Breeding biology of kakapo (*Strigops habroptilus*) on offshore island sanctuaries, 1990-2002

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Abstract The breeding biology of kakapo (*Strigops habroptilus*) was investigated on offshore island refuges between 1990 and 2002. Male kakapo typically attended their display territories between October to April, with the primary courtship display, "booming", usually beginning in January and ending in March. Mating was recorded from late December to March, with the median mating date falling in late January. Eggs were laid from early January to late March, with median dates of 24 January on Little Barrier Island and 7 February on Codfish and Pearl Islands. Females typically occupied a nest site eight days after their last mating (n = 44) and laid their first egg two days later (n = 40). Subsequent eggs were laid at three day intervals (n = 41). The mean and modal clutch sizes were 2.53 and 3 respectively, (range = 1 - 4, n = 54). Mean mass of fresh eggs was 40.53g (n = 122). Incubation began immediately after the first egg had been laid and the average incubation period was 30 days (n = 28). Mean nestling and fledgling periods were 72.4 (n = 27) and 246 days (n = 25) respectively. Male chicks began to grow more rapidly than females approximately one third through the nestling period. The mean fledging weights of 14 male and 14 female chicks were 1.93 and 1.72 kg respectively. Male kakapo are capable of mating at five years of age. Three known-age females first nested at 9, 10 and 11 years of age, respectively. Comparison with close relatives suggests that some aspects of kakapo breeding biology are evolutionarily conservative.

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INTRODUCTION

The kakapo (*Strigops habroptilus*) is a critically endangered parrot, endemic to New Zealand. The sole member of the psittacine sub-family Strigopini and the genus *Strigops* (de Kloet & de Kloet 2005), the kakapo is the heaviest parrot (male $\bar{x}$ = 2.11 kg, range = 1.24 - 3.60 kg, n = 40; female $\bar{x}$ = 1.45 kg, range = 0.85 - 1.88 kg, n = 25) and is unique in being the only flightless parrot and the only parrot with a lek mating system (Merton *et al.* 1984). In response to the discovery that feral cats were decimating the last known natural population, on southern Stewart Island, all birds that could be found were transferred to mustelid and cat-free offshore islands between 1980 and 1997 (Lloyd & Powlesland 1994; Powlesland *et al.* 1995, 2006). The present (2005) kakapo population, of 86 birds, lives on offshore islands from which mammalian predators have been eradicated.

The breeding biology and natural history of kakapo has been described by Merton *et al.* (1984) and Powlesland *et al.* (1992, 2006). Male kakapo establish a "court", or display territory, consisting of one or more shallow excavations in the soil, "bowls", linked by "tracks", which they maintain by biting off, or grubbing out, encroaching vegetation (Merton *et al.* 1984). Consequently, these sites are known as "track-and-bowl systems" (TBS). Each spring males typically move from their usual home-ranges to live in the immediate vicinity of their TBS where they spend up to three months engaged in courtship activity, mainly emitting the rhythmic, resonant call known as booming (Merton *et al.* 1984). Nesting does not occur every year but at intervals of two to seven years when certain fruits are sufficiently abundant (Powlesland *et al.* 1992; Elliott *et al.* 2001). More males participate in booming over a longer period in years in which nesting occurs (Powlesland *et al.* 1992). After mating, the male has no further contact with the female or her young (Merton *et al.* 1984; Powlesland *et al.* 1992).

No females or nests have been found in Fiordland since the early 20th century (Butler 1989) but Powlesland *et al.* (1992) described six nests on Stewart Island. These were situated in hollows in the ground, the base of standing, hollow

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tree-trunks, inside fallen, hollow logs, and on one occasion, on the surface of the ground under dense vegetation. Two to four eggs were laid and observations of one clutch indicated an incubation period of 25 days with chicks fledging after about 10 weeks.

Merton *et al's* (1984) and Powlesland *et al's* (1992) observations have been the only scientific accounts of the breeding biology of kakapo since the 19th century. Although only a few breeding seasons and nesting attempts were able to be observed, both these studies were conducted within the kakapo's last natural range.

This paper describes the breeding biology of kakapo since the transfer of all known birds to offshore island refuges. Most of the data presented here were collected on Little Barrier, Codfish (Whenua Hou) and Pearl Islands where most kakapo were between 1990 and 2002. Because of the close proximity and similarity in vegetation and climate of Codfish, Pearl and Stewart Islands, data from these islands have sometimes been pooled in analyses. Where this has happened these islands will be collectively referred to as the "Southern Islands"

METHODS

Monitoring male courtship activity

TBS were inspected for evidence of maintenance activity (grubbing or pruning) from September (the earliest males have been known to take up residency at TBS) until no further activity was detected. For the purposes of monitoring male courtship activity, a male was considered resident at a TBS when evidence of maintenance was recorded there over seven consecutive nights.

TBS were inspected daily during the usual peak of male courtship activity from December to March. In addition to noting maintenance activity, any kakapo feathers or droppings found at, or near, a TBS were recorded. As an aid to detecting a male's presence, four 5 - 10 cm upright twigs were pushed into the ground with two horizontal crossed sticks between them at each TBS site. Disturbance of these sticks indicated a male was still in residence. Booming was monitored using sound-activated tape recorders that were weather-proofed and hidden within 20 cm of active bowls.

