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On the skewed sex ratio of the Kakapo *Strigops habroptilus*: sexual and natural selection in opposition?

STEVEN A. TREWICK*
School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington, New Zealand

The Kakapo *Strigops habroptilus* is unique amongst parrots in many respects, not least its use of a lek breeding system. Since Merton *et al.* first described the phenomenon, little new information has come to light, chiefly as a result of the extreme rarity of Kakapo. Observation of an extreme sex ratio skew in favour of males has received little attention and has been considered spurious. I used subfossil material to examine the nature of the sex ratio prior to the arrival in New Zealand of humans and demonstrated that a sex bias in favour of males in the order of 2:1 existed at that time. Although apparently untenable on traditional theoretical grounds, this extreme skew has been persistent and has resulted from the interaction of sexual and natural selection on dimorphic male and female Kakapo. Relatively small, sole caring females may suffer the consequences of parental investment as a result of demands made by offspring over an extended rearing period. In particular, larger male chicks may exert a greater cost on the parent bird than do female siblings. Additionally, brood reduction in certain circumstances may favour the survival of dominant male siblings.

Sexual reproduction is expected to produce equal numbers of males and females when each sex requires equal investment and is of equivalent evolutionary "value" to the parent (Fisher 1930). Skewed sex ratios are predicted to occur when male and female offspring require different degrees of parental investment, such that fewer of the more expensive sex are produced, and when there are different evolutionary benefits to be gained from producing one sex over the other (Clutton-Brock *et al.* 1985, Griffiths 1992).

I present evidence of, and suggest explanations for, the occurrence of an extreme and persistent sex ratio skew in the Kakapo *Strigops habroptilus* that conforms to neither of these predictions. Available information about the nature of this bird indicates that it is anomalous in many regards and thus interpretation of its sex ratio requires treatment as a special case.

The Kakapo is the largest living parrot (Psittacidae) and the only species of that group to utilize a lek breeding system (Merton *et al.* 1984), other taxa being monogamous (Forshaw 1989). Kakapo are presumed to be long lived (Lloyd & Powlesland 1994), maybe to a greater extent even than other parrots, owing to expected metabolic features associated with flightlessness (Linstedt & Calder 1981). Individuals are generally flightless and terrestrial although they do use arboreal habitats when foraging (D. Merton, pers. comm.). In keeping with other parrots, Kakapo are herbivorous at all post-egg stages and more strictly so than many of their relatives (Forshaw 1989, Trewick 1996a). They are dependent on temporally unpredictable but abundant fruit crops (Kelly 1994) for successful breeding, and as a result, breeding takes place intermittently (2–4 years; Reischek 1890; Powlesland *et al.* 1992). At other times, Kakapo feed on leaves, roots and rhizomes and are solitary, seemingly unsociable and even intraspecifically aggressive (Reischek 1890; Henry 1903b).

A pronounced sexual dimorphism (see Plate 1) has been recorded in terms of body mass, with males averaging 2.06 kg and females 1.28 kg (Merton *et al.* 1984). This difference is presumed to be associated with the lekking behaviour (Höglund 1989, Oakes 1992, Webster 1992), with the largest males monopolizing matings. Shepard and Spitzer (1985) also recorded differences in body length and head size, females being smaller in both respects.

Kakapo are critically endangered, and success of conservation efforts, hindered by low net productivity, is further hampered by the relative scarcity of females. Studies of the only remaining populations revealed them to be dominated by males (although estimates vary), with a 4:1 ratio of birds captured in one study (12 males, three females) on Stewart Island (Shepard & Spitzer 1985) and 17 males and no females in Fiordland (Rasch 1989). A total of 65 Kakapo (43 males and 22 females, 2:1) have since been captured and translocated from these sites (Lloyd & Powlesland 1994). One suggested cause of this unusual sex ratio in the modern population is differential impact of introduced mammalian predators on female and male Kakapo (Shepard & Spitzer 1985), although there is no direct evidence for this. In fact,

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* Present address: Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand.

it is remarkable how little comment has been made regarding the excess of male Kakapo (other than by Shepard & Spitzer 1985), presumably because the excess was assumed to be a recent aberration, although even this has not generally been noted (but see Merton *et al.* 1984, Powlesland *et al.* 1995).

New data were obtained through the examination of subfossil material, which has the valuable potential of demonstrating trends in sex ratio over an extended multigenerational period (Gowaty 1993) whilst nullifying postulated effects of introduced predators by predating their presence.

I offer an hypothesis to explain this skewed sex ratio which proposes that a nonadaptive skew might persist in a species where conflicting evolutionary forces result in a trade-off within the constraints of the lek system. In evolutionary terms, female Kakapo are caught in a conflict between sexual and natural selection (Clutton-Brock *et al.* 1985).

METHODS

Quaternary fossil bones (subfossils) collected from three unassociated "pitfall"-type cave deposits at Waitomo (Waitomo Caves Museum [WO], Martinborough and Castle Rocks (Museum of New Zealand Te Papa Tongarewa [NMNZ]) were analysed (Fig. 1). These sites have yielded remains of a number of endemic birds and have been estimated to range in age from 8000 to 1200 years BP. The deposits predate the arrival of humans and other mammalian predators to New Zealand (Hamilton 1892, Yaldwyn 1958, Worthy 1984, 1988, P.R. Millener, 1981, unpublished PhD thesis, Auckland University). Remains of birds are likely to have accumulated over periods of hundreds or even thousands of years (Yaldwyn 1958, Worthy 1984).

