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FORAGING ECOLOGY OF THE RED-CROWNED PARAKEET (*CYANORAMPHUS NOVAEZELANDIAE NOVAEZELANDIAE*) AND YELLOW-CROWNED PARAKEET (*C. AURICEPS AURICEPS*) ON LITTLE BARRIER ISLAND, HAURAKI GULF, NEW ZEALAND

Summary: The diet of red-crowned parakeets (*Cyanoramphus novaezelandiae novaezelandiae*) and yellow-crowned parakeets (*C. auriceps auriceps*) was compared on Little Barrier Island, New Zealand between 1986 and 1987. Significant dietary differences were observed in these sympatric, congeneric species. Yellow-crowned parakeets ate significantly more invertebrates than red-crowned parakeets, which fed on a greater variety of plant foods. Red-crowned parakeets were found in all vegetation types depending on the availability of food and were commonly seen foraging on the ground in open habitats. In contrast, yellow-crowned parakeets were more arboreal and showed distinct preferences for forested habitats. The existence of both parakeet species in sympatry is examined as is the ecological importance of invertebrate food sources. Observed differences in the behaviour and ecology of parakeet species on Little Barrier Island are used to provide insight into the present day distribution and status of parakeets on mainland New Zealand.

Keywords: Red-crowned parakeet; yellow-crowned parakeet; kakariki; *Cyanoramphus novaezelandiae*; *Cyanoramphus auriceps*; parrots; psittaciformes; diet; foraging ecology.

Introduction

The red-crowned parakeet (*Cyanoramphus novaezelandiae novaezelandiae*) and the yellow-crowned parakeet (*C. auriceps auriceps*), known collectively as kakariki, are forest dwelling parakeets endemic to New Zealand. At the time of European settlement both species were common throughout forested areas of New Zealand (Buller, 1870; Reischek, 1884; Fulton, 1907). Persecution as crop pests (Buller, 1888; Oliver, 1955), deforestation, disease and introduced predators have probably all contributed to the present restricted distribution of these species (Harrison, 1970; King, 1984; Bull, Gaze and Robertson, 1985). Red-crowned parakeets are now uncommon or locally extinct in both the North Island and South Island and are now common only on Stewart Island and a number of smaller offshore islands (Falla, Sibson and Turbott, 1978; Taylor, 1985; O'Donnell and Dilks, 1986). Although the decline of the yellow-crowned parakeet is thought to have closely paralleled that of its congener (Taylor, 1985), it has been suggested that this species has since undergone a period of expansion, as it is now moderately common in some large indigenous forest remnants throughout the two main islands of New Zealand (Falla *et al.*, 1978; Taylor, 1985).

Previous anecdotal observations suggested that the diets of red-crowned and yellow-crowned parakeets were similar. Both species have been observed feeding primarily on flowers, fruits, seeds, leaves and buds with invertebrates forming a relatively minor component of both species' diet (Wilkinson and Wilkinson, 1952; Oliver, 1955; Moon, 1960; Williams, 1976; Falla *et al.*, 1978).

Recent studies which attempted more rigorous quantification of parakeet diets have, at least for the red-crowned parakeet, largely confirmed these earlier observations (Taylor, 1975; Dawe, 1979; Bellingham, 1987; Nixon, 1994). Nevertheless, these studies have not compared the diets of red-crowned and yellow-crowned parakeets where they occur in sympatry. Ecological relationships between parakeet species on the main islands of New Zealand are now difficult to determine due to the virtual disappearance of the red-crowned parakeet from mainland forests (Taylor, 1985). Only on the few (largely unmodified) offshore islands where both species occur can the feeding ecology of these species be examined within the same range of habitats.

This paper describes and compares the diets of red-crowned parakeets and yellow-crowned parakeets on Little Barrier Island, Hauraki Gulf, New Zealand.

