present a barrier to movement between forest patches and the forest canopy often spans trails and certain stretches of road. We identified forested areas on the vegetation map of the park, then defined a series of 50-m-wide buffers from the forest edge, which extended 200 m inside and outside of forest. The cumulative area covered by these buffers delineated our study area for these analyses (110 km^2). Outside of forest, the vegetation consisted almost entirely of maquis.

Using the GPS coordinates of 1049 records (including 243 of feeding birds) from PPRB, we counted the number of times we encountered each species in each of the 50-m buffer zones. We repeated this procedure with randomly defined points in the same area, which represented the expected number of encounters in each buffer zone. We analyzed edge selection with the Savage selectivity index, as described above.

RESULTS

ACTIVITY PATTERNS

Diel fluctuations in encounter rates were similar in all three species studied. Activity began at sunrise and reached a pronounced peak between 7:00 and 9:00 (Fig. 2). There was a lull in activity from late morning until the middle of the afternoon. A minor rise in activity levels was noticeable for all species in the late afternoon, peaking around 17:00 (16:30–17:30). Observations of feeding birds were most frequent several hours after dawn, and foraging activity declined as the morning drew to a close. Feeding gradually increased in the afternoon and appeared to reach a second smaller peak toward the end of the day.

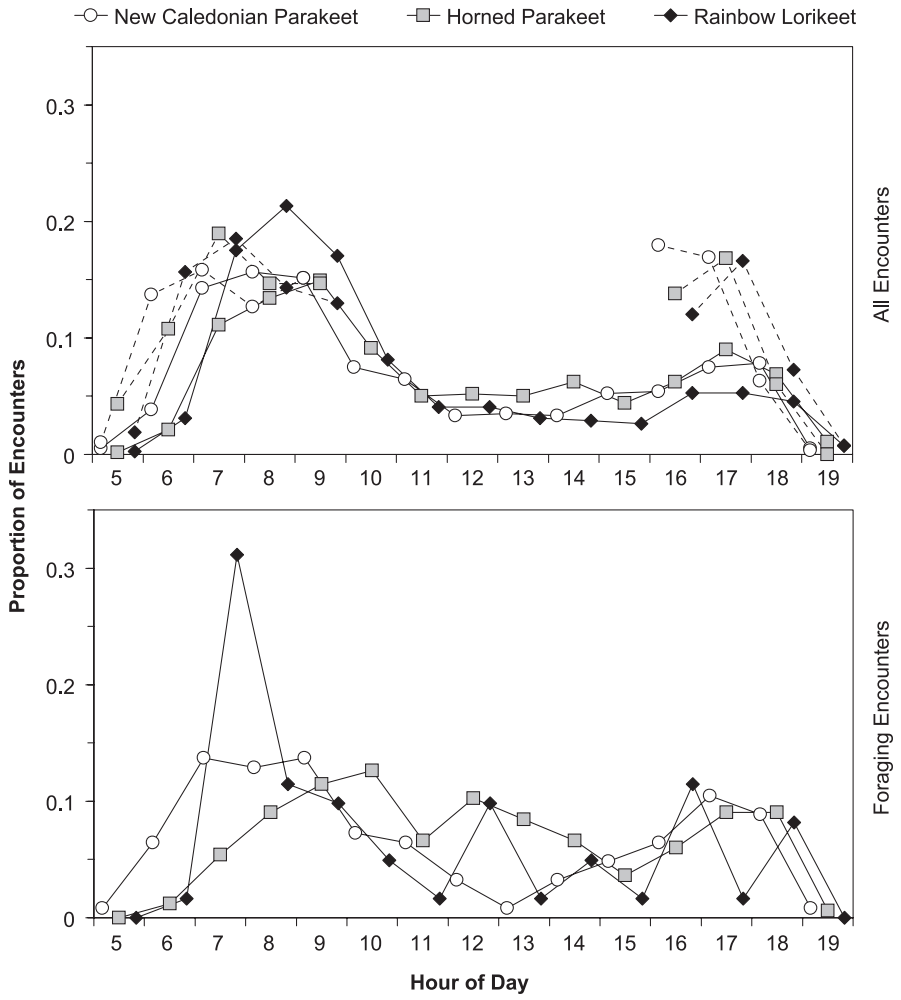

FIGURE 2. Proportion of encounters recorded per hour of the day for the New Caledonian Parakeet (n_{all} = 858; $n_{foraging}$ = 124), Horned Parakeet (n_{all} = 888; $n_{foraging}$ = 166), and Rainbow Lorikeet (n_{all} = 941; $n_{foraging}$ = 61). Dashed lines represent point-count data. Hourly intervals represent encounters recorded 30 min before and after the hour specified (i.e., 6 represents 05:30–06:30).

