

Comparative ecology of sympatric orange-fronted parakeets (*Cyanoramphus malherbi*) and yellow-crowned parakeets (*C. auriceps*), South Island, New Zealand

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Abstract: Sympatric orange-fronted (*Cyanoramphus malherbi*) and yellow-crowned parakeets (*C. auriceps*) were surveyed in a South Island beech (*Nothofagus* spp.) forest during the spring and summer of 1998/99. Habitat use, behaviour and diet were recorded for each parakeet identified. A single observer did all recording. Both species were seen most frequently in the upper-most 20% of the forest stratum. Orange-fronted parakeets were seen more frequently than yellow-crowned parakeets in the lowest 20% of the forest stratum. Orange-fronted parakeets were seen calling less frequently and comforting more frequently than yellow-crowned parakeets, and this may reflect a difference in breeding period behaviour. Both species were usually seen feeding. In summer, both species were seen feeding mostly on seeds, predominantly from mountain beech — but this was a beech mast year. The spring diet of both species appeared to be largely flowers and invertebrates. Orange-fronted parakeets were seen feeding on flowers less frequently and on invertebrates more frequently than yellow-crowned parakeets. We suggest factors that may have contributed to the decline in abundance of both species: (1) greater competition between the two species in a habitat substantially modified by humans; (2) competition with introduced finch species; (3) competition with wasps for invertebrates; and (4) vulnerability to introduced predators. These last two factors are likely to affect orange-fronted parakeets in particular, because they appear to feed more on invertebrates and make greater use of the ground and low-growing plants.

Keywords: conservation; *Cyanoramphus*; diet; foraging behaviour; mainland; *Nothofagus*; orange-fronted parakeet; predation; yellow-crowned parakeet.

Introduction

There are three species of *Cyanoramphus* parakeet endemic to mainland New Zealand. These three species have declined in abundance at different rates. The red-crowned parakeet (*C. novaeseelandiae*), although abundant on some offshore islands, is now recorded very rarely on the North and South islands (Higgins, 1999; Taylor, 1985). The orange-fronted parakeet (*C. malherbi*) is restricted to two valleys, both in the South Island (Higgins, 1999). By far the most common of the three species is the yellow-crowned parakeet (*C. auriceps*), which still inhabits extensive areas of indigenous forest on both main islands and on some offshore islands. At the time of early European settlement all three species appeared to be 'abundant' (Reischek, 1885; Buller, 1869), with the orange-fronted parakeet the least common (Potts, 1885; Phillpotts, 1919).

Both the red-crowned and yellow-crowned parakeets, described in 1787 and 1820 respectively, have always been accepted as distinct species (Turbott, 1990). In contrast the orange-fronted parakeet's taxonomy, first described in 1857 (Souancé), has been long debated (Finsch, 1869; Buller, 1869; Harrison, 1970; Holyoak, 1974; Taylor *et al.*, 1986; Nixon, 1981; Triggs and Daugherty, 1996; Taylor, 1998). Recent mitochondrial DNA sequence analysis suggests that the orange-fronted parakeet is a distinct species (Boon *et al.*, 2000) and not a colour-morph of the yellow-crowned parakeet (Taylor *et al.*, 1986). Orange-fronted and yellow-crowned parakeets have a very similar morphology but the bills of male orange-fronted parakeets have been shown to be significantly shorter than the bills of male yellow-crowned parakeets (Young and Kearvell, 2001).