Identification of resident males at TBS was initially done by radio-telemetry or by capturing males that were roosting nearby. Since 1997 "SNARKS" (combined radio frequency scanners and loggers) have been used to identify resident males and any visiting females. SNARKS automatically record the transmitter frequency and time of arrival and departure of any radio-tagged kakapo approaching within a radius of approximately 20 m. These monitoring methods allowed the intensity of male courtship activity to be recorded every summer on various islands. The overall intensity of male courtship activity was estimated as the percentage of males resident at TBS each week relative to the total number of males on the island.

Monitoring mating

Female kakapo leave distinctive feather clusters at TBS when they copulate (Powlesland *et al.* 1992, 2006). These are usually found within an area no more than 1 m^2 that is within 5 m of an active bowl. Such feathers are usually pressed well into the soil, and are mostly down feathers or fragments. The ratio of down to contour feathers indicates whether such a feather cluster was the result of a mating or a fight; a ratio of three or more down feathers to one contour feather is typical of mating sign. In contrast, feather sign left after fights is predominantly contour feathers that are often broken, rarely pressed into the soil and usually scattered over a wide area more than 5 m from active bowls.

Identification of mating females was achieved by regular radio-tracking during the breeding season. The location of every female was monitored by radio-telemetry almost daily during the booming season (mid December to the end of March) so that movements of females to TBS could be detected. Outside this period, the approximate locations of females are monitored at least every ten days. All known female kakapo carried radio transmitters since 1995. Females would usually leave their home range to mate, and were often found roosting near a TBS where mating sign had been found. The advent of data loggers in 1997 has since enabled more reliable identification of females visiting at TBS.

Monitoring nests

Prior to 1995 not all females were radio-tagged so some nests could only be found using trained dogs. Since then all females have been radio-tagged and all nests located by radio-telemetry. When a female's day-time location remained unchanged for seven days a visual inspection was made to see if she was nesting. If a nest was found, its location was marked to facilitate subsequent management and monitoring. A battery-powered infrared camera was installed while the female was away from the nest to allow remote viewing of the nest contents. The camera was connected by a cable to a television monitor inside a tent 20 to 60 m from the nest. An infrared beam was set up across the nest entrance that triggered an alarm at the tent site whenever the female left or returned to the nest. The sound of the alarm alerted nest minders to the departure of the female so that they could visually inspect eggs or chicks in her absence. Prior to the eradication of Pacific rats (kiore, *Rattus exulans*) from Codfish Island (Whenua Hou), the alarm also alerted nest minders to rats entering the nest chamber. Nest minders placed a battery-powered heat pad over the eggs and chicks to prevent chilling while the female was away. Nest minders used radio-telemetry to monitor the female's whereabouts and left the nest site as soon as they detected her returning. Nest sites were modified to allow ready access to eggs and chicks when required for health checks and weighing.

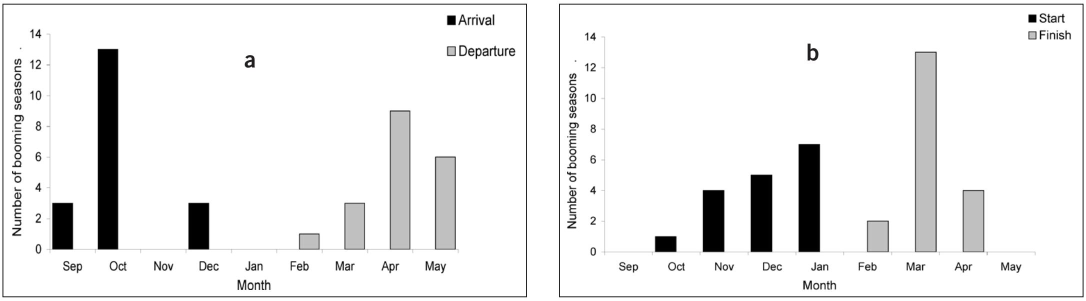

Figure 1 Timing of a) arrival and departure of male kakapo at track and bowl systems, and b) start and finish of booming on Little Barrier (*n* = 9 years), Codfish (*n* = 10 years) and Pearl (*n* = 1 year) Islands, 1991-2002.

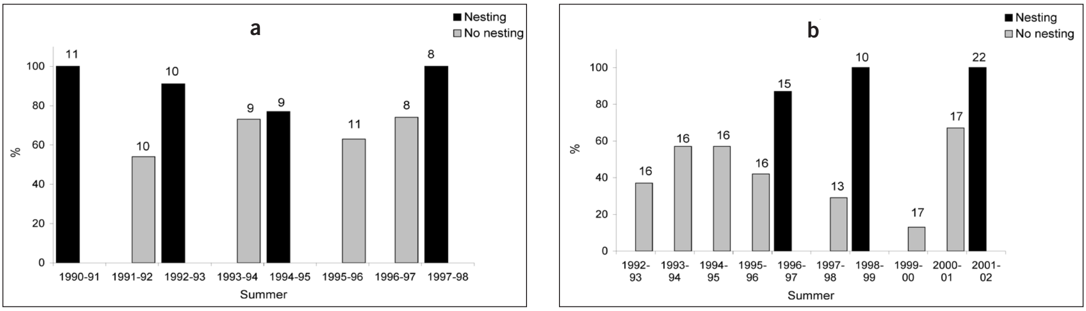

Figure 2 Maximum proportion of male kakapo resident at track and bowl systems during January in different nesting and non-nesting summers on a) Little Barrier, and b) Southern Islands. Numerals above bars indicate the total number of males present in different summers.

