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Adult sex ratios in wild orange-fronted parakeet (*Cyanoramphus malherbi*): are there conservation implications?

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Abstract Many globally threatened bird species have been shown to have highly male-skewed sex ratios. This is concerning for conservation as such populations have a higher extinction risk and lower reproductive population sizes. Our surveys of the remaining populations of orange-fronted parakeet (*Cyanoramphus malherbi*) indicate this species currently has a non-breeding season adult male population proportion of between 0.56 and 0.66. This male bias increased to between 0.68 and 0.74 during the breeding season. Limited data also suggest that prior to recent declines in the population size of orange-fronted parakeets, driven largely by introduced mammalian predators, the adult sex ratio (ASR) may have been closer to parity. The excess of males indicates that this species currently has a compromised population structure, despite intensive conservation management undertaken since 2000 to limit predation.

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INTRODUCTION

Adult Sex Ratios (ASRs), or tertiary sex ratios, are defined as the sex-ratio of all independent non-juvenile individuals (Mayr 1939). The causes of variation in ASRs and their effects upon future populations are varied but little understood (Donald 2007). This lack of information could have serious implications for understanding population dynamics in the conservation of endangered species. Recent studies have found that globally threatened species seem to have heavily skewed ASRs, which may suggest a smaller effective population size and a greater extinction risk (Donald 2007; Clout *et al*. 2002).

Allee effect modelling suggests this extinction risk is predicted to increase with increasing male skew (Bessa-Gomes *et al*. 2004). This risk was demonstrated with viability analysis in Spanish populations of little bustard (*Tetrax tetrax*), where population persistence was sensitive to a shortage of females. This is concerning for conservation, especially for populations that rely upon translocations for immediate negation of the risk of extinction, such as with the orange-fronted parakeet (*Cyanoramphus malherbi*; Kearvell 2013).

The orange-fronted parakeet is a globally threatened species that is endemic to New Zealand

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and listed as critically endangered and declining in the IUCN Red List (Birdlife International 2013). Recently, its threat status has been reduced by the New Zealand conservation authority to endangered (Kearvell 2013; Robertson *et al*. 2013) where the B (2/1) listing states the population is stable. This infers an improving situation as far as the species conservation is concerned. However, this decision may be premature based upon the latest population estimates, which shows further recent declines (*unpubl. data*).

In an extensive discussion on ASRs, Donald (2007) suggests 5 possible conservation implications for populations with highly skewed sex ratios. Firstly, ASRs in such populations "may represent one end of a general correlation between population trend or density and sex ratio," although the mechanism is unknown. The second suggests a skew in small populations may represent an effect of inbreeding, leading to the spread of deleterious alleles. This could lead to rapid loss of genetic diversity and "may exacerbate or result from inbreeding depression and asymmetric gene flow" (Eldridge *et al*. 1999). This may result in further increases in sex ratio skew and ultimately in population collapse (Telshow *et al*. 2006). The third possibility is a shortage of resources, where larger or more dominant males outcompete and reduce the survival of females. A fourth implication is that many threatened species are confined to small and isolated populations where male-skewed populations are common (Dale 2001). Here the suggestion is that females may disperse into unsuitable habitat (Steifetten & Dale 2001). The final implication is that many threatened bird species are in such a condition because of the effects of introduced predators (Innes *et al*. 2010), where the incubating sex, which is usually the female, suffers disproportionately high predation due to their naivety. For example, this has been documented in the 3:1 male to female ratio of the North Island kaka (*Nestor meridionalis septentrionalis*), which Greene and Fraser (1998) suggested was caused by greater predation on incubating females by introduced predators. The Norfolk Island green parrot (*Cyanoramphus cookii*) is also critically endangered, and similarly has a highly male skewed population; this is known to be a direct result of higher predation on females from introduced mammalian predators (L. Ortiz-Catedral, *pers. comm*.).

The orange-fronted parakeet survives on the mainland only in a single meta-population (Andrews 2013), comprising 3 sub-populations over 3 valleys. The habitat has been extensively changed by human activities (Innes *et al*. 2010), and there is some suggestion that resources in these habitats may be limited (Kearvell *et al*. 2002). As with other native species, there is considerable loss of nests and adults from introduced mammalian predators, which appear to depredate females disproportionately (Kearvell 2013). There is also anecdotal field evidence that the remaining mainland meta-population are male-skewed, and the 3 small remaining sub-populations exhibit a lack of genetic diversity (Andrews 2013).

The orange-fronted parakeet has recently been reintroduced to 4 islands as part of a strategy to ensure their conservation. All 4 island populations are also small and all were sourced from the single mainland meta-population. Three of these islands are less than 350 hectares in area and thus the population cannot expand indefinitely nor can they mix with other populations of the species. The population of orange-fronted parakeets on Maud Island was reported as being reduced to only a few individuals (Kearvell 2013), while the population on Tuhua Island, although having a larger area (1200 hectares), also has not been reported as increasing (Kearvell 2013). This highlights the importance of ensuring the mainland populations survive and their condition is monitored regularly.