The material was verified as originating from Kakapo by comparison with modern specimens, and metric data were taken from undamaged adult elements (WO: WO1.02; NMNZ: registered as Martinborough Cave 1 and Castle Rocks). Measurements were made using Mitutoyo dial callipers (accurate to 0.05 mm) for standard dimensions from femur, tibiotarsus and tarsometatarsus (Trewick 1996b). Equivalent comparative data were obtained from nine skeletonized modern corpses, the sex of which had been determined by dissection (Museum of New Zealand, NM23032, NM22954, NM2249 and recently prepared, unregistered material).

The data were analysed using SYSTAT 5.2.1 (Wilkinson 1990). Only bone samples exceeding 50 were used in subsequent analyses, thus femora, tibiotarsi and tarsometatarsi from Martinborough and femora alone from Castle Rocks and Waitomo were used.

Because of the extreme scarcity of living Kakapo and modern museum specimens, it was not possible to summarize the size distribution of an extant population and accurately determine suitable normal distributions for variables. Therefore, in order to derive values for the numbers of male and female Kakapo represented by the various subfossil populations, univariate and bivariate data plots were assessed by eye, and large and small forms (for each element examined) were defined by segregating bivariate data-point "clouds" on scatterplots with a straight line. Independent categorization (into two groups) was initially based on univariate (histogram) plots of each of two variables (length and breadth) for the leg bones examined. The smallest near-medial bar of each histogram was taken to indicate the region of overlap between two normal distributions, and half of the value of this bar was added to the sum of the bars in the presumed upper and lower distributions. Individual datum points that were categorized in this manner for one variable were generally assigned to the same group when subsequently categorized by the second variable. When two variables from individual specimens were plotted against one another and separated by eye with a straight line, the univariate categorizations were upheld with an error of one or two individual bones.

Density histograms of length and scatterplots of length *v* minimum shaft diameter were generated for each element and each site (Figs 2 and 3). The two visual size classes were coded and scatterplot symbols were used to differentiate the two groups. The reliability of the two groupings as being indicative of male and female Kakapo was tested as far as possible by plotting subfossil femora from all sites together

Plate 1. Female (left) and male (right) Kakapo encountered on Stewart Island, New Zealand, in 1980. The size difference evident here is typical of the species, with females averaging about 60% the weight of males. Photograph courtesy of Don Merton/Margaret Shephard, Department of Conservation, New Zealand.

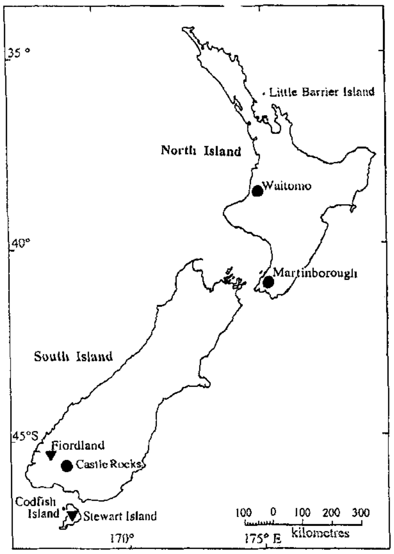

Figure 1. Map of New Zealand showing locations mentioned in the text. Filled circles indicate subfossil "populations" and filled triangles indicate recent wild Kakapo sites. Other island sites support translocated Kakapo.

with femora from previously sexed individuals from Stewart Island (Fig. 4). Tables of summary statistics were compiled using the scatterplot groups (Tables 1 and 2).

Measurements from modern sexed skeletons were used for comparison (Table 3). Estimated numbers of male and female elements and their ratios were summarized (Table 4) and tested against a null hypothesis of an expected 1:1 ratio with the use of chi-square tests. The consistency of the sex ratio from the different subfossil bones and sites was also tested using a contingency chi-square test.

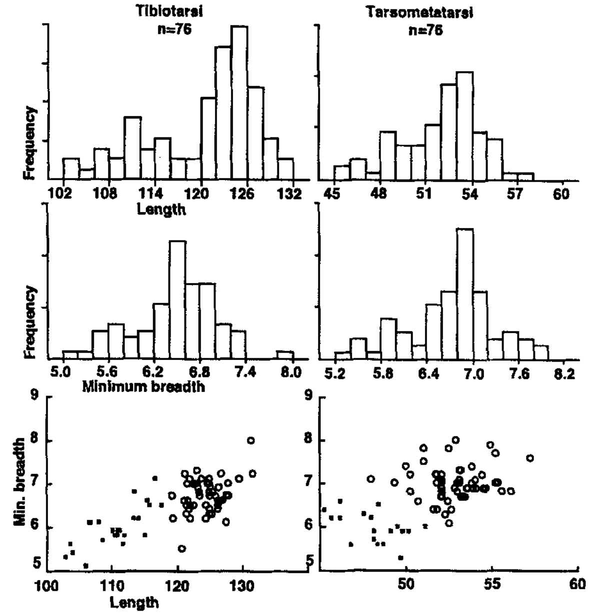

Figure 3. Size frequency histograms and scatterplots of length and minimum breadth data (mm) of subfossil Kakapo tarsometatarsi and tibiotarsi from Martinborough caves.

All data for femur lengths categorized by sex (size) and site were compared using two-way ANOVA.

