The timing of breeding in the kakapo (*Strigops habroptilus*)

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Abstract   The kakapo (*Strigops habroptilus*) is a nocturnal, herbivorous parrot that shows lek behaviour and does not breed every year. When breeding does occur, egg-laying and incubation in mid-summer are followed by a prolonged period of chick-rearing, with all parental care provided by the female. Breeding years for kakapo are associated with mast seeding years for a range of forest trees and plants, and the periodicity of kakapo breeding is linked with the periodicity of years of large seed and fruit production by their major plant foods. Kakapo are likely to have an annual cycle of gonadal growth and regression driven by the annual cycle of daylength, with breeding occurring in years when kakapo respond to cues from a range of plant species that undergo masting. Kakapo breeding is initiated in response to cues that appear in early summer, but in some years there is insufficient food for the rearing of young in the following autumn. Rimu (*Dacrydium cupressinum*) is an important food source for chick rearing and is likely to provide an important cue for kakapo in areas where rimu is present.

INTRODUCTION

Reproduction in the kakapo has some unusual features (Cockrem *et al*. 2004; Powlesland *et al*. 2006). The kakapo is the only parrot to show lek behaviour (Merton *et al*. 1984), with breeding attempts usually occurring at intervals of three or four years (Powlesland *et al*. 2006). Egg-laying and incubation in mid-summer are followed by a prolonged period of chick rearing, with all parental care provided by the female. Breeding in some years but not others has been linked with annual variations in food availability, but the factors that initiate breeding in the kakapo have not previously been clearly identified. Relationships between food availability and the timing of breeding in other birds, data on annual variation in seed production in New Zealand forests, and records of kakapo breeding were considered in this study in order to understand the timing of breeding in kakapo.

BREEDING SEASONS OF THE KAKAPO

Breeding activity in the kakapo varies from year to year and is related to annual variations in food availability (Cockrem 2002). The kakapo breeding season begins in late spring or early summer when males return to track-and-bowl systems. Males are active at their bowls and boom from late November until March in some years, whereas in other seasons there is virtually no activity (Powlesland *et al*. 2006). Mating has been reported from early January until early March (Powlesland *et al*. 2006). Incubation and feeding of the nestlings are performed entirely by the female. Incubation lasts for 30 days and is followed by a period of 10 weeks before chicks fledge in late May or early June (Eason *et al*. 2006).

Nesting by females since 1980 occurred twice with an interval of four years on Stewart Island, once on Maud Island, and five times at intervals of one to four years on Little Barrier Island (Fig. 1). Codfish Island has been the location for the majority of the kakapo population since 1987, except for a period in 1998 and 1999 when the birds were temporarily moved to Pearl Island whilst kiore (*Rattus exulans*) were eradicated from Codfish Island. Kakapo nested on Codfish Island in the summers of 1992, 1997, 2002 and 2005, and on Pearl Island in 1999. The mean interval between the nesting events on Codfish and Pearl Islands was 2.6 years.

CUES FOR THE TIMING OF BREEDING IN KAKAPO

Cockrem (1995) suggested that the kakapo, like other species of birds, is photoperiodic and hence that its reproductive system can respond to changes in daylength. The classical annual cycle for photoperiodic birds is that they become photosensitive in the autumn, are photostimulated by increasing daylengths in spring, breed in spring or summer and then, usually, lose their responsiveness to long days and become photorefractory during summer or autumn. Cockrem
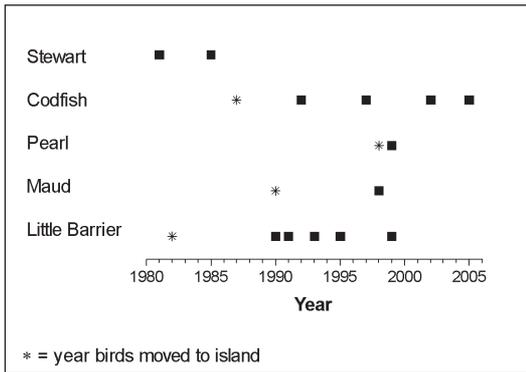
* = year birds moved to island

▶ **Figure 1**   Kakapo breeding years 1980 - 2005 on Stewart, Codfish, Pearl, Maud and Little Barrier Islands. Kakapo were rediscovered on Stewart Island in 1977. Predation of kakapo by feral cats (*Felis catus*) led to the transfer of birds from Stewart Island to other islands from 1982 onwards. The years that kakapo were moved to different islands are indicated by * symbols.