Determining egg size

The fresh egg mass of kakapo eggs was calculated following Hoyt (1979): Mass (g) = length (mm) x breadth^2 (mm) x k (a kakapo-specific constant). The kakapo specific constant "k", 5.449 x10^{-4} (*se* = 0.008 x 10^{-4}) was derived from a sample of 44 eggs weighed within hours of laying, or, in the case of infertile eggs, after the air cell had been filled with water.

Determining the nestling period

Nestlings were checked daily until they were two weeks of age and then every other day until they fledged. Nestlings were considered to have fledged when they left the nest and did not return.

Determining the fledgling period

Chicks were fitted with transmitters shortly before they left the nest so that their movements could be monitored and their health checked at monthly intervals. Fledglings were considered independent when they either left their mother's home range and did not return, or began consistently roosting separately from their mother.

RESULTS

Male courtship activity

Timing of TBS attendance and booming

Male kakapo became resident at TBS as early as September and left as late as May, however they usually arrived at their TBS in October and departed in April (Fig. 1a). Booming has started as early as October, but in most years began in January and finished in March (Fig. 1b). On Little Barrier Island, the mean start date for booming in nesting years was 24 November (*se* = 7.6 days), but in non-nesting years it was 2 January (*se* = 5.0 days). On the Southern Islands, the mean start date for booming in nesting years was 5 December (*se* = 5.7 days) compared to 27 December (*se* = 13.1 days) in non-nesting years.

Frequency of sustained booming

We recorded sustained booming in all but two of 11 summers for which the relevant data are available. The two summers in which we did not followed immediately those in which nesting had occurred. This frequency of sustained booming was significantly higher than that previously recorded in Fiordland (in three of 11 years 1973-1985; D Crouchley pers. comm.) and on Stewart Island (in six of 11 years; Powlesland *et al.* 1992) (2-tailed Fisher's Exact test, $P = 0.03$, $n = 33$).

Proportion of males attending TBS

The maximum proportion of males resident at TBS in January was higher in summers in which nesting occurred (Fig. 2). The numbers of males on different islands were too low to allow statistical comparison of TBS attendance in nesting and non-nesting years. However, pooling the data across years and islands indicates that

Table 1 Timing of mating by kakapo on different islands in different years (*n* = number of years in which mating was detected). Southern Islands are Codfish, Pearl and Stewart Island.

Island	**Maud (*n* = 1)**	**Little Barrier (*n* = 6)**	**Southern Islands (*n* = 4)**
Earliest	31 January	3 January	25 December
Latest	31 January	11 March	22 March
Median	31 January	23 January	30 January
Number of matings	1	13	67

Table 2 Number of copulations achieved and fertile eggs sired by the most successful five male kakapo.

Male & years	**% of total estimated fertile eggs sired**	**Number of breeding seasons**	**Number of copulations**	**Number of copulations per breeding season**
Felix 1997-2002	25.7	3	13	4.3
Sass 1997-2002	12.2	2	5	2.5
W'bo 1997-2002	10.8	3	11	3.7
Bill 1990-2002	10.8	8	8	1.0
Basil 1997-2002	9.5	3	7	2.3
Total	68.9	19	44	2.3

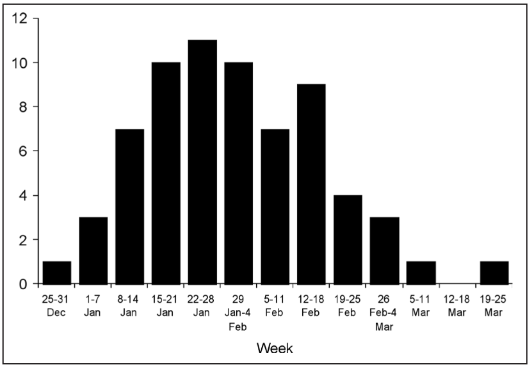

Figure 3 Timing of mating of kakapo on Codfish, Pearl and Stewart Islands.

TBS attendance was significantly higher in summers in which nesting occurred (95% *cf.* 48%) (Chi-squared test; $P < 0.0001$).

Mating

Female kakapo may leave their usual home range to spend several days in the vicinity of displaying males before mating. Females usually mate only once, but occasionally mate up to three times with the same, or different, males.

Timing

Mating has been recorded from late December to March with the median mating date falling in late January on all islands (Table 1). On the Southern Islands most mating took place between 15 January and 4 February (Fig. 3).

Variation in male breeding success

As is typical in lek species (Loffredo & Borgia 1986; Gibson *et al.* 1991; Westcott 1992), male kakapo have extremely unequal mating success; just 5 of 33 males (15 %) have performed 55.7% of all recorded copulations ($n = 79$) and sired 55 of 80 fertile eggs (68.9%) (Table 2). The most successful of these "Group A" males, Felix, has performed 29.5% of all copulations and fathered 28% of the 36 surviving progeny produced between 1991 and 2002.