RESULTS

Sexual dimorphism in size

Bone dimensions from all sites were distinctly bimodal for certain elements, although the use of bivariate plots dem-

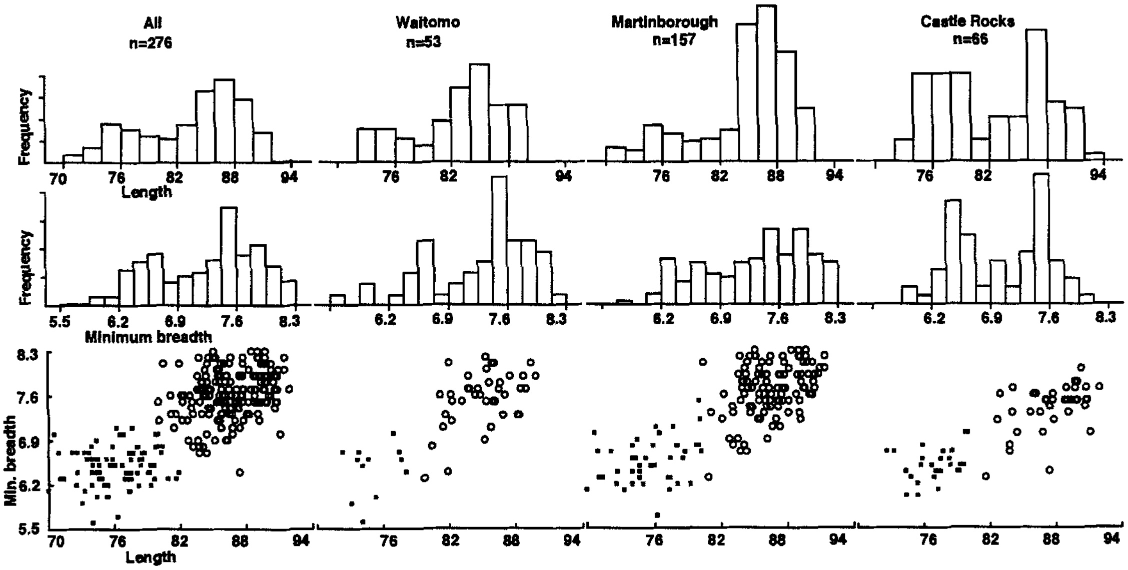

Figure 2. Size frequency histograms and scatterplots of length and minimum breadth data (mm) of subfossil Kakapo femora from various sites.

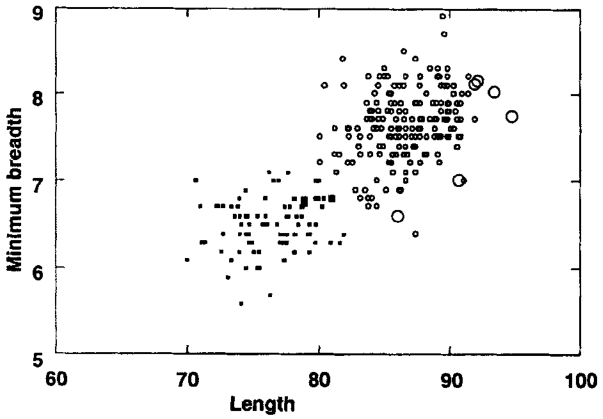

Figure 4. Comparison of femur dimensions of Kakapo sexed by dissection (as in Table 2) and subfossil size-sexed bones from all three sites (as in Fig. 2). Modern Kakapo are represented by larger symbols and subfossil bones by smaller symbols. Male Kakapo ($n = 6$) are indicated by open circles and females ($n = 3$) by filled squares. All modern material is from the Stewart Island population, which is the largest Kakapo studied (see Fig. 4), thus dimensions of modern individuals tend to be at the upper end of the male and female distributions.

Table 1. *Summary statistics or subfossil Kakapo femora, ordered by site and size category. Range is the total extent of size variation across the mean*

Site	Size group	*n*	Femur length (mm) Mean	s.d.	Range	% coeff. var.
Waitomo	Small	13	75.4	2.3	7.4	3.0
Waitomo	Large	40	85.1	2.5	9.4	2.9
Waitomo	All	53	82.7	4.9	17.5	5.9
Martinborough	Small	42	75.7	2.8	10.9	3.7
Martinborough	Large	115	86.6	2.6	6.7	3.0
Martinborough	All	159	83.7	5.6	21.5	6.6
Castle Rocks	Small	28	77.2	2.2	8.9	2.8
Castle Rocks	Large	38	87.8	2.6	9.4	2.9
Castle Rocks	All	66	83.3	5.8	19.3	7.0
All	Small	85	76.3	2.7	11.9	3.5
All	Large	191	86.6	2.6	11.9	3.0
All	All	276	83.4	5.5	22.0	6.6

onstrated the expected linear relationship of length and breadth of elements (Figs 2 and 3). Coefficients of variation (Table 1) were relatively large for unseparated data, but when divided according to the perceived bimodality, they were of a magnitude expected from a monomorphic species or single sex group of a dimorphic species (Engels 1938, Trewick 1996b). This differentiation was found to be consistent with that of modern specimens of Kakapo sexed by dissection (Table 3) and indicated in Figure 4. Means of various elements in each derived small and large "size" subgroup were not significantly different from those of data from modern material (Table 3) sexed by dissection or observation in life.

Analysis of variance between sex (=size) and site data for femur lengths revealed a highly significant difference between the two size groups ($F_{1,270} = 764$, $P < 0.001$), but also between sites ($F_{2,270} = 10.2$, $P < 0.001$). However, the interaction of the two terms was not significantly different. A Tukey HSD pairwise comparison probability matrix showed groups of small elements (female) from all three sites to be statistically inseparable, but amongst the large (male) groups, Waitomo was significantly different from Castle Rocks ($P < 0.0001$) and marginally different when compared with Martinborough ($P < 0.05$). Castle Rocks males (large bones) were not separable from Martinborough males (large bones). This slight difference in mean femur sizes is evident from Table 1 and is apparent on density plots for the three sites (Figs 2 and 3).