(1995) proposed that kakapo become photosensitive in the autumn, and that gonadal growth in the kakapo occurs in spring as photoperiodic drive increases. It is likely that birds become photorefractory and gonadal regression occurs in late summer, then photosensitivity develops and the annual cycle starts again. New information on kakapo breeding seasons and masting of New Zealand plants can now be used to explain the occurrence of breeding in some years but not others.

Seasonal breeding is controlled by environmental information called ultimate and proximate factors (Baker 1938). Ultimate factors select individuals that produce young at the optimum time for survival. The most important ultimate factor for birds is the availability of food for feeding young and for post-fledging survival. The timing of breeding in each species of bird must have evolved so that the hatching of eggs coincides with the maximum availability of food for the young birds, and clearly this is the case for the kakapo. Ultimate factors do not, however, regulate the precise timing of breeding each year. The annual reproductive cycle must start well in advance of the time of hatching, and other factors called proximate factors regulate gonadal development and the progression of the breeding cycle. Proximate factors have been subdivided by Wingfield (1980) into four types of information, the most important of which are initial predictive and essential supplementary information.

The primary source of initial predictive information for many birds is the annual cycle of daylength (Follett 1984). Initial predictive information brings birds into a physiological state in which breeding can begin, but usually does not induce the final stages of nest-building and egg laying. Complete gonadal development, mating, and egg-laying are stimulated by supplementary information, such as social cues, possession of a territory, and availability of

particular foods. These factors vary from year to year and between locations, and they determine the exact timing of breeding each year. The timing and extent of reproductive activity in the kakapo is quite variable from year to year. Extensive social displays by male kakapo may start in October, be delayed until December or January, or not occur at all (Powlesland *et al.* 2006). Similarly, egg-laying does not occur each year, and supplementary information from food availability is clearly very important for breeding in the kakapo.

Periodic breeding in other birds

Breeding in some years but not others is not uncommon in birds, and many species will delay breeding or, like the kakapo, not breed at all if the food supply is inadequate. For example, kaka (*Nestor meridionalis*), which are closely related to kakapo (de Kloet & de Kloet 2005), bred in six of 11 years at Nelson Lakes, with five of the six breeding seasons occurring in beech mast years (Wilson *et al.* 1998). Gonadal development in the tawny owl (*Strix aluco*) is correlated with body weight and food supply (Hirons *et al.* 1984), and the proportion of pairs that attempt to breed each year can vary from 0 to 85% (Hirons 1985), indicating strong effects of food availability on breeding in this species.

Two North American species that are similar to the kakapo in being dependent on variable seed crops for breeding are pinon jay (*Gymnorhinus cyanocephalus*) and red crossbill (*Loxia curvirostra*).

Pinon jays eat seeds of pinon pine (*Pinus edulis*) when they are available. The jays also collect and store seeds in autumn and then retrieve them for food during winter and early spring. Seed production is irregular: for example, it was abundant in only two of eight years in New Mexico, with a gap of five years between mast years, and elsewhere in south-western United States there was a mean period of 5.8 years between mast years over a 30-year period (Ligon 1978). Pinon jays will begin breeding in February (early spring) if pinon pine seeds from the previous autumn are plentiful (Ligon 1971), whereas if seeds are scarce or not available then breeding may start later in spring, or not occur. Ligon (1971) tested the gonadal response of captive pinon jays to the availability of intact, fresh green pinon pine cones, finding that the provision of green cones for one month reversed gonadal regression and led to some gonadal growth in three of ten birds with access to the cones. Thus, some birds responded to the availability of green cones when they were already receiving a nutritionally adequate diet.

Red crossbills feed almost exclusively on seeds from conifer cones. They can breed in spring, but breed most frequently in late summer and early autumn when cone crops mature (Benkman 1990). Testis growth is under photoperiodic control and begins before the birds discover new cone crops (Hahn 1998). Captive birds held on short daylengths then moved to long daylengths with restricted

food subsequently showed increased testicular growth when given access to *ad libitum* food, indicating a response to an increase in food supply that was independent of photoperiod (Hahn 1995). Captive crossbills underwent annual cycles of plasma luteinising hormone concentrations and testis size (Hahn 1995).

Annual gonadal cycle in kakapo

An annual cycle of faecal testosterone in kakapo has been found in samples from Little Barrier Island (Cockrem & Rounce 1995). Faecal testosterone concentrations increased to a peak in February at the time of copulation and maximum sexual behaviour, declined rapidly in April, then rose in the following spring when male sexual behaviour was starting again. These data indicated that kakapo might undergo gonadal development each year.