The next most successful males are a group of seven "Group B" males (Richard Henry, Nog, Ox, Luke, Blades, Merv and Gumboots) which have performed just 18.9% of all copulations and sired 16 fertile eggs, less than half the number sired by the five Group A males. At the other end of the spectrum, 61% of males have yet to fertilize a single egg. However, since any male believed to be responsible for an infertile clutch has been removed from the breeding population, the low mating success of these "Group C" males is an artifact of this management practice.

Fertility of successful versus unsuccessful males

The median fertility rate of Group A males was significantly higher than group B males (Mann-Whitney U-test; $P = 0.018$); Group A males fathered significantly more clutches that contained at least one fertile egg (Chi-squared test; $P = 0.003$) and produced significantly more fertile eggs per clutch ($\bar{x} = 0.674 \pm se\ 0.08$, $n = 32$ clutches). On average, two of every three eggs sired by Group A males were fertile compared to just one of every three eggs for Group B males ($\bar{x} = 0.359 \pm se\ 0.11$, $n = 20$ clutches).

Female mating preferences

Males that achieved more than three copulations were not significantly heavier than those that obtained three or less (Student's t-test, $P = 0.223$). Since male kakapo invest so much time and effort in courtship display (Merton *et al.* 1984; Powlesland *et al.* 1992) it seems reasonable to presume that some aspects of this influence female choice.

Table 3 Timing of egg-laying by kakapo on different islands (n = number of years in which nesting has occurred).

	Maud ($n = 1$)	**Little Barrier ($n = 5$)**	**Southern Islands ($n = 4$)**
Earliest	4 February	10 January	2 January
Latest	4 February	21 March	12 March
Median	4 February	24 January	7 February
Number of nests	1	11	37

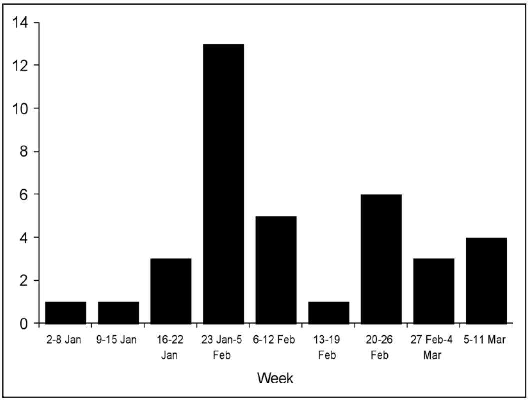

Figure 4 Timing of kakapo egg-laying on Codfish, Pearl and Stewart Islands, 1992-2002.

Nesting

Frequency

Nesting was recorded in five of the eight years kakapo were on Little Barrier Island and in four of the 11 years they were on Southern Islands. There was no significant difference in the nesting frequency of kakapo on Little Barrier compared to those on the Southern Islands (2-tailed Fisher's Exact test, $P = 0.65$) or between those on Stewart Island Powlesland *et al.* 1992) compared to those on offshore islands (2-tailed Fisher's Exact test, $P = 0.47$).

Timing

Eggs were laid from early January to late March with median dates of 24 January on Little Barrier Island and 7 February on the Southern Islands (Table 3). The peak of egg-laying on the Southern Islands was in the week of 30 January to 5 February (Fig. 4).

Nesting behaviour

Female kakapo occupied a nest site between one and nine days after their final copulation ($\bar{x}$ = 7.8 d, range 1 - 19, n = 44), and laid their first egg two days later ($\bar{x}$ = 9.6 d, range = 3 - 20, n = 40). Eggs appeared to be laid in the evening; one female was observed in the act of laying at 2330 h, and another is known to have laid an egg between 1700 and 2030 h. Subsequent eggs were laid at three to seven day intervals ($\bar{x} = 3.4 \pm se\ 0.90$ d, n = 41). Females usually left the nest for up to three hours each night until the clutch was complete. Thereafter, females usually left the nest for less than 90 minutes each night until the first egg hatched. Early in incubation it was not unusual for females to not leave the nest at all every second or third night.

Variation in female breeding success

The ability to raise young to sexual maturity is the only true measure of female reproductive success (Martin 1987). However, since kakapo require at least five years to reach sexual maturity (see below) we have used the number of young raised to independence as an approximation of female reproductive success.

Just seven of 22 adult females (32%) have produced 72% (28) of the 39 chicks fledged since 1985. The most productive female (Flossie) has produced an average of 2.5 fledglings per nesting attempt. Another eight females (36%) have each produced one or two of the remaining 11 fledglings (28%), and seven have yet to fledge a chick of their own. One female (Jane), which has impaired mobility in one leg, has never attempted to breed. Seven females consistently nested whenever nesting was recorded on the islands they were on, and only six that had experienced more than one nesting season produced one or more fledglings per season.