When two-way ANOVA was repeated with the inclusion of data from modern specimens, similar results were obtained. The difference between the size groups (males and females) was significant ($F_{1,277} = 418$, $P < 0.001$), as was the difference between sites ($F_{3,277} = 11$, $P < 0.001$). The interaction of site and sex was consistent at all sites and not significantly different. Females from each of the four sites were not separable, but males from all subfossil sites were significantly different from those on Stewart Island.

The slight difference in femora lengths (within the large size category) between sites had no effect on the overall relationship of the large and small categories across sites, but the separation of the original data into unimodal distributions unmasked differences in size not evident in the original data. Differences in size follow a north/south geographic cline between the four sites examined, with the smallest to the north (Fig. 5).

Sex ratio

Of the three subfossil "populations" examined, all had apparent sex ratios skewed towards males (Tables 1 and 4).

Table 2. *Summary statistics for subfossil Kakapo tarsometatarsi and tibiotarsi from the Martinborough site, ordered by size category. Range is the total extent of size variation across the mean*

Element	Size group	*n*	Length (mm) Mean	s.d.	Range	% coeff. var.
Tarsometatarsus	Small	18	48.2	1.6	5.8	3.4
Tarsometatarsus	Large	58	53.0	1.7	9.2	3.2
Tarsometatarsus	All	76	51.8	2.7	11.9	5.1
Tibiotarsus	Small	19	109.9	4.4	17.9	4.0
Tibiotarsus	Large	57	123.9	3.7	18.0	3.0
Tibiotarsus	All	76	120.4	7.2	28.8	6.0

Table 3. *Data and summary statistics (in mm) for modern Kakapo bones in the Museum of New Zealand, by individual*

Specimen name	Ring	Reference	Sex	Cr		Hu	Ul	Ca	Pe	Fe		Ti		Ta	
				l	b	l	l	l	l	l	mb	l	mb	l	mb
		NM23032	M	56.1	45.8	82.1	83.9	43.1	78	92	8.12	129.9	6.89	56.1	6.92
		NM22954	M						80	93.4	8.02	131.5	7.14	58	7.45
Jerry	R-44260	Unreg.	M			76.4	76.3			86	6.6	119.4	5.8	53.2	6.8
Lucky	0-12992	Unreg.	M	58.5	46.5	82.8	82.5	45.2	76.9	92.2	8.15	130.7	7.4	58.7	7.65
Ngawaka	No band	Unreg.	M			85	83.7			94.8	7.74	131.6	7.2	58.5	7.05
	0-25622	Unreg.	M							90.7	7	125	6.45	55.3	6.4
		NM2249	F	51.1	39.8	71.2	71.4	38.2	63.1	78.9	6.79	113.6	5.92	49.8	5.95
Bitch	M-38763	Unreg.	F	52.4	40					81	6.8	113.5	6.4	51	6.4
John-Girl	R-33427	Unreg.	F	52.2	40.3	73.1	72.8			78.9	6.75	114	6.3	50.2	6.4
Mean			M	57.3	46.1	81.5	81.6	44.2	78.3	91.5	7.6	128	6.8	56.6	7
Mean			F	52	40	72	72.1	38.2	63.1	79.6	6.8	113.7	6.2	50.3	6.3
Mean			M + F	54	42.5	78.4	78.4	42.2	74.5	87.5	7.3	123.2	6.6	54.5	6.8
% coeff. var.			M	2.9	1.1	4.5	4.4	3.4	2	3.3	8.5	3.8	8.7	3.8	6.4
% coeff. var.			F	1.3	0.6	1.8	1.7	—	—	1.5	0.4	0.2	4.1	1.2	4.2
% coeff. var.			M + F	5.7	7.9	7.2	7.2	8.5	103	7.4	9	6.6	8.7	6.6	8.1

Note: All specimens originated from Stewart Island between 1981 and 1991 and are presently held at NMNZ.

Abbreviations: Cr, cranium; Hu, humerus; Ul, ulna; Ca, carpometacarpus; Pe, pelvis; Fe, femur; Ti, tibiotarsus; Ta, tarsometatarsus; l, length; b, breadth; mb, minimum shaft breadth.

Table 4. *Sex ratios (number of males/female) of Kakapo at various sites as derived from subfossil leg bone elements grouped into two size categories. Chi-square values from comparison with 1:1 ratio are given*

Site	Element	*n*	Males	Females	Ratio Males : female	χ^2_1	*P*
Castle Rocks	Femur	66	38	28	1.36	1.5	n.s.
Martinborough	Femur	157	115	42	2.74	33.9	<0.001
Waitomo	Femur	53	40	13	3.08	13.7	<0.001
Martinborough	Tarsus	76	58	18	3.22	21.0	<0.001
Martinborough	Tibia	76	57	19	3.00	19.0	<0.001
All sites	All	428	308	120	2.57		

The ratio of males to females ranged from 1.36 to 3.22 (Table 4), with sample sizes of between 66 and 157 and a pooled sample of 428 elements. This ratio can be expressed alternatively as number of males/number of males and females, giving values of between 0.57 and 0.76 (parity being 0.5). The ratios of the two size groups (considered to be males and females) for each element/site combination were found not to differ significantly from one another (χ^2_4 = 8.28, n.s.). All element/site combination ratios were significantly different from a null 1:1 ratio at the $P < 0.001$ level except for Castle Rocks, although this site still had more males than females (Table 4). An average skew in the ratio of adult male to female Kakapo over multiple generations of 2.57:1 was obtained by pooling estimates from bone data of (large) males and (small) females (Table 4) from subfossil evidence from three sites.