Obtaining unbiased ASRs in wild populations of birds is difficult as they can vary seasonally, spatially, and between age groups (which is further complicated by defining a mature adult). On the other hand, the ASR in studies where the bias was not considered did not differ from those that did (Donald 2007). In a review of over 200 published estimates, Donald (2007) found that, on average, males outnumbered females by ~33%, and 65% of published estimates differed significantly from equality. He suggested that an equal sex ratio may not represent the norm in most species, even though there is evidence for most offspring sex-ratios being 1:1 (Sheldon 1998). Furthermore, a review of sex ratios in 80 species of captive parrots confirmed the sex ratio is seldom near unity, with 72% of species showing a male bias (Taylor & Parkin 2008). Although rare, sex ratios biased in favour of females can occur as Krebs *et al*. (2002) found in wild crimson rosellas (*Platycercus elegans*) in Australia.

Recent evidence suggests that female birds in some species, including parrots such as the critically endangered New Zealand kakapo (*Strigops habroptilus*), can even manipulate the sex ratio of their broods (Clout *et al*. 2002; Komdeur & Pen 2002; Pike & Petrie 2003). In birds, females are the heterogametic sex (ZW), which may allow them to more readily alter the sex of their offspring, although the mechanism of manipulation is not completely understood. Nevertheless, female control of the sex ratio is not universal, as Budden and Beissinger (2004) found no evidence for sex ratio manipulation in the green-rumped parrotlet (*Forpus passerinus*).

Table 1. Adult sex ratio (ASR) for orange-fronted parakeet (proportion of count made up of males, *p*m) in the Hawdon Valley from 2009-2012. Data from all observers and transects combined. Pre-breeding counts occurred before December (<December), while counts during breeding took place from January onwards (>January). Male = m, Female = f.

Year	*p*m < December	χ^2	*p*	*n* = m	*n* = f	*p*m > January	χ^2	*p*	*n* = m	*n* = f
2009	0.586	3.45	NS	68	48	-	-	-	-	-
2010	0.578	4.21	0.05	100	73	0.678	10.72	0.01	57	27
2011	0.574	3.84	0.05	93	69	0.704	10.26	0.01	43	18
2012	-	-	-	-	-	0.740	6.28	0.05	20	7

Extremes in sex ratio can be a concern to conservation managers as many globally threatened species seem to have skewed ASRs (Clout *et al*. 2002). Male-biased sex ratios have been shown to compromise reintroduced populations, to the extent that they can increase the probability of extinction as Lambertucci *et al*. (2013) detailed with the Andean condor (*Vultur gryphus*). They also demonstrated, through modelling, that the number released and the length of the release programme can be crucial to a positive outcome. While it appears that releasing individuals of differing age classes can affect the demography of a population (Sarrazin & Legendre 2000), the effect of releasing birds with a biased sex-ratio is not clear. There is also evidence that biased sex ratios can contribute to dissasortative mating in critically endangered species that otherwise mate assortatively. This has been indicated in black stilt (*Himantopus novaezelandiae*) and possibly the orange-fronted parakeet (Steeves *et al*. 2010; Kearvell & Steeves 2015).

There is an urgent need to investigate the sex ratios in both wild and captive populations of endangered parrots, to determine, firstly whether such ASRs are abnormal, and if so, what are the causes and effects of these ratios on the conservation of the species. In this study we investigate ASRs of wild populations of the orange-fronted parakeet.

METHODS

Study sites

Data on the ASRs of orange-fronted parakeets was collected from the 3 valleys in which the single remaining natural meta-population is still extant. The total number of orange-fronted parakeets in this population is difficult to assess accurately, largely because they are spread over a considerable area of high alpine (*Nothofagus* spp.) forest (13,237 ha) and the populations are not banded. However, a recent survey estimates the population at around 150-200 mature birds and this is distributed throughout the Hawdon (42° 58.18′ S, 171° 44.52′ E) and Poulter (42° 54.19′ S, 171° 51.97′ E) Valleys in Arthur's Pass National Park and the South Branch Hurunui River (42° 45′ W172° 5′ E) Valley in Lake Sumner Forest Park (Kearvell 2013).

