Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot

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Abstract

The kakapo (*Strigops habroptilus*) is a large, flightless, nocturnal parrot, endemic to New Zealand. It is critically endangered, with a world population of ca. 62 individuals and a male-biased adult sex ratio. The species has a polygynous "lek" mating system and adult males typically weigh 30–40% more than females. The kakapo is subject to intensive conservation efforts, including the provision of supplementary food to wild birds to encourage successful nesting. There is mounting evidence that, in polygynous species with large variance of male reproductive success, females in better condition may maximise their fitness by producing more offspring of the larger, more costly sex to be reared. We used data on the sex ratio of progeny of female kakapo that had or had not received supplementary food, to test the hypothesis that supplementary feeding might cause a male-biased offspring sex ratio. There was a significant excess of males in the clutches of females provided with supplementary food, suggesting that changes need to be made to the feeding regime to increase recruitment of females. This is an example of applying evolutionary theory to a practical conservation problem. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The kakapo (*Strigops habroptilus*) is a flightless, nocturnal parrot, endemic to New Zealand. It is the largest parrot species, (weighing up to 4.0 kg) and is classed as "critically endangered" (Hilton-Taylor, 2000), with a world population of ca. 62 individuals. Kakapo are usually solitary, inhabiting forests and shrublands where they feed on the fruits, seeds, foliage, stems, buds and roots of a range of plant species (Best, 1984; Best and Powlesland, 1985). The sex ratio of surviving adults (most of whom are older than 20 years, but are otherwise of unknown age) is biased 31:19 in favour of males (Clout and Merton, 1998; Robertson et al., 2000; Elliott et al., 2001). Males typically weigh 30–40% more than females, but the adult weights of both sexes fluctuate widely, both seasonally and annually (Elliott et al.,

2001), reflecting the storage and mobilisation of fat reserves. Breeding typically occurs in synchrony with the episodic mast fruiting of podocarp trees, which happens at intervals of 2–5 years (Merton et al., 1984; Powlesland et al., 1992). Kakapo have a polygynous "lek" mating system (Merton et al., 1984). In breeding years, adult males congregate in summer in loose associations ('exploded leks') at traditional sites, where they display vocally at night to attract females. Each displaying male maintains and defends a series of shallow excavated bowls, linked by tracks that are kept clear by the bird. Male kakapo are known to fight (and even kill one another) at lek sites (Clout and Merton, 1998). They play no part in nesting, incubation, feeding of females, or in the raising of young.

Males seem to come into breeding condition more readily than females. Even in years when some females mate, others in the same population do not. Nesting females lay their clutch of 1–4 eggs in natural cavities at ground level and incubate them for about 30 days,

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leaving the eggs whilst foraging at night. Nestlings remain in the nest for approximately 10 weeks after hatching and may be left unattended for several hours each night whilst the female forages. Normally only one or two young are raised to independence from each brood (Clout and Merton, 1998; Elliott et al., 2001).

The combination of flightlessness, solo parentage, nocturnal behaviour, altricial young and ground nesting makes the kakapo highly vulnerable to predation by introduced mammals (Best and Powlesland, 1985; Clout and Merton, 1998; Elliott et al., 2001). To protect them from such predation, surviving adult birds from the last natural population on Stewart Island were transferred to mammal-free islands. Most individuals are now on Maud Island and Codfish Island (Clout and Merton, 1998). Adult survival on predator-free islands is around 98% p.a. (Clout and Craig, 1995), but only 15 fledglings (nine males, six females) have been produced since 1982. Conservation efforts therefore focus on encouraging breeding and the successful raising of young (Clout and Merton, 1998; Elliott et al., 2001). The kakapo recovery plan (Cresswell, 1996) has a specific goal of ensuring the recruitment of at least eight more females by 2005, in recognition that greater female recruitment is essential for recovery of the species. A key technique to improve recruitment has been the provision of supplementary food.

In a recent paper Tella (2001) suggested that the provision of supplementary food to a lek-breeding species such as the kakapo could provoke the undesirable effect of a male-biased offspring sex ratio. His insight was based on mounting evidence that, in species with large variance in male reproductive success, females in better condition may maximise their fitness by producing more male offspring (Trivers and Willard, 1973; Nager et al., 1999; Westerdahl et al., 2000; Whittingham and Dunn, 2000).