FLOCK SIZE

Over the duration of the study, we recorded the size of 1276 flocks of parrots (Fig. 3). Flock sizes differed significantly by species (G = 190.72, P < 0.001, df = 8). Flocks of the New Caledonian Parakeet averaged 1.6 birds (SD = 0.8, n = 417), those of the Horned Parakeet 2.0 (SD = 1.1, n = 530). Approximately 98% of the flocks of the New Caledonian Parakeet and 90% of those of the Horned Parakeet comprised fewer than four individuals. We regularly saw Rainbow Lorikeets in large flocks, some of up to 40 birds, but observed no mixed-species flocks. The average flock size recorded for the Rainbow Lorikeet was 3.0 (SD = 3.5, n = 329).

The size of parakeet flocks did not vary considerably with the time of day (Fig. 4). The size of Rainbow Lorikeet flocks gradually increased in the afternoon and peaked in the early evening, as did variability in flock size. The size of New Caledonian Parakeet and Horned Parakeet flocks was consistent through the year (Fig. 5). During the warm, relatively dry season (September–December, when most nesting occurs), Rainbow Lorikeets formed small flocks averaging 2.4–3.1 individuals. The size and variability of Rainbow Lorikeet flocks appeared to increase during the latter part of the hot, wet season (January–April, when young fledge) and again during the latter part of the cool season (May–August). For all of the species, average flock sizes were similar from year to year, and the overlap of confidence intervals suggests that annual variation was minor (Table 1).

HABITAT USE

Horned Parakeets perched (G = 35.2, P < 0.001, df = 3) and foraged (G = 63.4, P < 0.001, df = 3) significantly higher than New Caledonian Parakeets (Table 2, Fig. 6). Horned Parakeets occasionally descended into the understory to feed, yet we seldom saw them foraging near the ground, and observations of feeding birds generally increased with height. In contrast, New Caledonian Parakeets foraged mainly at low heights. Although the

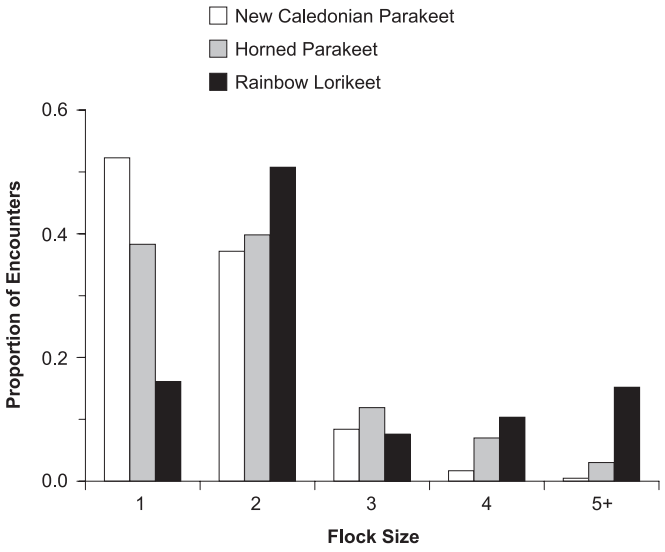

FIGURE 3. Proportion of encounters with variously sized flocks of the New Caledonian Parakeet (n = 417), Horned Parakeet (n = 530), and Rainbow Lorikeet (n = 329).

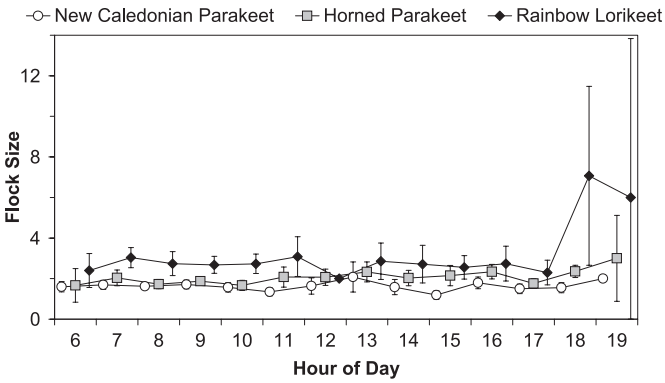

FIGURE 4. Average size (± 95% CI), by hour, of flocks of the New Caledonian Parakeet (n = 411), Horned Parakeet (n = 526), and Rainbow Lorikeet (n = 328). Hourly intervals represent encounters recorded 30 min before and after the hour specified (i.e., 6 represents 05:30–06:30).

