A parrot apart: the natural history of the kakapo (*Strigops habroptilus*), and the context of its conservation management

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Abstract Since the last review of kakapo biology, published 50 years ago, much has been learnt as a result of the transfer of all known individuals to offshore islands, and their intensive management to increase adult survival and productivity. This review summarises information on a diversity of topics, including taxonomy, plumage, moult, mass, anatomy, physiology, reasons for decline in distribution, present numbers and status, sex ratio, habitat, home range, foraging activities, diet, voice, breeding biology, nesting success, sexual maturity, and adult survival. In addition, those kakapo attributes that compromise its long-term survival in present-day New Zealand are discussed, along with management practises developed to overcome these problems.

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INTRODUCTION

The kakapo (*Strigops habroptilus*) is a large parrot (males 1.6 – 3.6 kg, females 0.9 – 1.9 kg) (Higgins 1999), with finely barred or mottled yellowish-green plumage. It has a conspicuous facial disc of sensory, hair-like feathers, a broad, pale grey beak, robust, short legs, large feet, short, rounded wings, and a relatively short, slightly de-curved tail. Fleming (1982) noted that the kakapo exemplified the tendencies that have characterised the evolution of birds on oceanic islands with abundant food and few predators: a tendency to "gigantism", gains in thermodynamic efficiency at the expense of flight, diminished keel on the sternum, reduced wing muscles, and robust legs and neck.

A combination of characteristics make the kakapo unique among parrots; heaviest parrot, pronounced sexual dimorphism in body size, flightlessness, nocturnal, herbivorous, low basal metabolic rate, probable well-developed sense of smell, distinctive and obvious scent, polygynous lek mating system, no male parental care, altricial young reared in a nest at ground level, and irregular breeding (intervals of 2 - 7 years: Henry 1903; Merton 1977a; Merton *et al*. 1984; Powlesland *et al*. 1992; Higgins 1999; Eason *et al*. 2006). Its many unusual characteristics made the kakapo a subject of great fascination to ornithologists in the late 19th century (Buller 1877; Haast 1864; Henry 1903; Lyall 1852; Potts 1873; Reischek 1884), although not all of these characteristics were known of at the time. Unfortunately, some aspects of the kakapo's biology also made it highly vulnerable to introduced mammalian predators (Merton 1977b, 1994; Best & Powlesland 1985). Adult males are particularly vulnerable to such predation during the breeding season when they cluster at traditional leks and advertise their presence by calling (booming) each night for about three months. Likewise, nesting females, eggs and nestlings are highly vulnerable because of the long (*c*. five month) nesting cycle and the species' ground nesting habit. The kakapo's vulnerability was recognised by Richard Henry, who was appointed by the New Zealand government to attempt establishment of a population on pest-free Resolution Island and neighbouring islands in Fiordland (Fig. 1) in the 1890s and early 1900s (Hill & Hill 1987). Also, a few kakapo were released on each of Little Barrier and Kapiti Islands (Fig. 1) (Williams 1956; Best & Powlesland 1985). These early attempts to establish kakapo on offshore islands failed because of the subsequent invasion of Resolution Island by stoats (*Mustela erminea*), the presence of feral cats (*Felis catus*) and Pacific rats (kiore, *Rattus exulans*) on Little Barrier Island, and the presence of cats, rats (*R. exulans*, *R. norvegicus*), possums (*Trichosurus vulpecula*) and weka (*Gallirallus australis*) on Kapiti Island. No further concerted attempts to locate or conserve kakapo were made until the 1950s and 1960s when the newly-established Wildlife Service, Department of Internal Affairs, searched more than 60 locations, mainly in Fiordland. Only eight males were found, all in Fiordland, six of which were taken into captivity. Most died within a few months although one lived for four years.

In 1974, another attempt was made to save the species, initially involving searches in Fiordland (Merton 1977a). By 1977, 18 kakapo had been located, three of which were transferred to Maud Island (Fig. 1), but all were males

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and so the species seemed doomed to extinction (Clout & Craig 1995). However, in 1977 a kakapo population of 100 - 200 birds was discovered on southern Stewart Island (Powlesland *et al*. 1995) (Fig 1). Although Stewart Island had feral cats, ship rats (*Rattus rattus*) and possums, it did not have mustelids, which was probably why this population managed to survive. It is thanks to the translocation of the remaining 62 birds of this last natural population between 1980 and 1997 to mustelid- and cat-free islands, intensive and innovative management of each individual kakapo and nest (Elliott *et al*. 2006), and perseverance and ingenuity by conservation staff, volunteers and advisers that the kakapo is now starting to make a comeback, albeit slowly.

The last comprehensive review of the status and biology of the kakapo was written 50 years ago (Williams 1956), but much has been learnt in the interim, especially as a consequence of the invigorated conservation programme. This up-date, then, is long overdue.

TAXONOMY

With its many distinctive characters, early authorities placed the kakapo alone in the family Strigopidae, but Smith (1975) used anatomical, morphological and ethological characters to place it in the endemic New Zealand subfamily Strigopinae, which has usually been followed since (Turbott 1990). Smith (1975) proposed that the closest taxonomic group to the kakapo was another New Zealand endemic parrot subfamily, Nestorinae, comprising the kaka (*Nestor meridionalis*) and kea (*N. notabilis*). De Kloet & de Kloet (2005), using DNA techniques, recognised a similar phylogeny, with the kakapo (subfamily Strigopini) and *Nestor* (kaka and kea) (subfamily Nestorini) genera comprising an ancient New Zealand lineage that diverged from all other parrots with the break-up of Gondwana *c*. 85 million years ago.

Triggs *et al*. (1989) examined the genetic status of kakapo using electrophoresis to estimate the level of allozyme variation in blood from 13 birds, 12 from Stewart Island and one from South Island. The heterozygosity was higher in the Stewart Island population, but the difference between the two populations was not significant owing to the small sample sizes. Genetic divergence between the two populations was similar to that of conspecific populations or subspecies of other birds. More recent study involving DNA profiling of 36 kakapo from Stewart Island has shown an unusually low level of genetic variability, and that the only known individual from the South Island has a significantly higher level of variability (Robertson *et al*. 2000; Miller *et al*. 2003; Robertson 2006).

APPEARANCE

For detailed descriptions of the kakapo, see Buller (1888), Oliver (1955), Williams (1956) and Higgins (1999). In brief, the upper parts of kakapo are predominantly yellowish moss-green or olive-green, finely barred or mottled with dark brownish-grey or black. Colour tones and intensity of barring vary between individuals. A delicate emerald-blue iridescence is often apparent, particularly on crown, nape and mantle. Breast and flanks are yellowish-green, streaked with yellow, and finely barred with brownish-grey in some birds, through to dark grey in others. The belly and undertail coverts are predominantly yellow, streaked with pale green and weakly barred or streaked with pale brownish-grey. The shade of yellow varies, being typically a pale lemon yellow in Stewart Island birds, and a richer canary yellow in Fiordland individuals (DVM pers. obs.). The tail, and both primary and secondary wing feathers, are barred brownish-grey or mottled with pale yellow. The tail feathers are often worn at the tip. Markings on the primaries are, in all age groups, useful in determining sex. In males, barring or mottling on the inner vanes of the four outermost primaries continues as an indistinct water-mark pattern to the tips, whereas in females the distal 3 - 4 cm of these feathers is virtually or entirely without markings (see Higgins (1999) and Robertson *et al*. (2000a) for illustrations).

The face, throat and chest are grey or yellowish-grey (most Stewart Island birds), or brownish-grey (most South Island birds) (Higgins 1999). A grey or brownish-grey ear patch is often conspicuous. A yellow superciliary line extends to above the ear patch. The shafts of the feathers at the base of the beak are prolonged into filoplumes resembling cat's whiskers. The broad upper mandible is bluish-grey, with an ivory-coloured tip and cutting edge. The lower mandible with its unique five longitudinal ridges is also ivory-coloured. The beak and throat feathers are often heavily stained brown by juices of foods, particularly on Fiordland birds. The eyes are dark brown with grey orbital rings of bare skin. The bulbous cere is blue-grey, and the nostrils are large, crescent shaped and more than 4 mm in length. The legs and feet are robust, smooth-scaled, and blue-grey in colour with cream soles.

In comparison to the male, the female's head is narrower and less domed, the beak is narrower and proportionately longer, the cere smaller, nostrils smaller and oblong in shape, the legs and feet markedly more slender and pale pinkish-grey, and the tail is proportionately longer (Higgins 1999). Plumage colour is similar to that of males. However, the female's tonings are generally more subtle, with less yellow, and less barring and mottling, on the underparts. The overall effect is a heightening of green, particularly on the underparts. Nesting females have a well-developed brood-patch of bare skin on the belly, and when handled, females tend to be more vocal and aggressive than males (Higgins 1999).

Juveniles are distinguishable from adults because their plumage is generally more dull olive-green with finer, more uniform, black barring, and less yellow (Westerskov 1981; Higgins 1999). The tail and wings are comparatively short, and the beak is shorter with a more pronounced curve near the tip than in adults. Juveniles have just three primordial struts on the under surface of the lower mandible, rather than the five prominent ridges of adults. The juvenile face is paler grey with darker grey lores than that of the adult (Reischek 1884). Their orbital ring is paler than of adults, and their irises are encircled by a ring of short feathers resembling "eye-lashes" not evident on adults. Juvenile primaries are narrower than those of adults, have pointed tips, and initially vestiges of down adhere to the tips of primary and tail feathers (Higgins 1999).

Newly-hatched kakapo nestlings are well covered in fine, long, white down through which pink skin is evident. This down is replaced within the first month by long, grey down, which is paler on the head. Their eyes are paler brown than those of adults, the beak is a glossy dark grey/brown, and the feet and legs pink, changing to uniform dark pinkish-grey at *c*.14 days old. Outer and inner toes rotate to the rear at 14 - 21 days of age. Secondary and greater wing covert quills irrupt at *c*.24 days old, and primary, tail, crown and facial quills at *c*.35 days old. Wing and contour feathers are well developed by 42 days old. By *c*.70 days old, when they fledge, fledglings are fully feathered with some down adhering to the lower back and crown, but with noticeably shorter wings and tail than adults (Higgins 1999).

The kakapo's cryptically coloured plumage blends perfectly with foliage so that even at close quarters birds are difficult to see. They use this camouflage and remain motionless to avoid detection when closely approached. Often only when touched will a roosting bird attempt to protect itself by moving a few metres before seeking shelter and remaining still again. Contrary to popular belief, kakapo are not able to glide, but use wing-assisted leaping or parachuting short distances at a steep downwards angle (Higgins 1999). This behaviour is most often seen when birds are descending from trees to avoid recapture by conservation managers. The wings are used regularly for balance, especially when climbing and running.

MOULT

Moult of the kakapo has been determined incidentally during the past *c*.20 years when birds have been caught and recaptured for other purposes, such as transmitter changes (DVM unpubl. data). As a result, little detailed information is available on the timing and sequence of moult, and the variation between individuals. Moult is protracted, and its timing and duration vary markedly according to whether birds are breeders or non-breeders. Non-breeders and males start moulting during March-May (austral autumn), and complete moult during October-November (spring). By comparison, breeding females delay the start of moult until September, by which time their young are approaching independence. For example, of two females that reared young to independence in 1981, one began moulting in September 1981 and had not finished by March 1982, and the other did not start to moult until after September 1981.

The sequence of primary moult recorded for *c*.40 live adults showed no obvious pattern (DVM unpubl. data). Moult began with any primary, and each primary replaced was not always adjacent to the previous one. The number of primaries in moult varied from just one to all 10. This highly variable rate of primary moult probably occurs because the kakapo is flightless.

The post-juvenile moult is apparently partial, involving only body feathers, and probably starts when birds are *c*.9 months old (DVM unpubl. data). Immatures probably go through a complete moult. One hand-reared female began to moult in May, when *c*.14 months old, and completed it in October (G. Climo pers. comm.). Moult began over the body, followed by the wings and tail two - three months later. All but one tail feather was dropped over a period of 17 days, the last being dropped 45 days after the first. In the following year, when this kakapo was two years old, it began to moult two months earlier in March, and had completed it in September.

MASS

The kakapo is the most massive and sexually dimorphic parrot (Livezey 1992), males typically weighing 30 - 40% more than females (Clout & Merton 1998). Weights of adult males range from 1.6 to 4.0 kg, although the average is *c*.2.0 kg (Powlesland *et al*. 1992; Clout & Merton 1988; Eason *et al*. 2006). In contrast, that of adult females ranges from 1.3 to in excess of 2.0 kg, with an average of *c*.1.5 kg (Powlesland *et al*. 1992; Clout & Merton 1998; Eason *et al*. 2006). Adult weights fluctuate seasonally, reflecting the deposition and use of fat reserves for breeding (Eason *et al*. 2006). The magnitude of such weight fluctuations appears to be greater than in any other terrestrial bird; seasonal weight gains averaging 25%, and occasionally as much as 100%, are normal in free-living, non-supplementary fed kakapo (Eason *et al*. 2006). Fledglings are within adult weight ranges when they leave the nest at 10 - 11 weeks of age (Farrimond *et al*. 2006a).