Male kakapo undoubtedly have high variance in reproductive success (Miller et al., 2000). Mating sign (female contour feathers pressed into the ground) and evidence from radio-tracking suggests that females tend to select large males, holding central or top sites at the lek (G.P. Elliott, unpublished data). There is therefore reason to suppose that male reproductive success rises with body size. Male nestlings grow faster and larger than females (Powlesland et al., 1992) and hence are more costly to raise. If female kakapo can control their offspring sex ratio [as can *Eclectus* parrots (Heinsohn et al., 1997)], they could increase their fitness by producing more male progeny when well fed and more female progeny when in poorer condition. In this paper we use data on the progeny of fed and non-fed female kakapo to test the hypothesis of Tella (2001) that supplementary feeding might cause an unwanted male bias in the offspring sex ratio of this critically endangered species.

2. Methods

2.1. Supplementary feeding and weighing

All known kakapo carry radio-transmitters and are regularly monitored, so their individual home ranges are well known. It is therefore possible to provide supplementary food to wild birds by placing it within their home range in specially designed dispensers, which most individuals readily learn to use. Since 1989, in attempts to encourage more frequent breeding and to provide nesting females with ready access to food, several birds have been provided with supplementary food (Elliott et al., 2001). This followed the finding by Powlesland et al. (1992) that kakapo on Stewart Island bred only when protein-rich foods, especially the seeds of mast-fruiting podocarp trees (*Dacrydium cupressinum, Lepidothamnus intermedium* and *Halocarpus biformis*), were abundant. In an attempt to encourage breeding, nuts, apples and sweet potatoes were first provided in food dispensers to free-living kakapo in 1989 (James et al., 1991). The frequency and intensity of male booming increased markedly and some nesting occurred in 4 of the 6 years after supplementary food was first provided (Clout and Craig, 1995). Since this initial experiment, supplementary food, usually consisting of nuts, apples and sweet potato, has been provided in dispensers to most adult kakapo at some stage (Elliott et al., 2001). Birds on Codfish Island were not fed until after 1992 (Clout and Merton, 1998). Kakapo provided with supplementary food have typically been given up to 200 g of mixtures of almonds, brazil nuts, walnuts, sunflower and safflower seeds every 3 days, placed in rodent-proof food dispensers within their home range. The composition of the mixture offered has varied between birds, with each bird being provided with larger amounts of the nuts that it preferred. They have also been provided with up to 100 g each of apple and sweet potato and up to 100 mls of honey solution (3:1 honey to water), once every 3 days. Most birds have shown a clear preference for nuts, with apple and sweet potato often being completely ignored. The normal supplementary feeding regime has been to provide sufficient food, so that when food dispensers are replenished after 3 days there is still a small amount left.

A few females have never been provided with (or have not accepted) supplementary food and others have been given it only recently. It is therefore possible, in retrospect, to confidently classify breeding females into those that have nested whilst taking supplementary food and those that have nested without taking it.

The effect of supplementary feeding on female weights was monitored by a combination of regular (at least annual) capture and weighing, and by automatic weighing on electronic scales at food dispensers.

2.2. Sexing

Broods were divided into those produced by fed and non-fed females, to test the effect of food provision on offspring sex ratio. Individual females could appear in both categories, since some have nested both with and without supplementary food. Although only 15 young have fledged since 1982, six others were produced on Stewart Island from 1977 to 1982, prior to any supplementary feeding. All fledgling kakapo were sexed by size and plumage (Robertson et al., 2000). In addition, several of the unhatched embryos and dead nestlings produced since 1982 were retained for subsequent molecular sexing, using sex-linked DNA markers. For this material, gender was identified using length polymorphism at the chromo-helicase-DNA-binding (CHD) gene (e.g. Griffiths et al., 1998), following the procedure described by Robertson et al. (2000).

3. Results

3.1. Effects of supplementary feeding on female weights

Weights of fed female kakapo are consistently higher than those of unfed ones (Elliott et al., 2001). Twelve females were weighed repeatedly at the same times of year, before and after they had access to supplementary food. They were significantly heavier after being provided with supplementary food (Paired t test $t = 5.06$, df $= 11$, $P < 0.001$), gaining an average of 310 g, which is equivalent to $>15\%$ of average body mass. In July 1996 supplementary food contributed, on average, 55% of the daily metabolised energy of 15 fed kakapo (G.P. Elliott, unpublished data).