The three parakeet species have not been studied in sympatry on the mainland, because a suitable

population no longer exists. Two studies on offshore islands have compared Chatham Island red-crowned (*C. n. chathamensis*) and Forbes' (*C. forbesi*) parakeets (Nixon, 1994), and red-crowned and yellow-crowned parakeets (Greene, 1998). Both studies have shown that the species differ in habitat use and diet and that these differences have implications for parakeet conservation. On Mangere Island, the near total destruction of forest has allowed the Chatham Island red-crowned parakeet, better adapted to an open grassland habitat, to thrive; whereas Forbes' parakeet has declined markedly (Nixon 1994). However red-crowned parakeets use the ground and lower levels for feeding and breeding more frequently than yellow-crowned parakeets (Greene 1998). This has made the red-crowned parakeet more vulnerable to predation from introduced mammalian predators. Single species studies of yellow-crowned parakeets on the mainland have also highlighted the vulnerability of parakeets to predators (Elliott *et al.*, 1996a; 1996b).

There is little published information on the ecology of the orange-fronted parakeet. There are a few brief notes or summaries in Buller (1869), Reischek (1885), Oliver (1955), Harrison (1970) and Taylor (1975; 1985) and in unpublished reports prepared in the 1980s for the New Zealand Wildlife Service (now the Department of Conservation) by A. Cox, D. Crouchley and R. Nilsson. Orange-fronted parakeets have been observed in a variety of habitats from sub-alpine scrub to sea level. The more recent reports have all been on parakeets in beech forest (*Nothofagus* spp.), mostly in North Canterbury, at altitudes of 600 to 1400 m. Birds have been observed feeding on a variety of berries, seeds, leaves, buds and invertebrates. Breeding biology is almost totally unknown, as are the reasons for this parakeet's decline.

We report on the comparative ecology of sympatric orange-fronted and yellow-crowned parakeets in a mainland beech forest. Ours is the first systematic study of two sympatrically occurring parakeet species on the New Zealand mainland and the first systematic study of the orange-fronted parakeet.

Methods

Study site

The study site is in the upper reaches of the South Branch of the Hurunui River (172° 5' E and 42° 45' W) in the Lake Sumner Forest Park, South Island, New Zealand. The valley is steep-sided with a tree line at approximately 1300 m and ridge tops at 1600 to 1800 m. The study site is confined to the valley floor on the true right of the river, at an altitude of 750 to 900 m, and is 7 km long by 600 m wide. The forest canopy has a mean height of 21 m and is dominated by red

beech (*Nothofagus fusca*). Both silver (*N. menziesii*) and mountain beech (*N. solandri* var. *cliffortioides*) are common. The understorey is generally open in nature and dominated by silver beech, but broadleaf (*Griselinia littoralis*), mountain toa toa (*Phyllocladus alpinus*), *Pseudopanax* spp. and *Coprosma* spp. are also common. Clearings contain native and introduced grasses and herbs.

Since 1995, the valley has been part of a Department of Conservation 'Mainland Island' habitat restoration project (Saunders and Norton, 2001). Sheep and cattle have been excluded and stoat (*Mustela ermine*) and brushtail possum (*Trichosurus vulpecula*) control programmes have been carried out every year.

Field methods

Parakeets were surveyed over 23 days in late spring (13 November to 17 December 1998) and over 25 days in summer (9 January to 24 February 1999). The study site was divided into two areas, each sampled on consecutive days. Each area had three starting points. A fixed route was followed each day from a starting point chosen at random to remove temporal bias. The observer (the same person in all surveys) followed the fixed route, but could leave the route for up to 100 m if necessary to locate a parakeet when a call was heard. Each day's sampling started an hour after sunrise and took around seven hours to complete.

For each parakeet species positively identified, habitat use, behaviour and diet were recorded (using the variables in Table 1). When parakeets were found in a group, the only observation made was of the first bird identified. Consecutive observations had to be at least one tree apart. All observations were given map co-ordinates, with each co-ordinate accurate to 50 m.

Data analysis

Data analysis was exploratory, identifying likely differences between the two species rather than testing pre-planned hypotheses. Logistic regression (SAS, 1997) was used to identify significant associations between a binary response variable representing the two species and predictor variables representing the observational variables in Table 2 and time of year and time of day. Time of year was expressed as a binary variable representing either late spring or summer. Time of day was not recorded; as a surrogate, time of day was represented by the number of observations made so far that day divided by the total number of observations made that day. The final logistic regression model contained only those predictor variables that would cause a significant change to model deviance if left out of the model. The fit of the final model was tested using the Hosmer-Lemeshow statistic.