ANATOMY

Livezey (1992) listed the limited anatomical studies that had been carried out on the kakapo prior to his own. These studies briefly described selected anatomical features, such as external characters, appendicular skeleton, musculature, trachea, hyoid apparatus, skull, tongue, alimentary tract, carotid arteries, uropygial gland, and feathers (Livezey 1992, and references therein). Livezey (1992) described and illustrated the functional morphology of the kakapo wing, and selected aspects of the leg and entire body, through measurements, and muscle, skeletal and feather characteristics. He compared these features with those of the flighted kea in order to highlight the changes that have come about in relation to the evolution of flightlessness of the kakapo. Livezey concluded that the kakapo is the heaviest and most sexually dimorphic parrot, and has the smallest relative wing size of any

Table 1 Measurements (mm) of live kakapo from Stewart Island

	Mean	*s.d.*	*N*	Range
Male				
Beak length	40.2	1.15	20	38.8 – 43.1
Beak width	23.7	0.95	20	22.0 – 25.7
Tarsus	60.1	2.02	17	56.8 – 63.8
Longer fore-toe	56.9	2.09	20	52.1 – 61.5
Claw (same toe)	21.7	1.08	19	19.5 – 24.1
Wing	268.5	12.5	19	240 - 280
Tail	224.5	21.7	17	195 - 272
Female				
Beak length	37.3	0.86	12	36.2 – 38.9
Beak width	20.6	0.43	13	19.9 – 21.4
Tarsus	54.1	1.34	12	51.9 – 56.7
Longer fore-toe	50.3	3.01	12	44.3 – 54.1
Claw (same toe)	20.4	0.96	13	19.1 – 21.9
Wing	266.2	14.5	13	250 - 285
Tail	222.5	9.7	13	210 - 240

parrot. Although its wing feathers are distributed similarly to other parrots, the primaries and secondaries are shorter, comparatively rounded, show less asymmetry of vanes, and have fewer interlocking barbules at their tips.

The skeleton of the kakapo is unique among parrots in a number of features, in particular the marked reduction in the carina sterni or keel, the primary anchor for the largest flight muscle. Most skeletal dimensions are highly variable within the sexes (Table 1). Males are larger in body length and head size than females (Shepard & Spitzer 1985). However, while females are smaller and lighter than males, their wing and tail lengths are proportionately larger (Henry 1903; Shepard & Spitzer 1985). Compared to kea, the kakapo is smaller in all wing dimensions but larger in leg dimensions, particularly the femur which has elongated disproportionately. The kakapo has the complete pectoral musculature typical of parrots, but most of these muscles are absolutely smaller than those of the lighter kea. Proportionately, the kakapo has the lowest pectoral muscle to body weight ratio of any parrot (McNabb & Salisbury 1995). The crop of the kakapo, enlarged to cope with its bulky vegetarian diet, is accommodated anatomically by the reduction of the keel and breast muscles.

PHYSIOLOGY

The difficulty of studying kakapo in the wild, together with the bird's critically endangered status, has limited opportunities for physiological studies such that inferences about function have often been made from anatomical descriptions. The distinctive features of kakapo biology that have been studied in varying detail include annual cycles of body weight, daily energy expenditure, the digestive system, and the physiological basis of seasonal breeding.

The tongue and beak of the kakapo appear well adapted for the grinding of plant material (McCann 1963; Gray 1977; Kirk *et al*. 1993; Butler 2006). The structure of the gastrointestinal tract with a distinct crop and gizzard that is larger than the proventriculus, but not the absence of caeca, are consistent with the fibrous nature of the diet (Kirk *et al*. 1993). With foods being finely ground in the beak, not surprisingly the gizzard is less muscular than in other parrots.

Hagelin (2004) observed the foraging behaviour of a male kakapo at a food station consisting of three food bins, only one of which contained food. The bird's response suggested it used olfaction to determine which bin contained food. In support of this finding she found that the 'olfactory bulb ratio' (OBR, longest diameter of the olfactory bulb / longest diameter of the brain; (Bang & Cobb 1968) of kakapo (30.2) indicated that it probably has a keen sense of smell. The kakapo has a larger OBR than most non-passerines (19.6), including parrots, and comparable to that of species with a known acute sense of smell (e.g. brown kiwi, *Apteryx australis*, 34.0; turkey vulture, *Cathartes aura*, 28.7; (Wenzel 1968). Thus, these findings are consistent with the hypothesis that the kakapo has evolved an enhanced olfactory capacity relative to most non-passerines.

The kakapo has a relatively small brain in relation to body weight compared with flying parrots (Iwaniuk *et al*. 2004). Since this is not generally the case for flightless birds (Iwaniuk *et al*. 2004), it may be a secondary consequence of the kakapo's relatively heavy gastrointestinal tract.

Flightlessness reduces the energetic costs of maintenance in birds. McNab & Salisbury (1995) predicted a low basal metabolic rate for kakapo on the basis of its relatively low pectoral muscle mass (Livezey

1992). Bryant (2006) determined the daily energy expenditure of free-living kakapo to be 799 ± 256 kj/d (n = 20), the lowest recorded for any bird. This was 1.39 times the basal metabolic rate predicted from an equation of Aschoff & Pohl (1970), compared with a multiplier of 2.75 times for the kea (McNab & Salisbury 1995). This is consistent with the ability of the kakapo to live on an entirely herbivorous diet of relatively low nutrient quality (James *et al*. 1991).

The lipid composition of kakapo eggs is similar to that of other birds, including the amount of linoleic acid, an important fatty acid for egg formation (Body & Powlesland 1990).

Reproductive steroids are excreted in the faeces, and faecal estradiol and testosterone levels were measured in kakapo faeces on Little Barrier Island (Cockrem & Rounce 1995). Although samples could not be ascribed to individual kakapo, since the majority of kakapo on Little Barrier Island were male it is likely that most of the samples were from males. There were clear annual cycles in faecal testosterone concentrations and in the testosterone: estradiol ratio in faecal samples. Testosterone concentrations and the testosterone: estradiol ratio reached peaks in February at the time of copulation and maximum sexual behaviour, declined rapidly in April, then rose the following spring when male sexual behaviour was starting again. This suggests that male kakapo undergo an annual cycle of plasma levels of testosterone and hence of gonad size, with peak hormone levels and maximum gonad size in late summer.

The timing of breeding in the kakapo is likely to be related to day length as well as to food availability (Cockrem 1995, 2006). Cockrem (*loc. cit.*) proposed that the kakapo has an annual cycle of gonadal growth and regression, with day length being the main proximate factor stimulating the growth of gonads in spring. Essential supplementary information (Wingfield 1980) was proposed to be crucial for the initiation of a complete breeding cycle, especially in the female. Supplementary information associated with food is needed to stimulate the full development of the booming sacs and an intense period of booming in males, and to initiate the final development of the ovaries and hence copulation and egg-laying in females. Presumably insufficient supplementary information is available most years, leading to the erratic occurrence of booming and mating (Cockrem 1995, 2006).

The time during which food is acting as supplementary information for the initiation of breeding could be in spring as this is when booming sacs develop. Alternatively, the availability of food could be crucial even as early as the preceding autumn and winter. This is the time when kakapo sometimes have large fat deposits. The physiological mechanisms by which nutrition influences breeding in the kakapo, and the time when they are important, remain unknown.

DECLINE IN DISTRIBUTION

As evidenced by subfossil records and observations by early observers, the kakapo was widespread throughout North, South and Stewart Islands (Fig. 1), including from sea level to alpine areas (Brunner 1848; Reischek 1884; Williams, 1956; Scarlett 1979; Millener 1981). The origin of kakapo on Stewart Island is still of debate (Williams 1956; Dawson 1962; Russ 1978); whether there was a resident population, or that it originated from liberations by Maori in pre-European times or from Fiordland birds liberated at Port Pegasus in the 1880s. That no fossil remains of kakapo have been found on Stewart Island (Worthy & Holdaway 2002) (however limited searching has been carried out there to date, and the highly acidic soils would result in the leaching of bones fairly quickly; T.H. Worthy pers. comm.), and the very high genetic similarity of all Stewart Island kakapo now alive (Robertson 2006) suggests a recent (i.e. human-aided) presence originating from a few founders.

Contrary to Williams (1956), there is no evidence of a significant decline in kakapo distribution prior to human settlement. However, its range contracted substantially following Maori settlement *c*.1200 years ago, particularly in the North Island. Larger birds, including kakapo, were an important food source for Maori, and subsequently for European explorers and settlers (Hall-Jones 1976; Best 1977; Cassels 1984). In addition, kakapo skins were highly sought after by Maori for cloak-making because of outstanding thermal insulation properties resulting from unusually dense layers of down and soft feathers (Higgins 1999; Tipa 2006).

Widespread burning of forest, scrub and tussockland habitats by Maori, and predation by their dogs (kuri; *Canis domesticus*) were probably contributing factors in the initial decline of kakapo distribution (Anderson 1981). The burning of forest may have caused local extinctions, especially in drier eastern and central regions of the South Island from the 13th century onwards. Maori used kuri to capture kakapo (Best 1977; Anderson 1981). Both kuri, and breeds introduced by European settlers in the early 19th century, became feral, at least in the South Island (Anderson 1981), and would have subsisted mainly on ground birds, such as kakapo and weka. Since kakapo have a strong odour and remain motionless when approached, feral dogs would have had a devastating impact on kakapo populations. Just how effective dogs were at finding kakapo is indicated by early explorers having to tie up their dogs each night to stop them regularly returning to camp with kakapo (Haast 1864; Henry 1903; Pascoe 1957; Wilson 1959). However, predation of chicks by Pacific rats (kiore) is more likely to have been the main cause of the dramatic and widespread retraction in kakapo range and decline in their numbers during this era (Merton 1975; Cassels 1984; Clout & Merton 1998).

At the time of first European contact during the late 18th century, kakapo still inhabited parts of the central

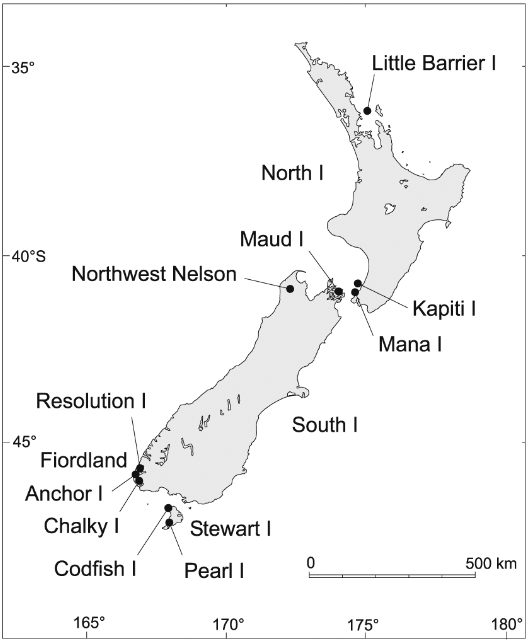

Figure 1 Map of New Zealand showing locations mentioned in the text

North Island; Kaimanawa Ranges, Urewera and Wairarapa districts (Best 1977), and was reported from the Hunua Range south of Auckland as late as 1912 (McKenzie 1979). It was extinct in the eastern South Island, but was abundant in some higher rainfall areas in northern, western and southern districts (Williams 1956; Lloyd & Powlesland 1994). Land clearance by European settlers after the early 1800s was unlikely to have greatly affected kakapo distribution because by then the species was generally confined to a few localities remote from human habitation. Also, predation by feral cats and habitat degradation by feral stock (goats *Capra hircus,* pigs *Sus scrofa* and cattle *Bos taurus)* are likely to have caused only local declines.

After 1880, remaining kakapo populations throughout North and South Islands declined rapidly. The species became extinct in the North Island and in north-west Nelson (Fig. 1) early in the 20th century, but survived in some remote subalpine valleys in Fiordland in south-western South Island (Williams 1956; Butler 1989). The decline in Fiordland, the kakapo's final mainland stronghold, was first noted in the late 1800s (Hill & Hill 1987; Clout & Craig 1995). The accelerated decline after 1880 coincided with the introduction and establishment of three species of mustelid (ferret *Mustela furo,* stoat, and weasel *M. nivalis*), ship rats, several species of deer (Cervidae), and possums. From the evidence of contemporary observers and present knowledge of the species involved, there is little doubt that predation by stoats was the main cause of this dramatic decline (Henry 1903; King 1984; Merton 1977b). The spread of ship rats, which would have preyed on eggs and chicks and competed with adults for food, would also have been a contributing factor (Wodzicki 1950; Atkinson 1973, 1978; Campbell 1978; Rasch 1989). Competition and habitat degradation by introduced browsers would have further reduced productivity. It is unlikely that competition from introduced birds was important in the decline of kakapo because even now such bird species are not abundant in extensive areas of unmodified or little-modified indigenous vegetation (Diamond & Veitch 1981). There is no evidence that introduced birds were vectors for exotic avian diseases that affected kakapo.