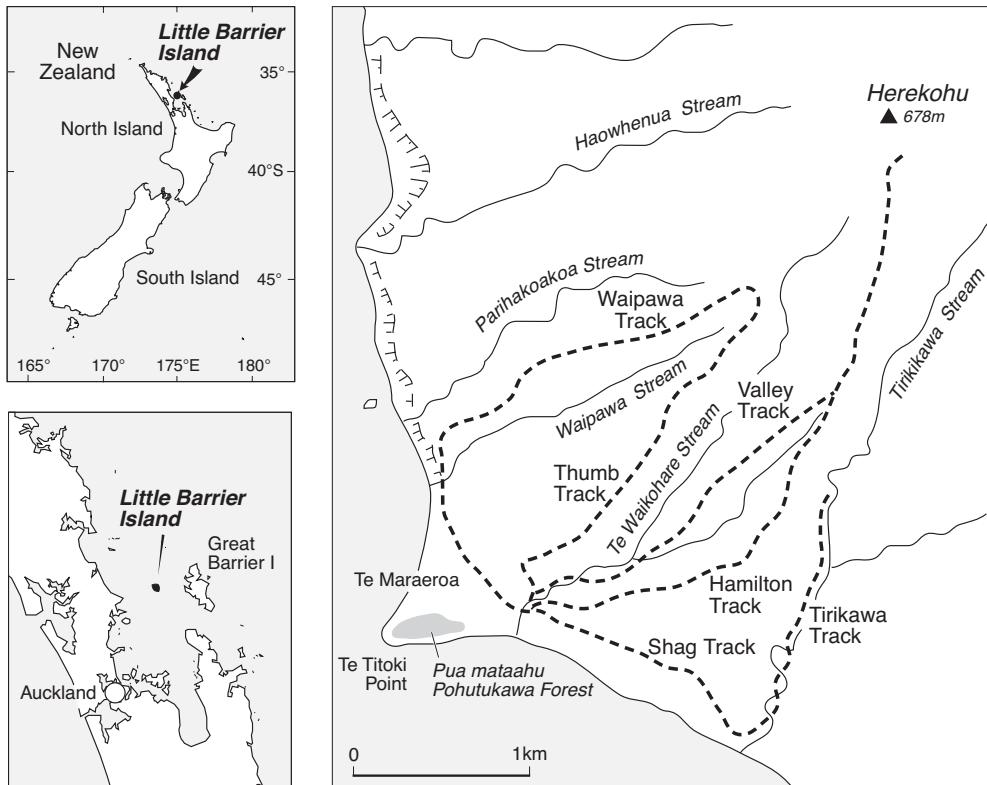


Figure 1: Location of Little Barrier Island (Hauturu) and study area.

Study Area and Methods

Little Barrier Island or Hauturu ($36^{\circ}12'S$, $175^{\circ}7'E$) lies approximately 24 km from Cape Rodney on the east coast of the North Island at the northern entrance to the Hauraki Gulf (Fig. 1). The study area was located on the southwestern quarter of the island and extended from sea-level to approximately 550 m a.s.l. Important vegetation types (Hamilton and Atkinson 1961) included coastal communities dominated by pohuehue (*Muehlenbeckia complexa*)¹, sedges (*Carex virgata*), introduced herbaceous weed species, rank pasture grasses, pohutukawa (*Metrosideros excelsa*) forest, areas of scattered kanuka (*Kunzea ericoides*) scrub and the occasional large puriri (*Vitex lucens*). Tall seral kanuka forest covered the lower third of the island with small stands of kauri (*Agathis australis*), hard beech (*Nothofagus truncata*) and northern rata (*Metrosideros robusta*) at mid-altitudes. At slightly

higher altitudes and in the larger and wetter valleys, the canopy was dominated by northern rata and tawa (*Beilschmiedia tawa* incl. *B. tawaroa*, C. Gardiner 1996). Above 450 m the forest was dominated by tawhero (*Weinmannia silvicola*) and tawaroa, with *Quintinia acutifolia*, Hall's totara (*Podocarpus hallii*) and miro (*Prumnopitys ferruginia*) co-dominating.

Diet

Feeding observations of red-crowned parakeets and yellow-crowned parakeets were collected during two-week periods every month (except for May 1987) over a 12 month period (October 1986 - September 1987). For each parakeet sighted, the first food item seen taken was recorded following the 'first food method' of Magrath and Lill (1983). The spatial organisation of the parakeets (non-exclusive home-ranges) and the collection of observations from a wide variety of habitats significantly reduced the risk of re-sampling the same individuals. The results can therefore be regarded as statistically independent.

¹Botanical nomenclature follows Allan (1961); Moore and Edgar (1970); Connor and Edgar (1987). Ornithological nomenclature follows Turbott (1990).

Temporal bias in observations of parakeet diet was minimised by varying both the time of day of observation (daylight hours from one hour after sunrise) and the time through which major vegetation types were traversed during each month. Each food item consumed was classified as one of five different food types: flowers/flower buds, fruits/berries, seeds/seed capsules/fallen seed, vegetative growth (e.g., leaves and leaf buds), or invertebrates. Frequencies of feeding observations for each month and for both parakeet species were pooled into four discrete seasons (spring; September, October, November, summer; December, January, February, autumn; March, April, May, winter; June, July, August) and the frequency data then analysed using Chi-square tests for independence. This data was then transformed into percentages from which 95% confidence limits were calculated and graphed. Seasonal differences in diet were compared between both parakeet species, except for summer months due to the very small sample size for yellow-crowned parakeets ($n=33$), which resulted in correspondingly high 95% confidence intervals. The importance of nectar within the diet of parakeets was not determined because of the species' tendency to either consume or destroy part or all of the flower.

The vegetation type and the vertical height above the ground of each individual when first sighted was also recorded. Data were scored as one of five groups: 0m, 1-4m, 5-9m, 10-14m, 15m+. The percentage of observations ($\pm 95\%$ CI) of parakeets within these height classes throughout the year was compared between species using a Chi-square test.