Annual weight trends of adult kakapo

The body weights of both male and female kakapo fluctuated significantly over a year, with weights of both sexes declining from December to May and increasing from May to November (Fig. 5). Birds which fed on supplementary foods (formulated pellets, nuts, fruits) were significantly heavier in most months than birds which did not, and, in contrast to the latter, continued to gain weight from November to December. Maximum weight fluctuations were 23% for non-fed females, 21% for fed females, 25% for non-fed males and 26% for fed males.

Eggs, nestlings and fledglings

Egg mass, width and length

Kakapo eggs had an average fresh mass of 40.5 g (Table 4). Comparison with Powlesland *et al's* (1992) data indicates that there has been no significant change in egg length or width since the transfer of kakapo to offshore islands (Mixed linear model; length: $P = 0.92$, width: $P = 0.29$). Although a relationship between egg mass and female size, or weight, has been documented in some other bird species (Carey 1996), no relationship between mean egg

Table 4 Size of 122 eggs in kakapo first clutches, 1990-2002.

	Fresh mass (g)	Width (mm)	Length (mm)
Mean	40.53	38.27	50.70
se	0.32	0.11	0.19
smallest	32.40	35.00	46.30
largest	48.41	41.15	55.80

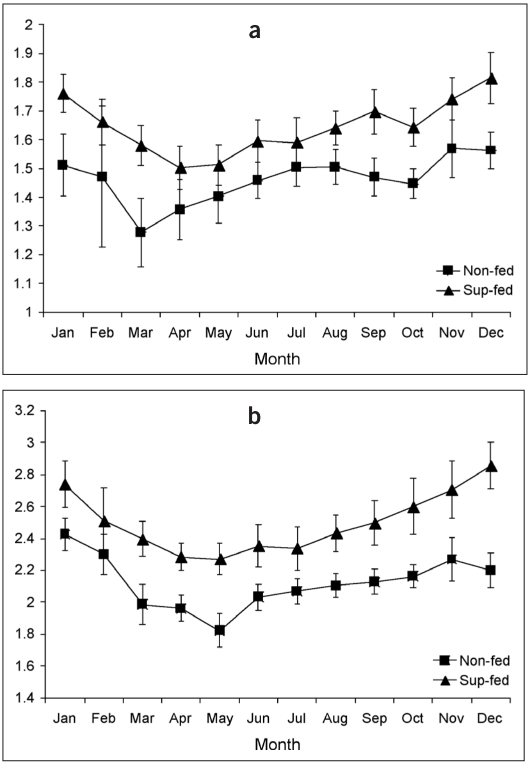

Figure 5 Annual weight trends in supplementary-fed (sup-fed) and non-fed a) female and b) male kakapo. Values shown are mean weights of the birds weighed in each month; error bars indicate 95% confidence limits. Monthly sample sizes varied from 5 to 26 for females and 20 to 40 for males.

size and mean maternal weight ($r^2 = 0.057$; $P = 0.34$), or size, (as assessed by measuring the sternum to shoulder distance) was found ($r^2 = 0.007$; $P = 0.75$). There was also no relationship between the mean egg size of six females and the amount of rimu fruit over three seasons (ANOVA, $P = 0.38$).

In some seasons, the first clutch laid by a female was removed to induce her to lay a second. Eggs from first and second clutches did not differ significantly in mass (Mann-Whitney U-Test, $P = 0.056$), or size ($F_{6,\,22} = 0.368$, $P = 0.89$), nor was there a significant difference in the viability of large and small eggs (Mann-Whitney *U*-test, $P = 0.35$).

Comparison of egg size between kakapo and related species

Recent genetic research indicates that the kakapo is most closely related to the kea (*Nestor notabilis*) and kaka (*N. meridionalis*) followed by the cockatoos (Cacatuini) (de Kloet & de Kloet 2005). Comparison of kakapo egg size and female body mass with that of its larger (> 400 g) close relatives suggests a significant positive relationship between female body mass and egg size (Fig. 6; Pearson correlation, $r = 0.66$, $P = 0.037$).

Clutch size

Clutch sizes of one ($n = 6$), two (16), three (29) and four (3) were recorded ($\bar{x} = 2.53 \pm se\ 0.10$). Powlesland *et al.* (1992) described three clutches of 2, 4 and 2 eggs on Stewart Island. The mean clutch size on Little Barrier Island was not significantly different from that on the Southern Islands (Kruskal-Wallis Test; $P = 0.23$).

Incubation Period

The typical incubation period was 28 to 31 days ($\bar{x} = 29.8 \pm se\ 0.13$ d, $n = 28$). Incubation began immediately after the first egg was laid and chicks usually hatched at intervals corresponding to when their egg was laid. First-laid eggs occasionally hatched up to two days later than expected, presumably because these had had less consistent incubation than subsequent eggs.

Nestling period

The average nestling period was 72.4 days (95% CI. = 70.6 - 74.2, $n = 27$) (see also Cockroft *et al.* 2006). The average nestling periods of male and female chicks were not significantly different (Independent Samples t-test; $P = 0.08$). There was no significant difference between the average nestling periods of male chicks in years of low fruit abundance ($\bar{x} = 68.4 \pm se\ 0.81$ d, $n = 5$) compared to that in one year (2002) of exceptional fruit abundance ($\bar{x} = 72.1 \pm se\ 1.96$ d, $n = 8$) (Mann–Whitney U test; $P = 0.14$) (all but one of the female chicks produced before 2002 were hand-reared).