By the 1970s, the Fiordland population had been reduced to a few aged males, scattered in less accessible parts of some remote valleys (Merton 1977a, 1985; Butler 1989). Of 18 males found in Fiordland during the 1970s, five were transferred to offshore islands. One of these, an adult of unknown age named "Richard Henry" found in 1975, was in 2005 the only known surviving South Island kakapo. None of the 13 males that were left in Fiordland are known to have survived beyond 1987 (Rasch 1989; Clout & Craig 1995).

In 1977, sightings of kakapo in southern Stewart Island (H. Vipond *in litt*. 1949) were investigated, and a population that included both females and males was found in an area of about 8,000 ha of fire-modified scrubland and forest. On discovery, this population probably consisted of 100 - 200 birds (Powlesland *et al*. 1995). Mustelids have never colonised Stewart Island, but feral cats were introduced by European settlers over a century ago. Soon after kakapo were discovered on Stewart Island evidence of cat predation on adult birds became apparent (Karl & Best 1982). The remains of 15 kakapo killed by cats were found during 1980 - 1982 (Best & Powlesland 1985), and the predation rate on adult radio-tagged kakapo reached 56% per annum in 1981/82 (H.A. Best cited in Moorhouse & Powlesland 1991). Since the Stewart Island kakapo population obviously could not have withstood this level of predation during the 100 years or more cats had been on Stewart Island, the most likely explanation for this increased predation was that one or more cats had learned to kill kakapo (Butler 1989). No cat-killed kakapo were found after intensive cat control started in 1982. However, to ensure the survival of the remaining birds, all that could be found (62; 38 males and 24 females) were transferred during 1980 - 1997 to islands free of feral cats and mustelids, but not of Pacific rats.

The last accepted North Island record was from the Huiarau Range in 1927 (Williams 1956), the last South Island record was of three males in Fiordland's Milford catchment in 1987 (Rasch 1989), and the last Stewart Island record was of a female found and transferred to Codfish Island (Whenua Hou) in 1997. Thus, the species is now likely to be extinct throughout its natural range (Higgins 1999). As of November 2005, kakapo reside on four islands, Codfish (Whenua Hou), Chalky (Te Kakahu), Anchor and Maud (Fig. 1).

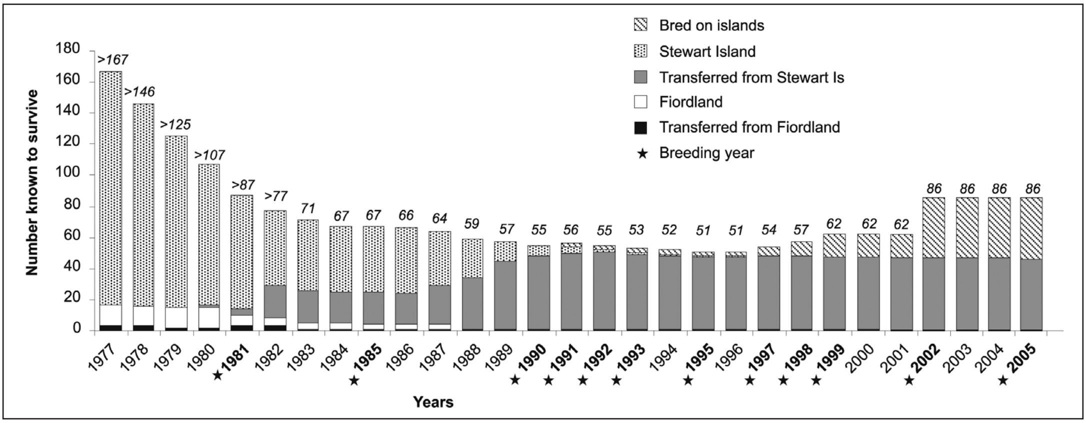

Figure 2 Annual number of kakapo present during 1977 to 2005, where they originated, where they were transferred to, and in which years breeding occurred

RECENT NUMBERS AND CONSERVATION STATUS

By 1992, the one surviving South Island kakapo and 61 from Stewart Island had been transferred to islands, with the exception of a female on Stewart Island whose presence was not known until 1997. In 1995, the population reached its nadir of 51 birds, including 21 females (Fig. 2). During 1992-1995, only three young were fledged. Although two adults have died since 1995, the survival of kakapo on islands has been remarkably high, averaging *c.*1.3% mortality per annum since the first transfers in 1980.

The introduction of a range of new management methods in 1995 was followed by significant improvement in kakapo productivity, reflecting the eradication of Pacific rats from Codfish Island (Whenua Hou), the support of nesting females through the provision of food supplements, and intensive monitoring and subsequent intervention when necessary (Elliott *et al.* 2006). As at November 2005, the population comprised 41 females and 45 males (Fig. 3), including four fledglings (3 females, 1 male) bred in 2005. Forty of the 86 kakapo (46.5%) have hatched on the refuge islands, the oldest of which was reared on Little Barrier Island in 1991.

The oldest surviving bird is "Richard Henry", found as an adult in Fiordland in 1975, and now probably more than 40 years old. The ages of 42 (48.8%) kakapo are known.

The New Zealand Department of Conservation has listed the kakapo as *nationally critical*, the highest conservation ranking available, because the total population was less than 250 mature individuals (Hitchmough 2002). This listing equates with the IUCN criterion of *critically endangered* (Hilton-Taylor 2000). In 1999, BirdLife International retained the status of *critically endangered* (a species that is facing a very high risk of extinction in the wild in the near future) for the kakapo, even though it no longer met the criteria (BirdLife International 2000). It was to be retained in the *critically endangered* category for a further four years after which it would be down-listed to *endangered*, assuming that none of the criteria for critically endangered were met. This down-listing would reflect the increase in numbers since 1995 (Fig. 2) (Elliott *et al.* 2006).

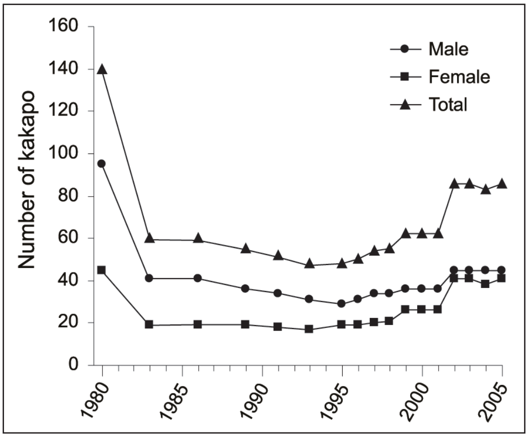

Figure 3 Annual number of male and female kakapo, and in total from 1980 to 2005

SEX RATIO

A skewed sex ratio of kakapo is apparent from subfossil bones (2.5:1 in favour of males; Trewick 1997), study skins in museum collections collected during the 1800s (2:1; Livezey 1992), and of kakapo transferred from Stewart Island in the 1980s and 1990s (2:1; Powlesland *et al.* 1995). Initially this was considered to have been the result of differential predation of adult females by introduced mammalian predators (Merton *et al.* 1984; Powlesland *et al.* 1995). However, Trewick (1997) considered that the male-biased sex ratio apparent from subfossil bones deposited well before mammalian predators were introduced was the result of differential mortality through gender-based brood reduction. He hypothesised that in mixed-sex broods, the larger, faster-growing male nestlings (Powlesland *et al*. 1992) would out-compete their female siblings when food was in short supply resulting in disproportionate mortality of the smaller, slower-growing female nestlings. This was followed by the finding that the sex of offspring can be influenced by the level of nutrition of the female (Clout *et al*. 2002); females whose body weights are high at the onset of breeding produce significantly more male than female offspring.

That all 24 of the last kakapo found in Fiordland were adult males (Merton *et al*. 1984) suggests that irrespective of any male bias in nestling survival, females in this population suffered significantly more predation than males. A male-biased sex ratio (2:1) has also been reported in adult kaka, where high levels of predation on nesting females is a feature at mainland sites where stoats and possums are not controlled (Wilson *et al*. 1998; Greene & Fraser 1998; Moorhouse *et al*. 2003). Like female kakapo, female kaka are confined within a cavity nest for many months and attempt to defend it from an intruder rather than flee. This may partially explain why female kakapo should be more vulnerable to predators, especially stoats and feral cats, than males.

During the breeding season the activity of both sexes is highly localised over a period of several months. The males spend each night displaying at “courts” for about four months, while females are on or near nests for approximately five months. However, females are smaller (*c*. 60% body weight of males), and thus likely to be more vulnerable to predators than males. Male kakapo have killed Cook’s petrels (*Pterodroma cookii*) that ventured on or near their courts at night (DVM pers. obs.), indicating an aggressive nature towards intruders. Likewise, an incubating female kakapo on Codfish Island (Whenua Hou) repeatedly attacked a Cook’s petrel when it approached the cavity in which both were nesting (Higgins 1999). Cook’s petrels have occasionally been found dead in or near kakapo nests on Little Barrier and Codfish Islands, and were considered to have been killed by kakapo (Higgins1999). Henry (cited in Hill & Hill 1987) also commented that female kakapo were fiercely protective of their young, charging his dog savagely when it approached their nests. Therefore, it seems likely that nesting female kakapo would attack a stoat or cat near their nests, rather than fleeing, and as a result were frequently killed during such encounters. This behaviour contrasts with that of bird species that have evolved with predatory mammals and so developed a survival strategy whereby they readily desert their nests.

HABITAT

Kakapo were habitat generalists, having inhabited a range of vegetation types in relation to altitude and climatic zone (Lyall 1852; Hector 1863; Reischek 1884, 1930; Henry 1903; Williams 1956; Higgins 1999; Atkinson & Merton 2006; Butler 2006).

From both subfossil and Maori midden remains kakapo are known to have occurred throughout the three main islands of New Zealand, from the far north of the North Island (35° S) to southern Stewart Island (47° S) (Williams 1956; Dawson 1962; Millener 1981; Holdaway 1989). Kakapo occurred from near sea-level to the subalpine zone (> 1200 m a.s.l.) and in rolling to extremely steep land-forms. Also, it occurred in areas of high rainfall (Milford catchment, > 6000 mm per annum), and those of low to moderate rainfall (parts of Otago, Canterbury and Marlborough, < 800 mm) (Williams 1956; Lyall 1852; Hector 1863; Reischek 1884, 1930; Henry 1903; Gray 1977; Johnson 1976; Millener 1981; Holdaway 1989; Wood 2006). Despite severe winter frost, snow and ice for four to six months each year, some kakapo lived year-round in subalpine habitat in Fiordland (Henry 1903; Gray 1977; Merton 1977a; Westerskov 1981; Morris & Smith 1995). At the other extreme, kakapo withstood high summer temperatures (> 30° C) and dry conditions in parts of Otago, Marlborough, Nelson and northern North Island. On the two more northerly islands to which kakapo were transferred (Little Barrier and Maud Islands), most individuals inhabited the relatively cool, moist and shaded south or south-western slopes (Moorhouse & Powlesland 1991; Merton 1994). Males transferred to islands have tended to establish home ranges on the upper slopes, high plateaus and summit regions, whereas females have generally settled at slightly lower elevations on the mid slopes.

Although kakapo occurred in temperate rainforests from lowland podocarp to upland beech (*Nothofagus* spp.) (Williams 1956; Johnson 1976; Gray 1977; Atkinson & Merton 2006), it was not an exclusively forest-dwelling species. During historic times, kakapo were most frequently associated with grassland habitats (Brunner 1848; Lyall 1852; Haast 1864; Henry 1903; O’Donoghue 1924; Pascoe 1957; Merton 1975; Johnson 1976; Gray 1977; Wood 2006) and ecotones (transition zones between two or more diverse communities, as between forest and tussock grasslands) where they had access to varied food resources available from forest, scrubland, herbfields, tussock grassland and seral associations (Henry 1903; Johnson 1976; Gray 1977; Best 1984; Butler 1989; Higgins 1999). While kakapo formerly occupied lowland parts of Fiordland, those found after 1970 were invariably in the subalpine zone, especially head-basins and steep walls of glaciated valleys at 700 - 1200 m.a.s.l., where their home-ranges included beech forest margins, subalpine scrub, tussock grassland and herbfield communities (Henry 1903; Merton 1977a; Morris & Smith 1995; Atkinson & Merton 2006).