Table 1. Variables recorded for each parakeet identified in the South Branch of the Hurunui during spring and summer of 1998-1999.

Variable	Measurements made ¹
Date:	Date.
Co-ordinate:	The map co-ordinate of each observation.
Weather:	Brief description for each day.
Activity:	Call, fly, comfort (bathing, preening, drinking, day roosting), breeding (courtship feeding, display, entering nest, feeding young, mating, nest hole search, and antagonistic chasing/display), glean, probe, rip, scan, browse.
DBH:	Tree diameter at breast height (cm).
Canopy height:	The height of forest at point of observation (m).
Plant species:	<i>Nothofagus fusca</i> , <i>N. solandri</i> var. <i>cliffortioides</i> , <i>N. menziesii</i> , <i>Coprosma</i> sp., <i>Phyllocladus alpinus</i> , standing dead trees/shrubs, ground herbs.
Stratum:	Above canopy, unshaded and shaded canopy, upper and lower understory, ground.
Bird height:	The height of the bird above the ground (m).
Station:	Trunk, large and small branch, twig ² , ground, dead, aerial.
Substrate:	Bark, lichen, moss, leaf, ground, flower, new growth, dead plant structure, bud.
Behaviour:	Feeding, breeding, comfort, calling.
Food:	Seed, flower, leaf, bud, moss, lichen, wood, invertebrate, non-specific new growth.

¹Only those categories used during the study are listed; for a full list see O'Donnell and Dilks (1988)

²Twig was deemed to be any branch where the parakeet was amongst leaves

Table 2. Resource use by orange-fronted and yellow-crowned parakeets in the South Branch of the Hurunui during spring and summer of 1998-1999: for each species the number of observations (n) and percentage (%) in each category.

	Orange-fronted parakeet		Yellow-crowned parakeet	
	n	%	n	%
Plant species				
<i>Nothofagus fusca</i>	118	37.0	125	34.2
<i>Nothofagus menziesii</i>	62	19.4	90	24.6
<i>Nothofagus solandri</i>	108	33.9	115	31.4
<i>Phyllocladus alpinus</i>	8	2.5	22	6.0
Other ¹	23	7.2	14	3.8
Forest stratum				
Unshaded canopy	56	17.5	68	18.6
Shaded canopy	125	39.2	147	40.2
Upper understory	60	18.8	84	22.9
Lower understory	66	20.7	60	16.4
Ground	12	3.8	7	1.9
Bird height as a % of canopy height²				
80+	178	55.8	225	61.5
60-79	51	16.0	59	16.1
40-59	39	12.2	39	10.7
20-39	27	8.5	26	7.1
0-19	24	7.5	17	4.6
Station				
Trunk	24	7.6	23	6.3
Large branch	3	0.9	3	0.8
Small branch	147	46.1	173	47.3
Twig	130	40.7	157	42.9
Dead plant structure	3	0.9	3	0.8
Ground	12	3.8	7	1.9
Diameter of tree at breast height				
1-25 cm	83	27.0	88	24.7
26-50	130	42.3	156	43.8
51-75	49	16.0	52	14.6
76-100	29	9.5	39	11.0
>100	16	5.2	21	5.9