The relative seasonal abundance of fruits and berries, seeds and seed capsules, flowers and flower buds and vegetative growth for a number of the more common plant species was assessed using a logarithmic scale (0-10,000) to provide a subjective estimate of the variation in food availability throughout the study. Seasonal abundance of potential food sources was estimated on a monthly basis:

- | | |
|--------------|---|
| (1) absent | nothing (0) of a specific food type available on any of the plants examined; |
| (2) present | only small amounts (ones - tens) of a given food type present on scattered individual plants; |
| (3) common | food type widespread (hundreds - thousands) and available on the majority of plants but not abundant; |
| (4) abundant | large amounts (tens of thousands) of a given food type present on most plants. |

Results

Red-crowned parakeets were recorded eating parts of 57 different food species ($n=1745$ observations) throughout the study period. Only 17 species of this total accounted for more than 5% of the diet in any one month and were therefore considered 'important' dietary components (Table 1). In comparison, yellow-crowned parakeets had a much less diverse diet with only 17 species of plant and insect ($n=237$ observations) consumed during the same period. The

Table 1: Major food items (accounting for >5% of the diet in any one month) of red-crowned parakeets and yellow-crowned parakeets on Little Barrier Island, October 1986-September 1987.

Food species	Food type
Red-crowned parakeets	
Plants	
<i>Agathis australis</i>	male cones, seed
<i>Coprosma arborea</i>	fruits
<i>Coprosma macrocarpa</i>	flower buds
<i>Holcus lanatus</i>	seed
<i>Knightia excelsa</i>	flower buds
<i>Kunzea ericoides</i>	flower buds, seed capsules
<i>Metrosideros excelsa</i>	flowers, seed capsules
<i>Muehlenbeckia complexa</i>	flower buds, flowers, seed
<i>Nothofagus truncata</i>	leaf buds, flower buds, flowers, seed
<i>Phytolacca octandra</i>	fruit
<i>Pittosporum umbellatum</i>	flower buds, flowers
<i>Poa annua</i>	seed
<i>Pseudopanax edgerleyi</i>	fruit
<i>Solanum americanum</i>	flowers, fruits
<i>Vitex lucens</i>	flower buds, flowers
Invertebrates	
<i>Ctenochiton viridis</i>	
<i>Sensoriaphis nothofagi</i>	
Yellow-crowned parakeets	
Plants	
<i>Alseuosmia macrophylla</i>	fruit
<i>Coprosma arborea</i>	fruit
<i>Dianella intermedia</i>	fruit
<i>Dysoxylum spectabile</i>	flower buds
<i>Kunzea ericoides</i>	flower buds
<i>Meliczytus ramiflorus</i>	flowers
<i>Metrosideros excelsa</i>	leaf buds, flower buds
<i>Myrsine australis</i>	fruits
<i>Nothofagus truncata</i>	leaf buds, flower buds, flowers, seed
<i>Pittosporum umbellatum</i>	flower buds, flowers, seed
<i>Pseudopanax arboreus</i>	fruit
Invertebrates	
Beetle larvae/caterpillars	
<i>Eriococcus orariensis</i>	
<i>Sensoriaphis nothofagi</i>	

majority of these species (14), however, accounted for 5% or more of the yellow-crowned parakeet diet in any one month. The number of feeding observations made on yellow-crowned parakeets was more than enough to record the range of food types taken by this species (Fig. 2).

Thirteen food species, consisting of a number of food types, were consumed by both species of parakeet (Greene, 1988). Seven of these species were important dietary components (>5% of the monthly diet) for both red-crowned and yellow-crowned parakeets (Table 1). Four other plant species were important to only yellow-crowned parakeets. The remaining two species (*Pyrossia serpens* and *Metrosideros fulgens*) formed an insignificant part of both species' diets.

Both red-crowned parakeets and yellow-crowned parakeets exhibited significant differences in the food types consumed both within and between seasons (Fig. 3a and 3b, Table 2). Flowers (including flower buds) and seeds were important components of the red-crowned parakeet diet throughout the year (Fig. 3a). Fruits and berries were also important, but only from March through to the end of July (autumn and winter). Vegetative growth and invertebrates were relatively minor components of this species diet. Vegetative growth only became important during winter and spring and the two species of invertebrates seen consumed were only important in spring (Table 1).

Invertebrates, such as homopterans and various coleopteron and lepidopteran larvae, formed the basis of the yellow-crowned parakeet diet throughout most of the year (Table 1, Fig. 3b). Invertebrates were particularly important from

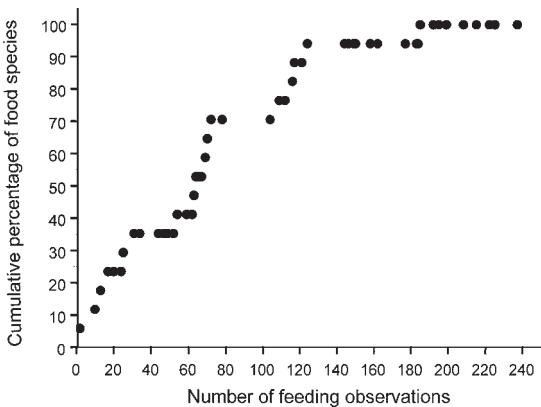


Figure 2: Relationship between number of feeding observations and number of food species consumed by yellow-crowned parakeets on Little Barrier Island.