Kakapo tended not to penetrate far into tall forest but lived adjacent in areas of dense and varied pioneer or seral vegetation, such as along the banks of streams, old slip-faces, subalpine terraces, areas of wind-thrown trees, and regenerating avalanche screes (Johnson 1976; Gray

1977; Higgins1999; Atkinson & Merton 2006). Such rich feeding areas were termed "kakapo gardens" by some early writers (Henry 1903).

On Stewart Island, kakapo occupied rolling to hilly peatlands 100 - 400 m.a.s.l. supporting a mosaic of rata/podocarp forest, subalpine *Dacrydium, Halocarpus*, *Lepidothamnus, Olearia* and *Dracophyllum* scrub, and peat-bog communities. Some of these vegetation mosaics were created in the late 1800's and early 1900's as a result of vegetation clearance by miners' activities.

Kakapo transferred from Fiordland and Stewart Island to Little Barrier and Maud Islands quickly adapted to unfamiliar habitat types and food plants (Moorhouse & Powlesland 1991), including exotic pasture grasses and herbs (Gray 1977) and the needles and conelets of *Pinus radiata* (Higgins 1999).

ROOST SITES

Kakapo roost within their home ranges, typically on the ground under dense cover, or in natural cavities, such as caves, hollow tree stumps and logs (Higgins 1999). Occasionally they will roost on a horizontal branch in the forest understorey or canopy with heavy overhead cover. Generally, roosts are on steep, damp, shaded, heavily-vegetated slopes, often with a southerly aspect. However, after wet weather kakapo have occasionally been found roosting in direct sunlight, such as in shrubs, the crown of a tree (Higgins 1999), or stretched out on a rock (Westerskov 1981). Individuals often display a preference for roosting either above or on the ground. Some sites may be used repeatedly or irregularly over many weeks or even years (Higgins 1999). Favoured sites are dark, dry, sheltered from strong winds, and sufficiently large to allow the bird to turn. Some former roost sites in caves and under dry overhangs in Fiordland are today still carpeted with desiccated droppings, even though kakapo died out there many decades ago. There seems no obvious difference between roost sites and roosting habits of males and females. For the first few months after fledging juveniles are unable to climb well, and so generally roost on or near the ground.

Non-breeding kakapo usually roost about an hour before sunrise, and become active about an hour after sunset (Higgins 1999). Similarly, nesting females have often left their nests within about an hour of sunset and, except when food has been limiting, returned before sunrise. Breeding females with one or two month-old nestlings, or without access to abundant food, will often leave the nest to forage in the late afternoon and continue to forage after daylight in the early morning (Higgins 1999). Males involved in courtship display maintain a similar routine as breeding females, with the exception that on dull days courtship activity may sometimes continue well into daylight hours. During roosting, adults and most juveniles adopt a near-horizontal posture with the head and beak resting on the back above one wing.

Groups of up to six individuals were found roosting together during the 19th century (Gould 1865; Henry 1895-1908; Best 1977). These kakapo were likely to have been family parties (i.e. female and juveniles), or groups of juveniles (Higgins 1999). It is rare for adult males and adults of opposite sex (other than on the lek) to roost in close proximity of one another, although two or more adult females have been found occasionally roosting in loose association with one another (DVM pers. obs.).

HOME RANGE

Both sexes are solitary, and generally remain within individual, overlapping home-ranges throughout much of the year. On Stewart Island, home ranges have been determined as being of 15 - 50 ha (Best & Powlesland 1985) or 50 ha for males and 100 ha for females (Shepard 1989), and on Little Barrier Island, of 21 - 38 ha (Moorhouse & Powlesland 1991). Kakapo transferred to Maud Island have occupied ranges up to 50 ha in area, but ranges varied seasonally and also in response to patterning of the vegetation (Trinder 1998; Walsh *et al.* 2006). These various observations of home range size were determined for remnant kakapo populations, probably at lower density than the species would have occurred at in the same habitat types prior to the arrival of mammalian predators.

On Codfish Island, where the population was denser (approx. 1 bird per 30 ha in 2002), Farrimond *et al.* (2006b) recorded mean home ranges of adult females and of newly-fledged juveniles to be approx. 15 ha, using the minimum convex polygon method. Only one home range (an adult female) exceeded 30 ha.

MOVEMENTS

Movement on the ground when travelling between distant sites is often by way of a rapid "jog-like" gait along tracks when these are available (Westerskov 1981; Higgins 1999). A female with nestlings on Stewart Island made two return trips each night from her nest to a food source 1 km away, running at speed throughout each trip (Powlesland *et al.* 1992).

Kakapo spend most of the year within their usual home range (Moorhouse & Powlesland 1991; Powlesland *et al*. 1992). However, during October-January, adult males may leave their home-range to visit a lek or arena (courtship display-ground) to claim and/or maintain their display "courts', known as track-and-bowl systems. Such visits may entail walking a few hundred metres to several kilometres. One radio-tagged male is known to have moved more than 5 km from his home-range to a track-and-bowl system (Best & Powlesland 1985).

Individuals of either sex occasionally walk up to several kilometres from their core home-ranges to sites where they may remain for several days, weeks or even months (Best & Powlesland 1985). Such movements can often be related to the availability of a preferred food, such as a localised and abundant fruit crop. They may also be related to climatic factors; in Fiordland, where home-ranges within the subalpine zone were snow-covered for three or four months in winter, males occasionally descended to snow-free areas (DVM pers. obs.).

Adult females commonly move beyond their core home-ranges during late December-early February, particularly in years when intense booming occurs (Higgins 1999). Why they make such movements is not known, but perhaps it is to assess the location and quality of males prior to mating. Females also make brief visits of one - three nights to leks to mate. The distances travelled by these females varied from a few hundred metres to a few kilometres.

Juveniles on Codfish Island remained within or close by their natal home range until six to ten months of age (males: $\bar{x}$ = 235 ± 44 days, range = 191 – 291 d; females: $\bar{x}$ = 234 ± 31 d, range = 183 – 301 d) (Farrimond 2003). On Stewart Island, one 14 month-old male was recaptured more than 5 km from his natal home-range, and a nine-year-old female was recaptured *c*.3 km from her natal nest. Being confined to relatively small islands, kakapo are now restricted in their post-natal dispersal movements. Juveniles and subadults generally occupy peripheral, and seemingly suboptimal, habitats at lower altitudes than adults. These habitats often include coastal and sea-cliff associations.

FORAGING AND DIET

Although foraging occurs mainly on or near the ground, kakapo are skilled climbers (Westerskov 1981; Higgins 1999), reaching the canopy of 20 - 30 m tall trees via vines, lianes and understorey shrubs, and often move from tree to tree through the canopy. Such arboreal foraging is characterised by periods of silence while the bird is feeding, interspersed by noisy episodes involving much wing flapping as the bird changes position. The wings are used frequently for balance (Westerskov 1981; Higgins 1999) and, as in other parrots, the beak is used extensively when climbing for balance and to assist with hauling themselves forward. Given that females are smaller, lighter and have proportionately longer wings than males (Henry 1903; Shepard & Spitzer 1985), they are, perhaps, better able to reach foods in the canopy, especially on the outermost branches where fruit tends to be most abundant (DVM & R. Buckingham cited in Trewick 1997). Descent to the ground is often by wing-assisted leaping or parachuting for a few metres at a steep (< 45^{o}) downward angle. Foraging is normally interspersed with periods (< 60 minutes) of inactivity (DVM pers. obs.).

Although the kakapo has a facial disc resembling that of an owl, with eyes orientated forward providing it with some degree of binocular vision, apparently its sight is not well developed (Higgins 1999). The sense of smell, however, is believed to be well developed and important in locating food (Best 1977) (see Physiology above). When walking, kakapo adopt a near-horizontal posture bringing the lower rictal bristles into contact with the ground. Sensory perception may be of importance not only when traversing unfamiliar terrain in the dark, but also when feeding at night on certain foods, such as *Aciphylla* spp. which have long, rigid, leaves with spiny tips.

The kakapo is entirely herbivorous. Observations by 19th century and early 20th century observers well-acquainted with the bird (Haast 1861, 1864; Potts 1873; Henry 1895-1908; Best 1908; Pascoe 1957) recorded that kakapo fed on leaves, twigs, bark, nectar, fruit, seeds, fern pinnae, rhizomes and fungi. However, Von Hugel (1875) reported finding remains of lizards in the crop of a male. This is the only record of carnivory in kakapo, and in light of more recent findings is clearly erroneous. Field observations of kakapo (1960-present) by Wildlife Service and Department of Conservation staff, and others in Fiordland, on Stewart Island, and of transferred island populations, as well as dietary studies by Gray (1977), Best (1984), Trewick (1996), and Wilson *et al*. (2006) confirm that the kakapo is a vegetarian. With the exception of occasional seeds from a few species of fruit plants and tussocks, only finely ground material is ingested.

The kakapo's method of feeding is unusual. The short, stout, powerful beak and short, broad, thick tongue are adapted for cutting, crushing and grinding to extract juices from fibrous plant tissues (McCann 1963; Kirk *et al*. 1993). The lower mandible and tongue form an efficient grinder against the finely-grooved upper mandible and palate (Henry 1903; Gray 1977; see also Butler 2006).

The kakapo is a selective feeder, not only in its seasonal exploitation of food species and parts of plants, but also in its selection of individual plants of a species. An individual tree, shrub or tussock is often selected to the exclusion of neighbouring individuals of the same species. Best (1984) found on Stewart Island that kakapo feeding sign was most evident on herbs, ferns and shrubs, especially on developing and young growth (buds and leaves), and subterranean portions (rhizomes, bulbs and roots). Their versatile feeding activities, from the grubbing of rhizomes to the eating of flowers and fruit in the canopy, enable kakapo to utilise a wide variety of plant foods, some of which are available for only short periods each year or occur in some years but not others.

Features of the kakapo's alimentary tract are typical of parrots, though vitelline diverticulum and caeca are absent. In view of the species' bulky and fibrous diet a more muscular gizzard might be expected. The limited muscular development of the gizzard suggests that the kakapo relies on its specialised tongue and palate, and vigorous chewing to break coarse plant material into small fragments suitable for digestion (Kirk *et al*. 1993). Much fibrous material is ejected in the form of characteristic kidney-shaped, tightly compressed pellets known as "chews", which may remain attached to the plant, but more often litter the ground beneath (Williams 1956; Best 1984). These soon bleach and may remain intact for many months. Fibrous foliage is chewed while attached to the plant, grass and tussock blades being consumed from the tip downwards. Because of their terminal sharp spines, leaves of *Aciphylla* species are browsed at the mid-blade. The tillers of snow tussock (*Chionochloa* spp.) and robust leafy sedges (*Gahnia*) are wrenched or bitten from plants and the basal portions eaten. Grass and tussock seed is obtained by running the spikelet through the partially open beak with an upward scythe-like motion (Gray 1977; see Butler 2006). Berries and fruit, including most seeds, are pulped in the beak, but a few hard seeds are swallowed whole.

As in other parrots, kakapo use their feet to hold food items (Westerskov 1981), but rarely use them to lift items to their beaks (Higgins 1999). The beak is used extensively as a grubber to excavate subterranean foods, including roots, tubers, rhizomes and stolons (Best 1984). Grubbing for fern rhizomes can leave a fist-sized depression in the ground, and many square metres of *Lycopodium* or moss may be grubbed intensively in a night (Higgins 1999). The beak is also used to remove bark and so gain access to the underlying soft, nutritious phloem tissue and sap of trees such as rata (*Metrosideros* spp.), totara (*Podocarpus* spp.), manuka (*Leptospermum scoparium*) and *Pseudopanax* species (Higgins 1999).

For a detailed appraisal of kakapo food species in Fiordland and Maud Island see Gray (1977) (summarised in Butler 2006), of Stewart Island see Best (1984), and of Little Barrier Island see Trewick (1996). Plant parts most sought after were subterranean storage organs, meristematic tissue and new growth, and reproductive tissue, thus the more nutritious and digestible portions. Feeding sign tended to be concentrated on drier, elevated sites, such as hillocks and ridge crests. At such sites the low woody, open canopy vegetation often graded through to areas of dispersed cover, providing a mosaic of food species and sheltered feeding sites.