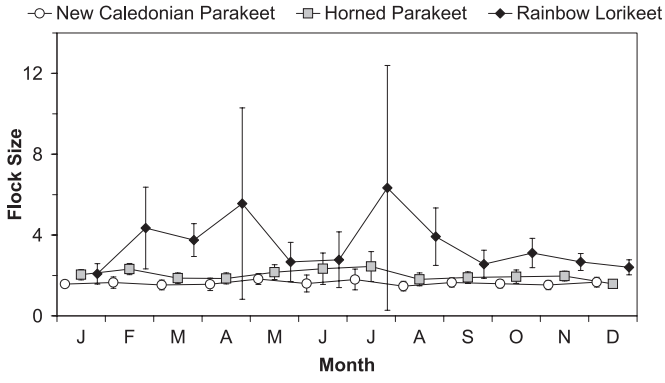

FIGURE 5. Average size (± 95% CI), by month, of flocks of the New Caledonian Parakeet (n = 417), Horned Parakeet (n = 530), and Rainbow Lorikeet (n = 329).

TABLE 1. Average size (± 95% CI), by year, of flocks of the New Caledonian Parakeet (n = 417), Horned Parakeet (n = 529), and Rainbow Lorikeet (n = 329).

Year	New Caledonian Parakeet	Horned Parakeet	Rainbow Lorikeet
2002	1.5 ± 0.3	1.7 ± 0.2	2.8 ± 0.5
2003	1.6 ± 0.2	2.1 ± 0.2	3.5 ± 0.8
2004	1.7 ± 0.2	1.7 ± 0.2	2.4 ± 0.3
2005	1.6 ± 0.3	1.7 ± 0.3	2.5 ± 0.8
2006	1.7 ± 0.2	1.6 ± 0.2	3.3 ± 0.9
2007	1.5 ± 0.2	2.0 ± 0.3	4.2 ± 2.4
2008	1.7 ± 0.2	2.3 ± 0.2	3.3 ± 1.1
2009	1.5 ± 0.2	2.1 ± 0.3	7.8 ± 7.4

number of encounters with foraging Rainbow Lorikeets was relatively small (n = 39), their feeding habits appeared to resemble those of the New Caledonian Parakeet, with a general decline in foraging as height increased. Despite this, the Rainbow Lorikeet's feeding heights were not distinctly stratified within forest. The heights at which each species flew were not significantly different (G = 3.6, P = 0.73, df = 6).

In PPRB, New Caledonian Parakeets preferred slope forest and maquis to valley forest (Fig. 7). While foraging, they favored maquis but also used slope forest. In contrast, Horned Parakeets selected valley forest and avoided maquis, whether they were feeding or not. Rainbow Lorikeets selected valley forest, yet they also used maquis, and most encounters with foraging lorikeets were in this habitat. At PGF, parakeets used rainforest, secondary regrowth, and scrub and plantations according to their availability. In urban areas, Rainbow Lorikeets selected parks and gardens but also used urban land with few trees. On average, Rainbow Lorikeets were located much closer (0.10 km, SD = 0.15 km, n = 24) than random points (1.05 km, SD = 1.88 km, n = 100) to settlements (t-test, P < 0.001).

Habitat use in PPRB varied seasonally (Fig. 8). New Caledonian Parakeets selected slope forest during the hot, wet season and maquis in the warm, dry season. For most of the year, Horned Parakeets preferred valley forest and consistently avoided maquis. Rainbow Lorikeets selected maquis during the warm, dry season and generally avoided slope forest.

In PPRB, New Caledonian Parakeets selected forested habitat, yet they particularly favored habitat at the edge of forest (Fig. 9). Despite this, New Caledonian Parakeets mostly avoided areas beyond 50 to 100 m from forest. Horned Parakeets preferred forested areas, especially to feed, yet selection decreased toward the edge of forest, and the species avoided areas outside of forest. Rainbow Lorikeets selected areas close to forest edges and often fed at the verge of forest, yet selection declined sharply in the forest interior and beyond 50 m from forest.