Table 2. Continued from previous page

	Orange-fronted parakeet		Yellow-crowned parakeet	
	n	%	n	%
Behaviour				
Feeding	194	60.8	214	58.5
Breeding	40	12.5	37	10.1
Comfort	45	14.1	37	10.1
Calling	40	12.6	78	21.3
Diet				
Invertebrates	86	44.8	71	33.3
Flowers	21	11.0	40	18.8
Seeds	69	35.9	81	38.0
Other ³	16	8.3	21	9.9
Invertebrate source				
<i>Nothofagus fusca</i>	46	54.1	37	51.4
<i>Nothofagus menziesii</i>	20	23.5	19	26.4
<i>Nothofagus solandri</i>	18	21.2	15	20.8
Dead vegetation ⁴	1	1.2	1	1.4
Invertebrate substrate				
Bark ⁵	46	53.5	40	58.0
Leaves	35	40.7	26	37.7
Other ⁶	5	5.8	3	4.3
Seed source				
<i>Nothofagus fusca</i>	1	1.5	1	1.2
<i>Nothofagus menziesii</i>	10	14.5	16	20.0
<i>Nothofagus solandri</i>	45	65.2	41	51.3
<i>Coprosma</i> spp.	5	7.2	0	0.0
<i>Phyllocladus alpinus</i>	8	11.6	22	27.5
Food substrate				
Flower	22	11.7	39	18.2
Bark	46	24.3	41	19.2
Leaf	46	24.3	31	14.5
Seed	65	34.4	85	39.7
Other ⁷	10	5.3	18	8.4

¹*Coprosma* spp., standing dead trees or shrubs, and ground herbs²Bird height and canopy height were recorded separately but are not shown³Leaf, bud, moss, lichen and non-specific new growth⁴Removed directly from a part or wholly dead plant⁵Bark not covered by epiphytes⁶Lichen and moss-covered bark⁷Lichen, new growth and moss

Pseudoreplication

The method of maximum likelihood was used to estimate the parameters of the final logistic regression model. This method requires independent observations. If observations are in fact correlated, then the probability of making a Type I error (concluding there is an association when there is not) could well be greater than the stated *P*-value (Hurlbert, 1984; McArdle, 1996). Even though observations were made at least one tree apart, such observations could still be correlated for two reasons. First, while parakeets are in general mobile, breeding parakeets are more likely to be found in the same place in a subsequent survey ['temporal pseudoreplication' (Hurlbert, 1984)]. Second, multiple observations may have been made on the same flock of

parakeets and members of the same flock may not behave independently ['simple pseudoreplication' (Hurlbert, 1984)].

Two strategies are available for analysing potentially pseudoreplicated data. First, observations that may be correlated can be discarded so that the remaining observations are independent. Second, correlations in data can be identified and modelled explicitly (McArdle, 1996). Both these strategies were used to make sure the final logistic regression model was robust to potential pseudoreplication.

Observations potentially on the same breeding pair were identified from observation co-ordinates. Co-ordinates were accurate to ± 50 m so the distance between two observations was accurate to ± 70.7 m, assuming independent and unbiased co-ordinate errors

(Cook and Rabinowicz, 1963). This implies that two breeding observations less than 141 m apart could be observations on the same breeding pair. Therefore any observation of breeding behaviour was discarded if not at least 150 m from every previous observation of breeding behaviour. This gave a reduced data set of 650 observations (95% of the initial sample size of 685).

Observations potentially on the same flock were identified in the reduced data set from the distance between observations and the breeding status noted for each observation. Each bird showing breeding behaviours was assumed to be in a flock of its own. Birds not showing breeding behaviours were assumed to be in the same flock as birds previously observed if they were within a certain minimum distance from the previous observation. A range of plausible minimum distances was considered; from 50 m to 400 m in 50 m steps.

First, the full data set was analysed assuming its observations were independent. Parameters in logistic regression models were estimated using the method of maximum likelihood. Second, the final logistic regression model was fit to the reduced data set, with an extra parameter for the correlation between observations on birds within the same flock. Parameters were estimated using the method of generalised estimating equations (Liang and Zeger, 1986), assuming that observations on birds in different flocks were independent but observations on birds within the same flock were correlated.

Results

Data analysis

There were no significant associations between the two parakeet species and their use of forest stratum, station, beech tree species or tree size. Nor were there significant associations between the two species and their height above ground, height as a percentage of canopy height or height in categories. There were no significant associations between the two species and either time of year or time of day.

