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Nest site selection by sympatric orange-fronted (*Cyanoramphus malherbi*) and yellow-crowned parakeets (*C. auriceps*) in Nothofagus spp. forest: interspecific competition between two closely related species?

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Abstract Orange-fronted (*Cyanoramphus malherbi*) and yellow-crowned parakeets (*C. auriceps*) are sympatric congeners that are secondary cavity nesting species, with the former being critically endangered. Both currently inhabit anthropogenically-modified *Nothofagus* forest. We compared the characteristics of nest sites in both species and found the majority of nest site parameters (tree height, height of hole above ground, DBH, tree condition and aspect) were similar. However, orange-fronted parakeets selected nest cavities with a significantly narrower entrance, and when situated in red beech (*Nothofagus fusca*), nest entrances were significantly smaller in area than in yellow-crowned parakeets. As the male orange-fronted parakeet is smaller in body mass than the male yellow-crowned parakeet (only males feed nestlings when laying multiple clutches), the difference in nest hole size may simply indicate that they are capable of utilising smaller entrances. We also found that orange-fronted parakeets selected nest holes in standing dead trees more frequently and nest sites in silver beech (*N. menziesii*) less frequently than expected. While the lack of differences in nest site characteristics suggests some interspecific competition may be occurring between these species (*i.e.*, they occasionally use the same nest holes), it is difficult to establish this experimentally and to determine whether these differences are artefacts of former niche separation in unmodified forest.

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Keywords orange-fronted parakeet; yellow-crowned parakeet; *Nothofagus*; nest sites; competition

INTRODUCTION

The orange-fronted (*Cyanoramphus malherbi*) and yellow-crowned parakeet (*C. auriceps*) are endemic to the forests of New Zealand. Both have declined as a result of habitat destruction and introduced mammalian predators (Innes *et al*. 2010). Orange-fronted parakeets have been reintroduced to 4 offshore islands with varying success (Birdlife International 2012, Hitchmough 2007, Kearvell 2013a), and as a consequence, its threat status has recently been reduced from critically endangered to endangered (Kearvell 2013a). However, with less than 250 birds surviving in the wild on the mainland (Kearvell 2013a) and recent field evidence suggesting ongoing declines in the mainland populations, we believe this classification should be reconsidered. The yellow-crowned parakeet,

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although more common and recorded as having declined in many mainland areas, is classified as not threatened by Elliott (2013).

There have been few studies on any New Zealand species of parakeet and none where all 3 species (the red-crowned parakeet [*C. novaezelandiae*] is now extinct on the mainland) were sympatric on the mainland. The ecology (Elliott *et al*. 1996a) and nest site selection of the yellow-crowned parakeet has been examined on the mainland in Fiordland and although no other parakeet species was present, nest site selection overlapped with the sympatric yellowhead (*Mohoua ochrocephala*), a small (28 g) secondary cavity-nesting species of insectivorous passerine (Elliott *et al*. 1996b). Their conclusion was that the 2 species may 'compete for the odd nest site', but that competition for sites probably does not influence the density of either species (Elliott *et al.* 1996b).

The only study of 2 sympatric species of parakeet on the mainland have been ecological studies on habitat use (Kearvell *et al*. 2002) and nesting sites (Kearvell 2002) of orange-fronted and yellow-crowned parakeets in the forests along the South Branch Hurunui River (hereafter Hurunui) on the South Island. Interspecific competition was suggested based on overlap in diet between the 2 species, although this overlap may be a result of habitat modification (Kearvell *et al*. 2002). In a preliminary study of nest site selection (based on 32 nests), Kearvell (2002) suggested that the 2 species may also select similar nest sites, and that competition for nest sites might occur. However, there was a significant difference between the 2 species in their selection of tree species. Kearvell (2002) further suggested that, if nest sites were limiting, as may occur in a modified forest, then one species could be placed at a competitive advantage.