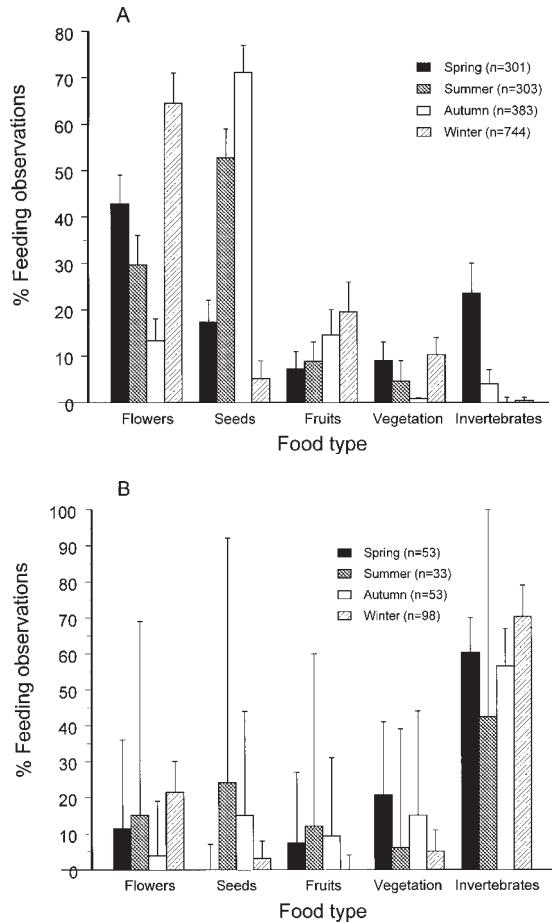


Figure 3: Seasonal variations in major food types consumed by (A) red-crowned parakeets (n=1731) and (B) yellow-crowned parakeets (n=237) on Little Barrier Island, October 1986-September 1987, expressed as percentage of feeding observations (+ 95% confidence limits).

autumn until spring but the small sample size in the summer data prevents determination of the most important food category in that season. Flower buds and flowers were also important, but not statistically so, when large numbers became available in spring (Fig. 3b). Fruits, berries and seeds were only occasionally important elements of the yellow-crowned parakeet diet.

Yellow-crowned parakeets consumed significantly more invertebrates than red-crowned parakeets ($\chi^2 = 41.7, d.f. = 2, P < 0.0001$) in autumn, winter and spring. No other significant differences in the seasonal diet of red-crowned parakeets and yellow-crowned parakeets were detected.

Table 2: Variation between food types consumed and between seasons for red-crowned parakeets (n=1731) and yellow crowned parakeets (n=237).

Parakeet species	Variation between food types	Between season variation
Red-crowned parakeets	χ^2_{12} 163.7 p<0.0001	χ^2_{12} 128.9 p<0.0001
Yellow-crowned parakeets	χ^2_{12} 34.8 p<0.001	χ^2_{12} 27.8 p<0.006

Diet in relation to food availability

Seasonal variations in the percentage of particular plant foods consumed by both parakeet species reflected changes in the temporal availability of these foods. Flowers were available year round, but seeds (as well as fruits and berries) were generally only available for a relatively small part of the year (Fig. 4). Large amounts of seed only began to become readily available during summer (December and January), and had almost completely disappeared by winter (June).

Red-crowned parakeets fed primarily on seed for as long as it was available (Fig 3a and Fig. 4). Sequential changes in the consumption of plant foods generally reflected temporal differences in their availability (Fig. 4). For example, beech seed was an important component of the diet from October to February, followed by kanuka seed as it became

available in February then kauri seed in March (Fig. 4). The fruits of inkweed (*Phytolacca octandra*), an introduced weed, were the most important dietary component (26.2 ± 10%) during winter (Table 1). Flowers became important in July (Fig. 4) with the mast flowering of hard beech. Subsequent months (August - September) saw a decrease in the percentage of beech flowers consumed, and an increase in the consumption of flowers of other species such as haekaro and puriri (Greene, 1988).

Marked seasonal changes in diet were not as evident for yellow-crowned parakeets, possibly because of their greater reliance on invertebrates throughout the year (Fig. 3b). Pooling of invertebrate feeding observations, however, obscured seasonal variations in the species of invertebrates consumed and their relative abundance. For example, scale insects were particularly abundant on kanuka between April and July, and aphids were abundant