TABLE 2. Average height (m) of New Caledonian Parakeets, Horned Parakeets, and Rainbow Lorikeets observed in New Caledonia.

	Flying			Perching			Feeding		
Species	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
New Caledonian Parakeet	13	6	55	10	6	138	7	5	101
Horned Parakeet	12	6	41	12	4	237	12	5	143
Rainbow Lorikeet	14	7	113	13	7	57	7	6	39

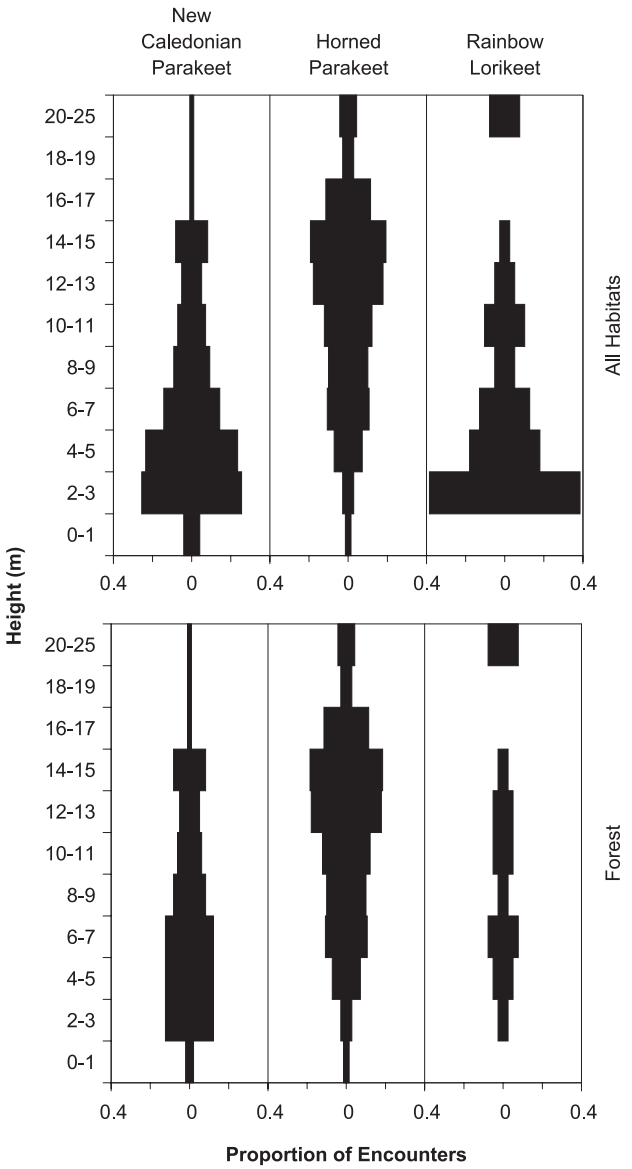

FIGURE 6. Proportion of New Caledonian Parakeets (n_{all} = 98; n_{forest} = 68), Horned Parakeets (n_{all} = 140; n_{forest} = 139), and Rainbow Lorikeets (n_{all} = 39; n_{forest} = 15) encountered foraging at various heights in all habitats studied and within forest.

