

What triggers nesting of kakapo (*Strigops habroptilus*)?

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Kakapo (*Strigops habroptilus*) are unusual in that, although some males may engage in courtship activity every year, nesting occurs only at three - four year intervals (Powlesland *et al.* 1992; Eason *et al.* 2006). Because productivity is low (Elliott *et al.* 2006) increasing the frequency of nesting has been a management priority. Powlesland *et al.* (1992) hypothesized that the frequency of nesting on Stewart Island had been limited by the availability of natural foods with sufficient protein to allow females to raise young successfully. Powlesland & Lloyd (1994) suggested that the provision of supplementary food to kakapo on Little Barrier Island had increased the frequency of nesting there. However, although there appeared to be an initial increase in nesting frequency on Little Barrier following the provision of supplementary food this was not sustained in subsequent years and supplementary feeding had no effect on nesting frequency on Codfish Island (Elliott *et al.* 2001).

Elliott *et al.* (2001) concluded that there is no evidence that supplementary feeding has induced nesting, although it may have allowed females to reach the nutritional threshold required for nesting to occur. Identifying the triggers for nesting may allow its frequency to be increased. On Codfish, Stewart and Pearl Islands in southern New Zealand, nesting has occurred only when the podocarp species, rimu (*Dacrydium cupressinum*) or pink pine (*Halocarpus biformis*) fruit has been abundant (Powlesland *et al.* 1992; Elliott *et al.* 2001). In this note, we describe the relationship between nesting and rimu fruit abundance on Codfish Island, evaluate potential

triggers of nesting on Little Barrier Island in northern New Zealand, and present a generalized model for the initiation of nesting in kakapo.

Phenological data on the temporal distribution and abundance of rimu fruit on Codfish Island have been collected since 1996 by counting the proportion of fruiting tips on four marked branches of the same 10 trees each year. Meteorological data were obtained from weather stations on Stewart Island (adjacent to Codfish Island) and Leigh (near Little Barrier Island). Nesting was detected by monitoring the behaviour of radio-tagged female kakapo as described by Eason *et al.* (2006).

On Codfish Island, nesting has only occurred when >10% of rimu branch tips bore fruit in October (Fig. 1). As it ripens, rimu fruit differentiates into a black seed and red, fleshy aril but in October is green and undifferentiated (Salmon 1991). Since female kakapo begin feeding on green rimu fruit in late October and early November, it is likely that some characteristic of this triggers them to mate and nest in January and February. Although higher in energy, green rimu fruits are lower in protein and fat than the nuts and food pellets that have been provided to kakapo as supplementary food (RJM unpubl. data). Therefore, it seems unlikely that it is nutritional value of green rimu fruit alone that triggers nesting.

It has not been practical to collect and store sufficient green rimu fruit to feed to female kakapo. Therefore, in spring 2004, female kakapo were fed freeze dried, ripe rimu and kahikatea (*Dacrycarpus dacrydiodes*) fruit (another podocarp species) in an attempt to simulate an abundant rimu fruit crop. No females subsequently nested. Since it was possible that some aspect of the unripe nature of rimu fruit, rather than rimu fruit specifically, triggers nesting, in spring 2005 green walnuts and green pine cones were fed to 20 females on Codfish Island in an attempt to simulate an abundant, unripe fruit crop. Ten females nested but this result was confounded by the simultaneous occurrence of a moderate rimu fruit crop. However, since this was the lowest abundance of rimu fruit to coincide with nesting it is possible that the green walnuts and pine cones did induce females to nest. Further feeding trials of these foods in a low rimu fruit year are required to clarify this.

It is possible that the trigger provided by green rimu fruit is cognitive, rather than nutritional, or even, chemical. For example, captive pinon jays (*Gymnorhinus cyanocephalus*) can be induced to breed simply by allowing them to manipulate, rather than eat, green pinon pine (*Pinus edulis*) seed (Lignon 1974, 1978).