DISCUSSION

> "males are also very fat, while the mother is like skin-and-bone, and once I thought that, Phoenix-like, she might die when she reared a brood, but I soon found that idea untenable"
>
> (Kakapo when breeding; Henry 1903a)

Data: source and reliability

Authors of previous studies of Kakapo who have commented on morphology have not been in the position to comment on sex ratio because the data most commonly used have originated from the extensive resource of Kakapo skins held in museums. This material has generally not been sexed on collection (during the last century), and when such data are included with specimens, there is no guarantee that infallible assessments were made or that the collection was not biased by differential trapability, seasonal variation in numbers (Meyer 1939) or the greater value to collectors of "pairs" of specimens (real or perceived). Although an apparently reliable method for sexing by wing feathers is available (Powlesland 1989), this method appears not to have been widely used on museum specimens, and dissection, where possible, is to be preferred as an accurate sexing method. Standard study skin measurements such as tarsometatarsus length do not clearly distinguish males and females in unsexed skins, although this study has shown that lengths of clean limb bones (not available in skins) are bimodal. Live tarsus-lengths from intrapopulation samples, however, show little modal overlap (Lloyd & Powlesland 1992).

Despite recognizing the large "dimorphism ratio" of Kakapo on the basis of body mass, Livezey (1992) found only few and "marginally significant differences" between bone elements. This inconsistency is most likely to have resulted from some inaccurate sexing of the original museum material used. However, despite suspicions about sexing of study skins, samples used by Livezey (1992) show a preponderance of males (2:1). Payne (1984), in his review of lekking birds, described sexual dimorphism in Kakapo as small (1%), and his conclusion that sexual size dimorphism is not associated with lekking in parrots is therefore incorrect. The dimorphic nature of Kakapo osteology has not previously been accurately noted.

The discovery that dimensions of femora and other elements differ between males and females is not surprising given the extreme difference (33%) in body mass of living Kakapo (Livezey 1992, Powlesland *et al.* 1995); linear dimensions of femora and other long bones are known to correlate with body mass (McMahon 1973). Although the sample of modern skeletal material previously sexed by dissection or field observation is small, dimensions of elements from this material fit the bimodal distribution of bone dimensions from all material examined, as predicted by differences in body mass (Fig. 4).

The average apparent sex ratio skew from subfossil bones of 2.57 (in favour of males) coincides with field observations of 2:1 (Merton *et al.* 1984), 4:1 (Shepard & Spitzer 1985), 2:1 (Lloyd & Powlesland 1994) and 2:1 (Powlesland *et al.* 1995) and evidence from museum collections in the form of study skins collected last century (2:1; Livezey 1992). Variation in the degree of skew indicated by various methods (and, in the case of subfossil material, various bone elements) is considerable, but this is to be expected given the inconsistent nature of sampling and the possibility that sex ratio may have been locally variable. However in most cases,

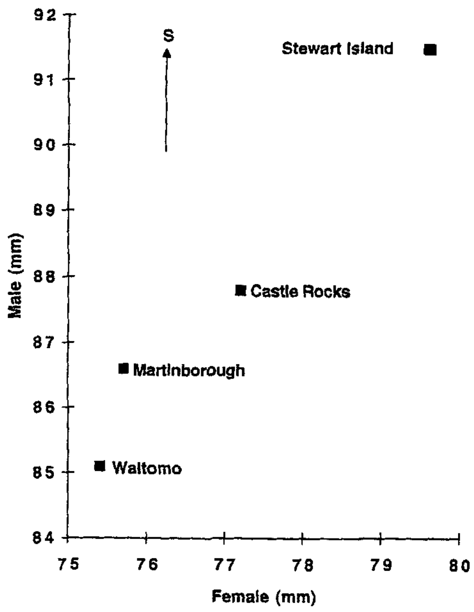

Figure 5. Mean length of "male" v "female" Kakapo femora from various sites. Arrow indicates south–north bearing.

the skew indicated is considerable and in itself is noteworthy when compared with other nonequal sex ratios recorded in birds (Meyer 1939, Lack 1966), especially because it appears to be persistent and not related to ephemeral phenomena such as season.

The direction of the skew is consistent in all samples and is contrary to the theoretical expectations normally applicable to size dimorphic lekking birds. Parent–offspring conflicts (Trivers 1974) ought to favour the production of fewer (large) males than females, and, given the operational sex ratio found in leks, the higher fitness value of female offspring should again favour greater production of this sex.

All subfossil material examined originated from mainland sites (Waitomo, Martinborough, Castle Rocks) not recently populated by Kakapo, whilst modern data came from Stewart Island. Size variation was observed between all sites and was found to be significant in the case of comparisons of the large bone groups (assumed males), possibly forming a cline of increasing size from north to south (Fig. 5). The difference between data from Stewart Island birds and those from mainland subfossil sites was the most distinct, although this may have resulted in part from the persistence of a thin cartilaginous layer that remained on the epiphyses of freshly prepared bones. In addition to other sources of variability, differences in the plumage colour of Fiordland and Stewart Island Kakapo have been noted from living animals (D. Merton, pers. comm.), indicating that size variation observed in this study may result from a combination of genetic, phenotypic and temporal factors. These factors are unlikely to have a significant bearing on the determination of sex ratios using bone size because consistency within locality is to be expected.