Analysis of plant cuticles from *c*.400 faecal samples collected on Stewart Island, mainly during 1983-85 (Wilson *et al*. 2006), revealed marked seasonal and annual variations in diet. The following foods were eaten throughout the year; *Blechnum* spp. rhizomes and fronds (2.5 - 39.7% of diet), *Cyathodes juniperina* fruit (0.5 - 8.8%), *Dracophyllum longifolium* leaf bases (0.1 - 11.2%), *Gahnia procera* tiller bases (2.7 - 18.3%), *Lycopodium* spp. rhizomes (0.4 - 33.7%), *Leptospermum scoparium* leaves (0.4 - 17.8%) and *Olearia colensoi* leaves (0.1 - 11.2%). However, when available, the following foods were preferentially eaten, often to the exclusion of the previously listed staple foods; fruit of *Halocarpus biformis* (up to 77.6% of diet in February during the 1985 breeding season on Stewart Island) and *Dacrydium cupressinum* (1981 breeding season on Stewart Island, 1992, 1997 and 2002 breeding seasons on Codfish Island), seeds of *Leptospermum scoparium* (1999 breeding season on Pearl Island), fruit of *Coprosma* spp., kernels of miro (*Prumnopitys ferruginea*) endocarps (an important winter food), reproductive fronds of various ferns, and nectar of *Meterosideros umbellata* (Henry 1903; DVM pers. obs.). In spring and summer, when new growth was available, a large proportion of the diet was leaf material. However, if available at this time of year, immature pollen cones, fruit and seeds were eaten in preference to leaf material. An assessment of the nutritional quality of kakapo diet on Stewart Island indicated that the non-breeding and breeding diets contained about 37 g and 59 g of crude protein per kg of dry matter respectively, and 38 g and 23 g of lipid per kg of dry matter respectively, which would be barely adequate for adult survival or the rearing nestlings respectively (James *et al*. 1991).

Wilson *et al*. (2006), using cuticle analysis data, analysed kakapo diets from Stewart Island and Codfish Island during 1977-99. They found that in December-March of breeding years (*n* = 21 females, 27 males), females were significantly more likely than males to have eaten podocarp (trees of Family Podocarpaceae) fruit, *Dracophyllum* leaves, *Podocarpus hallii* leaves, and *Meterosideros umbellata* leaves. Males were more likely to have eaten *Lycopodium* rhizomes and monocotyledons. In the same period in non-breeding years (*n* = 29 female, 43 male), females were more likely than males to have eaten podocarp leaves and fruit, and males to have eaten *Leptospermum scoparium* seeds, and rhizomes of *Lycopodium* spp. and *Blechnum* spp. These results probably reflect differences in foraging behaviour between the sexes, particularly in breeding years, when females gather food mainly in forest habitats for their nestlings, while males feed mainly in tussock and subalpine scrub in the vicinity of their track-and-bowl systems (Merton *et al*. 1984).

Comparing the diets in breeding and non-breeding years for the period December to April, female kakapo (21 adults in breeding years, 40 of all ages in non-breeding years) were more likely to have eaten podocarp fruit and *Blechnum* fronds, and less likely to have eaten leaves of *Dracophyllum longifolium* and *Olearia colensoi* (Wilson *et al*. 2006). In comparison, males of all ages (32 in breeding years, 50 in non-breeding years) were more likely to have eaten podocarp fruit, and less likely to have eaten *Dracophyllum longifolium* leaves and *Lycopodium* spp. rhizomes in breeding years compared with non-breeding years. Also, females were more likely to have eaten all fruits combined in May-July (chick-rearing period) of breeding years (*n* = 19) than in non-breeding years (*n* = 8) (Wilson *et al*. 2006).

Little is known of the natural diet of nestlings and fledglings. One female rearing two nestlings on Stewart Island in 1981 fed heavily on ripe rimu (*Dacrydium cupressinum*) fruit throughout the nestling phase (Powlesland *et al*. 1992). Likewise, Trewick (1996), from an analysis of five droppings collected from nests containing nestlings in April 1992 from Codfish Island, found that they contained the remains of only fruit and leaves of rimu. Interestingly, he found that as well as supplementary foods and *Blechnum* fern fronds, another important component of nestling diet on Little Barrier Island in 1990/91 was kauri (*Agathis australis*), probably indicating that kauri seeds were being fed to nestlings, even though this food was infrequent in the diet of adults.

The diet of three nestlings in a nest in a pine (*Pinus radiata*) plantation on Maud Island in 1998 comprised a high proportion of pine needles (> 70% of cuticles identified from droppings) in addition to food supplements (N. Parker *unpubl. report*). What important nutrients for chick health are available in pine needles is unknown.

During the 1997 breeding season on Codfish Island, females rearing young fed heavily on *Dracophyllum longifolium* leaf-bases in addition to walnuts and almonds provided *ad. lib.* as food supplements (Higgins 1999). In contrast, in 2002 when ripe rimu fruit was readily available on Codfish Island, kakapo nestlings appeared to be fed a diet almost exclusively of such fruit (Cottam *et al*. 2006). Each fruit, consisting of a seed and fleshy aril, weighed *c*.0.1 g. After foraging for 113 minutes on 5 April 2002, one female fed her two 6-week old nestlings 90 g of food each, or *c*.900 rimu fruit. Thus, she must have eaten *c*.16 fruit per minute during her absence from the nest. The gross nutrient composition of rimu fruit (seed and aril) in 2002 consisted of 34.0% dry matter, 95.8% organic matter, and on a dry matter basis 7.2% crude protein, 14.9% lipid, and 77.7% carbohydrate (Cottam *et al*. 2006). The nutrient composition of crop samples from nestlings 27 and 35 days of age whose mothers were not taking food supplements during the 2002 breeding season were similar to those of entire fruit (94.9% organic matter, 7.6 - 9.2% crude protein, 7.7 - 7.9% total fatty acids, and 78.1 - 79.5% carbohydrate). These results suggest that the nestlings were fed almost solely on either entire ripe rimu fruit or the ripe aril component of it (Cottam *et al*. 2006).

AGONISTIC BEHAVIOUR

Both sexes are usually solitary, each bird maintaining a distance of several hundreds of metres from its neighbours. Henry (1903, 1895-1908) and Pascoe (1957) found kakapo to be highly unsociable, and that if confined together one would eventually kill the other. Aggressive behaviour between males on the lek is characteristic of the pre-booming period, and is sustained over many nights. Agonistic activities include vigorous chasing, aggressive screeching and fighting (Westerskov 1981; Higgins 1999). Fights between males for possession of particular courts have resulted in injuries and deaths (Henry 1903); at least two males were killed and another severely injured in such fights on Little Barrier Island (Clout & Merton 1998). Screeching, chasing and fighting by males on the lek continue at a reduced level throughout the booming period (Merton *et al*. 1984; Powlesland *et al*. 1992). The loud, harsh "skraark" call given infrequently at night apparently serves to advertise a bird's location. Thus, vocal rather than visual displays would seem to be the main tactic for this solitary, nocturnal species to maintain individual distance. Nevertheless, kakapo do have a range of visual displays, most of which have been observed only being given by a few males displaying on their track-and-bowl systems in Fiordland (Morris & Smith 1995; Higgins 1999). A bird performing a threat display faces its opponent, raises and holds its wings over its back until almost touching, raises its head and neck feathers with neck outstretched and beak partly open, and makes a low drawn-out growling call. In response, the defensive bird stands upright facing its opponent, and has one foot raised ready to strike downwards. Harper & Joice (2006) describe raising of crest feathers as a threat or dominance display at a feeding site.

VOICE

No specific studies of kakapo vocalisations have been made. The kakapo has a varied repertoire of calls, which includes a mechanical sound, and a range of calls associated with courtship activities (Williams 1956; Merton *et al*. 1984; Powlesland *et al*. 1992; Morris & Smith 1995). In keeping with their secretive behaviour, kakapo seldom call, except during the courtship season when males occupy track-and-bowl systems and are highly vocal.

Outside the breeding season birds are relatively silent, except when in relatively close proximity to other kakapo. At such times, brief isolated calls may be heard, such as the characteristic "skraark" call (see 'Courtship' below for a description of this call). Other calls include pig-like grunts and squeals, duck-like "warks", and donkey-like braying. An additional range of vocalisations, including hisses and screeches, screech-crowing, humming and beak-clicking (a mechanical sound), are known from only Fiordland males (Higgins 1999). Vocal activity may be induced at night or day by brief loud sounds, such as an avalanche, thunder, a rifle shot or an animal calling nearby. They may also be induced to call by playing taped kakapo calls.

Until recently females were known only to make a "hoarse cough" (Henry, 1903). However, a hand-raised female that was kept in captivity for five years (Climo & Ballance 1997) displayed a similar vocal repertoire to males, except that she did not give boom or ching calls (see 'Courtship' below for descriptions of these calls). Females and juveniles often produce a series of long, drawn out, vibrant, croak-like distress calls when handled, whereas males are usually silent.

BREEDING BIOLOGY

Courtship

Track-and-bowl

The kakapo has a lek mating system (Merton *et al*. 1984), with adult males congregating in loose association at traditional sites known as "arenas" where they call and display competitively to attract females for mating. Lek breeding is not known in any other parrot or flightless bird (Merton *et al*. 1984). Typically, arenas occur on relatively open ridge tops above the bush-line at 400 - 1200 m.a.s.l (Henry 1903; Merton *et al*. 1984). Each male defends and maintains a "court", known as a "track-and-bowl system", where he calls and displays. Each system consists of one or more shallow bowls (*c*.600 mm diameter x *c*.100 mm deep) linked by tracks (*c*.500 mm wide) that are pruned of vegetation. Systems having more than one bowl generally have one that is relatively exposed and the remainder sheltered from the prevailing wind by vegetation or rocks.

A bowl is formed by a male standing at the centre of his selected site, biting off vegetation within reach, and grubbing up beakfuls of soil which are thrown away with a sideways flick of the head. In addition, soil is removed from the bowl by the bird lying across it and making raking movements with a foot (Powlesland *et al*. 1992). Any branches and roots too big for the bird to bite through are removed by being chewed over many nights, and even successive seasons. At the height of the breeding season the soil of frequently used bowls is grubbed to a fine tilth, and may be lower near the circumference of the bowl and well consolidated at the centre (Henry 1903). This is because males stand for much of the night in the centre of the bowl, but occasionally grub soil from just inside the edge and tossed it out of the bowl.

Track-and-bowl systems have no connection with food or nest sites, but appear to be located for their acoustic properties (Merton *et al*. 1984). Where topography allows, bowls are excavated against the base of an overhanging bank, rock face or tree trunk, which acts as a sound reflector. Usually at least one bowl is at a commanding position, such as on a ridge crest overlooking a valley. Track-and-bowl systems may be within a male's core home-range, but more often are situated up to several kilometres away. A system may extend for 50 m or more along a ridge-crest, or occupy an area 10 - 20 m in diameter on a hilltop. Distances between systems of neighbouring males may vary from 15 to several 100 metres, with groups of up to 50 systems extending over several km^2 (Merton *et al*. 1984). Each male occupies and defends a particular system from one breeding season to the next. However, occasionally a male on Stewart Island left a system and occupied an abandoned one or developed a new one. The term "exploded lek" describes the spatial distribution of male courts of kakapo, where displaying males are within hearing but usually not in sight of each other (Gilliard 1963, 1969).

The marked variation in distance between occupied systems in Fiordland and on Stewart Island was probably not just due to topography, but reflects the relict nature of the populations as a result of predation (Merton *et al*. 1984; Powlesland *et al*. 1992). Even so, a few males on Stewart Island persisted at isolated systems where they could not hear other males booming, rather than moving to be nearer other males.

Calls

Aggressive "skraarking" is frequently heard at arenas during the breeding season (Merton *et al*. 1984; Powlesland *et al*. 1992). Skraaking birds stand erect and may emit a single skraark or several in quick succession. Skraark calls vary markedly in intensity, from a few short, soft calls to loud drawn-out, braying. Vigorous skraarking often occurs after a chase or fight between two males, as though the victor was vocally proclaiming or reaffirming ownership of his court.

The most frequently heard call during the courtship season is "booming", a low-frequency (< 100 Hz), non-directional, resonant call (Higgins 1999), which under ideal conditions can be heard at distances of up to 5 km (Merton *et al*. 1984). Standing in or near a bowl, the male progressively lowers his head and inflates his thoracic region, simultaneously producing three - four quiet measured grunts on a descending scale at *c*.2 sec intervals (Fig. 4). At maximum thoracic inflation the grunts become soft booms which increase in volume so that maximum volume is reached after 6-8 booms. The loud booms of *c*.1 sec duration are repeated 15 - 20 times at *c*.2 sec intervals, after which the volume gradually decreases during a further 10-20 booms. Except at close quarters (< 50 m), only the loud booms are heard. During booming, the head is held low against the chest and is partially concealed in chest feathers (Fig. 4). Rhythmic muscular contractions are apparent throughout the body, particularly in the lower thorax, causing carpal flexures of the wings to flick outwards immediately after each contraction. The wing tips, which are at first crossed over the tail coverts, droop lower with each successive boom, ending up beneath the tail. Following a booming sequence the bird stands alert for 20 - 30 seconds before repeating the sequence (Merton *et al*. 1984).