Similarly, the testicular size and song rate of male spotted antbirds (*Hylophylax n. naevioides*) could be increased simply by allowing them to see, but not eat, live insects (Hau *et al.* 2000). ;

If green rimu fruit provides no significant nutrients, other than energy, to female kakapo why should it trigger nesting? We hypothesize that female kakapo nest in response to unripe podocarp fruit crops because these predict an abundant supply of nutritious ripe fruit during autumn, the period in which they raise their young. Ripe rimu fruit is both higher in protein and fat and easier to collect and process than many staples of the kakapo diet (Eason & Moorhouse 2006). If sufficiently abundant, it appears to be the predominant, if not only, food provided to nestlings (Cottam *et al.* 2006). The hypothesis that kakapo are adapted to nest in response to rimu fruit crops is supported by the fact that three young females without exposure to rimu for five to 17 years (Heather, Hoki, Zephyr) bred on Codfish Island during the first or second rimu fruit crop they had ever experienced as adults. This suggests that female kakapo can be triggered to breed by rimu fruit despite having only previously eaten it as nestlings.

No mating or nesting was recorded on Little Barrier Island in the seven years before supplementary feeding began in 1989 (Lloyd & Powlesland 1990, 1992) but was subsequently recorded in five of the eight years kakapo were on the island (1990, 1991, 1993, 1995, 1998) (Eason *et al.* 2006). Although no information on the size of fruit crops on Little Barrier Island is available, several plants are known to have produced above average fruit or seed crops elsewhere in New Zealand during these five summers (Schauber *et al.* 2002). These include kauri (*Agathis australis*), the seeds of which were fed to kakapo nestlings on Little Barrier Island (Trewick 1997). Because kauri pollination occurs only if September temperatures 17 months before seed-fall are warmer than average (Ecroyd 1982), we evaluated September temperatures at Leigh (24 km from Little Barrier Island) two years before each breeding season as a possible predictor of kakapo nesting on Little Barrier Island.

Nesting on Little Barrier Island may also have been triggered by abundant beech (*Nothofagus* spp.) seed, which also triggers nesting in some populations of kaka (*Nestor meridionalis*) (Wilson *et al.* 1998), another endemic New Zealand parrot. Beech seeding is synchronous over large areas of New Zealand (Schauber *et al.* 2002) and, in the absence of phenological information on beech from North Island sites, we evaluated seed fall data in Nelson Lakes National Park (J. Beggs & M. Maitland unpubl. data) in conjunction with September temperatures. The best predictor of nesting on Little Barrier Island was the average September temperature two years prior to nesting (Table 1).

Although Powlesland and Lloyd (1994) suggested that nesting on Little Barrier Island was triggered by supplementary feeding, supplementary-fed females did

Table 1 Logistic regression of the relationship between kakapo mating on Little Barrier Island (1990-1999) and models incorporating September temperature 2 years before nesting, above average beech seed fall and spring temperature in the year of nesting. September temperatures are those recorded 2 years prior to nesting. AIC = Akaike's Information Criterion (corrected).

Model	AIC
September temp. + beech mast (NLNP) + spring temp.	21.278
September temp. + beech mast (NLNP)	16.128
September temp.	15.252

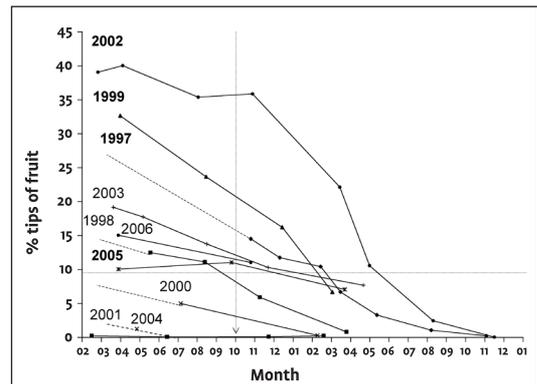


Figure 1 Relationship between kakapo nesting and yearly variation in the rimu fruit crop on Codfish Island. Years in which nesting has occurred are in bold type, dashed lines are extrapolated fruit abundance. Horizontal dotted line indicates the threshold of fruit abundance below which nesting has not occurred. Vertical dotted arrow indicates the critical month of October. Nesting has only occurred when fruit abundance was $\geq 10\%$ in this month.