The cave samples are presumed to be representative of the standing population of healthy adult Kakapo over time. Thus, individuals dying as a result of predation, the costs of parental care (females), intrasexual aggression at lek sites (males), intraspecific aggression at other times and nestling mortality are absent from the sample. The cave sample is expected to reflect the living population no less accurately than do field observations.

Possible explanations for the sex ratio skew

Differential predation against females

Though proposed previously (Merton *et al.* 1984, Shepard & Spitzer 1985, Powlesland *et al.* 1995), no evidence has been produced to support this suggestion. The smaller size of females and their presumed greater agility combined with their reputed more feisty response on capture as compared with males (Shepard & Spitzer 1985) do not indicate a greater susceptibility to predation. Although, during the breeding season, female Kakapo are solely responsible for egg/chick incubation and might therefore be considered easy prey, during the same time males are equally vulnerable to predation because they cluster together and advertise their presence by booming (Powlesland *et al.* 1992, Lloyd & Powlesland 1994). When not breeding, male and female Kakapo have overlapping ranges. The new data from subfossil remains indicate that a male bias existed in Kakapo populations prior to the arrival of mammalian predators.

Differential self-entrapment in caves

No evidence exists to support this suggestion, although larger males might be less capable of climbing out of pitfall-like traps in cave systems. However, sites from which Kakapo bones have been collected are of various forms, and all are unlikely to present the same entrapment potential. There is no evidence that male Kakapo range farther or more actively than females so they are not expected to encounter caves more often. Furthermore, both males and females roost in burrows that are sometimes among rocks, and both are therefore likely to be equally susceptible to accidental entrapment when searching for new roosts. Variation in the proportions of large and small bones of various elements indicates that collection sampling or the susceptibility of elements of different sizes (tibiotarsi v tarsometatarsi) to disturbance by underground water are as likely causes of different male : female ratio estimates as are differences in entrapment or actual skewed sex ratio. The congruence of male bias estimates from museum skins, field observation and subfossil bones indicates that this latter source of data is reliable, at least in terms of the direction of the sex ratio bias.

Facultative control of chick sex

The evidence for facultative sex ratio manipulation in birds is not strong (Gowaty 1991), and a male bias would not be expected to be preferable in such a lek system. Both the presumed greater cost of rearing (larger) males and the skewed operational sex ratio would seem to favour greater production of females, despite the possible biased selective value of males in such breeding systems (Patterson & Emlen 1980).

Intraspecific aggression

According to early field observations, scarred Kakapo of both sexes were relatively common, and attempts to keep two individuals in a cage usually ended in the death of one (Reischek 1890, Henry 1903b). During lekking, intraspecific competition can be fierce between males (D. Merton, pers. comm.), and evidence of fighting is quite common (Lloyd & Powlesland 1992). Whether or not females are able to avoid such aggression by passive response is not known. Between breeding seasons (intervals which may extend for several years), Kakapo are seemingly solitary and unsociable, and old males are said to attack younger males and females indifferently (Reischek 1890) and thus are unlikely to have a marked effect on females in particular. The predicted (see below) greater agility of females is expected to give them an advantage in escaping from aggressive encounters with other, in particular male, Kakapo.

The previous hypotheses have little evidential support but there are two other possible explanations, which are not mutually exclusive, and for which supporting and circumstantial evidence exists.

Sole care costs

Parental care makes considerable demands on adults and can directly affect mortality rates of parents (Lack 1954). In particular, efforts associated with provisioning have been shown to be significant determinants of parental survivability (Owens & Bennett 1994). Kakapo chicks are altricial and remain in the nest for 10–12 weeks, during which time they attain body-weights in excess of the adult female (Powlesland *et al.* 1992). The effort of providing food is borne entirely by the female and must be considerable. Henry (1903a) noted that whilst Kakapo chicks and males were "like balls of fat", mothers were "like skin and bone". Both male and female Kakapo show considerable seasonal weight variation as fat reserves developed prior to breeding are gradually depleted. Although successful males probably refrain from leaving their lek sites to feed during the display period (and the energetic costs of booming and fighting must be high), the extent of investment in this phase is greatly exceeded by that of females incubating eggs and feeding chicks beyond fledging (about 8 months; D. Merton, pers. comm.). At times when the fruit on which females are reliant to feed chicks fails to ripen, chicks starve to death, but, despite weight losses recorded in the region of 70%, females do not desert chicks whilst they are alive and, whilst foraging for chicks during the short summer nights, do not appear to take much food themselves (D. Merton, pers. comm.). Male chicks, being larger and apparently growing faster (Fig. 5), may be assumed to impose a greater cost on mothers than do female chicks (Lack 1954).

Differential mortality as a result of gender-biased brood reduction

Arguments have been proposed to support opposing interpretations of such phenomena. Examples have been found where larger-sex chicks were apparently disadvantaged by lack of food (Clutton-Brock 1986, Weatherhead & Teather 1991, Griffiths 1992) because of higher maintenance diet requirements and therefore increased susceptibility to starvation. Conversely, there is good evidence that in some cases larger chicks were better able to dominate scarce food supplies to the peril of smaller siblings, and in sexually dimorphic species this could lead to a disproportionate mortality amongst smaller-sex siblings (Edwards & Collopy 1983, Bartolotti 1986, Edwards *et al.* 1988, Smith *et al.* 1989).