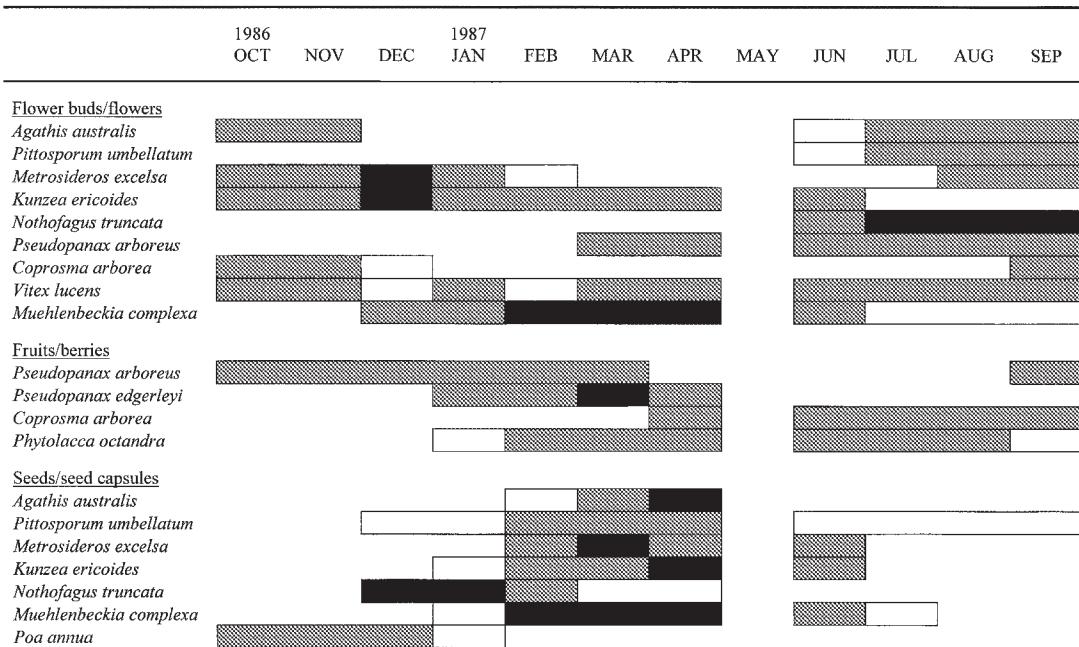


Figure 4: Availability of plant food species and food types within the Little Barrier Island study area, October 1986-September 1987 (no data collected for May 1997). Open bars = present; shaded bars = common; solid bars = abundant.

on the new leaves of hard beech in August and September. The invertebrate component of yellow-crowned parakeets diet changed accordingly. The increased importance of flowers and buds in July, August, and September followed similar trends to that of red-crowned parakeets.

Seeds, seed capsules and fallen seed were of minor importance in the diet of yellow-crowned parakeets (Fig. 3b) except during January and February when hard beech seeds were particularly abundant (Fig. 4). Fruit was even less important (Fig. 3b) even though considerable quantities were available during some months (Fig. 4).

Habitat selection

Red-crowned parakeets were particularly well represented in the more open vegetation types with $29.6 \pm 3.0\%$ of observations in *Muehlenbeckia* and pasture/rank grass communities (Fig. 5a). In contrast, yellow-crowned parakeets preferred heavily forested vegetation types, with $90.6\% \pm 4.0\%$ of observations in the *Leptospermum* and Kauri/Beech forest types (Fig. 5b), and were only rarely seen frequenting the more open habitat types ($<7\%$ of observations). Both parakeet species occurred at all altitudes on Little Barrier Island with no suggestion of altitudinal separation.

Of the seven major forest types examined, Rata/Tawa (particularly during the winter months) and Tawhero/Tawa were the least favoured by both parakeet species (Figs 5a and 5b) although differences in forest structure (e.g., canopy height and foliage density) within these vegetation types

may have affected the detectability of parakeets.

Both parakeet species were common within *Leptospermum* forest throughout the year. The number of yellow-crowned parakeets in this habitat peaked in December coinciding with a peak in foraging on the scale insect *Eriococcus orariensis* (Hoy), decreased suddenly during January and February (reflecting the relative importance of hard beech seed), then increased again over the following months until June as scale insects became a more important part of the diet (Fig. 5a). Between March and April the abundance of yellow-crowned parakeets was higher than red-crowned parakeets within *Leptospermum* forest as most red-crowned parakeets had moved into coastal plant communities to feed on the abundance of pohuehue seed (Fig. 5b). Apart from these two months, red-crowned parakeet numbers in *Leptospermum* forest remained high throughout the year (Fig. 5a).

Numbers of red-crowned parakeets were also high throughout the year within Kauri/Hard Beech/Northern Rata forest areas (Fig. 5a), although numbers did decline between April and June following rapid declines in the availability of kauri and beech seeds and when pohuehue seed and inkweed fruit were still readily available (Fig. 4). A dramatic increase in the number of red-crowned parakeets in Kauri/Beech/Rata forest occurred from July to August when hard beech flowering reached a peak. Yellow-crowned parakeet numbers within this forest type followed similar trends (Fig. 5b), utilising the abundance of beech flowers and seeds (Fig. 4) as well as the large numbers of aphids (*Sensoriaphis nothofagi* Cottier) occurring on new leaves.