Direct interspecific competition between bird species in New Zealand's forests intuitively seems unlikely, given the low diversity of species present and because most species have been established for a considerable time (Trewick & Gibb 2010). For example, stitchbird (*Notiomystis cincta*) and saddleback (*Philesturnus* spp.) separated around 39-28 Ma (millions of years before present), and *Nestor* and *Strigops* parrots soon after the K/T boundary at <65 Ma. Species boundaries have thus had a considerable time to establish themselves and for competition to be reduced. This does not seem to be the case for *Cyanoramphus* parakeets. They appear to be a recent radiation with most speciation originating recently and in New Zealand (Trewick & Gibb 2010). Boon *et al*. (2001), in their investigation of the molecular systematics of *Cyanoramphus* spp., suggest that the genus may have split from *Eunymphicus* around 450,000-650,000 years BP (before present). They proposed that the New Zealand *Cyanoramphus* evolved from a common ancestor between 20,000 and 2,000,000 years BP. The orange-fronted parakeet is thought to have appeared only between 279,000 and 14,000 years BP.

Despite the reduced likelihood of interspecific competition among birds in New Zealand, there is some evidence for direct competition for nest sites, especially in some species of cavity or burrow-nesting birds in which the suitable nest sites may be limiting. For example, the broad-billed prion (*Pachyptila vittata*) has been recorded as "interfering with" the chicks within the nesting burrows of the endangered Chatham petrel (*Pterodroma axillaris*). This interference is due to prions prospecting for nesting burrows (Sullivan & Wilson 2001), but indicates there is direct competition for burrows between the species. As the habitat where these 2 species currently occur has undergone major anthropogenic changes, it has been suggested that competition is partly due to habitat degradation (West & Nilsson 1994). There are also 2 records of introduced common starling (*Sturnus vulgaris*) stopping orange-fronted parakeet from using nests they had used in previous seasons (Kearvell 2013b). Starlings use secondary cavities similar to those of parakeets and this raises the possibility that cavities suitable for use as nests by parakeets in *Nothofagus* forest may be limiting, and contrary to previous views that nest cavities were not thought to be limiting (Elliott *et al*. 1996b). Research in sub-tropical moist Atlantic forests has suggested that useable cavities may be fewer in number than earlier appreciated and that competition for suitable sites can be intense (Cockle *et al*. 2010). A study by Blakely *et al*. (2008) in *Nothofagus* forest found only an average of 8 holes per hectare was suitable for all hole-nesting species. This intuitively seems to be a small number and suggests the potential for competition between parakeet species.

Given the potential importance of competition for nest sites in the management of endangered cavity-nesting species such as the orange-fronted parakeet, in this paper we examine nest site selection by 2 closely related congeners of endemic New Zealand parakeet where they occur in sympatry. Our objective is to measure the characteristics of the nest sites selected by each species and to determine whether this overlap could lead to interspecific competition.

METHODS

Nests of orange-fronted and yellow-crowned parakeets were studied between 2001 and 2012 in the Hawdon (42° 58.18′ S, 171° 44.52′ E) and Poulter Valleys (42° 54.19′ S, 171° 51.97′ E) in Arthur's Pass National Park, and the Hurunui (42° 45.50′ S, 172°

1.64′ E) in Lake Sumner Forest Park. Nests were located by observers following pairs of birds, or by locating a bird already at an active nest. Nests (where the female had at least one egg or nestlings were already present) were confirmed either by climbing and inspecting the nest cavity, or if unable to climb, by repeated ground observations of parental activity at the nest site.

For all nests the following parameters of the nest cavity and nest tree were measured: tree species (except standing dead trees [SDT] were not separated to species), tree height (using either a Sunto height meter or Leica laser measure), canopy height (by measuring either nest tree if canopy or nearest canopy tree to the nest tree using Sunto meter or Leica laser measure), diameter of nest tree at breast height (DBH) using a tape measure), height above ground of nest hole (measured either directly with tape measure or a Leica Laser measure), nest hole exposure (scored from 1 to 5, where 1 = covered/shaded and 5 = exposed) and tree condition (scored from 1 to 4, where 1 = tree entirely dead and 4 = tree entirely alive). For the nest hole we measured aspect (with a compass), height and width of entrance hole (using a tape measure), depth of the nest bowl (either directly with tape or estimated), hole type (being either knot hole or slit), nest hole site (being either trunk or branch) and number of entrances. A knot hole was defined as a circular or oval entrance which originated from a rotted out branch. A slit was an entrance that was several times higher than wide and tended to be narrow and rectangular in shape. Trunk refers to the single main trunk of the tree, while the branch can be any part of the tree coming off the main single trunk. From measurements of the entrance hole, we calculated the area of the nest entrance, depending on its shape. For a slit entrance we calculated area of nest entrance assuming it was a simple rectangle (height x width). Knot hole areas were either calculated as a simple circle (πr^2) or as a simple oval (πab); where a = half the major axis and b = half the minor axis. The aspect was not measured in a standard format over the period. Some were measured in degrees (0 to 360) while some used the 16 cardinals of the compass (i.e., 'N' or 'SE'). For analysis all were converted to the 16 cardinals and placed within the relevant 22.5 degree sector e.g. 'WNW' to 'W'. Sectors were then compared.