Data collection

All data originated from field records from the Department of Conservation's work on this species. Birds were sexed using a combination of morphological traits as well as phenotypic differences and behavioural interactions. Known sexed birds in captivity were used to verify traits. Males (40-52 g) are on average larger than females (30-41 g), with minimal overlap (Kearvell 2014; Kearvell 2013). Males tend to be more brightly coloured and with a bolder frons, while the plumage colours in females often appear slightly faded (Kearvell 2014; Kearvell 2013). The bill of males is also significantly longer than the bill of females (Young & Kearvell 2001). When observed in pairs, differences in size and coloration were usually visible, and in combination with behaviours such as courting, mating and breeding, sex could be assigned reliably. Solitary birds can be more difficult to sex, but with experience, sex could be assigned to most individuals based on plumage, size and behaviour. No individual was allotted sex unless the observer was certain.

Observers spent each day traversing the forested valleys identifying all orange-fronted parakeets to sex, where possible. Field data was collected, mostly in the austral summer between 2007 and 2012 and during each season between October and April. Team numbers varied between 4 and 6 each season. As birds were unbanded, there was some risk of double-counting individuals. While this could not be reduced to zero, every effort was made not to double-count. Each team member was allotted a separate area each day and asked not to retrace their steps where ever possible. Once a team member found possible breeding birds, the count was stopped while these individuals were studied.

Here we express the ASR as the proportion of the count made up by males (Wilson & Hardy 2002), calculated m/(m + f). We tested the departure from an expected 0.5 ratio using Pearson's χ^2 goodness-of-fit statistic. Counts were analysed separately for those undertaken in the pre-breeding season (before December) and those during breeding (January onwards).

RESULTS

The proportion of males in the orange-fronted parakeets in the Hawdon Valley, in the pre-breeding period, ranged between 0.574 to 0.586 for the 3 seasons from 2009 to 2011 (Table 1). The pre-breeding counts were similar across the 3 seasons, indicating a consistent male bias in the population. Only one count did not differ significantly from a 0.5 ratio; this occurred in the pre-breeding period in 2009 (Table 1). For the 3 counts taken during the breeding season, all differed significantly from a 0.5 ratio, with ratios varying from 0.678 to 0.740. This greater male bias during breeding is not surprising, as from January onwards most females spend much of their time incubating (Kearvell 2013).

When survey data from all 3 valleys were analysed (Table 2), there was an indication of a male bias during the pre-breeding phase of the season from 2007 to 2011. However, only 2 of the counts differed significantly from a 0.5 ratio and so care must be considered with this interpretation.

Table 2 also lists survey data from the South Branch Hurunui in 1998, the only data available on the sex ratio of the orange-fronted parakeet from before a rat plague in 2001 reduced the population by ~85% (J. van Hal, *pers. comm.*; J. Kearvell, *unpubl. data*). This result (0.518; n = 189; 98 males) does not differ significantly from a 0.5 ratio.

Table 2. ASR for orange-fronted parakeet (proportion of count made up of males pm) in all 3 valleys combined during the pre-breeding period (October to December). The 1998 data refers to the only sexed data from the Hurunui prior to the 2001 rat plague. Male = m, Female = f. NS = not significant.

Year	pm	χ^2	p	n = m	n = f
2007	0.565	1.06	NS	43	33
2008	0.576	0.94	NS	30	22
2009	0.666	4.68	0.05	32	16
2010	0.577	0.8	NS	26	19
2011	0.625	4.01	0.05	45	27
1998	0.518	0.19	NS	98	91

DISCUSSION

There are many variables to consider when obtaining unbiased estimates of sex ratio in populations of wild birds, and our results have indicated the importance of accounting for time of season. Our method of estimating the ASR produced different ratios over a season, with fewer females observed during the breeding season. This bias is not unexpected if we examine the breeding behaviour of orange-fronted parakeet, as the female incubates the clutch exclusively over ~26 to 30 days. If a second brood is commenced the female will lay again around 2 weeks after the first brood hatches (Kearvell 2013) and she will stay in the nest to transfer food to the young nestlings. Therefore females during the breeding season can be inside the nest hole for considerable lengths of time, only coming off a few times each day to be fed by the male.

Although we found the male bias increased during the breeding phase and this leads to an over-estimate of the number of males in the population, this also suggested that our count method was sensitive enough to pick up this difference. This supports our observations made in the pre-breeding period (when females are not on nests) of a smaller, though mostly significant male bias in the wild orange-fronted parakeet ASR of around 0.56 to 0.66. We suspect this male bias may result from high levels of predation from introduced mammalian predators (Kearvell 2013; Innes *et al*. 2010) that falls disportionately on nesting females, although data is needed on the mortality of females at the nest to test this hypothesis.