3.2. Sex ratio of offspring

Kakapo offspring of known sex consist of 33 individuals from 18 different broods produced since 1978. They include five unhatched embryos, seven dead nestlings, and 21 fledglings. Thirteen male and five female offspring were produced by supplementary-fed females, whereas four male and 11 female offspring were produced by unfed females. The sex ratio of the two sets of offspring is significantly different (Chi-square $= 6.798$, df $= 1$, $P = 0.009$), but individuals in this analysis are not independent samples of the sex ratio of offspring, since some are from the same clutches. However, the sex ratios of the clutches themselves (Table 1) do comprise a set of independent samples. Clutches of supplementary-fed females comprised 67% males, whereas those of unfed females comprised only 29% males (Table 1). A maximum likelihood model (analogous to ANOVA but with binomial errors) showed that supplementary feeding had a significant effect on clutch sex ratio ($F = 5.567$, df $= 1,16$, $P = 0.031$).

Table 1
Sex ratio of 18 clutches produced by supplementary fed and unfed female kakapo

	Supplementary fed		Not supplementary fed	
	Proportion males	Clutch size	Proportion males	Clutch size
	1	3	0.33	3
	1	2	0	3
	0.67	3	0	1
	1	1	0.5	2[a]
	0.5	2	0	2[a]
	0	1	1	1[a]
	0	1	0	1[a]
	1	1[a]	0.5	2[a]
	1	2		
	0.5	2		
Average	0.67		0.29	

[a] Clutches in which not all siblings were sexed.

Of the five female offspring that have fledged since 1992, only one (from a brood also containing two males) was produced by a fed female. Three of these most recent female recruits were from a single-sex brood, produced in 1999 by a female that had never taken supplementary food.

To investigate the possibility that the biased sex ratio was caused by differential survivorship of nestlings, we repeated the above analyses, but excluded six clutches in which some siblings died before we were able to sex them. In this subset of the data 12 male and five female offspring were produced by females taking supplementary food, whereas one male and six female offspring were produced by unfed females (Chi-square $= 6.331$, df $= 1$, $P = 0.012$). Analysis by clutch revealed a significant difference in offspring sex ratio between fed and unfed birds ($F = 5.142$, df $= 1,10$, $P = 0.047$; Table 1). This result suggests that the change in offspring sex ratio due to provision of supplementary food occurs before laying (i.e. acting on the primary sex ratio), not through differential mortality during chick raising.

There were only seven clutches (containing a total of 16 eggs or chicks) for which the laying order was known. They included five clutches (containing eight males and three females) that were produced by supplementary fed females. In each of these, the first egg laid was a male. In both of the clutches with known laying order that were produced by unfed females, the first egg laid was a female. Although there is a slight suggestion that males were more likely to be laid first in clutches produced by fed females, the sample sizes are too small for rigorous analysis.

Analysis of the effects of female age on sex of offspring is similarly frustrated by lack of data. Most female kakapo are of unknown age and only two have laid three or more clutches for which the sex ratio is known.

The clearest result is therefore that supplementary fed females produced more male offspring, with a strong suggestion that this was due to an effect on the primary sex ratio.

4. Discussion

4.1. Kakapo sex ratios

This male-biased adult sex ratio of kakapo (31 males:19 females) is of considerable conservation significance, given the risks of stochastic sex ratio fluctuations in small populations (Courchamp et al., 1999). Concern about the recruitment of new females to the kakapo breeding population is reflected in the recovery plan goal of achieving recruitment of at least eight new females by 2005 (Cresswell, 1996).

The current male bias among adult kakapo may be a result of past differential mortality in the presence of introduced mammalian carnivores, with nesting females being more vulnerable than males. A similar male bias in the adult sex ratio of another cavity-nesting New Zealand parrot, the kaka (*Nestor meridionalis*) has been attributed to the higher vulnerability of nesting females to introduced mammalian predators (Moorhouse, 1999). The fact that all 18 of the last kakapo found in Fiordland were adult males (Clout and Craig, 1995) accords with the hypothesis of higher mortality of females in the presence of mammalian carnivores.

An alternative view, based on an analysis of sub-fossil kakapo bones, is that a male-biased sex ratio is normal for this species (Trewick, 1997). Trewick considered that the male-biased sex ratio of surviving kakapo and an apparent 2:1 male bias in sub-fossil remains were the result of nonadaptive differential mortality through gender-based brood reduction. He argued that males were larger because of sexual selection associated with lek breeding and contended that in mixed-sex broods the larger, faster-growing male chicks dominate, resulting in disproportionate mortality of the smaller, slower-growing female chicks. Trewick (1997) dismissed the possibility that maternal control of the sex of chicks was responsible for the apparent bias towards males, arguing that the greater costs of rearing males would seem to favour greater production of females, despite the possibly higher selective value of males in a lek breeding system.