While many of the parameters were collected for most nests, some measurements were not collected at all nests. DBH was not recorded for yellow-crowned parakeet nests in the Poulter and Hawdon Valleys, and an exposure rating for yellow-crowned parakeet nest holes was not recorded. It should also be noted that some nest parameters could not be recorded at each nest, as not all nests were accessible through climbing. No systemic surveys of the vegetation are available for the 3 study sites, although all 3 valleys are dominated by *Nothofagus* beech forest.

Where appropriate, comparisons were made with the Hurunui data previously reported in Kearvell (2002) by analyzing our data for that valley only. We assumed variances were equal and that the data was distributed normally and have therefore used the Student *t*- test. We have also used Pearson's Chi-squared (χ^2) goodness-of-fit statistic, including Yate's correction, where departure from an expected 1.0 ratio was considered.

RESULTS

Nest site description

Orange-fronted parakeet

A total of 138 orange-fronted parakeet nests were found, with 39 in the Hurunui, 41 in the Poulter Valley and 58 in the Hawdon Valley. All nests in living trees were built in beech trees (*Nothofagus* spp.), with 94 (69%) found in red beech (*N. fusca*), 3 (2%) in silver beech (*N. menziesii*), and 13 (9%) in mountain beech (*N. solandri* var.*cliffortioides*). The remaining 28 (20%) nests were located in SDT. The mean nest height was 10.87 m (SD = 5.1, *n* = 131, range 2 to 21 m), and the mean tree height was 20.6 m (SD = 5.74, *n* = 133), with a mean DBH of 79.6 cm (SD = 26.4, *n* = 120, range 30 to 141 cm). The majority of nests were in larger trees. The mean overall condition of the nest tree was 3.10 (SD = 1.17, *n* = 135).

The majority of nests were located in trunks (83.7%, *n* = 98), with fewer in branches (16.3%, *n* = 19) and all were accessed through either knot holes (87.2%, *n* = 123) or slits (12.8%, *n* = 18). Entrance holes varied in size, with the smallest being 20 x 40 mm (628 mm^2), and the largest 250 x 150 mm (29456 mm^2); both were knot holes. The mean area of the entrance was 4252 mm^2 (SD = 4841.8, *n* = 111). The smallest single dimension recorded was a width of 20 mm.

Seven nest bowls (9.1%, *n* = 77) were level with the entrance. The deepest nest was measured at 1000 mm from the nest entrance. The mean depth of the nest bowl was 245 mm (SD = 238.9, *n* = 77). The majority of nests faced the northeast quarter ('N' to 'E', 40.8%, *n* = 56), while 43.1% (*n* = 59) faced the south half ('E' through 'S' to 'W').

Yellow-crowned parakeet

A total of 119 yellow-crowned parakeet nests were found with 74 in the Hurunui, 33 in the Hawdon Valley and 12 in the Poulter Valley. All were in beech trees, with 79 (66%) nests in red beech, 20 (17%) nests in silver beech, and 7 (6%) nests in mountain beech. The remaining 13 (11%) nests were built in STD. The mean nest height was 10.6 m (SD = 3.7, *n* = 110, range 3 to 22 m), the mean tree height was 21.3 m (SD = 5.01, *n* = 96). DBH was only measured

Table 1. Mean values for nest site comparisons between orange-fronted parakeet and yellow-crowned parakeet. STD = standing dead tree.