The final logistic regression model for the complete data set of 685 observations had three predictor variables. Removing any one of these variables led to a significant change in model deviance. The final model suggests significant associations between the two species and their choice of plant species (Δ deviance = 12.6, d.f. = 4, $P = 0.01$), their behaviour (Δ deviance = 10.3, d.f. = 3, $P = 0.02$) and their diet (Δ deviance = 9.5, d.f. = 4, $P = 0.05$). There were no interactions between these three predictor variables in their association with the two species. The model appeared

to fit the data well (Hosmer-Lemeshow statistic = 2.4, d.f. = 8, $P = 0.96$).

The final model was fit to the reduced data set of 650 observations, assuming observations made on different flocks were independent but observations made on the same flock were correlated. For all minimum distances between flocks, the within flock correlation was negligible (Table 3). The final logistic regression model was then fit to the reduced data set assuming all its observations were independent. All three predictor variables were still significant; hence the final logistic regression model appears robust to potential pseudoreplication in the data.

Table 3. Correlation between individual parakeets within the same flock.

	Minimum distance (m) between flocks							
	50	100	150	200	250	300	350	400
Number of flocks	575	518	412	406	348	340	310	297
Maximum flock size	6	6	11	11	12	12	12	12
Within flock correlation	0.004	0.003	-0.022	-0.013	0.016	0.013	0.004	0.022

Of the 685 observations in the full data set, 319 (47%) were of orange-fronted parakeets (Table 4). If a predictor variable were independent of the two species, then one would expect the same 47:53 ratio of two species within each of the variable's categories. Therefore orange-fronted parakeets were seen: less frequently on mountain toa toa and more frequently on 'other' plants than expected; less frequently calling and more frequently comforting (i.e. bathing, preening, day roosting) than expected; and less frequently feeding on flowers and more frequently feeding on invertebrates than expected.

Habitat use similarities

Both species spent most of their time in the upper-most 20% of the forest stratum — 56% and 62% of observations for orange-fronted and yellow-crowned parakeets respectively (Table 2). They both favoured the shaded canopy over all other strata (39% and 40%) and both used small branches and twigs for most of their activities (87% and 90%). They were both seen on beech far more often than on any other plant species (90% and 90%) and both targeted a very similar size range of trees.

Behavioural similarities

Both species were often seen feeding — 61% and 59% of observations for orange-fronted and yellow-crowned

Table 4. Significant associations between the two species and plant choice, behaviour and diet: for both species, the number of observations observed (o) and expected (e) in each category.

	Total n	Orange-fronted parakeet		Yellow-crowned parakeet	
		o	e	o	e
Overall	685	319		366	
Plant species					
<i>Nothofagus fusca</i>	243	118	113.1	125	129.8
<i>Nothofagus menziesii</i>	152	62	70.8	90	81.2
<i>Nothofagus solandri</i>	223	108	103.8	115	119.2
<i>Phyllocladus alpinus</i>	30	8	14.0	22	16.0
Other ¹	37	23	17.2	14	19.8
Behaviour					
Feeding	408	194	190.0	214	218.0
Breeding	77	40	35.9	37	41.1
Comfort	82	45	38.2	37	43.8
Calling	118	40	55.0	78	63.0
Diet					
Invertebrates	157	86	73.1	71	83.9
Flowers	61	21	28.4	40	32.6
Seeds	150	69	69.9	81	80.1
Other ²	37	16	17.2	21	19.8

¹*Coprosma* spp., standing dead trees or shrubs, and ground herbs

²Leaf, bud, moss, lichen and non-specific new growth

parakeets respectively (Table 2). Breeding had started in the valley by mid summer and associated behaviours were common for both species (13% and 10%).