If kakapo do have an annual gonadal cycle, then its amplitude is likely to differ between individual kakapo. Some females breed in each year that breeding activity occurs, whereas others breed less frequently. The birds that breed less frequently presumably require stronger supplementary information than the birds that breed more regularly. Birds that breed most often are likely to have high levels of gonadal activity in all years (Fig. 2A), whereas birds that breed irregularly may have low levels of gonadal activity in some or most years (Fig. 2B – D). The question then arises of the nature of the supplementary information that acts as a cue for breeding in the kakapo.

Masting and kakapo breeding

Although it is well recognised that the availability of food is important in determining the timing of breeding in kakapo (Cockrem *et al.* 2004), the cues that kakapo use as supplementary information remain unclear (Elliott *et al.* 2001). Kakapo breeding on Codfish Island is associated with years of increased rimu fruit production (Harper *et al.* 2006), yet kakapo have also bred on Maud and Little Barrier in the absence of podocarps (Family Podocarpaceae). Kakapo feed on a wide range of plant species (Gray 1977; Best 1984; Trewick 1996; Powlesland *et al.* 2006) and there are differences in diet composition between breeding and non-breeding years (Wilson *et al.* 2006). Masting (mast seeding) is the intermittent production of large seed crops by plants (Kelly 1994) and some kakapo food plants exhibit masting. The occurrence of masting is related to weather, and masting is generally associated with higher then average temperatures in the preceding summer (Schauber *et al.* 2002). Years can be designated as mast years, although since seed production varies on a continuum there are no absolute criteria for determining which years are mast years for a plant species. Mast years with heavy flowering in spring followed by seed production in summer and autumn are a feature of the New Zealand flora (Webb & Kelly 1993), Masting has been reported in podocarp trees such as rimu (*Dacrydium cupressinum*; Norton & Kelly 1988) and totara (*Podocarpus totara*; Wilson & Owens
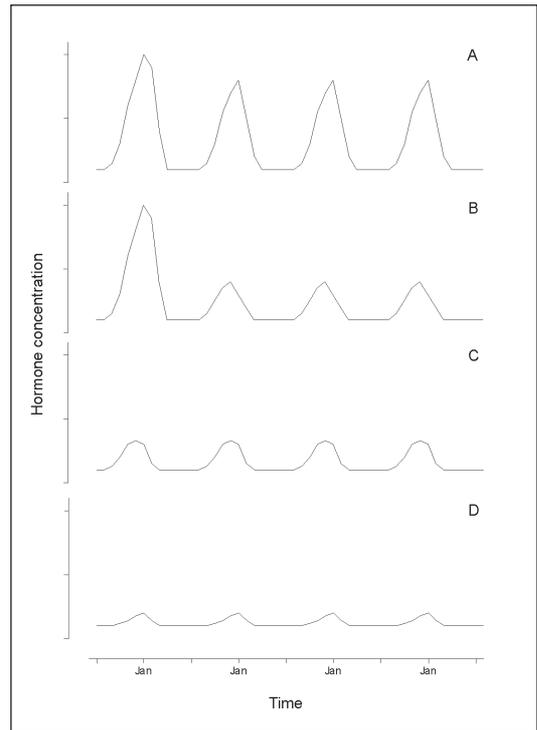
Figure 2 Hypothetical steroid hormone profiles of four kakapo. A. Breeding in first season and high levels of gonadal activity in other years; B. Breeding in first season and low levels of gonadal activity in other years; C. Low levels of gonadal activity each year; D. Very low levels of gonadal activity every year.

1999), beech trees (*Nothofagus* sp.; Salmon 1980; Wilson *et al.* 1998; Alley *et al.* 1998), snow tussock (*Chionochloa rigida*; Connor 1966; Mckone 1990; Rees *et al.* 2002) and flax (*Phormium tenax*; Brockie 1986; Craig & Stewart 1988). There is a high degree of synchrony in mast years between species and also within species across different areas of New Zealand (Schauber *et al.* 2002).

Kakapo are entirely herbivorous, so an abundance of food in summer and autumn depends on whether it is a mast year or not. Kakapo young can be found in nests in autumn from late February until early June (Powlesland *et al.* 2006), and breeding appears to be timed so that the rearing of young coincides with the increased abundance of fruits and seeds in mast years. *Chionochloa* (snow tussock) and *Nothofagus* (beech) mast years often occur together and both these groups of plants flower and produce seed within one season from spring until autumn. The development of rimu seed, however, takes at least two years with initial growth of female cones in one season and further growth of the cones, the development of seeds and the fleshy receptacle and finally seedfall during a second season (Norton *et al.* 1988).