Variable	Orange-fronted parakeet	Yellow-crowned parakeet	Test statistic	*P*
Tree height	20.6 m	21.39 m	*t*-test	0.28
DBH (Hurunui only)	84.2 cm	85.5 cm	*t*-test	0.81
Tree condition	3.103	3.129	*t*-test	0.86
Site (trunk or branch)	98-19	84-26	χ^2	0.16
Hole type (knot or slit)	123-18	98-11	χ^2	0.48
Nest bowl depth	245.1 mm	183.9 mm	*t*-test	0.052
Height of hole above ground				
Overall	10.87 m	10.66 m	*t*-test	0.73
STD only	8.01 m	8.37 m	*t*-test	0.78
Mountain beech only	6.66 m	5.53 m	*t*-test	0.53
Silver beech only	14.66 m	10.61 m	*t*-test	0.06
Red beech (Hurunui Valley)	13.55 m	11.58 m	*t*-test	0.052
Red Beech (Hawdon Valley)	12.42 m	11.84 m	*t*-test	0.59
Entrance hole				
Height	96.7 mm	108.9 mm	*t*-test	0.32
Width	51.1 mm	62.6 mm	*t*-test	0.025
Knot hole only (height)	77.2 mm	98.4 mm	*t*-test	0.026
Knot hole only (width)	52.5 mm	64.2 mm	*t*-test	0.041
Red beech only				
All valleys hole height	98.3 mm	114.0 mm	*t*-test	0.34
All valleys hole width	48.9 mm	67.4 mm	*t*-test	0.008
SDT only				
All valleys hole height	73.2 mm	132.3 mm	*t*-test	0.047
All valleys hole width	56.1 mm	60.9 mm	*t*-test	0.582
Area of entrance				
Knot and slit	4252 mm^2	8086 mm^2	*t*-test	0.076
Knot only	3541 mm^2	7947 mm^2	*t*-test	0.067
All valleys Red Beech	3027 mm^2	10590 mm^2	*t*-test	**0.0349**
Orange-fronted parakeet nest hole aspect			χ^2	**<0.001**
Yellow-fronted parakeet nest hole aspect			χ^2	**0.0506**

in nests in the Hurunui and averaged 85.1 cm (SD = 262.2, n = 67, range from 28 to 170 cm). As with the orange-fronted parakeet, the majority of nests were in larger trees. The mean overall condition of the nest tree was 3.13 (SD = 1.23, n = 116).

The majority of nests were positioned in trunks (76.3%, n = 84), with fewer in branches (23.7%, n = 26) and all were accessed through either knot holes (86.7%, n = 98) or slits (13.3%, n = 11). Entrance holes varied in size, with the smallest being 40 x 30 mm (942 mm^2) and the largest 550 x 400 mm (172810 mm^2); both were knot holes. The mean area of the entrance was 8086 mm^2 (SD 22135.1, n = 107). The smallest single dimension recorded was a width of 25 mm.

Twelve (11.4%, n = 110) nest bowls were level with the nest hole entrance, while the deepest nest bowl was 750 mm. The mean depth was 183.8 mm (SD = 184.4, n = 105). The majority of nests faced the northwest quarter ('N' to 'W', 32.4%, n = 25), while 42.9% (n = 33) faced the south half ('E' through 'S' to 'W').

Nest site overlap

Table 1 lists the results of statistical comparisons between the 2 species. There were no significant differences between the 2 species and their choice of nest site for tree height, height of nest hole above ground, DBH and tree condition. The selection of site of nest hole and type of nest hole were also similar between the 2 species. Over all nests selected, the vertical height (maximum vertical diameter) of the entrance holes was similar.

The height of nest hole above the ground also did not differ significantly if the different tree species were considered (Table 1), except for nests in red beech in the Hurunui Valley, where orange-fronted parakeet nests were higher than yellow-crowned parakeet nests.

Nest hole width dimensions, for all holes, were significantly different between the 2 species with orange-fronted parakeet using a narrower entrance. As several of the 'slit' measurements had extreme heights (*e.g.*, between 400 and 700 mm) and were few in number, we compared nests with knot holes only. Knot hole width varied significantly between the 2 parakeet species, indicating that orange-fronted parakeet use narrower nest holes. SDT entrance hole vertical height was significantly different between the species with the yellow-crowned parakeets using nests with a higher height.

Although we found several significant differences between the height and width of the entrance hole dimensions, we did not find that the area of the hole was significantly different between the species, even if we considered just knot holes. However, when we compared entrance hole area for red beech only, which for both species constitutes the greatest number of nests (69% and 66% for orange fronted and yellow crowned parakeets, respectively), we found that over all valleys, orange-fronted parakeets selected holes with a significantly lower entrance area than did yellow-crowned parakeets.

There were near significant differences in the depths of the nest bowls between the 2 species. It should be noted that only 70.8% (n = 182) of confirmed nests were measurable for nest bowl depth and so this data must be interpreted with some caution.