A local dialect of booming was evident in Sinbad Gully, Milford Sound, Fiordland (Higgins 1999). Males there consistently produced a two-syllable boom in contrast to the single-syllable boom produced by Stewart Island males. Fiordland birds recorded in the 1970s boomed more slowly (*c*.2 sec. intervals) and with greater resonance than Stewart Island males (1.0 - 1.5 sec. intervals) (Higgins 1999). The fully inflated airsacs of booming males do not prevent them making vigorous movements; booming males often made quick turns of up to 180°, and one ran 3 m from one bowl to another while maintaining his calling sequence with only a brief pause (Powlesland *et al*. 1992).

Two four-year-old males were heard attempting to boom late in a booming season on Little Barrier Island. Their calls were hardly recognisable as booming, being significantly higher in pitch than those of adult males, phrases were of shorter duration, and elements were delivered at a more rapid tempo of *c*.0.5 sec intervals (Higgins 1999).

Booming usually begins about an hour after dark and ceases about an hour before first light, i.e. six - eight hours per night. However, individuals have boomed for

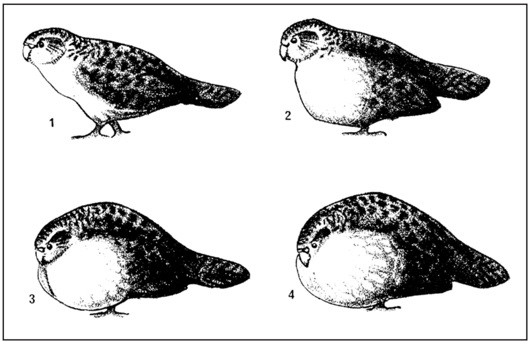

Figure 4 Postures of male kakapo during booming. 1. normal stance; 2. alert static pose between booming sequences; 3. commencement of booming – inflation of thorax while giving preliminary booms; 4. maximum thoracic inflation during loud booming (from Figure 4, Merton *et al*. 1984).

up to 17 hours during foggy weather (Merton 1985). Neighbouring males frequently duet, but whether this is by chance or is deliberate is unknown. The combined booming of numerous males sounded like distant thunder to early naturalists (Buller 1877; Henry 1895-1908). In years when nesting occurs, males typically boom nightly for more than four months (late November - early April) whatever the weather, but in years when nesting does not occur, booming typically continues for just two - three months (January-February) (Merton *et al*. 1984; Powlesland *et al*. 1992).

Booming undoubtedly serves to advertise a male's location, and possibly stimulates and synchronises sexual activity in both males and females. For a call to be as widely heard as possible, it should be of intermediate frequency (1 - 4 kHz), especially if the signaller is on the ground, and it should have repetitions of pulses at relatively low rates (Wiley & Richards 1978) – a fairly accurate description of booming. While such low frequency sounds can be heard over much greater distances through forest than high frequency sounds (Wiley & Richards 1978), they are relatively non-directional. In contrast, the "ching" call, also given by male kakapo in the breeding season, is highly directional. Chings are higher pitched (2 - 5 kHz), metallic and nasal in quality, and are *c*.1 sec duration, and repeated at *c*.1 sec intervals (Higgins 1999). Chinging birds stand erect with mandibles wide open (Powlesland *et al*. 1992). Chings are given in bouts of 20 to 50, and bouts of chings are often interspersed between bouts of booms. A male on Stewart Island gave 185 bouts of chings and 359 bouts of booms (1:1.94) in a single night (Powlesland *et al*. 1992). Under ideal conditions, a chinging male can be heard up to *c*.1 km away (DVM pers. obs.). This directional call is believed to enable females that are seeking mates to pinpoint a male's location.

Males in Fiordland have also been heard giving low amplitude "humming" and "beak-clicking" sounds at their track-and-bowl systems (Merton *et al*. 1984; Morris & Smith 1995). The former is audible within 3 - 4 m of a bird. The latter is a mechanical sound made by drawing the lower mandible across the tip of the upper mandible. Beak-clicking may be repeated every 5 - 10 seconds and interspersed with humming during visual courtship displays. This combination may be maintained for many minutes. The significance of each sound is not known.

A sustained "screech-crowing" call interspersed with wing flapping was made by a male from a bowl in Fiordland (Merton *et al*. 1984). In response to a brief high-frequency radio sound from a nearby hide, the bird screeched loudly, then vigorously and noisily flapped its wings, then immediately repeated this sequence 13 times in succession. The calls and associated wing flapping continued for 75 seconds, and were reminiscent of the repeated crowing of a rooster (*Gallus domesticus*).

Displacement activities of males at track-and-bowl systems included mock-feeding and grubbing, pulling at roots or other vegetation, carrying items in the beak, beak whetting (in which males wipe the sides of their beaks on the ground, tree trunks or rocks), and biting or tossing twigs or leaves while raising or flapping the wings (Higgins 1999). Such displacement activities are typical of lekking species (Armstrong 1947).

Timing and extent

The proportion of adult males occupying track-and-bowl systems, the extent to which they visit them on a nightly basis, and how long they call each night varies markedly from year to year (Merton *et al*. 1984; Powlesland *et al*. 1992; Eason *et al*. 2006). Male occupancy of track-and-bowl systems on Little Barrier Island (1991 - 1998) and Codfish Island (1992 - 2002) varied annually from 5 - 10% to 100%, and typically there was little occupancy in a year following nesting (Eason *et al*. 2006). On Stewart Island in a breeding year, males arrived at their track-and-bowl systems between early November and early January, and dispersed from them during late March - early April (Powlesland *et al*. 1992). Some were booming by mid-December and continued to do so through to April. They remained in the vicinity of their track-and-bowl systems for some weeks after booming ceased (Higgins 1999). In contrast, in non-breeding years, few males occupied their bowls, and those that did were mainly those whose bowls were within their non-breeding season home ranges or close by (Powlesland *et al*. 1992). Track-and-bowl attendance in such years was intermittent and, although males engaged in maintenance activities, such as trimming vegetation and grubbing, little or no booming was heard.

In the 1980s it seemed that availability of nutrient-rich foods was important in initiating breeding in kakapo. To test this, supplementary foods were provided to free-living kakapo on Little Barrier Island from 1989, and on other islands in later years (Powlesland & Lloyd 1994; Elliott *et al*. 2001). Kakapo did breed on Little Barrier Island for the first time in seven years in the summer after supplementary food was introduced (Powlesland & Lloyd 1994). Body weights of seven males on Little Barrier Island increased by 42% and of five females by 36% after the provision of supplementary foods (Powlesland & Lloyd 1994), whereas other females not receiving supplementary foods gained approximately 15% in body weight (Clout *et al*. 2002). However, it is now evident that while supplementary foods improve nesting success in years when kakapo breed, it does not itself increase the frequency of breeding (Elliott *et al*. 2001; Harper *et al*. 2006).

Mating

Henry (1895 - 1908) observed that kakapo did not breed every year in Fiordland. He noted that in some years the birds accumulated large fat deposits in autumn, and found that the development of the booming sacs in males started several months before booming and up to six months before mating. Henry (1903) claimed that breeding in Fiordland occurred only in years when booming was heard, and that booming occurred at about two year intervals. However, other observers of kakapo in the same region and elsewhere found that sometimes five years elapsed between breeding seasons (Reischek 1952; Williams 1956). Furthermore, Henry considered that there was unanimity throughout a population: in those years when booming occurred all adult females bred, and no breeding occurred in the intervening years. However, observations on Stewart, Little Barrier and Codfish Islands since 1981 have shown that the intensity of booming and breeding is variable from year to year (Powlesland *et al*. 1992; Clout & Merton 1998; Eason *et al*. 2006). The proportion of females that mated and laid clutches on Little Barrier Island (Elliott *et al*. 2006) and Codfish Island (Fig. 5) has varied between breeding years. Since males have boomed at their systems without any females visiting for mating it seems that males attain breeding condition more readily than females (Clout & Merton 1998).

Breeding of geographically separated populations has not always been synchronous (Higgins 1999). Breeding occurs in synchrony with the abundant fruiting or seeding of certain food species at two - seven year intervals (Merton *et al*. 1984; Powlesland *et al*. 1992). Only in years when more than 90% of males attended track-and-bowl systems, or males started booming before 5 December has mating occurred (Eason *et al*. 2006). Nesting has been recorded in 12 of the 29 years since 1977 when female kakapo were rediscovered on Stewart Island (Fig. 2).

Kakapo mating has never been observed, but the behaviour of some males in Fiordland towards people suggests that it is preceded by an elaborate courtship "dance" by the male (Merton *et al*. 1998; Morris & Smith 1995). In response to surrogate females, males at Fiordland track-and-bowl systems have indulged in elaborate, ritualised displays and posturing. This includes side-to-side rocking movements, walking backwards while slowly raising and lowering fully extended wings like a basking butterfly, vigorous wing-flapping, and a variety of calls, including a mechanical bill-clicking sound. Attempted copulation with objects and people that were in or near a male's bowl was recorded on a number of occasions in Fiordland (Merton *et al*. 1984; Morris & Smith 1995; Higgins 1999). During such copulation attempts, the male crouched with his head held high, tail depressed and partially-open wings held loosely by his sides drooping almost to ground level. He maintained a rhythmic motion involving the swaying of his body from side to side in synchrony with pronounced alternate swinging of half-open wings and rapid, audible panting through partly-open beak. The duration of attempted copulation with surrogates was 2 - 14 minutes. Male copulatory behaviour and its duration are similar to that described of the kaka (Jackson 1971).

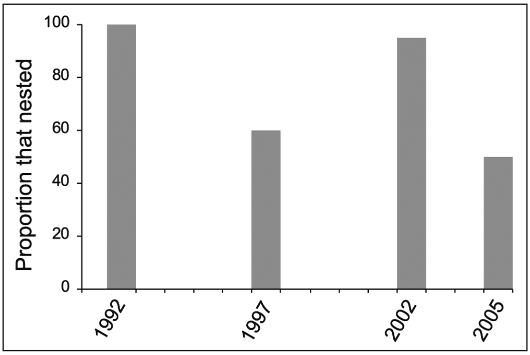

Figure 5 Proportion of adult female kakapo on Codfish Island that bred during each breeding year, 1992-2005

Characteristic sign is left where kakapo have mated (Merton *et al*. 1984; Powlesland *et al*. 1992; Eason *et al*. 2006). Ten to 50 down feathers and often a few contour feathers remain trampled into litter or soil in an area of <1 m^2, generally at or within 5 m of a track-and-bowl system.

Mating occurs mainly between early January and early March, with the peak period of mating on Codfish and Pearl Islands (Fig. 1) occurring during 15 January - 4 February (Eason *et al*. 2006). No pair bond is formed, and females visit an arena solely for mating. They may spend just a few hours and mate with only one male, or stay for up to five nights and mate with two or more males (DVM pers. obs.). In keeping with their lek-mating behaviour, male kakapo take no part in incubation, rearing of young, or feeding of nesting females.

As would be expected in a lek species, male kakapo vary markedly in their mating success. Eason *et al*. (2006) found that just five of 33 (15%) males fertilised 76% of the 33 clutches containing fertile eggs produced during 1990-2002. Factor(s) influencing female mating preference are unknown.

Nests

Of 67 nests found since 1980, each has been within or nearby (one instance of a nest being < 500 m beyond) the female's home range. Fifty-seven were in forest and 10 in open scrub/tussock habitats. Three of five nests (60%) on Stewart Island were in open scrub/tussock habitats, whereas seven of 62 nests (11%) on offshore islands were in this habitat type. Since scrub/tussock habitats are poorly represented on the islands to which kakapo have been relocated and nested on, this result may reflect the relative scarcity of this habitat type rather than a preference for forest as a nesting habitat.

Nests are formed in natural cavities at or below ground level, such as small caves or holes, under boulders, or in standing or fallen hollow tree-stumps. Of 67 nests, 40 (60%) were in caves or holes, 18 (27%) in standing tree-stumps, five (7%) under tussock or other dense ground vegetation, and four (6%) in fallen tree-trunks.

Each nest comprised a shallow bowl-shaped depression 250 - 300 mm in diameter and 20 - 50 mm deep (Powlesland *et al*. 1992). Cavity diameter ranged from *c*.400 mm to more than 2 m (mean *c*.500 mm), and height from 350 mm to more than 1 m (mean *c*.450 mm). The distance from nest entrance to nest bowl ranged from *c*.200 mm to over 4 m (mean *c*.500 mm). The contents of 23 (34%) nests were visible from 2 m away, presumably making eggs and chicks particularly vulnerable to predation by rats (*Rattus* spp.) and weka (Elliott *et al*. 2002).