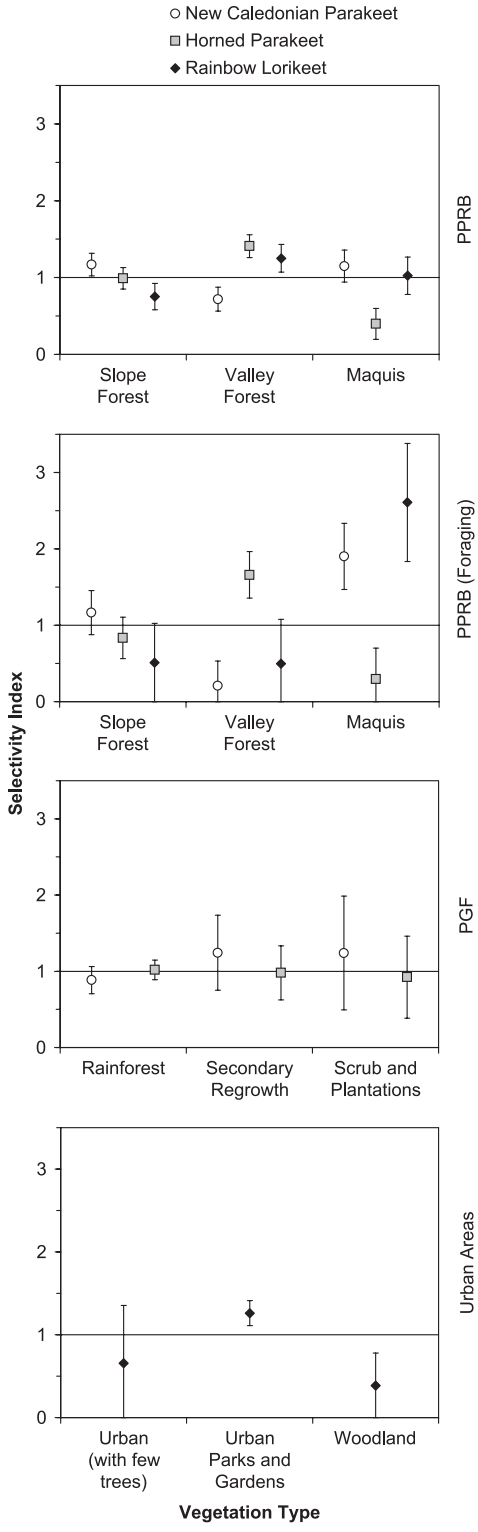

FIGURE 7. Habitat selection by the New Caledonian Parakeet (n_{PPRB} = 407; $n_{PPRB(foraging)}$ = 99; n_{PGF} = 86), Horned Parakeet (n_{PPRB} = 443; $n_{PPRB(foraging)}$ = 112; n_{PGF} = 165), and Rainbow Lorikeet (n_{PPRB} = 305; $n_{PPRB(foraging)}$ = 31; n_{urban} = 120) based on observations in PPRB, PGF, and urban areas. Selection is significant if confidence intervals do not contain the value 1.

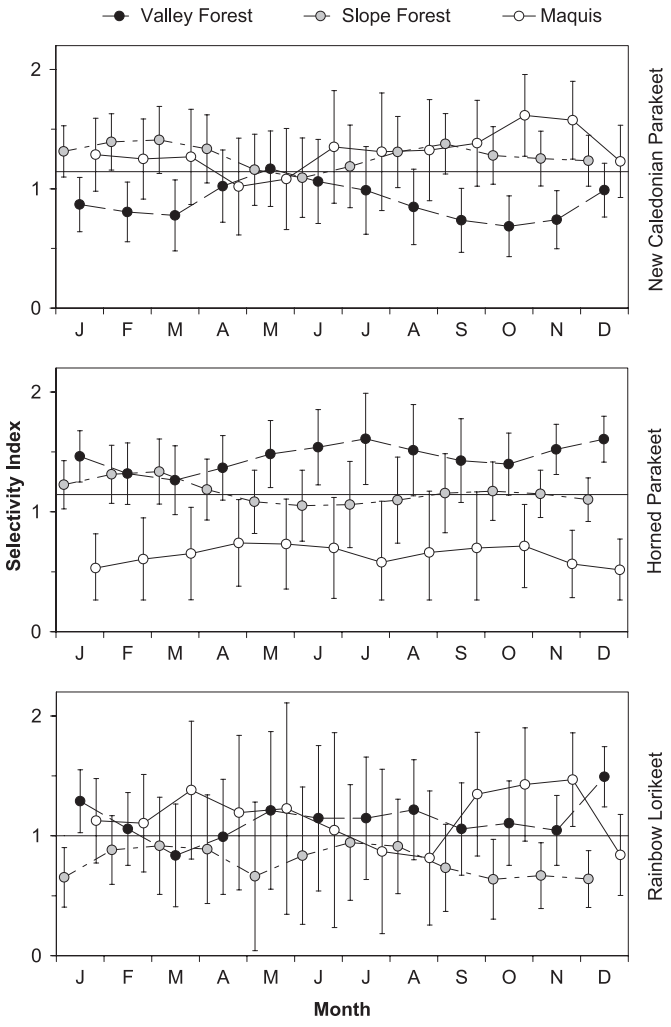

FIGURE 8. Seasonal habitat selection by the New Caledonian Parakeet (n = 407), Horned Parakeet (n = 443), and Rainbow Lorikeet (n = 305) in PPRB, calculated as 3-month running means. Selection is significant if confidence intervals do not contain the value 1.