Comparison of clutch size, incubation and nestling period with those of related species

Comparison of kakapo clutch size, incubation period and nestling period with those of its closest large (> 400 g) relatives indicates that the kakapo, kea and kaka have a higher maximum clutch size than all but one of the six cockatoo species for which comparable data were available (Table 5). Incubation and nestling periods are very similar between species.

Fledgling period

The average fledgling period was 246 days (95% CI = 229 - 263, $n = 25$). The fledgling period of males ($\bar{x} = 237.6$ d, range = 197 - 316, $n = 11$) and females ($\bar{x} = 252.6$ d, range = 183 - 350, $n = 14$) were not significantly different (Independent Samples t-test; $P = 0.39$).

Table 5 Clutch size, incubation and fledgling periods (days) of kakapo, kea, kaka and large (> 400g) cockatoos. Data sources: 1 Heather & Robertson (1996); 2 Jackson (1963); 3 R. G. Powlesland (unpubl. data); 4 Murphy *et al.* (2003).

Species	Clutch	Incubation	Fledging	Source
Kakapo	1 - 4	28 - 31	71 - 74	
Kea	2 - 4	23 -25	90 - 100	1, 2
Kaka	1 - 8	23 - 25	60 - 70	1, 3
Sulphur-crested cockatoo (*Cacatua galerita*)	1 - 4	30	66 - 73	4
Red-tailed cockatoo (*Calyptorhynchus banksii*)	1 - 2	28 - 32	71 - 100	4
Glossy cockatoo (*C. lathami*)	1 - 2	28 - 33	60 - 105	4
Yellow-tailed cockatoo (*C. funereus funereus*)	2 - 3	28 - 31	90	4
Short-billed cockatoo (*C. f. latirostris*)	1 - 2	28 - 29	70 - 77	4
Palm cockatoo (*Probosciger aterrimus*)	1	30 - 32	66 - 79	4

Chick weight trends from hatching to independence

Nestlings increased rapidly in weight until just before fledging when their weights mostly declined (Fig. 7). The mean weight of male and female chicks beganto diverge approximately one third through the nestling period, with this separation becoming most marked between fledging and independence. After independence, both male and female chicks generally lost weight until they were just over two years old. The post-independence mean weight of male chicks fluctuated more than that of females, but the overall trend was similar (Fig. 7).

There was no significant difference between the fledging weights of male chicks of supplementary-fed females in a year of poor fruit abundance ($\bar{x}$ = 1.90 ± *se* 0.02 kg, *n* = 2) compared to a year of exceptional fruit abundance ($\bar{x}$ = 1.99 ± *se* 0.06 kg, *n* = 8) (Mann Whitney U-test; *P* = 0.19). There was, however, a significant difference between the mean fledging weights of two male chicks raised on Little Barrier Island ($\bar{x}$ = 1.71 kg) and those reared on Codfish Island between 1997 and 2002 $\bar{x}$ = 1.97 ± *se* 0.04 kg, *n* = 11). The average fledging weight of female chicks in an exceptional fruiting year was 1.73 ± *se* 0.04 kg (*n* = 13). The only female chick to fledge in the wild before then was 1.51 kg at 73 days of age. Farrimond *et al.* (2006) reported that, on Codfish Island in 2002, chicks from broods of one were significantly lighter at fledging than those from broods of two.

Age at sexual maturity

Young male kakapo are capable of mating at five years of age, when, apart from occasional differences in pitch and tempo, their booming is otherwise identical to that of adult males (Powlesland *et al.* 2006). Males less than five years of age appear incapable of sustained booming. Because nesting in female kakapo is contingent on relatively infrequent fruit crops (Harper *et al.* 2006), it is difficult to determine the exact age at which females become sexually mature. Three known age females first nested at 9, 10 and 11 years of age respectively.

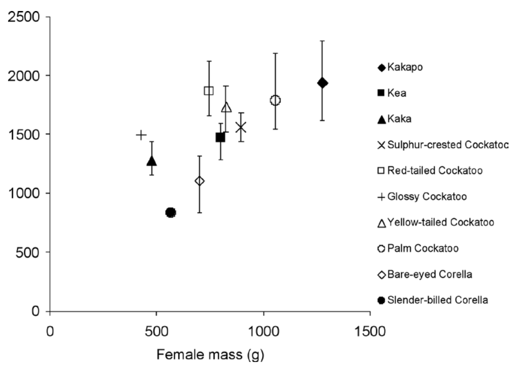

Figure 6 Relationship between an index of egg size (egg length x width) and female mass in large (> 400 g) New Zealand parrots and cockatoos for which the relevant data are available. Values are midpoints of the range of female mass for each species versus mean egg length x width. Error bars indicate the range in egg size of each species (where available). All data other than those on kakapo egg size (Table 4), and species names are from Forshaw (1989).