An existing cavity is used for a nest site. The nest bowl is developed from materials on site, such as dry rotted wood, bark and soil. The female grubs litter in the cavity to a depth of *c*.100 mm, and may incorporate material from the walls and roof of the chamber. Any large pieces of soil, peat and rotten wood are bitten or chewed to form a deep, well aerated dry tilth on which she develops a nest-bowl measuring 250 - 300 mm in diameter and 20 - 50 mm deep. Every few hours during incubation and nestling-rearing stages, the female grubs deeply into and turns the substrate of the nest bowl (Higgins 1999).

Three instances are known of nest sites being reused, in each case by the same female. Two females on Stewart Island that nested in successive breeding seasons used different sites, one 500 m and the other 1500 m from their previous nest-site (Powlesland *et al*. 1992). Nests may be situated close by or several kilometres from the nearest arena. For example, two nests on Stewart Island in 1981 were 600 m and 1200 m from an arena (Powlesland *et al*. 1992). Female home-ranges, and thus nests, are generally at a lower altitude than male home-ranges and arenas. Of 67 nests found on Stewart (max. altitude in kakapo area, 637 m.a.s.l.), Codfish (190 m.a.s.l.), Maud (400 m.a.s.l.) and Little Barrier Islands (722 m.a.s.l.) since 1980, all were between 150 - 400 m.a.s.l (Higgins 1999). Unlike male arenas, nests are invariably associated with prime feeding sites, typically involving a masting plant species (Kelly 1994).

Eggs

Egg-laying occurs mainly in January-February (austral summer), and with occasional clutches being laid in March (Reischek 1884; Williams 1956; Higgins 1999). The median date of egg-laying on Little Barrier was 24 January, and on Codfish and Pearl Islands combined was 7 February (Eason *et al*. 2006). The first egg of a clutch is generally laid *c*. 10 days after copulation (range = 3 – 20 d), and eggs are laid at *c*.3 day intervals (range = 1 – 7 d) (Eason *et al*. 2006). Females that lay early in the breeding season are capable of laying a replacement clutch if the first is lost or removed early in incubation. Two females have laid in successive years, having bred unsuccessfully in the first (Elliott *et al*. 2001).

Kakapo eggs are white and ovate with a fine granular surface (Merton 1985). Combining 122 eggs from Little Barrier, Codfish, Pearl and Maud Island nests during 1990 - 2002, mean length was 50.7 ± *se* 0.2 mm (range = 46.3 - 55.8 mm), mean breadth was 38.3 ± *se* 0.1 mm (range = 35.0 - 41.1 mm), and mean weight was 40.5 ± *se* 0.3 g (range = 32.4 - 48.4 g) respectively (Eason *et al*. 2006). The mean weight of an infertile 4-egg kakapo clutch after 6 - 7 weeks of incubation on Stewart Island in March 1985 was 32.7 g (range = 30.9 - 33.7) (Body & Powlesland 1990).

Kakapo eggs are small relative to the body-weight of the female; 3.2% of a 1.3 kg female's body weight (Eason *et al*. 2006). By comparison, the fresh egg weights of six Cacatuidae species are 3.7 - 5.1% of female body weight (Saunders 1974; Saunders & Smith 1981; Higgins 1999).

Clutch size

Early observers noted that kakapo clutches were mainly of two to four eggs, and rarely five (Reischek 1884; Henry 1903; Williams 1956). Mean clutch size for 67 clutches found during 1981 - 2005 on Stewart, Little Barrier, Maud, Pearl and Codfish Islands was 2.5 eggs; nine 1-egg clutches, 19 2-egg clutches, 36 3-egg clutches, and three 4-egg clutches (DVM unpubl. data; Eason *et al.* 2006).

Incubation

Incubation lasts an average of 30 days (range = 28 – 31 d) (Eason *et al*. 2006), is initially intermittent, and starts with the first egg laid. The behaviour of an incubating female on Stewart Island was assessed by radio-tracking (Powlesland *et al*. 1992). Each night she left the nest to feed, on 11 occasions leaving 1 - 2 hours after sunset, and on three occasions at about midnight. Her time away from the nest averaged 108 min ($n = 14$, range = 60 - 165 min).

On Codfish Island, the behaviour of incubating females has been monitored by remote, infra-red video systems. Prior to completion of the clutch, females usually left the nest nightly, often for up to three hours at a time. Subsequently, females usually left the nest for less than 90 minutes each night until hatching (Eason *et al*. 2006). During the first 10 - 14 days, females generally left their

Table 2 The mean number (± *s.d.*) (*n*, range) of egg rolls per hour, total time (minutes) spent away from the nest per night, maximum time spent away from the nest per trip by incubating female kakapo that fed on food supplements and those that did not, Codfish Island, 1997.

	Females that	
	Fed on supplements	**Did not feed on supplements**
Egg rolls per hour		
1st 2 weeks	2.14 ± 0.68 (19, 1.08-3.15)	1.45 ± 0.52 (9, 0.78-2.08)
2nd 2 weeks	2.00 ± 0.55 (69, 0.91-2.95)	1.66 ± 0.82 (21, 0.25-3.13)
Total time away		
1st 2 weeks	57 ± 41 (19, 0-144)	207 ± 138 (9, 0-440)
2nd 2 weeks	74 ± 62 (70, 0-304)	229 ± 262 (22, 0-913)
Maximum time away		
1st 2 weeks	50 ± 38 (19, 0-109)	174 ± 128 (9, 0-440)
2nd 2 weeks	67 ± 56 (70, 0-304)	176 ± 205 (21, 0-727)

nests every second or third night to feed, but during the second two weeks they normally left to forage each night. However, when food was not readily available during the first fortnight, females left their nests nightly, occasionally departing before dark and returning after first light. The impact of such food shortages on female incubation attentiveness was most evident during 1997 when the behaviour of females that fed on food supplements was compared to those that did not (Table 2). Females with an adequate food supply (supplementary food) were absent from their nests about one third of the duration of females that relied on natural foods. A similar result was also evident when the mean maximum time off the nest per trip was compared between females eating food supplements and those that did not (Table 2).

Female kakapo roll their eggs, an activity essential to the normal development of embryos, 1.45 to 2.14 times per hour (Table 2). There was no significant difference in the mean egg-rolling rates of the first and second fortnights of incubation for females that fed on supplements, or between the two periods for females that did not feed on supplements. However, the difference in mean egg-rolling rates between the two classes of females for the first fortnight (*t*-test = 2.97, *df* = 27, $P < 0.01$), and second fortnight (*t*-test = 1.79, *df* = 89, $P < 0.05$) were significant.

The time females were absent from their clutches in 1997 on Codfish Island differed significantly depending on whether they fed on food supplements or not (Table 2). This was the case whether total time away per night in the first fortnight of incubation (*t*-test = 3.19, *d.f.* = 27, $P < 0.01$) or second fortnight was considered (*t*-test = 2.75, *d.f.* = 91, $P < 0.01$), or maximum time away per trip in the first fortnight (*t*-test = 2.85, *d.f.* = 27, $P < 0.01$) or second fortnight (*t*-test = 2.41, *d.f.* = 90, $P < 0.05$). The results presented in Table 2 were from four females taking supplements and two that did not. The latter had three fertile eggs of which two hatched, but neither nestlings survived, possibly because of the chilling they endured as embryos.

Nestling rearing

Hatching occurs during late February to early April. Chicks generally hatch at intervals corresponding to the egg-laying interval, but occasionally eggs laid three days apart hatch at one or two day intervals (Eason *et al*. 2006). For example, the hatching interval between the eggs of two 2-egg clutches under video surveillance on Codfish Island in 1997 was 10 h 57 min, and 38 h 35 min.

Although females were observed chewing fragments of shell from hatched eggs, they made no attempt to carry fragments from the nest. Within two - three days, all fragments had become very small as a result of being chewed and/or broken under the female's feet. They became incorporated into the nest substrate by the female's frequent grubbing of the nest floor (Higgins 1999).

Nestling kakapo weigh *c*. 28 - 35 g, and are blind and helpless at hatching (Higgins 1999; Farrrimond *et al.* 2006a). They (and fledglings) often sleep lying on their ventral surface or on their sides with their necks and legs outstretched. Rapid growth and weight gain generally occur from three to eight weeks of age (Farrimond *et al.* 2006a), after which growth almost plateaus (Eason *et al*. 2006; Fig 7). Provided food is not limiting, weight may then continue to increase at a modest rate to a maximum at around 14 - 16 weeks of age. Sibley (1994) presented growth curves for three nestlings that were partially hand-raised in 1992. Mean weights of male and female nestlings begin to diverge when they are about three weeks old, and this difference becomes most marked between fledging and independence (Eason *et al*. 2006; Fig 7).

From the night they hatch, nestlings are left unattended for several hours each night while the female forages. On Stewart Island in 1985, a female with nestlings one - five days old, left the nest an average of 259 min each night, departing an hour after sunset for 165 min (range = 120 – 210 min) and again about an hour before sunrise for 94 min (range = 73 – 120 min) (Powlesland *et al*. 1992). Nestlings three - five weeks old in two nests on Stewart

Island in 1981 received little brooding each night; they were fed twice nightly, at about 2300 h and 0200 h, and these visits lasted 10 - 40 min. The ambient temperature near ground-level at one of these nests was 0 - 10°C during three nights. Females returned to these nests again at dawn, fed the broods, and then brooded throughout the day (Powlesland *et al*. 1992). When nestlings of these two broods were 8 - 10 weeks old, the females roosted away from their nests by day. At night the broods were fed once or twice, and again at dawn. Such feeding visits lasted only 10 - 20 min, the female leaving immediately after she had fed the brood. Similarly, during the first week after hatching three females on Codfish Island in 1997 were absent from their nests each night for a mean of 305 min, and by the fifth week this non-attendance averaged 478 minutes per night (Higgins 1999).

Vocalisations by females to communicate with their nestlings have seldom been heard. One call used for this purpose is a low amplitude, pig-like grunt (Higgins 1999). Soon after leaving the nest, females often give a loud skraark call. Nestlings are vocal from hatching, giving a "purring" or "grunting" call, which becomes progressively louder and lower in pitch with age. Rapidly repeated, low amplitude purring or grunting is given when soliciting food, being fed, and during inter-sibling rivalry for food (Sibley 1994; Higgins 1999). By fledging age, the purring call is remarkably similar to the grunting of a young pig. Nestlings have not been heard to give distress or alarm calls, but once fledged juveniles develop a low amplitude, drawn-out croaking or growl call, similar to the female distress call.

Preening of nestlings by the female is common throughout the nestling stage, particularly in the latter stages when feathers are sprouting.

Nestlings are fed on vegetable matter (Cottam *et al*. 2006) regurgitated by the female directly into the nestling's beak. Faeces of kakapo nestlings have virtually no smell. Once the nestlings are a few days old they move to the periphery of the nest bowl to defecate, where the droppings quickly desiccate and become incorporated into the nest rim. The female's regular grubbing of the nest base results in many droppings being buried, and the frequent brushing action of the female's tail as she turns in the nest tends to sweep droppings beyond the nest bowl.

Fledging

Fledging occurs in late May - early June, just before the winter solstice, thereby ensuring maximum foraging time for the young of a nocturnal species. Leaving the nest cavity is often a gradual process. Provided egress from the nest is not difficult, young may spend progressively longer periods a few metres from the nest from about nine weeks of age (Higgins 1999) until, finally, they do not return. If egress is difficult, fledglings may not have the strength and co-ordination to climb from the cavity until 10 - 12 weeks of age.

The ages at fledging varied from 65 to 88 days, with an average of 76.1 ± 6.37 days. Males fledged 3.5 days before females from broods of the same size but this difference was not significant (F = 2.86, df = 1.18, P = 0.074). Chicks from broods of two fledged 5.5 days later than chicks from broods of one, a statistically significant difference (F = 2.864, df = 1.18, P = 0.010) (Farrimond *et al.* 2006a).

Chicks from most broods of two roosted away from the nest after their mothers had started roosting away, whereas chicks from all broods of one, roosted away from their nests before or at the same time as their mothers. This difference was statistically significant (Fishers exact test, P = 0.011) (Farrimond *et al*. 2006a).

When 11 - 12 weeks of age, most young roost on the ground <10 m from the nest. A month later, fledglings are usually 50 - 100 m from the nest. The area about the nest becomes well trodden, littered with faeces, and low-growing vegetation in the area may be well chewed (DVM unpubl. data). Initially fledglings do not have the strength or co-ordination to climb shrubs and trees well, but are capable climbers by the time they become independent.

Reischek believed that kakapo fledglings were abandoned by their mothers as soon as they left the nest (Westerskov 1981). However, radio-tracking and observations with night-vision equipment indicate that fledglings continue to receive some food from their mothers for at least three months after leaving the nest (Higgins 1999). They remain within or close to their mother's home range until 6.5 - 8.4 months of age, and may roost in close association with her (Farrimond 2003).