We found a significant difference between the 2 parakeets in their choice of nest tree species (Table 2). Orange-fronted parakeets selected standing dead trees more frequently and silver beech less frequently than expected while yellow-crowned parakeets selected fewer standing dead trees and more silver beech than expected. In the Hurunui, orange-fronted parakeets selected fewer silver beech as nest trees than expected, while yellow-crowned parakeets selected more.

A comparison of nest aspect combined across all valleys indicates that orange-fronted parakeets appeared to select a northeast direction significantly more than expected ($\chi^2 = 22.0$, $df = 1$, $p < 0.001$), whereas yellow-crowned parakeet showed a significant preference for a northwest direction and avoidance of the southwest ($\chi^2 = 3.82$, $df = 1$, $p = 0.05$). However, the orientation of the respective valleys and the numbers of nests for each species in each valley may play a part in this result. Both the Poulter and Hawdon Valleys are orientated approximately north to south while the Hurunui runs east to west. We found that both the Poulter ($\chi^2 = 5.79$, $p = 0.016$) and Hawdon Valleys ($\chi^2 = 4.49$, $p = 0.034$) had a significant number of nests facing northeast and not northwest, while the Hurunui had a significant number of nests facing northwest ($\chi^2 = 13.16$, $p = 0.0002$). Overall, 71.7% of orange-fronted parakeet nests were located in the predominantly northeast facing sites of the Hawdon and Poulter Valleys, while 62.1% of yellow-crowned parakeet nests were in the predominantly northwest facing Hurunui Valley. It is possible that there is no difference in the selected aspect of either species and the differences may have more to do with the valley orientation.

Table 2. A comparison of nest tree species selected by orange-fronted parakeet (OFP) and yellow-crowned parakeet (YCP). As only 12 nests recorded for YCP in Poulter Valley (OFP $n = 41$) no comparison was possible.

	OFP	YCP	χ^2	*P*
All valleys				
Red beech	94	79		
Silver beech	3	20		
Mountain beech	13	7		
Standing dead tree	28	13	19.83	<0.001
Hurunui Valley				
Red beech	28	48		
Silver beech	3	16		
Mountain beech	2	1		
Standing dead tree	6	9	4.88	0.027
Hawdon Valley				
Red beech	36	21		
Silver beech	0	2		
Mountain beech	7	6		
Standing dead tree	15	4	5.97	0.014

Nests used by both species

There were 13 nests known to have been used by both species in sequence, with 3 each in the Poulter and Hurunui Valleys and 7 in the Hawdon Valley. Not all had complete data sets: 8 (61.5%) were in red beech, 3 (23.07%) in SDT and one each in mountain

Table 3. Mean nest site characteristics for 13 nests used by both orange-fronted and yellow-crowned parakeets.

	Tree height (m)	DBH (cm)	Nest height above ground (m)	Nest entrance hole width & height (mm)	Cavity depth (mm)
Mean	20.5	69	10.5	49.7 x 83.7	301.5
Range	6.5-26	32-117	3.8-17.6	(30-120) x (45-140)	20 - >1000

and silver beech. Twelve nests were situated in trunks, one in a branch, 12 were accessed through knot holes and one through a slit. Table 3 lists a summary of the characteristics of these nest size but no statistical tests were carried out because of the few data points.

DISCUSSION

It is not surprising, perhaps, that we found limited differences in nest site selection between these 2 recently speciated parakeets (Trewick &Gibb 2010; Boon *et al* 2001). In fact, it appears that they select very similar nest sites regardless of the features we examined, including tree species selection, nest height and size of nest tree. The large degree in overlap in nest site characteristics is aptly illustrated by observations that about 10% of the nests were used by both species at varying times (Table 3).

Given the highly 'modified' nature of their current environment occupied by both orange-fronted and yellow-crowned parakeets (*e.g.,* introduced predators and herbivores, forest clearance; Inness *et al*. 2010), it is not clear if nest site features were more dissimilar prior to habitat modification given that old growth and unlogged forests tend to have a greater diversity and abundance of tree hollows that could be used as nest sites (Spurr 1987; Stewart & Burrows 1994). Testing the hypothesis will be difficult given the current lack of unmodified forests but it may also be the case that nest site may be similar across a variety of forest types.