Our finding that the ASR of wild orange-fronted parakeets appears to be male biased is supported by data on other New Zealand parakeet species caught in the wild. Elliot *et al.* (1996) caught 106 yellow-crowned parakeets (89 males) in the Eglington Valley, Fiordland. Although they did not quote a proportion, their data indicates the proportion of males in the population is 0.83. Within this valley there is considerable predation from introduced mammals. However, on the Poor Knights Islands where there are no introduced mammalian predators, Sagar (1988) found a male proportion of 0.64 (total of 311 birds mist-netted, 200 males). Using mist nets and call birds, the senior author caught 19 parakeets (both orange-fronted and yellow-crowned; 11 males) in the South Branch Hurunui, a male proportion of 0.58, but using the same method in the Eglington Valley, all 28 parakeets captured were males (J. Kearvell, *unpubl. data*). Two visits to predator-free islands produced a similar male bias: Chalky Island (surveyed in 2012) had 10 males to 6 females (0.62) and Maud Island (surveyed in 2010) had 15 males to 11 females, 0.57 (J. Kearvell, *unpubl. data*). While these estimates are based on a small sample, a male bias is evident in all. As Sagar (1988) suggests the true ASR in wild populations of New Zealand parakeets may be a bias towards males, but both Sagar (1988) and Elliott *et al*. (1996) also state that mist netting to survey parakeets is likely a biased sampling method. Indeed, Greene and Fraser (1998) found that mist nets captured male North Island kaka twice as effectively as females. Nevertheless, the male bias observed in netting studies is consistent with sex ratio estimates obtained from other methods.

Our method of surveying *Nothofagus* forests are likely to be less biased than using mist nets, taped calls and call birds. It was designed to search for this cryptic species, to locate and sex all individuals in the population, and to find their nests to protect them from introduced mammalian predators. We have no evidence that the method is biased towards a single sex (at least in the non-breeding season when females are not incubating) and thus appears to confirm a male bias in the wild ASR. Even though some of the counts were not statistically significant in some years, overall they indicate the population exhibits a male bias in most years. As Donald (2007) suggests, "…there is currently no quantitative evidence that an ASR of one male to one female represents the norm in birds", and our results suggest this is also the case for orange-fronted parakeets.

The potential effect of increased predation risk on changing the sex ratio was clearly illustrated by surveys from the South Branch Hurunui for 1998 (Table 2). This was collected before a rat (*Rattus* spp.) plague in 2001 devastated this population and indicated that both orange-fronted and yellow-crowned parakeet (*C. auriceps*) occurred at a sex ratio close to parity (Kearvell *et al*. 2002). The male proportion of 0.518 is the closest to parity we observed and raises the possibility that, prior to recent declines, the sex ratio may have been much closer to parity. The male proportion of 0.64 collected by Sagar (1998) on the predator-free Poor Knights Island seems to contradict this; however, he used mist nets and calls and this method is known to bias in favour of males (see Greene & Fraser 1998), as they are caught in nets much easier than females. More work on island populations, without the use of mist nets, might provide some data that helps to resolve this issue. The extant meta-population of wild orange-fronted parakeets does seem to have a male bias, even though the population is protected by large scale integrated pest control (Kearvell 2013) which should have been reducing the level of predation on females occupying nest holes. This suggests predator control has not been sufficient to prevent a male bias in the population.

As a result of the currently skewed population, a potentially unusual behaviour has been noted by field staff. Extra-pair males of both species have been noted to persistently 'hang around' active nests, including inter-species aggressive courtship behaviour. Here the more common yellow-crowned parakeet (possibly also with a male-skewed population), have been observed aggressively courting female orange-fronted parakeet which appeared to have an attendant male orange-fronted parakeet. It should be noted that male yellow-crowned parakeet are larger (mean 51 g), than male orange-fronted parakeet (40-52 g; Elliott 2013; Kearvell 2013). While these behaviours have not been monitored in detail, it is a potential example of increased aggressive competition by 'spare' males, which can result in nest intrusion by unpaired males resulting in egg loss or infanticide, or even established pair disruption. If this behaviour is indeed occurring within the small male-skewed orange-fronted parakeet meta-population, then it is another factor that will have a negative long term effect upon that population and thus the future conservation of the species. This warrants further investigation.

The general consensus in the literature is that skewed ASRs are common amongst wild bird populations. Interestingly, and rather worryingly, Donald (2007) found that birds listed by the IUCN as Globally Threatened or Near-threatened showed both significantly more male-skewed ASR and a greater deviation from parity than non-threatened species. Certainly the critically endangered orange-fronted parakeet seems to have a male-skewed wild population. Even if a male skew is normal in this species, it has probably been exacerbated by increased predation on secondary cavity-nesting females. It is also possible that other causal factors may include reduced fitness, inbreeding and environmental and ecological factors.

The reduction in the number of females has an obvious conservation issue within the meta-population. There are simply fewer mature females to produce the next generation, which in turn will reduce the overall genetic diversity of the meta-population. This also means that the effective population size is less than the census population size any survey has produced and this should be taken into account when undertaking any future threat status designations.

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