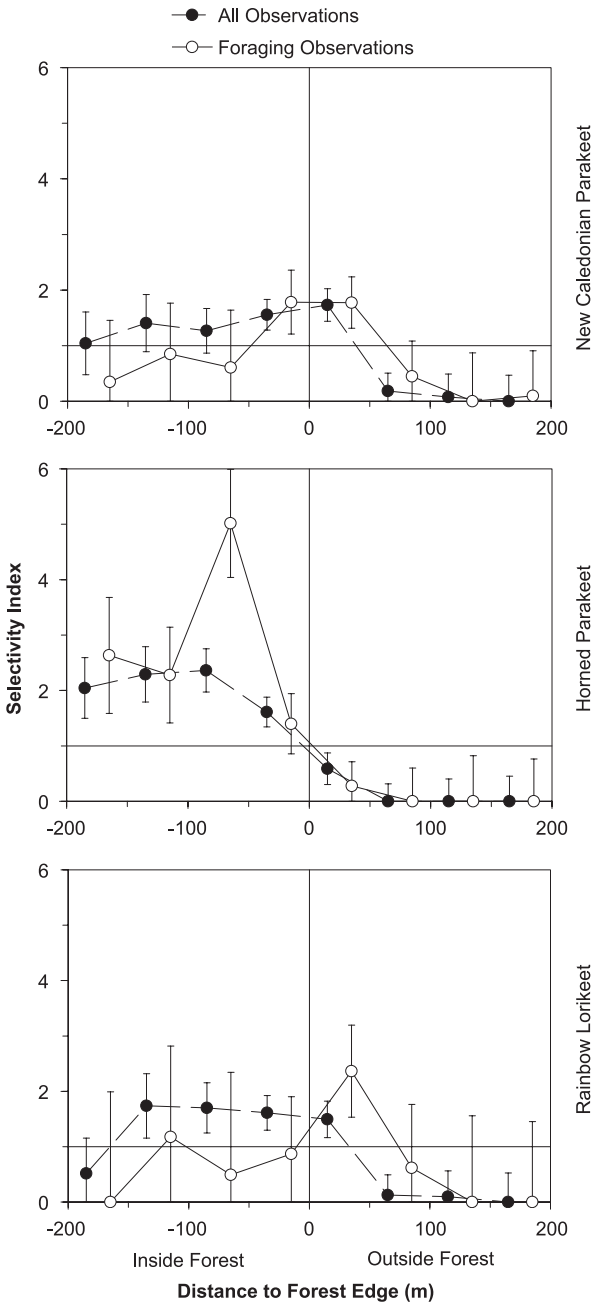

FIGURE 9. Selection relative to forest edges, based on observations of the New Caledonian Parakeet (n_{all} = 368; $n_{foraging}$ = 100), Horned Parakeet (n_{all} = 391; $n_{foraging}$ = 112), and Rainbow Lorikeet (n_{all} = 290; $n_{foraging}$ = 31) in PPRB. Selection is significant if confidence intervals do not contain the value 1.

DISCUSSION

PATTERNS OF ACTIVITY AND FLOCKING

The parrots of mainland New Caledonia have a bimodal pattern of activity, with peaks during the morning and late afternoon, separated by a period of reduced activity. This is typical of Psittaciformes in the tropics (e.g., Hardy 1965, Pizo et al. 1997, Gilardi and Munn 1998) and corresponds with patterns of activity of the Ouvéa Parakeet (*Eunymphicus uvaeensis*) on the neighboring island of Ouvéa (Robinet et al. 2003). Daybreak provides diurnal parrots with an opportunity to replenish their energy reserves, and we found that parrots (particularly Rainbow Lorikeets) often spent the early hours foraging. Temperatures are generally lower during the morning and evening, so parrots probably expend less energy to keep themselves cool during these periods than they would at other times of the day. However, it is unknown whether the inactivity at midday is associated with rising temperatures (Wyndham 1980, Pizo et al. 1997) or whether parrots use this time to rest and digest their morning meal (Gilardi and Munn

1998). Research on Meyer's Parrot (*Poicephalus meyeri*) in the Okavango Delta, Botswana, suggests that such patterns of activity may be due to an interaction of physiological (e.g., crop size), behavioral (e.g., roosting and dispersal), and weather-related factors (e.g., fluctuations in temperature and rainfall) (Boyes and Perrin 2010). Predation may influence activity patterns as well (Westcott and Cockburn 1988, Gilardi and Munn 1998). However, New Caledonian parrots are likely to be active during the same periods as avian predators, such as goshawks (e.g., Rutz 2006).