Fledging weights vary markedly according to sex and food availability during the nestling period. Provided food is not limiting, weights at fledging equal or exceed mean adult weights. For example, the weights of two Stewart Island sibling fledglings in 1981 were 2.16 kg (male) and 1.68 kg (female) (Higgins 1999). The mean fledging weights of males and females on Codfish Island in 2002, when rimu fruit was exceptionally plentiful, were 2.0 kg (n = 8) and 1.7 kg (n = 13) respectively (Farrimond *et al.* 2006a).

By fledging age, the tempo of the grunt call has slowed considerably from that of nestlings, grunts now being given at *c.*1 sec duration, and repeated at 1-2 sec intervals. This fledgling call is remarkably pig-like, and can be heard for up to 5 m. A hand-raised fledgling three to seven months old gave this call while foraging and at eight months started giving skraark calls (Climo & Ballance 1997). Skraarking by subadults is distinctive, being higher in pitch and less protracted than those of adults.

Like adults, individual fledglings vary in their response to perceived danger; while some are silent, others are highly vocal. Fledglings are generally more vocal than nestlings, and can sometimes be located from some distance by their constant grunt or croak calling when approached (Higgins 1999).

Anti-predator responses at the nest

A ship rat was observed eating food dropped when a female was feeding a 9 - 10 week old nestling in a nest on Stewart Island in 1981. The nestling lunged repeatedly at the rat (Rasch 1989). In contrast, a five - nine week-old nestling showed no apparent reaction to a Pacific rat that briefly entered its nest once on Codfish Island in 1997 (DVM unpubl. data). After fledging, young adopt the same predator avoidance strategy as adults, remaining motionless when danger threatens.

An incubating female kakapo on Codfish Island was observed vigorously attacking a Cook's petrel that was nesting within the same cavity. Even though the petrel was not a threat to her or her eggs, whenever it approached the cavity, the kakapo rushed at it screeching loudly with beak open and neck outstretched. Cook's petrels that have occasionally been found dead in or near kakapo nests may have been killed by nesting female kakapo. Females make no attempt to cover or conceal their eggs or young while away from the nest at night, and exhibit no distraction display when approached by people on or near their nests. When approached closely by people, nesting females often continue incubating or brooding making it necessary to reach beneath them to check their nest's contents. However, some females may stand, or even back off their nests a little when approach to within one - two metres. No female has deserted a nest as a result of disturbance by a person, even though in recent years nests have been routinely visited and modified, including being moved into nest-boxes.

NESTING SUCCESS

Early observers (Henry 1903; Reischek 1884; Williams 1956) and recent observations (Powlesland *et al*. 1992; Higgins 1999; Clout *et al*. 2002) indicate that only one or two nestlings are fledged from each successful nest. Of 166 eggs monitored during 1981 - 2005, 66 were infertile (39.7%), 68 hatched (40.9%), 48 nestlings fledged (28.9% of eggs, 70.5% of nestlings), and 47 nestlings reached independence (28.3% of eggs, 97.9% of fledglings) (Elliott *et al.* 2006, updated by DVM). The large proportion (98/166 = 59%) of eggs that failed to hatch can be compared with a hatching failure of <10% for most species (Briskie & Mackintosh 2004) and is likely to be the result of very low genetic variation between individuals (Jamieson & Ryan 2000; Miller *et al*. 2003; Robertson 2006). Most of the 47 nestlings that reached independence would not have survived without human intervention: 17 were partially or entirely hand-raised, and at least 16 of the remainder received crucial supplementary food via their mothers. Just 19 (27.5%) of the 69 nesting attempts during 1981 - 2005 succeeded in fledging young. Overall, 0.76 fledglings per nesting female were reared, and 1.53 fledglings per successful nest.

Successful breeding can occur only in the presence of unusually abundant, enduring and high-quality food resources within *c*.1 km of the nest (Powlesland *et al*. 1992; Clout & Merton 1998). These foods must be readily available throughout the incubation, nestling and fledgling periods of *c*.six months. The periodic abundant fruit/seed crops that have coincided with kakapo nesting occur irregularly at up to seven-year intervals, and are believed to be determined by climatic conditions during the preceding summer (Norton & Kelly 1988). Climatic conditions following pollination determine whether the crop develops and ripens. During the 1990s, two rimu fruit crops developed on Codfish Island, but both failed to ripen, resulting in nesting failure of those females that had not learnt to take supplementary food.

SEXUAL MATURITY

The precise age at which male and female kakapo attain sexual maturity is not known. However, two four-year-old males on Little Barrier Island that visited an arena at the end of a booming season made barely-recognisable attempts to boom there on several nights (Higgins 1999). At five years old, these same males had established track-and-bowl systems, and their booming was similar to that of older males. Seven males reared subsequently have shown similar behaviour at this age.

Three known-age females bred for the first time at nine, 10 and 11 years old (Eason *et al*. 2006). However, since the abundant fruit crops that trigger nesting did not occur in the years preceding those in which these birds first bred it is possible that they may have been sexually mature a year or two earlier. Thus, males may reach sexual maturity at about five years of age, and females at about nine years of age.

ADULT SURVIVAL

Kakapo are believed to be exceedingly long-lived. The oldest known bird, a male ("Richard Henry") first captured when an adult in Fiordland in 1975, was alive and in good health in 2005. Clout (2006) speculates he may be almost 100 years old.

The survival rate of kakapo transferred from Stewart Island between 1980 and 1992 has been remarkably high despite the fact that all but three were adults of unknown age when transferred. At least 44 of the original 61 (72%) were still alive in 2005. Forty-two of these are now at least 24 years old, and most are likely to be considerably older than this. Mean annual survival between 1982 and 2005 of adult kakapo transferred to offshore islands was 0.99 (Elliott 2006).

Only one of 18 kakapo found in Fiordland during 1974-1977 is known to have survived beyond 1987. Five were relocated to island refuges, of which only one, 'Richard Henry', remains alive. None of the 13 males left in Fiordland survived beyond 1987 (Rasch 1989).

Survival following independence is high: 41 of 46 juveniles which reached independence since 1981 survived in 2005. Annual survival of juveniles in the present managed population is estimated at 0.91 (Elliott 2006).

CONSERVATION PROGNOSIS

Much has been written in the popular literature about the kakapo being a parrot taxonomically and structurally, but in many other respects showing little similarity with other parrots (Higham 1992; Trewick 1999; Grzelewski 2002; Hilburn 2002; Pain 2002). Features which set it apart from other parrots include being flightless, nocturnal, solitary, having pronounced sexual dimorphism in body size, and a lek-mating system.

The kakapo was superbly adapted to the New Zealand environment prior to the arrival of people. During this era the terrestrial environment of New Zealand was dominated by birds, reptiles and invertebrates; birds comprised the megafauna, and exploited niches occupied elsewhere by mammals (Worthy & Holdaway 2002). In this environment the predators of kakapo were predatory birds (e.g., *Harpagornis moorei*, *Circus eylesi*, and possibly the two *Aptornis* species) that relied mainly on sight to detect their prey. Thus, despite being flightless, by becoming nocturnal and cryptic the kakapo would have been difficult for these predators to detect.

The absence of mammalian predators and competitors enabled the kakapo to evolve in ways that no other parrot has done. Becoming flightless was accompanied by it becoming the giant of the Psittaciformes, and in combination with an unusually low metabolic rate, enabled it to subsist on an entirely herbivorous diet that is generally low in nutrients. Even so, by selectively feeding on the more digestible and better quality foods, such as subterranean storage organs (bulbs, rhizomes), growing soft tissues and reproductive organs (pollen cones, flower buds and flowers, developing and ripe fruit and seeds), kakapo could sustain themselves and also periodically accumulate prodigious reserves of fat. Although much of their diet consisted of fibrous plant parts, such as leaves and stems, their ability to grind these in the beak and spit out most of the indigestible fibre enabled the species to survive on low quality foods. This combination of diet and metabolism enabled the kakapo to be a successful habitat generalist, inhabiting forests, shrublands and tussocklands, from sea-level to the subalpine zone, throughout the length and breadth of New Zealand.

Even though nocturnal and flightless, kakapo were well able to take advantage of seasonally and spatially available nutrient-rich foods. Their strong legs and running gait enabled them to cover several kilometres in a night to reach patchily distributed food sources. Also, their probable sense of smell may have enabled kakapo to detect and locate certain foods from a distance, such as ripening fruit. Rictal bristles, near the eyes and beak, may have helped them to avoid injury when moving about in the dark, functioning much like the whiskers of a cat. Even though flightless, they were agile climbers, reaching and foraging in the canopy of tall forest trees when seasonally abundant and nutrient-rich foods were available, such as flowers, nectar, pollen cones and fruit. Also, kakapo were more able than flighted species to store the energy obtained from periodically super-abundant foods as fat which they subsequently metabolised when food was scarce, or when breeding or moulting. Indeed, kakapo appear to have a greater capacity to accumulate fat than any other terrestrial bird. Such fat reserves may also aid thermoregulation in a cool temperate climate, particularly in colder parts of their range, such as the subalpine Esperance Valley, Fiordland, where the mean annual temperature is *c.* 6^{o}C (Atkinson & Merton 2006).

Masting is a feature of some New Zealand trees and tussocks whereby they produce a super-abundance of fruit or seed at irregular (1 - 7 yr) intervals, but little or no seed in the intervening years (Kelly 1994; Norton & Kelly 1988). Kakapo are well adapted, for the reasons described above and by being long lived, to exploit such periodically abundant food sources. The emancipation of males from incubation and nestling-rearing duties would only have been possible because these abundant food sources enabled females to rear young without male assistance. Lek mating presumably evolved because individual males were unable to either coerce females to mate with them, or to gain access to females by controlling the resources that females required. As in all lek-mating species, male kakapo relied solely on "sex-appeal" to gain mates, which in turn led to intense inter-male competition for females and a marked increase in sexual size dimorphism.

As well as male emancipation from parental care, another prerequisite of this breeding system was the necessity for embryos and nestlings to be able to survive without being incubated or brooded for periods of 1 - 2 hours at a time while the female was absent foraging. Little is known about how kakapo eggs and young nestlings differ from those of other parrots other than that kakapo nestlings have much more down at hatching than those of other parrot species. Is it possibility that kakapo nestlings are able to go into torpor, or some physiological analogue, to cope with the cooling resulting from long periods of no brooding while females forage?

All the features mentioned above combined to make the kakapo one of New Zealand's more widespread and abundant species (Worthy & Holdaway 2002) in pre-human times. However, with the arrival of predatory mammals many of the characteristics that had made kakapo so successful now predisposed them to predation. It is hard to imagine that any kakapo eggs or nestlings could survive once mammalian predators, such as stoats and ship rats, became common. In addition, adult kakapo are highly vulnerable to predation by cats, stoats and dogs. Whether competition for food with mammalian herbivores, such as possums, mice (*Mus musculus*), rats, goats and deer, contributed to the decline of the kakapo is unknown. However, given the vulnerability of kakapo to mammalian predators, kakapo populations would in all probability have been decimated before such competition had an effect.

The persistence of kakapo into the 21st century owes much to the bird's longevity, its ability to exploit a wide range of habitat types, and to its extra-ordinary tolerance of what has become a highly intrusive conservation programme. Once removed from their principal threat, the natural longevity of the remnant survivors has afforded time to develop appropriate conservation responses. In the development of those responses, the remnant survivors have been plucked from their alpine (Fiordland), and scrub and forest (Stewart Island) environments, and shuttled between islands into habitats as diverse as sub-tropical rainforest (Little Barrier Island), dry coastal grassland, scrub and pine plantation (Maud Island), and low-altitude scrub and podocarp forest (Codfish, Pearl, Chalky and Anchor Islands). That the birds have accepted not just the effect of transportation the length of the country, but have maintained condition, and even bred, in all of these habitats (Eason *et al*. 2006) is extra-ordinary. So too has been their tolerance of regular captures, weighings and bleedings, of carrying radio-transmitters and transponders (Low *et al*. 2005), of having nest sites modified and continuously monitored, and of a persistent close human presence, all of which now characterise the kakapo recovery programme (Creswell 1996; Clout & Merton 1998; Elliott *et al*. 2001).

The current management vision for kakapo is "to establish at least one viable, self-sustaining, unmanaged population of kakapo as a functional component of the ecosystem in a protected habitat, and to establish two or more other populations which require ongoing management" (Cresswell 1996). To this end, the ecological restoration of two large Fiordland islands, Resolution (20,860 ha) and Secretary (8140 ha) is a newly accepted conservation challenge. If successful, and kakapo are placed once again on Resolution Island, a remarkable journey will have gone full-circle; the vision of New Zealand's first wildlife conservator, the remarkable Richard Henry (Hill & Hill 1987), finally will have been fulfilled.

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