In Kakapo, male chicks appear to grow bigger and faster than females (Powlesland *et al.* 1992, Fig. 6) and may therefore be better able to appropriate (with or without aggression) food brought by the mother, especially when the food available to the mother is limited; this phenomenon is known to be common for Kakapo which rely on highly variable food sources. Lyall (1852) made observations that are consistent with more recent evidence (Fig. 6) and recorded that, amongst two-chick broods (the most frequent size among Kakapo), chicks at quite different stages of development were generally found, and this may well reflect unequal apportioning of food between siblings and different growth rates.

Breeding ecology

Combining sole care and lekking emphasizes the probable influence of the mating system used by Kakapo on the development of a skewed sex ratio, which, instead of showing evidence of being of direct adaptive value to the species, appears to have developed as a consequence of Kakapo breeding ecology. The effects of size dimorphism in the nest have in several other species led to the evolution of hatching asynchrony as an adaptation to counter the development of extreme gender skews. By downweighting the significance of sex in the feeding rank hierarchy in favour of one that is based on age and thus size (Slagsvold 1990, Griffiths 1992), mortality is spread more equally between the sexes. Asynchrony, whilst expressed in Kakapo as a laying and hatching interval of 2–3 days between eggs (Williams 1956, Lloyd & Powlesland 1992), is common to all parrots (Forshaw 1989), and in some species it is far more extreme (Beisinger & Waltman 1991). Because of the long brood time (Fig. 5), which is sometimes sustained at temperatures below 10°C (Powlesland *et al.* 1992), and initially only brief absence by the mother for foraging (Lloyd & Powlesland 1992), hatching asynchrony of 1–2 days probably offers

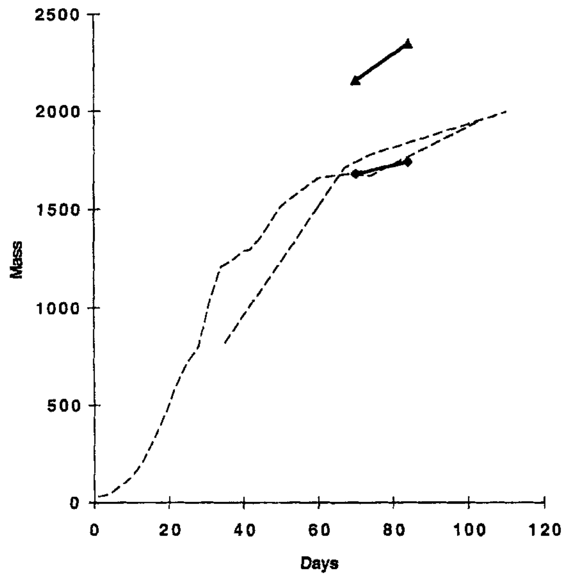

Figure 6. Mass (g) gain of Kakapo chicks. Dashed lines represent growth of two chicks in separate nests on Little Barrier Island in 1991 (redrawn from Lloyd & Powlesland 1992); black lines are for two sibling chicks on Stewart Island in 1981 (data from Powlesland *et al.* 1992). Filled triangles = male, filled diamonds = female.

negligible advantage to the small sex sibling (female) if it hatches first.

Sexual dimorphism is a common feature of birds that utilize polygamous or lek breeding systems (Höglund 1989, Oakes 1992, Webster 1992) and arises through sexual selection (Darwin 1871), such that males that are successful in defeating other males and gaining matings with females by virtue of the expression of certain traits are favoured. If, as it appears, sexual size dimorphism evolved through sexual selection operating on males, it is disadvantaging the smaller female Kakapo, and it would seem we require an explanation for why natural selection has not favoured larger females.

The role of natural selection in the development of size dimorphism has been proposed to allow for the partitioning of resources between males and females, thus reducing intersexual competition for food and other resources (Selander 1966, Yom-Tov & Ollason 1976, Slatkin 1984, Shine 1989). In the case of Kakapo, which lead very separate lives, a combination of sexual and natural selection might lead to the development of males and females with quite different physical and behavioural traits (Moore 1990). Female fitness in Kakapo is principally reliant on success in obtaining food for the altricial chicks, and any improvement in a female's ability to do so will directly favour both her own survival and the survival of her offspring. If females choose the largest males when selecting mates on leks (or lek sites controlled by large males), it is clear that a conflict of processes will arise if remaining small is in some way a significant component of being a "good mother" (i.e. being able to ensure chick survival). Selection for large males and small females may favour species survival even at the expense of compromised female survivability if no better alternative arises to free females from this bind.

Presumably, when a female chooses a mate at the lek, she is selecting for male genes that represent both the potential to be big and the temperament to compete for and hold a lek site. This decision may carry a considerable cost if the demands of any resulting male offspring are such that her subsequent reproductive value is compromised or the fitness of female chicks is impaired.

Male size

If males with traits such as aggressiveness and large size are able to dominate mating on a lek, then sexual selection must, for some traits at least, be acting most directly on the phenotypic character of individuals. In birds, achievable skeletal size in life is fixed early on in development when the shaft and epiphyses of bones fuse, only the potential phenotypic range being set by the inherited genotype. If a male Kakapo is to be a successful "lekker" in the generally understood sense, then he will need to be big (a trait linked with large skeletal frame size), and this potential must be realized in the nest, long before it can be realized on the lek.