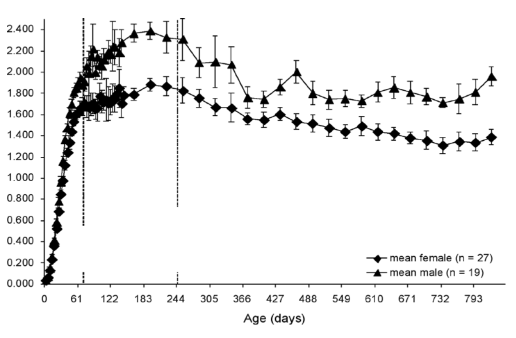

Figure 7 Weight changes over time of male (*n* = 4 - 51) and female (*n* = 12 - 61) parent-raised kakapo chicks from hatching to 18 months after independence. Error bars are 95% confidence intervals.

DISCUSSION

Male courtship activity

Male kakapo on offshore islands typically spent about seven months at their TBS (Fig. 1a), considerably longer than the period in which they are actually engaged in booming (Fig. 1b). The timing of booming (Fig. 1b) was similar to that reported by Merton *et al.* (1984) in Fiordland (November or January to March or April) and Powlesland *et al.* (1992) on Stewart Island (December to March). We recorded an earlier start of booming, in October, than previous studies, but this is probably explained by the fact that this occurred on Little Barrier Island, 1000 km further north than Fiordland, Stewart Island or the Southern Islands.

Henry (1903) heard booming in every second or third summer in Fiordland but did not indicate whether this was sustained (heard nightly over a period of months) or sporadic. More recent records indicate that sustained booming occurred in Fiordland in three of 11 years and in six of 11 summers on Stewart Island. The higher frequency of booming we recorded on offshore islands could be a consequence of supplementary feeding. Booming is probably energetically demanding; a male kakapo on Stewart Island produced between 5390 - 8400 individual booms over eight hours each night (Powlesland *et al.* 1992). It is possible therefore, that the provision of supplementary food has allowed males to gain the condition they need to sustain booming more easily, thereby increasing the frequency of sustained booming.

That male attendance at TBS was higher in years in which nesting occurred suggests that either males can detect when nesting is more likely so that more of them boom in these summers, or that females are stimulated to nest only when a sufficient number of males are booming. We think the first hypothesis is more likely to be true, primarily because females have failed to nest even when a relatively high proportion of the male population was booming. Moreover, nesting still occurs despite there being far fewer males than there were 200 years ago.

Mating

The median mating dates on Little Barrier, Maud, and the Southern Islands (Table 1) were similar despite the islands' different latitudes. This suggests that either the timing of the fruit or seed crops that triggered nesting on each island was similar, or that the timing of mating is largely controlled by endogenous factors. Like most birds, kakapo have an annual cycle of reproductive hormones that is mediated by changes in day-length (Cockrem & Rounce 1995; Cockrem 2006).

The unequal breeding success of male kakapo (Table 2), as in other lek species, is primarily due to female choice; females preferentially mating with just a small proportion of the male population. This has almost certainly been further exacerbated by the removal of putative infertile males from the breeding population. However, the removal of such males doesn't explain the significantly higher fertility of Group A relative to Group B males. This suggests that, either more frequent mating improves male fertility, or, that females are able to identify which males are more fertile, or genetically compatible with them, than others. Kakapo appear to have a well-defined sense of smell for a bird (Hagelin 2004) so a potential mechanism for this could be olfactory discrimination of variation in males' major histocompatablity complex (Zelano & Edwards 2002).

The male attributes that influence female choice are unknown, but given the amount of time and effort males expend booming, it is likely that some aspect of this influences female choice. Although the number of booms per bout appears to be unimportant, other features of booming, like frequency range (Loffredo & Borgia 1986) or the inter-vocalization time period (Gibson *et al.* 1991) might be.

Hotspots or hotshots

Leks are generally thought to form either around "hotspots" of female density, or around individual males ("hotshots") that are preferred by females (Bradbury 1981; Beehler & Foster 1988). We suggests that the formation of kakapo leks is more consistent with the hotspot hypotheses, except that TBS are primarily clustered on prominent landforms such as ridges and hilltops rather than sites where females are relatively abundant (Merton *et al.* 1984; Powlesland *et al.* 1992). On Little Barrier Island, two males were killed in fights for possession of a TBS on the island's summit where most mating occurred. Given that kakapo were once both widespread and common (Henry 1903), and that, under ideal conditions, booming can carry for up to 5 km (Merton *et al.* 1984), it is likely that males would have attracted more females by booming from such vantage points than by any other strategy. Once established, such leks may be so conspicuous that they become the only hotspots of female activity in breeding years. If so, young males establishing their first TBS would significantly improve their chances of encountering females by joining them. Powlesland *et al.* (1992) found that a young male on Stewart Island did just this. The behavior of the human-imprinted Sirocco suggests that male kakapo would also establish TBS near any obvious hotspots of female activity. However, since the spatial distribution of female kakapo is more regular than clumped (Moorhouse & Powlesland 1991) the situation of Sirocco's TBS is probably an artifact of the clumped distribution of humans on Codfish Island.

Nesting

Kakapo nested infrequently on offshore islands despite being provided with supplementary food. This supports the hypothesis that nesting is triggered by infrequent, above average abundance of certain fruits rather than female condition *per se* (Harper *et al.* 2006). Moreover, the similar frequency of nesting on the Southern Islands and Stewart Island suggests that the same fruit crops have triggered nesting at both locations.