Despite the overall similarity in nest site characteristics, some features differed between the 2species. Kearvell (2002) recorded a significant difference between the 2 species in the selection of nest tree species. Our study also found similar significant differences (Table 2), with yellow-crowned parakeet selecting silver beech (16.8%) more than expected (compared to 2.1% in orange-fronted parakeet) and orange-fronted parakeet selecting STD (20.2%) more often than expected (yellow-crowned parakeet 10.9%). It is interesting to note that Elliott *et al*. (1996b) also found that yellow-crowned parakeet selected a lower percentage (3%) of STD, and a higher percentage of silver beech (21%) in their single species study in the Eglington Valley, Fiordland; they found a large majority of nests were in red beech (77%). In Western Australia, red-tailed black cockatoo (*Calyptorhynchus magnificus*) likewise was found to favour STD more so than the other 5 parrot species in woodland (Saunders *et al*. 1982).

We found a consistent difference between the 2 species with their selection of nest hole entrance width and in some cases, with hole height. Orange-fronted parakeets tended to use smaller holes, although there was much overlap. If we consider the body sizes of the 2 species then perhaps this difference is not surprising, with male orange-fronted parakeet averaging 44 g ($n = 159$) in captivity (Anne Richardson, *pers. comm.*) and a reported 51 g for male yellow-crowned parakeet (Elliott 2013). This difference in body size parallels our finding that the area of their nest hole entrances tends to be significantly different. In both species the female is smaller, but because the male alone feeds nestlings while the female lays the next clutch in another site (when laying multiple clutches), then the male must be able to enter the selected hole or the clutch will fail.

The other cavity nesting species, the congener red-crowned parakeet, formerly part of the avifauna, is a magnitude larger, with males on the Poor Knight's Islands averaging 82.1 g (Sagar 1988). While information on nest site selection is available only from a study on Little Barrier Island (Greene 2003), it is interesting to note that their nest holes were, on average, 9960 mm^2, with a minimum dimension recorded of 30 mm. This is larger than for both the yellow-crowned parakeet and for orange-fronted parakeet. Perhaps when the 3 species occurred in sympatry, they did show a niche separation based on the size of the nest hole. The larger nest holes of red-crowned parakeet, and propensity to nest low or even on the ground (Greene 2003) may explain why they no longer survive on the main islands in the presence of introduced predators.

Elliott *et al* (1996b) considered that mohua (yellowhead) and yellow-crowned parakeets may compete for individual nest sites, but that they considered there were many sites available for both species and thus competition for nest sites probably did not influence either species' populations. Deciding whether the availability of nesting cavities is limiting is difficult, as the observation that many cavities remain unused does not necessarily mean that the availability of cavities is not limiting. Elliott *et al* (1996b) could not be categorical about cavity availability being limiting, though thought that the high density of holes available made it seems unlikely. Nevertheless, as recent studies have found fewer nest sites than were first proposed to be available (Blakeley *et al.* 2008), competition for sites cannot be ruled out (Cockle *et al* 2010).

In other avian communities, competition between parrot species for natural cavities is fairly well documented (Garnett *et al*. 1999; Robinet & Salas 1999), as are some of the actual and potential conservation implications of interspecific competition (Chang *et al*. 2006; Green 1998). That New Zealand parakeets have a significant overlap in their selection of cavity should not be a surprise and is in no way unique. The detailed study by Saunders *et al.* (1982) on cavity use by 6 species of Psittaciformes in 15 ha of woodland in Western Australia, also found extensive overlap in the size of the cavities selected. They too found that size of the bird is related to the size of the cavity hole, where smaller parrot species tended to use smaller holes. Where species were of a similar size, behaviour dictated cavity use (*e.g.*, a species with a long tail had to have a cavity large enough to be able to back into). The antagonistic behaviours of 4 species at the nest site also varied, with one protecting the site all year, 2 only during breeding and one unable to breed within 2 km of other members of the same species. They also found that depth of the cavity and aspect were not significant predictors of site selection. Within their study area they found 47% of 'hollows' were occupied (Saunders *et al.* 1982).

Behavioural limitations may render many potential cavities of no use. For example, the proximity of a cavity to an already occupied cavity may prevent its use. Field observations on both orange-fronted parakeet and yellow-crowned parakeet indicate that they will only defend the hole and immediate nest hole surrounds (~5 m radius; *pers. obs.*). However, we cannot rule out that their influence is greater than this and so several trees with potential holes could be excluded. Greene (2003) suspected that the tolerance for red-crowned parakeet to nest in sub-optimal cavities closer than 10 m, on his highly modified study site, was because of a scarcity of cavities.