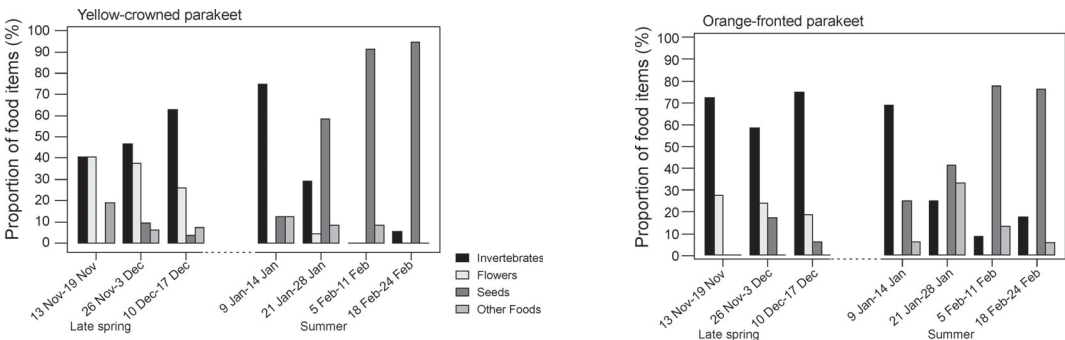
Diet similarities

In summer, the diet of both species consisted almost entirely of seeds (Fig. 1). As it was a beech mast year, a large quantity of beech seed was available from around late January. Mountain beech was the most common source of seed — 65% and 51% of seed

source observations for orange-fronted and yellow-crowned parakeets respectively (Table 2).

Invertebrates were a significant part of the diet of both species, especially in spring (Fig. 1). The main source of invertebrates for both parakeets was red beech bark — 53% and 58% of invertebrate substrate observations for orange-fronted and yellow-crowned parakeets respectively (Table 2). Both species took small leaf roller larvae (*Tortricidae* spp.) from under the leaves of sub-canopy silver beech and much larger leaf roller larvae and unidentified caterpillars

Figure 1. The diet of orange-fronted (n = 192) and yellow-crowned parakeets (n=213) in the South Branch of the Hurunui during the late spring and summer of 1998-1999. Other foods include leaf, bud, moss, lichen and non-specific new growth.



(*Lepidoptera* spp.) from red beech leaves. From early December aphids (*Aphidae* spp.) and leaf miners (*Tineidae* spp.) were commonly taken, notably from heavily infested red beech trees. Honeydew aphids (*Margarodidae* spp.) were eaten by both parakeets (particularly from mountain beech), as were adult and larval scale insects (*Coccidae* spp.). Invertebrate foraging techniques were very similar for both parakeet species.

The flowers of all three beech species were also an important part of the spring diet (Fig. 1). Parakeets were never seen feeding on the flowers of other plants, nor on the cones of mountain toa toa. Both parakeet species were recorded browsing on herbs and ferns on the ground, e.g. on *Pratia angulata*, *P. perpusilla*, *Oreomyrrhis colensoi*, *Parahebe lyallii*, *Leptinella maniototo* and *Blechnum penna-marina*.

Habitat use differences

Orange-fronted parakeets were seen on mountain toa toa less frequently and yellow-crowned parakeets more frequently than expected (Table 4). All observations of parakeets on mountain toa toa were of individuals taking seed. Orange-fronted parakeets were seen on 'other' plants more frequently and yellow-crowned parakeets less frequently than expected. This category included observations of parakeets on the ground, on *Coprosma* sp. (< 2m) and on dead trees and shrubs. There were only three observations of parakeets on dead trees or shrubs for each species. This suggests that orange-fronted parakeets were seen more frequently in this 'other' category than expected because of their use of the ground and low-growing plants. Orange-fronted parakeets were also seen more frequently than yellow-crowned parakeets in the lowest 20% of the forest stratum (Table 2).