Amongst male Kakapo, competition for preferred lek sites and, therefore, matings is fierce. In recent years on Little Barrier Island, in two sequential breeding seasons, the dominant male, occupying the single preferred lek site, died or was killed during the display season and a new male took over (D. Merton, pers. comm.). Furthermore, male chicks that express the same traits in the nest that will later lead to success in obtaining mates on the lek are likely to be able to dominate access to food supply to the detriment of smaller siblings. Because it is likely that smaller siblings in mixed sex broods are females, big fathers are therefore, indirectly, "bad fathers" as far as female chicks are concerned. Selection for larger adult females, which would be an expected evolutionary response to this situation, is apparently constrained by traits that constitute a "good mother".

Female size

For Kakapo, which probably occurred at high densities in natural circumstances (Hügel 1875), dimorphism may be maintained if this reduces competition for food resources during the nonbreeding period. This explanation seems unlikely, however, because Kakapo maintenance diets can include any of a very wide range of plant material and species (Best 1984, Trewick 1996a).

Female Kakapo are both smaller (Table 2) and lighter than males, and yet their wing and tail lengths are proportionately larger (Henry 1903a, Shepard & Spitzer 1985). Greater wing size of females (Table 5) hints at rather different aerial capabilities over males, and it seems therefore reasonable to consider these characteristics as traits which fulfill the requirements needed to be a "good mother".

Just as 5% of an eye is better than no eye at all (Dawkins

Table 5. *Mean values for mass and external dimensions of a sample of modern male and female Kakapo on Stewart Island.*[a] *Calculated wing and tail loadings are expressed as a function of the length of those structures*

	Male	Female
n	12	3
Mass (g)	2.12	1.43
Wing-length (cm)	262	273
Tail length (cm)	238	232
Wing loading (cm/g)	0.12	0.19
Tail loading (cm/g)	0.11	0.16

[a] Data from Shepard and Spitzer (1985).

1988), being even slightly less flightless may make female Kakapo sufficiently better mothers than if they were the same size and shape as males. Even without flying, a female that can move rapidly between foraging sites (trees) and feed amongst the canopy (D. Merton, pers. comm.) and on outermost branchlets where fruits are concentrated (R. Buckingham, pers. comm.) would presumably be relatively more efficient in foraging for food to feed chicks. Although rarely seen feeding in the wild, one female was observed on Codfish Island using short, descending, but controlled flapping "flights" to move rapidly between foraging sites (R. Buckingham, pers. comm.), and evidence from radio telemetry has shown that females run rapidly between nest and foraging site to obtain food for chicks.

Skewed sex ratio

In hypothetical two-chick broods where the first-hatched larger sex chick always kills the second hatched smaller sex chick, the maximum sex ratio that can result is 0.75 (M/M + F; Bartolotti 1989), or 3:4 (smaller: larger sex). Taken a step further, if the larger sex always kills the smaller sex in mixed two-chick broods, then the most extreme ratio can only be 1:2, and if only one chick is allowed to survive from each two-chick brood, then a figure of 1:3 can theoretically be derived.

Data for Kakapo from translocation and subfossil bones give ratios ranging from 1:1.36 to 1:3.22 and an average (from pooling male and female numbers) of 1:2.57. Male Kakapo chicks do not always kill their sisters, but because Kakapo breeding is so dependent on the superabundance of food, it is quite possible that, in marginal breeding years, dominance by male chicks will lead to reduced survivability of female chicks. In addition, the costs of sole care are likely to be considerable, and female Kakapo mortality may be increased when raising chicks in poor fruiting years and more so when raising male chicks relative to female chicks.

Although apparently not an evolutionarily stable strategy, the proposed origin of the observed sex ratio skew may be a persistent phenomenon amongst Kakapo because of the breeding system that evolved, presumably in response to phylogenetic features of Kakapo and the nature of the local New Zealand environment (e.g. freedom from ground predators, temporally unpredictable food sources). The unique nature of the Kakapo seems to provide the basis for the development of the observed sex ratio. By comparison, other bird species that share some characteristics with Kakapo differ in other respects. For instance, size dimorphic raptors feed their chicks meat, have relatively rapid growth and have two caregivers, whilst other terrestrial lekking birds, such as grouse (Tetraonidae), have precocial young and include animal components in the diet during early development. Chick survival in grouse is to a larger degree self determined and is not so likely to have an intense mortality effect on the mother or siblings. Sharp-tailed Grouse *Tympanuchus phasianellus* studied by Oring (1982) had a population sex ratio of 1:1. Other frugivorous lekkers like manakins (Pipiridae) utilize more reliable fruit food sources and are not dimorphic (Höglund 1989).

It will be some years, given successful management, before sufficient Kakapo are living to provide quantitative data about the interaction and ecology of males and females, but some useful observations may be made in the interim. In particular, observation of female foraging behaviour, chick growth patterns (utilizing genetic early sexing techniques) and mate selection will be of relevance. The implication that the survival of smaller chicks (and sisters in particular) might be limited by sibling competition will have relevance to future conservation efforts, especially because the abundance of females is crucial to the survival of the Kakapo.

Such evidence as there is supports the unexpected notion that Kakapo live with a bizarre and nonadaptive bias in the sex ratio. The extreme rarity of this species will continue to hamper understanding of its ecology and behaviour. It is probably not coincidental that an anomalous phenomenon is encountered in a species which is rare. The features of the Kakapo's autecology and environment that have allowed the evolution of such a bird are likely to be the same as those that have subsequently made it susceptible to the effects of habitat clearance and predation. Most studies have rightly concentrated on abundant and observable species to test theory-based predictions, but there is much to be learnt from the exceptions and rarities, the "dazzling perfection of some parental adaptations should not lead us to assume that all aspects of parental behaviour [or indeed species] are equally finely adapted" (Clutton-Brock & Godfray 1991).

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