The bimodal pattern of activity we observed should be taken into consideration during censuses, as it may influence the outcome of density estimates (Marsden 1999). For a reasonable estimate of the density of parakeets in New Caledonia (e.g., Barré et al. 2010), we recommend that counts be concentrated during one of the peak activity periods, preferably in the morning before 10:00, when detectability is likely to be highest.

Some species of parrots typically form pairs or small flocks (e.g., the Red Shining Parrot, *Prosopeia tabuensis*; Rinke 1988), while others aggregate into large flocks, sometimes of hundreds (e.g., the Burrowing Parrot, *Cyanoliseus patagonus*; Masello et al. 2006) or even thousands of individuals (e.g., the Budgerigar, *Melopsittacus undulatus*; Wyndham 1980). There are a number of theories on the advantages of flocking, yet it is generally considered to be a behavioral adaptation to either compensate for variations in food availability (Cannon 1984b) or assist with predator detection and avoidance (Westcott and Cockburn 1988). New Caledonian Parakeets and Horned Parakeets consistently formed small flocks whose sizes remained relatively constant through the day and through the year. As granivores, these species have apparently not had an evolutionary incentive to form large flocks to search for food. Rainbow Lorikeets, on the other hand, are gregarious birds that form substantial flocks, particularly while tracking nectar (Franklin and Noske 1999, Symes and Marsden 2007). We occasionally observed large flocks, of up to 40 individuals, yet most flocks consisted of only a few birds. We suspect that we would have recorded a larger average flock size for the Rainbow Lorikeet if we had spent more time in urban areas, where there is a high concentration of flowering plants.

Rainbow Lorikeet flocks were fairly consistent in size through most of the day, and the observed increase in flock size at the end of the day reflects communal roosting (Symes and Perrin 2003). Sizes of Rainbow Lorikeet flocks also varied on a monthly basis, as is typical of many parrots (Chapman et al. 1989, Collins and Kares 1997, South and Pruett-Jones 2000). Numerous factors may induce seasonal changes in flock size, yet our results suggest that food supply (Cannon 1984b) and breeding behavior (Chapman et al. 1989) are likely to have contributed to these patterns.

In New Caledonia, the Rainbow Lorikeet breeds mainly from November to January (Hannecart and Létocart 1980), so the smaller flock sizes observed during this period may be associated with the formation of breeding pairs (Higgins 1999). During the breeding season, there is a sharp increase in the number of flowers and fruits being produced, with flowering peaking in October and fruiting peaking in December (Carpenter et al. 2003). As a result, food is probably plentiful at this time of the year, which may encourage breeding. After February, the size and variability of flocks increased considerably. We suspect that this is due to the arrival of new offspring and to a decline in flowering plants, which might promote a shift to large feeding flocks (Cannon 1984b, Carpenter et al. 2003). The formation of large flocks may be critical to the survival of young Rainbow Lorikeets, as flocking is likely to minimize their risk of predation (Westcott and Cockburn 1988) and the young are probably able to forage more efficiently in a flock than on their own (Cannon 1984b, South and Pruett-Jones 2000). However, the observed daily and monthly variations in flock size are likely to make density estimates more difficult for this species than for the parakeets.

HABITAT USE

The habitat preferences of the New Caledonian Parakeet appear to be similar to those of its close relatives, the Red-crowned Parakeet (*Cyanoramphus novaezelandiae*), the Yellow-crowned Parakeet (*C. auriceps*), and the Orange-fronted Parakeet (*C. malherbi*) of New Zealand, which inhabit forest (including forest edges) yet are occasionally found in scrublands and open areas (Taylor 1985, Greene 1998). We encountered New Caledonian Parakeets most often in the forest interior, but they also selected areas just beyond the edge of forest. In PPRB, maquis is the main vegetation type bordering forest, and our results suggest that this habitat is likely to be used only if it is close to forest. There is minimal shelter in maquis, so large expanses of maquis are unlikely to be suitable for the New Caledonian Parakeet unless they are interspersed with patches of forest. New Caledonian Parakeets also had a close association with slope forest. Compared to valley forest, slope forest is richer in plant species, has a greater number of plants with small stems, and fewer large trees (Jaffré and Veillon 1991). Preliminary research into the New Caledonian Parakeet's diet suggests that this species may frequent relatively open habitats such as maquis, slope forest, and forest edges because of a preference for food species that occur mainly in early successional vegetation (unpubl. data). At PGF, scrub and secondary regrowth (including savanna) are likely to offer similar opportunities for foraging, and New Caledonian Parakeets seem to cope well with the habitat composition there.