Behavioural differences

Orange-fronted parakeets called less frequently and yellow-crowned parakeet more frequently than expected (Table 4). Most calls were restricted to the upper levels of the forest, with 77% of orange-fronted parakeet calls and 87% of yellow-crowned parakeet calls coming from the shaded canopy and upper understory combined. There were no calls recorded on the ground and only three in the unshaded canopy, although 18% of all observations were in this stratum.

Orange-fronted parakeets were seen comforting more frequently and yellow-crowned parakeets less frequently than expected. Comfort activities were almost exclusively performed on small branches (95% of all comfort activity observations) with both species often leaving their feeding station to undertake such activities.

Diet differences

Orange-fronted parakeets were less frequently seen feeding on flowers and more frequently seen feeding on invertebrates than expected (Table 4). Their intake of invertebrates throughout the spring was consistently high (Fig. 1). The spring diet of yellow-crowned parakeets was also largely flowers and invertebrates, but the proportion of invertebrates increased over time (Fig. 1).

Discussion

Habitat use

Studies of *Cyanoramphus* parakeets on largely unmodified offshore islands (Greene, 1998; Nixon, 1994) and on the mainland (Elliott *et al.*, 1996a; 1996b) have provided important insights into the possible reasons for the present distribution of mainland parakeets. Island studies have shown that red-crowned parakeets spend considerable time foraging on the ground, whereas yellow-crowned parakeets are more arboreal (Greene, 1998). Heavy understory browsing may have led to increased predation on the red-crowned parakeet (Greene, 1998) because of increased visibility for predators (Taylor, 1979). As Greene (1998) points out, there are some islands with large numbers of red-crowned parakeets where the vegetation has been reduced to near grassland by browsers, but there are no predators on these islands. On Macquarie Island the red-crowned parakeet only became extinct after the introduced rabbit (*Oryctolagus cuniculus*) became firmly established (Taylor 1979). Taylor suggests that the rabbit supported a huge increase in the number of introduced predators, namely the cat (*Felis catus*) and weka (*Gallirallus australis*), with subsequent heavy predation on the parakeet. The parakeet was extinct within 20 years.

On the mainland, changes in the structure of the beech forest over the last 1000 years have been extensive (Veblen and Stewart, 1982). Introduced animals, such as the brushtail possum and red deer (*Cervus elaphus*), have heavily browsed much of the vegetation (Mark and Bayliss, 1975; Payton, 2000). Introduced mammals, possums, birds, forest clearance and the disappearance of many native bird species (Holdaway, 1989) have all contributed to large changes in the forest ecosystem. With the increase in browsers, the red-crowned parakeet has become all but extinct on the mainland (Taylor, 1985). The ability of the yellow-crowned parakeet to forage higher may well have placed it at an advantage on the mainland, reducing the risk from predators such as the stoat, rat and cat (Elliott *et al.*, 1996a). Our study has shown that orange-fronted parakeets appear to use the ground and low

growing shrubs more frequently than yellow-crowned parakeets and, like the red-crowned parakeet, this may place the orange-fronted parakeet at greater risk of predation.

Behaviour

There are likely to be other factors contributing to the decline of the orange-fronted parakeet on the mainland. Yellow-crowned parakeets are known to be capable of producing up to five broods in a season (Elliott *et al.*, 1996b) and are known to start breeding early and be capable of breeding for long periods (Taylor, 1985; Elliott *et al.*, 1996b). During our study yellow-crowned parakeets were seen calling more frequently and comforting less frequently than orange-fronted parakeets. This may indicate some differences in breeding period behaviour, and casual observation suggests that yellow-crowned parakeet fledglings appear around 4 weeks before the first orange-fronted parakeet fledglings. We know almost nothing about the breeding strategy of the orange-fronted parakeet, and this should be studied because of its implication for the conservation of these parakeets on the mainland.