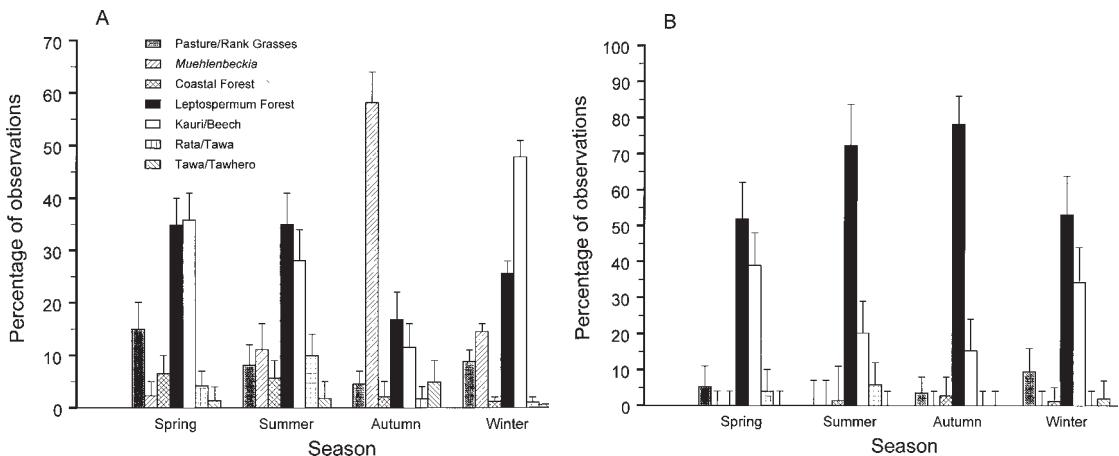


Figure 5: Seasonal variations in habitat preferences exhibited by (A) red-crowned parakeets ($n=2634$) and (B) yellow-crowned parakeets ($n=415$) on Little Barrier Island, October 1986-September 1987, expressed as percentage of habitat preference observations (+ 95% confidence limits).

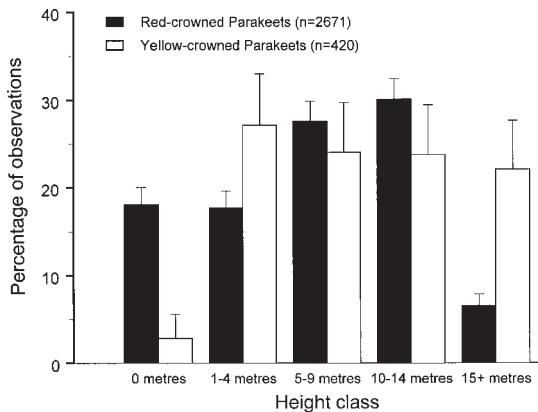


Figure 6: Seasonal variation in vertical distribution of red-crowned parakeets and yellow-crowned parakeets on Little Barrier Island, October 1986-September 1987, expressed as percentage of vertical distribution observations (+ 95% confidence limits).

Vertical distribution

The yellow-crowned parakeets were observed on average higher in the canopy than red-crowned parakeets ($\chi^2_{4df} = 178.0$ $p < 0.0001$) (Fig. 6). The vertical distribution of red-crowned parakeets varied with seasonal changes in diet and food availability. This relationship was particularly obvious during autumn when most observations were of birds foraging on the ground for pohuehue seeds. Similarly, use of the higher (10-14m) vegetation strata by red-crowned parakeets in August was associated with increased feeding on the flowers of canopy trees (hard beech and haekaro) and leaf-dwelling insects (*Sensoriaphis nothofagi* Cottier).

Yellow-crowned parakeets' use of the higher vegetation strata reflected their preference for tall forest habitats and a diet of arboreal invertebrates, such as scale insects, aphids and leaf miners. No yellow-crowned parakeets were ever seen foraging on the ground in open habitats.

Discussion

Competition

The competitive exclusion principle (Krebs, 1978) predicts that competition between closely related or ecologically similar species such as red-crowned parakeets and yellow-crowned parakeets will exist for a particular resource, or set of resources that are limiting and essential to continued existence (Weins, 1977). As a result the species must differ in some

morphological, ecological, or behavioural feature to coexist. Both "character displacement" (divergence of morphological characters such as bill size permitting the exploitation of alternative niches) and "differential colonisation" (the process of competitive exclusion resulting from separate colonisation of habitats by species with similar ecological requirements) have been suggested as mechanisms promoting coexistence of similar species (Grant, 1986). Interspecific and intraspecific morphological variation (especially bill size) has been suggested by Smith (1975) as an adaptation to reduce competition both within and between New Zealand parakeet species. Coexistence should therefore be mediated by morphological features that determine dietary composition - the 'optimal phenotype' for a species resulting from 'competitive forces' (Wiens, 1977), hence the dietary differences seen between parakeet species today.

There are, however, two main difficulties with the perception that morphological, ecological and behavioural differences necessarily have anything to do with minimising competition between species. Firstly, it is unwise to regard individual morphological differences occurring between closely related sympatric species as an adaptation "permitting coexistence" (Lawton, 1985). Morphological differences (which are significant for red-crowned parakeets and yellow-crowned parakeets; Nixon, 1982) usually do not display sufficient correlation with differences in food necessary to support the character displacement hypothesis; changes in climatic conditions, competition for nest sites (Dawe, 1979) or having less specialised diets than many other bird species (Nixon, 1982) may provide equally plausible explanations of intraspecific variation thereby reducing the effect that interspecific competition is thought to have on morphology (Wiens, 1977; Strong, 1983). Investigations of bill morphology for New Zealand parakeet populations also imply that bill size is unlikely to have evolved to minimise competition (Taylor, 1975; Nixon, 1982) and observations of foraging behaviour for the two parakeet species occurring on Little Barrier Island (Greene, 1988) support this conclusion.