Our data strongly suggest that maternal control of offspring sex ratio does indeed occur in kakapo and that it results in a male-biased offspring ratio for well-fed females, as hypothesised by Tella (2001). The evolutionary context for this production of more male offspring by well-nourished females is likely to be the kakapo mating system and the relative costs of producing males and females. Male reproductive success probably increases with body size, but male nestlings grow faster and larger than females (Powlesland et al., 1992) and are therefore more costly to raise.

It is often difficult to distinguish if females only invest in male offspring when they can 'afford' it (Clutton-Brock et al., 1985) or if they invest in this more 'costly' sex when future indirect fitness returns merit it (Trivers and Willard, 1973). In the case of kakapo, another contending hypothesis might be that of 'resource competition', whereby females should bias production towards the dispersive sex when competition for resources (such as food) is high and to the non-dispersive sex when food is plentiful. For most birds, females tend to disperse from their natal area more than males (Greenwood, 1980), but this might not be the case for kakapo, given their unusual mating system. The dispersive sex remains unknown for kakapo, because so few young have been raised to independence recently.

Whether or not there is any gender-based brood reduction, caused by higher mortality of female kakapo in mixed broods when food is limited, also remains an open question. Such an apparently non-adaptive effect (resulting in male-biased fledging success under poor conditions) has been experimentally demonstrated for great tits (*Parus major*; Oddie, 2000), but we detected no evidence of any such gender-based brood reduction for kakapo. Female kakapo may be able to reduce the sex-biasing effects of sibling competition for food in mixed broods because (unlike great tits) they are not 'single-loaders', but feed their young by regurgitation over an extended period.

In some bird species, females manipulate the order in which sexes are produced within a clutch, so that the larger, faster growing sex tends to be produced later (Bortolotti, 1986; Legge, 2000). There is no evidence for this (or for any effect of female age on offspring sex ratio) in kakapo, but the sample sizes are too small for rigorous analysis.

Our data provide no indication of the likely natural sex ratio of kakapo. If anything they suggest that unfed kakapo normally produce an excess of females, although the effect of this on the adult sex ratio depends on mortality patterns later in life. The selective environment that kakapo now inhabit is certainly very different to the one in which they evolved. Whatever the natural sex ratio, the conservation imperative right now is to produce as many females as possible to speed the recovery of the species.

4.2. Management implications

Elliott et al. (2001) showed that the provision of supplementary food to kakapo increased their breeding rate on one island, but they were unable to determine if the supplementary food itself triggered breeding or just raised birds above a nutritional threshold that

allowed breeding. They concluded that supplementary feeding had no effect on the likelihood of breeding in years when there was abundant fruit from a masting tree species. The suggestion is therefore that supplementary feeding facilitates breeding, but does not trigger it (G.P. Elliott, unpublished data). However, the provision of supplementary food does increase the survival rate of eggs and chicks when natural food supplies fail later in the breeding season. Elliott et al. (2001) therefore concluded that the provision of supplementary food was prudent conservation management.

Unmanaged kakapo typically nest only when there is abundance of fruit from a masting species, so females are probably always relatively well nourished when they lay. Supplementary fed birds are likely to be in even better condition, since they are on average 15% heavier after receiving supplementary food. It is therefore probably the better condition of fed females that affects the sex ratio of clutches, rather than the provision of supplementary food per se.

Supplementary feeding, as applied to date, does not by itself seem to trigger kakapo breeding when it would not otherwise occur. This feeding therefore has three aims: to raise as many birds as possible above the nutritional threshold for breeding (when this is triggered by other factors), to facilitate the production of as many eggs as possible, and to improve egg and chick survival by providing extra food for nesting females. A practical implication of our findings is that, in meeting these other aims, supplementary feeding also has to keep the condition of female kakapo low enough to avoid male-biased clutches. One option would be to give female kakapo just enough supplementary food to keep them above a threshold minimum condition in winter and then to give more food just prior to mating and laying. This approach might maximise clutch sizes and the proportion of females breeding, but would risk raising body condition so high that male progeny predominate. A surer way of obtaining female progeny would be to delay increased provisioning until after the eggs have been laid, but this might entail lower egg production overall and poorer survival of eggs in the early stages of incubation, due to 'unfed' females spending more time foraging. Fine-tuning of the feeding regime to maximise production of female chicks clearly presents a considerable challenge for the kakapo conservation programme.

In conclusion, the results presented here illustrate that the application of evolutionary theory can sometimes provide valuable guidance for achieving the goals of practical conservation.

Acknowledgements

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