Diet

Forshaw (1973), in his review of all parrots, recorded only a few that ate invertebrates, but suspected that the importance of invertebrates had been greatly underestimated. Since then Taylor (1985), O'Donnell and Dilks (1994), Nixon (1994) and Greene (1998) have all shown that invertebrates are an important part of the diet of New Zealand's *Cyanoramphus* parakeets, especially in winter and spring. Invertebrates are also important in the diet of Australian parrots closely related to *Cyanoramphus* (Ovenden *et al.*, 1987; Magrath and Lill, 1983; Long, 1984). Most Psittaciformes are now recognised as having at least some invertebrates in their diet (Higgins, 1999).

Our study has shown that invertebrates are a major part of the diet of orange-fronted and yellow-crowned parakeets in a mainland beech forest. In late spring, up to 70% of feeding observations were of parakeets taking invertebrates (Fig. 1). Removal of invertebrates from beech forests by such introduced agents as birds, mice (*Mus musculus*), wasps (*Vespula vulgaris* and *V. germanica*), rats (*Rattus* spp.) and hedgehogs (*Erinaceus europaeus*) may have had a significant impact on parakeet abundance. In honeydew beech forest in the north of the South Island, the invertebrate intake by two species of introduced wasp was similar to that of the entire insectivorous bird fauna (Harris, 1991). Some invertebrate species were so heavily preyed on that their survival through the wasp season was "virtually nil" (Beggs, 2001). The recent invasion of honeydew beech forest by wasps (Sandlant and

Moller, 1989) and subsequent competition for invertebrates may help explain why the orange-fronted parakeet disappeared from these forests some time after 1965.

Beech seeds are also important in the diet of both species, at least in a beech mast year. In the summer of our study, up to 90% of feeding observations were of parakeets taking seeds (Fig. 1). Both species took predominantly mountain beech seeds but this could just reflect a better supply of this seed. Seed production in a mast year can vary between beech tree species (Wardle, 1984). High abundance of seed can lead to an extended breeding season. Following a heavy beech mast, yellow-crowned parakeets were observed to breed "not only during their normal late summer breeding season, but right through the following winter, spring and summer" (Elliott *et al.*, 1996a). These authors also found two dead yellow-crowned parakeet chicks whose crops contained "almost nothing but beech seeds". Cardueline finches in Europe have a breeding strategy that is also heavily reliant upon seed for successful reproduction (Newton, 1967). Two of these finch species, the redpoll (*Carduelis flammea*) and goldfinch (*C. carduelis*), are abundant in mainland New Zealand beech forests while a third, the greenfinch (*C. chloris*), is present but less common. All are found in the South Branch of the Hurunui, often in very large flocks. Cardueline finches may directly compete with *Cyanoramphus* parakeets for seed.

Our study has shown that sympatric orange-fronted and yellow-crowned parakeets have similar diets during the summer of a beech mast year. In spring, the two species place different emphasis on invertebrates and flowers. Studies of sympatric *Cyanoramphus* parakeets on offshore islands have shown that diets do generally overlap (Taylor, 1975; Nixon, 1994; Greene, 1998; 1999), but on those islands that are largely unmodified, significant dietary differences do occur (Greene, 1998; 1999). Studies of closely related species (*Cyanoramphus* parakeets on Mangere Island by Nixon, 1994; Fringillinae and Carduelinae finches in Europe by Newton, 1967) have shown that diets overlap to a much greater extent in habitats substantially modified by humans than in unmodified habitats. Our study has shown considerable overlap in diet between orange-fronted and yellow-crowned parakeets in a mainland beech forest that has been substantially modified by humans (Veblen and Stewart, 1982). The two species may now compete with each other more than they used to.

Conclusions

The conservation of a species requires a thorough knowledge of its breeding biology and its ecology. The effects of introduced predators such as the rat, cat and stoat are beginning to be understood. The less dramatic, but equally damaging effects of introduced food competitors such as wasps, birds, mice and rats and introduced herbivores and omnivores are not well understood. The orange-fronted parakeet only survives on the mainland. If we wish to maintain populations of parakeets on the mainland, then a thorough understanding of our modified forest ecology is a prerequisite.

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