Data on seed production and mast years can be compared with the occurrence of kakapo breeding

Table 1 Mast years (M)[1] and kakapo breeding.(Explanations: [1] A year with markedly greater than average seed production for a species of plant. The amount of seed produced each year by a species at a given location varies along a continuum, so the designation of a year as a mast year is not based on absolute criteria; [2] Year refers to the summer of that year e.g. 1981 refers to the summer that extended from late 1980 into early 1981; [3] Mast years for multiple sites in the North and South Islands identified from standardised masting intensity data in Schauber *et al.* (2002) from 1981 to 1999; [4] Mast years for a site at Nelson Lakes identified from seedfall data from 1981 to 1996 (Wilson *et al.* 1998), from seedfall data in Schauber *et al.* (2002) for 1997 to 1999, and from seedfall data from Department of Conservation publications for 2000 to 2003; [5] Mast years for a site on the West Coast identified from seedfall data from 1981 to 1986 (Norton & Kelly 1988), and identified for Codfish Island from data on the proportion of rimu branch tips bearing fruit from 1997 to 2005 (R. Moorhouse (*pers. comm.*) and Harper *et al.* (2006)).

Year[2]	*Chionochloa* and *Nothofagus* mast New Zealand (1981-1999)[3]	*Nothofagus* mast Nelson Lakes (1981-2003)[4]	Rimu mast West Coast (1981-1986) and Codfish Island (1997-2005)[5]	Kakapo breeding (islands on which breeding occurred each year)
1981	-	-	M	Stewart
1982	M	M	-	-
1983	-	-	-	-
1984	-	-	-	-
1985	M	-	M	Stewart
1986	-	M	-	-
1987	M	-		-
1988	-	-		-
1989	-	M		-
1990	M	M		Little Barrier
1991	-	M		Little Barrier
1992	-	-		Codfish
1993	M	M		Little Barrier
1994	-	-		-
1995	M	M		Little Barrier
1996	-	-		-
1997	M	-	M	Codfish
1998	-	-	-	Maud
1999	M	M	M	Little Barrier, Pearl
2000		M	-	-
2001		-	-	-
2002		M	M	Codfish
2003		-	-	-
2004			-	-
2005			M	Codfish

seasons (Table 1). Kakapo breeding on Stewart Island in 1981 and 1985 was associated with rimu mast years on the West Coast, and breeding on Codfish Island has been associated with increased presence of rimu fruit on the island. Kakapo breeding on Codfish and Pearl Islands also coincided with mast years for *Nothofagus* at Nelson Lakes or *Chionochloa* and *Nothofagus* in New Zealand in three of the four breeding years for which matching data are available. Two of three years in which kakapo bred on Codfish Island coincided with mast years for *Nothofagus* at Nelson Lakes. Kakapo on Little Barrier Island have fed their young on kauri (*Agathis australis*) (Trewick 1996), but records of seedfall in kauri are not available. However, all five breeding years on Little Barrier Island coincided with *Nothofagus* mast years at Nelson Lakes, and four of the five breeding years coincided with more widespread mast

years for *Chionochloa* and *Nothofagus* in New Zealand (Table 1). It is clear from these data that kakapo breeding is generally associated with mast years in a range of forest trees and plants.

Kakapo feed on a range of plant species that experience mast years, and it is likely that kakapo receive cues for breeding from a variety of species during a mast year. Booming by male kakapo can start in November, so birds must respond to cues that become available from October or November. Responses of birds to increases in the availability of particular foods can be mediated by visual and tactile cues in addition to or instead of direct responses to the nutrient content of foods. For example, gonad growth and song rates increased in captive spotted antbirds (*Hylophylax n. naevioides*) in Panama that were already receiving food *ad libitum* when live crickets were provided (Hau *et al.* 2000), whereas antbirds

that could eat dead crickets did not increase their song rates. Kakapo are likely to respond to a range of cues that may be a combination of increases in the intake of specific nutrients, together with visual and tactile cues from the sight of particular foods and from the ingestion of those foods. The relative importance of these various cues for kakapo may differ between plant species, and will vary between islands. Rimu may provide the major cue for kakapo on Codfish Island, whereas breeding on islands such as Little Barrier that do not have rimu indicate that cues from rimu are not essential for kakapo breeding.