It is possible that the 2 species of parakeet in our study do not, in fact, require different types of nest site and that they could have co-existed in formerly unmodified South Island beech forests because they were nutritionally and cavity rich habitats. In most years the apparent abundance of nest sites would allow the congeners to exist without competition. It may have been that the orange-fronted parakeet always existed at the reported lower densities (Phillpotts 1919), when compared to the other 2congeners. However,now that we have substantially modified their habitats this balance has been affected, resulting in the extinction of the red-crowned parakeet on the mainland and the orange-fronted parakeet is severely threatened and has thus produced a system that can no longer support parakeets at former levels.

Establishing if there is interspecific competition, either direct or indirect, between these 2 species of parakeet is difficult. Our data appears to show considerable overlap within nest sites selected and that some holes are used immediately by one species after the other has finished with it.This has included instances where the other species has intermittently sat outside the hole for the entire active period of the nest. We do not know if this was a member of a breeding pair with a nest elsewhere, or a single bird responding to the stimulus of nesting behaviours (*unpubl. data*). However, the large overlap and use of the same nest site would suggest the presence of some level of interspecific competition. Both intraspecific and interspecific antagonistic behaviours are fairly regularly observed in the wild, although only rarely at or near the nest (Kearvell & Steeves 2015).

Competitive exclusion (Hardin 1960) theory states that 2 similar species cannot exist together and that some behaviour or morphology must be different for them to exist. Often these differences can be hard to isolate and are often quite subtle, such as resource partitioning where one species of bird feeds by going up the trunk (*e.g.*, brown creeper *Certhia americanna*) while another feeds by going down the trunk (*e.g.,*white-breasted nuthatch, *Sitta carolinensis*); as a result different invertebrates will be scanned and taken by the two species (Pravosudov & Grubb 1993). Are the differences found between the 2 sympatric parakeets we studied different enough for them to exist together? These differences include some diet and habitat use differences (Kearvell *et al.* 2002), plus the differences in nest tree species selection (Kearvell 2002), and nest hole size differences we found in this study. Some significant differences also occur within their vocalisations (Kearvell & Briskie 2003) and bill lengths are also significantly different (Young & Kearvell 2001). Even considering the extensive overlap and the loss of the red-crowned parakeet, it is possible that these species could co-exist when their numbers were low, because the habitat was nutritionally and cavity rich. Only after a period of intense breeding, as with a mast seeding year (Wardle 1984), would numbers increase and competition intensify, perhaps to the point of exclusion. A mast season occurs approximately every 2 to 6 years, where the *Nothofagus* spp. produce seeds in vast amounts, providing a huge amount of food and thus an explosion in breeding for birds, especially the parakeet species. This could then have triggered the massive eruptions of all 3 species that were recorded from the 1880's (Phillpotts 1919) as they seek new sources of nutrition and possible breeding sites.

Given the current distribution and threatened status of parakeets in New Zealand, we cannot undertake comparative or experimental removal studies where one species is absent or present, which would allow us to study nest site selection without a competitor in the same habitat. The orange-fronted parakeet no longer inhabits the Eglington Valley, although the data found in Elliott *et al.* (1996b) suggests nest site selection by yellow-crowned parakeets is similar to that on our study sites. Furthermore, all remaining habitat is now considerably modified and so it will be difficult to determine how much overlap and thus competition may have occurred under previous conditions (Inness *et al.* 2010). Nevertheless, the evidence we have does point to some level of competition at the 3 mainland sites where both orange-fronted and yellow-crowned parakeets presently occur. Nest site selection at these 3 sites is similar, although orange-fronted parakeet are able to use slightly smaller holes and do appear to select significantly different tree species to their sympatric congener. Whether this latter difference is a remnant of former behaviours, former niche differentiation, where now the species find themselves 'closer together', is impossible to verify at the present. It may be possible to compare these 2 species in the future, when orange-fronted parakeet populations are established on islands where another congener does not yet exist, or they return in numbers to the mainland sites.

Competition between closely related species is often exacerbated by modification of the habitat (Sauders *et al.* 1982; Garnett *et al.* 1999; West & Nilson 1994) and it seems likely here that these 2 species have been forced closer together since the anthropogenic manipulation of their habitat (Innes *et al.* 2010). Whether or not this has resulted in a decline of one or both species requires further research.

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