The earlier occurrence of nesting on Little Barrier compared to the Southern Islands (Table 3) is curious since there was no difference in the timing of mating between these sites (Table 1). The timing of nesting on the Southern Islands (Fig. 4) was essentially the same as that documented by Powlesland *et al.* (1992) on Stewart Island, presumably because the same fruit crops are involved.

Despite the provision of supplementary food, female kakapo spent up to three hours per night away from their nest until their clutch was complete, suggesting that natural foods were important to females at this time.

Variation in female breeding success

Some of the observed variation in female breeding success reflects the fragmentation of the female population on islands that differ in their suitability for nesting (Elliott *et al.* 2006). Just seven females nested every time nesting occurred on the island they were on, suggesting some females are more likely to breed than others. Such individual variation in female breeding potential presumably reflects either the patchiness of the fruit crops that trigger breeding or differences in female condition. There is evidence to suggest that both underweight (Moorhouse & Powlesland 1991) and overweight (Elliott *et al.* 2001) females nest less frequently than others. Other sources of variation in female breeding success are probably chance events e.g., mating with infertile males or with those with which they tended to produce unviable embryos.

Annual weight changes of adult kakapo

Although breeding did not occur every year, the timing of the marked seasonal weight increases of male and female kakapo (Fig. 5a, b) suggests that these weight changes are related to breeding. In other words, kakapo appear to gain the condition required for breeding each year despite the fact that they don't breed in most years. Since booming males have little time to forage, they probably rely to a large extent on fat reserves accumulated over winter and spring to sustain them through a summer of booming. Females may gain weight before the breeding season so that they are better condition to produce eggs and incubate effectively.

Eggs, nestlings and fledglings

The lack of any significant difference in egg or clutch size on offshore islands compared to Stewart Island suggests that these parameters have been unaffected by supplementary feeding. This is consistent with the lack of relationship between egg size and the amount of rimu fruit present. Kakapo eggs are actually smaller than might be expected on the basis of female body mass (Fig. 6). The higher maximum clutch size of the kakapo, kea and kaka relative to all but one of the large cockatoos (Table 5) may reflect less frequent breeding by the New Zealand species. Kaka have been known to breed at two - three year intervals (Wilson *et al.* 1998; Greene *et al.* 2004), and, although kea usually breed annually, they occasionally miss a year (Elliott & Kemp 2004).

Although the estimated incubation period of 30 days is longer than the 25 days reported by Powlesland *et al.* (1992) their estimate was based on just one clutch. The average nestling period of 72.4 days is consistent with the 10 weeks recorded by Powlesland *et al.* (1992). The similarity of the incubation and nestling period in kakapo compared to their closest large relatives (Table 5) suggests that these aspects of breeding biology are evolutionarily conservative in parrots. Powlesland *et al.* (1992) were unable to determine the fledgling period of chicks on Stewart Island because they found so few and none were radio-tagged. The average fledgling period on offshore islands was 3 months longer than the 6 months reported for kaka (Moorhouse & Greene 1995; Wilson *et al.* 1998).

Although some chick growth rates (Fig. 7) may have been increased by the provision of supplementary food to their mothers this effect was probably slight since in 2002, when most chicks were produced, most mothers did not take supplementary food for most of the nestling period. The fact that some nestlings on Stewart Island were similar weights at the same age as those on offshore islands (Powlesland *et al.* 1992) suggests that chicks can achieve similar growth rates without supplementary food so long as there is sufficient fruit. The general post-independence decline in chick weights (Fig. 7) probably reflects the inexperience of fledglings at foraging for food and the difference in the weights of male chicks fledged on Little Barrier and those on Codfish Island suggests that raising chicks was more difficult on Little Barrier. It remains uncertain if females can raise chicks on Little Barrier without supplementary food.

Age at sexual maturity

Kakapo require longer to reach sexual maturity than either kaka (females breed at one year and males at two years; R. Berry pers. comm.) or kea, (females breed at three years and males at five years; Diamond & Bond 1999). Female kakapo may require more time to learn the spatial and temporal distribution of the fruit crops that trigger breeding while young male kakapo may also require more time to learn the best location to establish their TBS, or, to become sufficiently proficient foragers to gain the weight required to sustain booming. That females require several years to learn which fruits can sustain nesting is demonstrated by two females, transferred to Little Barrier Island, first nesting 10 and 17 years, respectively, after their release on the island. Neither female ate supplementary food. Conversely, three young females, taken from Stewart Island at less than two years of age, bred on Codfish Island during the first or second rimu fruit crop they had experienced since fledging.

CONCLUSIONS

Except for an increase in the frequency of sustained booming and chick growth rates as a result of supplementary feeding, the breeding biology of kakapo on offshore islands has been fundamentally the same as that described by Powlesland *et al.* (1992) on Stewart Island. Despite its many unusual characteristics, the kakapo's clutch size, incubation and nestling period are similar to those of its closest relatives, although its egg size appears smaller than expected on the basis of female body mass. The kakapo's lek mating system is unique among parrots but their requirement for above-average fruit crops to trigger nesting is shared with their close relative, the kaka.

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