The second difficulty arises when considering the availability of ecological resources. Species do not compete unless some resource, for example food or nest sites, is in short supply. For this reason it is critical to the argument to have an accurate estimate of resource availability and limitations which may operate on a given species (Schluter and Grant, 1982; Lawton, 1985). Even though the majority of foods consumed by yellow-crowned parakeets were also utilised by red-crowned parakeets, most were

either relatively minor components of the latter species diet, or highly abundant during specific seasons. Interspecific competition for food, therefore, appears to be substantially less than previously thought (see Williams, 1963; 1976 and Taylor, 1975). Behavioural differences, such as movement between and within habitats, also appears to be a direct response to the availability of food items at any one time, rather than a response to the presence of sympatric species.

Alternatively, Nixon (1982) suggests that the reduction in variety and availability of food species on islands when compared with the mainland may result in the competitive exclusion of yellow-crowned parakeets by preventing their colonisation or continued survival on smaller islands. Circumstantial evidence for this later mechanism has been reported by Cooper *et al.* (1986) who noted that red-crowned parakeets appear to have displaced yellow-crowned parakeets on the Solander Islands between 1948 and 1973.

Intraspecific competition may, therefore, be an important stabilising influence on the existence of sympatric populations of parakeets on relatively large and floristically diverse islands (Birch, 1979; Boer, 1986; Nixon, 1982) by preventing either species reaching population levels at which resources become limiting and interspecific competition can occur. However, it is also plausible that both species of parakeets are only able to coexist in sympatry where there is sufficient ecological complexity to allow this. Previous studies of parakeet populations occurring in allopatry (Dawe, 1979; Taylor, 1985; Bellingham, 1987) may simply have obscured any evidence of ecological displacement.

The importance of invertebrates

Both species of parakeet fed on phyt parasitic invertebrates (mainly coccids, aphids and the larvae of coleopterans and lepidopterans), although there was substantial variation in the quantity eaten and the time of year they were consumed by the two species. *Sensoriaphis nothofagi* (Cottier), the small aphid fed on by red-crowned parakeet is apparently only found on the new leaves of hard beech (*C. Butcher pers. comm.*). It was particularly common during August and September. *Ctenochiton viridis* (Maskell) or 'six-penny scale', a relatively large scale insect, was common on the leaves of a number of plant species. It was actively sought from October and December. Although red-crowned parakeets their consumption of insects in spring, the overall contribution invertebrates made to their diet remained much less than for yellow-crowned parakeets.

In contrast to red-crowned parakeets, yellow-crowned parakeets consumed invertebrate food sources throughout the year although accurate estimates of the importance of this (and other) food type(s) may have been significantly affected by the relatively small sample size; a direct result of yellow-crowned parakeet's lower abundance on Little Barrier Island (Greene, 1988). Arguably the most important of these invertebrates was the scale insect *Eriococcus orariensis* (Hoy) which formed a significant part of this species' diet. This scale insect is host specific to the genera *Leptospermum* and *Kunzea*. Most feeding observations involved scales on kanuka, the most common host of this insect on Little Barrier Island by virtue of its abundance. Kanuka appeared to provide a less suitable environment for this insect than manuka (*Leptospermum scoparium*), with fewer crevices for colony establishment as a result of periodic exfoliation of the bark (Hoy, 1961). As a result individual scale insects were more visible and exposed to predation.

Both invertebrate species commonly taken by red-crowned parakeets were also taken by yellow-crowned parakeets using identical foraging techniques. Other invertebrate elements of the yellow-crowned parakeet's diet, such as caterpillars and beetle larvae found within dead twigs and branches, were more cryptic and call for more specialised foraging methods (Greene, 1988).

The largely insectivorous diet of yellow-crowned parakeets may be advantageous during the breeding season. There is some evidence to suggest that yellow-crowned parakeets may begin breeding much earlier and continue for far longer than red-crowned parakeets (Oliver, 1955; Taylor, 1985; Elliott, Dilks and O'Donnell, 1996). The length of the breeding season for each species may be related to the type of food provided to their offspring (Newton, 1967). Insects may be a more reliable protein source for nestlings and for adults than plant foods.

Forshaw (1973) has suggested that insects play a generally far more important role in the diets of parrots than previously thought. Studies of closely related rosella species (*Platycercus* sp.) and other parakeets in Australia appear to confirm this (Cannon, 1981; Magrath and Lill, 1983; Long, 1984). In New Zealand early observations underestimated the importance of invertebrates within the diets of mainland parakeets species (Buller, 1888; Guthrie-Smith, 1914; Richdale, 1958). Although St. Paul (1977a) indicated that insects were consumed by yellow-crowned parakeets on the mainland, he considered them relatively unimportant within their diets. More

recent observations by Taylor (1985) in South Island beech forests showed that yellow-crowned parakeets actively seek out scale insects (*Ultracoelostoma assimile* Maskell) and caterpillars (*Heliostibes vibratrix* Meyrick) from beneath the bark of beech trees. The importance of invertebrates to the diet of yellow-crowned parakeets is given further weight by O'Donnell and Dilks' (1986) observations of foraging behaviour in South Westland. Approximately 90% of feeding observations were classified as 'gleaning', a behaviour consistent with the removal of invertebrates from the surface of various substrates such as leaves and bark.