not attempt to nest every year and some never nested. One explanation for the apparent coincidence between nesting and the beginning of supplementary feeding on Little Barrier Island is that supplementary food may have allowed females to reach the nutritional threshold required for nesting to take place after which a suitable fruit crop was required to trigger nesting. Female kakapo on Little Barrier Island were known to be consistently lighter than females on Stewart Island before the implementation of supplementary feeding (Moorhouse & Powlesland 1991) so it is possible that they were incapable of nesting before then.

An alternative explanation for the absence of breeding during the first seven years kakapo were on Little Barrier Island is that females had not yet learned which fruits could sustain breeding (Moorhouse & Powlesland 1991). Fruit crops suitable for raising chicks are relatively infrequent. For example, there were probably only two beech masts before kakapo first bred on Little Barrier Island in 1990 (Schauber *et al.* 2002). This hypothesis is supported by two females, apparently never having taken supplementary

food (Jean and Lisa), nesting on Little Barrier Island 10 and 17 years respectively after their release on the island.

We hypothesize that there is a minimum weight threshold below which female kakapo are incapable of nesting. Such thresholds have been documented in petrels and albatross, which are also relatively long-lived (Weimerskirch 1992, Chastel *et al.* 1995). Above this putative threshold, female kakapo respond to a developing fruit crop by releasing reproductive hormones, but the amount of hormones produced are proportional to the magnitude of the fruit crop. When the amount of hormone reaching the ovaries is sufficient, nesting occurs. As well as triggering nesting, green fruit abundance may influence breeding intensity; female kakapo tend to produce larger clutches when more green rimu fruit is available (Randomisation test, $R = 0.927$; proportion of bootstrapped samples with a lower coefficient = 0.996).

Recent analysis (Elliott *et al.* 2001) suggests that relatively fat females are less likely to breed than those in more moderate condition. This could be because the hormones that induce breeding are fat soluble and therefore smaller amounts of hormones reach the ovaries of fat birds. Another potential mechanism for the inhibition of nesting in fat females is leptin, a hormone which increases in proportion to total fat mass (Golan *et al.* 2005). At high levels in the bloodstream, leptin restricts the response of human and rat ovaries to gonadotrophins (Duggal *et al.* 2000; Messinis & Domali 2003), and appears to restrict egg production in poultry fed *ad libitum* (Bruggeman *et al.* 2000). Whatever

the mechanism, we predict that fat birds require bigger fruit crops to trigger them to nest.

This model can explain some of the anomalous aspects of kakapo breeding biology observed over the past 25 years, such as the initial flurry, then decline, of nesting frequency on Little Barrier Island following the implementation of supplementary feeding there. We suspect that breeding frequency declined on Little Barrier Island because, as individual females grew progressively fatter following the provision of supplementary food, they required progressively larger, less frequent, fruit crops to induce them to breed. The lack of a relationship between supplementary feeding and breeding frequency on Codfish Island is also explicable in terms of the model. We suspect that female kakapo have been able to maintain sufficient condition on Codfish without supplementary feeding and so have been able to nest in response to rimu crops there (Elliott *et al.* 2001).

If true, this model has important implications for kakapo management. If fat females are less likely to nest it follows that limiting the amount of supplementary food should increase the proportion of females that nest, particularly when fruit is not abundant. It is possible that a record number of females nested on Codfish Island in 2002 (Elliott *et al.* 2006), not only because there was an exceptional rimu crop in that year, but also because this was the first year in which the quantity of supplementary food provided to females had been limited. This hypothesis can only be rigorously tested when there are poor or moderate rimu fruit crops.

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