SUPPLEMENTARY FEEDING AND KAKAPO BREEDING

The possibility that food availability might be insufficient for breeding on Little Barrier Island led to the provision of supplementary food to free-living birds from 1989 onwards. Body mass of kakapo had declined after they were moved from Stewart Island to Little Barrier Island. Body mass remained relatively low until supplementary food was provided, then increased to reach similar levels to those before transfer (Moorhouse & Powlesland 1991). Kakapo nested on Little Barrier Island in 1990 after not breeding for seven years (Powlesland & Lloyd 1994), indicating that increased food availability could lead to increased breeding frequency in kakapo. Supplementary food has also been provided to kakapo on Codfish Island since 1993. However, kakapo on Codfish Island were not lighter than before transfer from Stewart Island and supplementary feeding has apparently not increased the frequency of breeding on Codfish Island (Elliott *et al*. 2001). Explanations that have been suggested for the varying responses of kakapo to supplementary food include that the food could raise birds above a nutritional threshold for breeding, there could be both a nutritional threshold and other triggers, and breeding could occur in response to the initial increase in food availability (Elliott *et al*. 2001). Body condition is generally known to be important for breeding in birds (Drent & Daan 1980). It seems likely that kakapo respond in spring and early summer to a variety of cues associated with flowering and the development of seeds and fruit, and that breeding may occur in individual birds that are in sufficiently good condition for breeding.

It was noted by Elliott *et al*. (2001) that heavy supplementary-fed birds on Codfish Island were less likely to breed, although heavier birds did breed in 1997 when rimu fruit was especially abundant. The relationship between body fat levels and reproduction is complex. Whilst "adequate" amounts of fat are needed for birds to breed, high levels of fat are associated with reproductive problems in broiler chickens (Hocking & Whitehead 1990). However, broiler chickens are genetically selected for high growth rates and are not a good model for wild birds. Fat is an important endocrine tissue that produces a range of hormones including estradiol and leptin (Ahima & Flier 2000). Leptin is a protein hormone that inhibits food intake and has an important role in the control of body weight by providing a negative feedback signal to the brain about the level of fat in the body. Leptin is also involved in the relationship between nutrition, body fat levels and reproduction. It has been suggested that leptin has dual actions on reproduction: Caprio *et al*. (2001) proposed that leptin concentrations above a minimal threshold are necessary in the hypothalamus to activate the reproductive axis from the hypothalamus in the brain to the pituitary gland and the gonads, whereas high leptin levels, such as found in obesity, might impair testicular and ovarian function and have negative effects on reproduction.

Leptin has been identified in birds (Taouis *et al*. 2001), and it is possible that high levels of body fat in birds could be associated with a negative effect of leptin on the reproductive system. However, for the kakapo it seems more likely that any reduction in breeding frequency in heavier birds is simply a consequence of these birds spending less time feeding on natural foods and hence receiving fewer natural cues that may lead to breeding. This conclusion differs from the suggestion of Harper *et al*. (2006) that smaller amounts of reproductive hormones reach the ovaries of fat birds. Ovarian function is stimulated by luteinising hormone and follicle stimulating hormone which are protein hormones and not fat soluble, so the amount of body fat will not affect concentrations of these hormones in the blood.

CONCLUSIONS

Kakapo breeding depends on the frequency of years of large seed and fruit production by their major plant foods, and involves both a postulated annual cycle of gonadal growth and regression driven by the annual cycle of daylength, and responses to cues from the environment. Male kakapo can begin booming many weeks before females lay eggs, and booming but not egg-laying occurs in some years, indicating that males may respond to different natural cues from females. The kakapo egg is small in relation to body mass (Powlesland *et al.* 2006), possibly because the low metabolic rate of kakapo (Bryant 2006) means that it is harder to accumulate the resources needed for egg-laying in kakapo than in other species. The female also makes a long investment in parental care through incubation and chick-rearing, so it is more important for females than males to respond to cues that are likely to accurately predict adequate food supplies for the entire breeding cycle.

Kakapo are very long lived, so kakapo populations can be maintained even though breeding occurs in some years but not others and some breeding attempts fail due to insufficient food for rearing chicks. However, if the frequency of breeding could be increased artificially then the conservation efforts needed to ensure the long term survival of the kakapo could be reduced. The challenge for increasing breeding frequency in kakapo is to find cues that can be provided for female kakapo.

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