Status of mainland parakeet populations

Significant differences in diet and habitat use are highlighted by this study. The diet of red-crowned parakeets is confirmed as being highly diverse and generalised. This should be advantageous to species such as red-crowned parakeets with wide geographical distributions where the physical environment varies dramatically (Forshaw, 1973; Taylor, 1985). However, despite this ability to utilise a variety of food species (both native and introduced) red-crowned parakeets have virtually disappeared from mainland habitats. Introduced browsers such as brushtail possums (*Trichosurus vulpecula* Kerr) could conceivably have had a significant impact on preferred food species. However, 90% of possums' diet consists of leaves (Fitzgerald and Wardle, 1979) which are a relatively small part of red-crowned parakeet's diet. Red-crowned parakeets have also persisted in good numbers on islands (for example, Codfish and Kapiti) with previously large possum populations. On Macauley Island, the Kermadec Island parakeet (*C. n. cyanurus*) persisted despite the total transformation of the island's vegetation from forest to a completely denuded goat (*Capra hircus* L.) browsed grassland (Veitch and Bell, 1990).

Yellow-crowned parakeets with their much less diverse diet and apparent preference for forested habitats (this study; Elliott *et al.*, 1996) are potentially even more susceptible to the impacts of introduced browsers. However, the reliance of yellow-crowned parakeets on invertebrates (a food source which is often assumed to be more stable and reliable over time; Moeed and Fitzgerald, 1982) for a significant part of their diet may have reduced the overall impact of browsers on the population.

There is circumstantial evidence to suggest that the annual variation in the abundance of invertebrates may affect numbers of yellow-crowned parakeets. Data collected by St. Paul (1976; 1977a,

b), showing the average number of birds seen per day over a number of years, indicate that the years from 1951 to 1953 were particularly poor in terms of the number of yellow-crowned parakeets seen. This period also includes those years (1952 and 1953) when other insectivorous birds, particularly whiteheads (*Mohoua albicilla*) and the pied tits (*Petroica macrocephala*), were also found in low numbers. St. Paul (1977a) thought insects were an unimportant component of the diet of yellow-crowned parakeets and considered "some other reason" to "account for the temporary drop in its numbers." However, the evidence from Little Barrier Island suggests otherwise. The long-term impact of such events on the status of parakeet populations does not, however, appear to have been significant. More recently, large variations in Fiordland yellow-crowned parakeet populations (rapid increases and equally rapid decreases in numbers as well as extended breeding seasons) were shown to be closely related to mast cycles of beech seed production (Elliott *et al.*, 1996).

Differences in foraging behaviour may be of greater significance particularly where the two species of parakeet choose to forage. Results from this study show that red-crowned parakeets spend significantly greater periods of time foraging on the ground, in low vegetation or in open habitats. In contrast yellow-crowned parakeets tend to forage at levels significantly higher above the ground. Red-crowned parakeets will therefore be at much greater risk of predation within mainland habitats. Heavy understorey browsing pressure may also significantly increase the risk of predation as foraging birds will be more visible to predators such as cats (*Felis catus* L.) and mustelids (Dawe, 1979). It is worth noting that offshore islands on which browsers such as goats occurred with a predator such as cats (e.g., Raoul and Cuvier Islands) red-crowned parakeets were quickly extirpated. However, on islands with cats but no significant browsers (e.g., Little Barrier Island) red-crowned parakeets were able to persist in good numbers (Greene, 1988; Veitch and Bell, 1990).

Sympatric populations of red-crowned parakeets and yellow-crowned parakeets are now few (Taylor, 1985) and opportunities for direct comparison of ecological and behavioural differences within similar habitats are limited. That significant differences in diet and foraging behaviour do occur between parakeet species seems certain but the role of competition in shaping these remains speculative. Evidence that these differences may have influenced the distribution and abundance of parakeet species on mainland New Zealand is highly suggestive and warrants further investigation.

Acknowledgements

I wish to thank the Hauraki Gulf Maritime Parks Board (now Department of Conservation, Auckland) for permission to carry out field work on Little Barrier Island. Transport was kindly provided by GMV Hauturu and crew and hospitality on the island by Mike and Alex Dobbins. I also thank Prof. Euan Young and David Allen for their respective contributions to this endeavour and Ralph Powlesland, Ron Moorhouse, Brenda Greene, Kay Clapperton and one anonymous referee for critical comments on the manuscript which had a very long gestation period! This study was supported by grants from the Wildlife Service Department of Internal Affairs, New Zealand Lottery Board and the Royal Forest and Bird Protection Society.

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