Horned Parakeets are particularly dependent on forest and rarely venture far beyond its limits. Although they appear to prefer rainforest, they enter nearby pine plantations and areas of secondary regrowth when there is food available. They seldom occur near urban settlements and tend to avoid maquis and other low, open habitats. Horned Parakeets feed mostly in tall trees and are generally found higher above the ground than are New Caledonian Parakeets. Their

preference for valley forest is probably associated with the types of food plants found there rather than with slope per se. As the New Caledonian Parakeet and Horned Parakeet are both granivorous, it is plausible that the type of vertical stratification and habitat segregation we observed is the result of resource partitioning, which allows these similar species to coexist. The species appear to have distinct habitat niches with minimal overlap, probably reducing the potential for interspecific competition. A thorough examination of their diets might help to clarify this matter, particularly if consideration is given to the habitat type and height of each species' favorite food species. Dietary preferences certainly exist, as only 23 of the 140 plants recorded as food for the New Caledonian Parakeet and Horned Parakeet are consumed by both species (unpubl. data). It is unlikely that there is competition for nest sites, as the availability of tree hollows does not appear to be a limiting factor for parakeets on the New Caledonian mainland (Theuerkauf et al. 2009a).

The Rainbow Lorikeet is mostly nectarivorous (Cannon 1984a), so there is little potential for dietary overlap between it and the two parakeets, and it is unlikely that variations in its use of habitat are the result of resource partitioning. Rainbow Lorikeets cope well in most environments where food is readily available, especially in areas with trees near human habitation. Their diet includes many exotic plant species (unpubl. data), and the introduced flowering shrubs and trees in urban parks and gardens probably provide them with an abundant source of nectar. The floristic composition of valley forest differs considerably from that of slope forest (Jaffré and Veillon 1991) and maquis, and we suspect that the selection of these habitats by Rainbow Lorikeets is influenced by the seasonality of flowering plants. The relatively high incidence of Rainbow Lorikeets feeding low is due primarily to observations in maquis and gardens. In forest, we found no clear pattern of vertical stratification, although we often observed Rainbow Lorikeets foraging high. In northern Australia, the closely related Red-collared Lorikeet (*T. h. rubritorquis*) also forages in the highest stratum available (Brooker et al. 1990). Rainbow Lorikeets are easily spotted in open habitats, including the top of the forest canopy, yet they are relatively difficult to observe if they are feeding quietly on nectar in forest. It is much easier to detect parakeets feeding in the canopy because fruits, leaves, and other plant parts fall to the ground as a result. Consequently, we have probably underestimated the number of times Rainbow Lorikeets foraged in the upper levels of the forest canopy.

Although the New Caledonian Parakeet and Rainbow Lorikeet both use maquis and occupy forest edges, there is no shortage of these habitats in New Caledonia. The New Caledonian Parakeet is dependent on forests, particularly for nest hollows (Theuerkauf et al. 2009a), yet our results reveal that they are tolerant of forest fragmentation and are closely associated with areas in the early stages of succession. The natural habitat of this species probably comprises a mosaic of forest interspersed with small areas of primary maquis (on ridges) and successional maquis (e.g., regrowth in natural clearings). In contrast, Horned Parakeets appear to prefer large, mature tracts of forest and are probably more susceptible to habitat modification. Forest degradation from mining, logging, and fire is likely to increase edge effects and reduce the availability of tall trees, on which this species depends. Forests also provide critical habitat for many other endemic species, including the endangered Kagu (*Rhynochetos jubatus*; Létocart and Salas 1997), whose reproductive success is influenced by habitat quality (Theuerkauf et al. 2009b). Preservation of primary and mature forests should therefore be viewed as an essential element of bird conservation in New Caledonia.

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