How could all these extraordinary features have come together to make a viable species?

KAKAPO: THE PARADOXICAL PARROT

BY STEVE TREWICK

AMONG BIRDS, THE PARROTS ARE A GROUP that few people would fail to recognise. The hooked beak, clasping foot and intelligent eye, coupled with a well-developed and sometimes destructive curiosity, distinguish members of the group. All these attributes are expressed in New Zealand's Kakapo (*Strigops habroptilus*), yet there is much about this bird that renders it utterly distinct from other parrots and, in fact, any other bird. The extreme rarity of the Kakapo does nothing to ease the task of interpreting its nature and this is unfortunate as it is our lack of knowledge that has impeded conservation efforts. Even after differentiating between the bird's inherited and unique characteristics, the Kakapo remains a paradox.

ROD MORRIS

The face of a Kakapo is quite different from that of other parrots. A disk of fine pale feathers around the eyes gives the bird an owl-like appearance and this, combined with the nocturnal habit and seemingly thoughtful countenance that Kakapo often adopt, led to the use of the name 'owl-parrot' by early biologists. The generic classification, *Strigops*, reflects this.

The Maori name Kakapo means night parrot (*po* = night; *kaka* = the name of the common New Zealand parrot). Although unusual, the Kakapo is not the only nocturnal parrot. Australia's aptly named Night Parrot (*Pezoporus occidentalis*) and its near relative the Ground Parrot (*P. wallicus*) are also largely nocturnal. Because of this and similarities in plumage, these parrots would appear to be closely related to the Kakapo. However, genetic studies have shown that the Australian and New Zealand species are very different and have closer relatives in their own countries. The morphological and behavioural similarities are instead the result of evolutionary convergence for similar reasons such as camouflage.

The most extraordinary behavioural characteristic of Kakapo is that they do not fly. Although well feathered, the wings of Kakapo are relatively small and the keel of the breastbone to which wing muscles would normally attach is tiny. The Kakapo is the only known flightless parrot and ranks with the Dodo (an anomalous pigeon) as an oddity in this respect. As with the Dodo and other birds that have evolved flightlessness on islands, Kakapo are large and heavy compared with their flying relatives. The Kakapo, in fact, ranks as the world's heaviest parrot, with males typically weighing 2–3.5 kilograms. By comparison the Sulphur-crested Cockatoo (*Cacatua galerita*), which is one of the larger flying parrots, has a maximum weight of less than a kilogram.

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Gigantism in birds is often associated with herbivory, perhaps because a low-quality plant diet requires the consumption of large volumes of food; and here again the Kakapo is unusual. Although parrots are predominantly vegetarian, many if not all species other than Kakapo also eat animals (usually invertebrates). However, field observations and microscopic examination of droppings have shown that Kakapo are strict herbivores even as chicks, a time when many otherwise herbivorous birds utilise animal protein in their diet.

As some compensation for this dietary restriction, Kakapo forage in a wide range of vegetation both on the ground and in trees, which they climb proficiently using their beak and zygodactylous feet (two toes forward and two back). They feed on a diversity of plant species and plant structures, depending on the availability and nutrient quality, and use a specialised ridged palate to help grind food. In some instances Kakapo will feed on tough leaves, swallowing only the soft tissue and soluble component and leaving characteristic fibrous 'chews' hanging on the plant. At other times they will carefully bite out only the softest parts of leaves, avoiding hard midribs and stems altogether. Fruits, roots and the seeds of grasses are also eaten when available.

As a flightless and strictly herbivorous parrot, the Kakapo is wholly dependent

KAKAPO

Strigops habroptilus

Classification
Order Psittaciformes, family Psittacidae.

Identification
Very large, mottled green parrot. Length 63 cm. Weight about 2 kg for males, 1–2 kg for females.

Distribution
Endemic to NZ. Once present throughout scrub and forested areas and hilltops of North, South and Stewart Islands. Today, all surviving individuals are translocated to predator-free islands including Little Barrier, Codfish and Maud. No natural populations known to remain.

Behaviour
Nocturnal, flightless and cryptic. Solitary except for mating; large home range. A strict herbivore feeding on leaves, fruits and roots of many plants. Forages on ground and in trees using feet to hold food and beak to assist climbing. Typically leaves distinctive 'chews' on or near fibrous plants. Usually silent but may emit various squeals and screeches. Males produce low-frequency 'booming' and 'ching' calls when breeding. Roost by day in natural cavities often beneath tree roots, in hollow logs, or in dense foliage.

Reproduction
The only lek-breeding parrot. Breeding attempts coincide with abundant fruiting of native plants. Males aggregate at night on 'track-and-bowl' sites and use 'booming' vocalisation to attract females. After mating all nesting and rearing undertaken by female, a period of up to 8 months. Nests built in burrow as with roosts; 2–4 eggs laid. Adult sex ratio significantly skewed to males.

Status
Endangered. Total 1997–98 population 54 (20 females, 34 males).

DON MERTON

Most of the habitat in which Kakapo have been found this century is mixed shrubby vegetation in southern New Zealand. Early observations and evidence from recent fossil bones indicate a widespread use of forests in the past.

on nutrient-rich fruits and seeds to feed the chicks. However, many of New Zealand's grasses and trees do not produce abundant fruit crops throughout Kakapo habitat every year. In some years and places there will be almost no fruit and in others there will be a glut. The frequency of these fruiting or 'masting' events varies from every second to fifth year. It has long been known that Kakapo attempt to breed only in years of fruit abundance. This synchronism exists despite the fact that mating and egg-laying has to take place before the fruit arrives. How the parrots know when it's going to be a good year is unclear.

Unlike all other parrots, which are monogamous, Kakapo are 'lek' breeders. In this system males advertise themselves, and females choose the best mates. Males, however, take no further role in producing offspring.

At the start of breeding, male Kakapo construct special arenas on hill tops and ridges by clearing vegetation from small patches of ground, often near a rock or tree stump, and along paths in between. These are known as track-and-bowl systems and the males perform in the bowls during the night. The display consists of a series of low-frequency vocalisations called 'booming'. Male Kakapo have a special air chamber in their chest that helps resonate the sounds they make and, in combination with the acoustic properties of the bowls, allows them to be heard up to a kilometre away. Females, attracted by the noise, visit the leks and select a male to mate with. It appears that it is the largest males that are generally chosen. Copulation takes place in one of the bowls and soon after the female returns to her own home range in the forest. Here she builds a nest, lays two to four eggs and raises her chicks alone. Meanwhile, the males carry on booming every night for several months in the hope of securing further matings, although most will achieve no matings at all.

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Male Kakapo construct display arenas by clearing vegetation from the ground. A series of hollows (bowls) are interconnected by tracks. Bowls are usually positioned beside a suitable acoustic reflector such as a log, boulder or in this case a small vegetated bank.

WHY LEKKING BEHAVIOUR HAS evolved in the Kakapo and other species is an active area of research. One feature that is common to many different lekking species is an inability of males or pairs to control an important resource. Commonly this resource is food, and if the availability of preferred foods is not predictable (either in space or time), then defending territories becomes pointless and the mutual benefits of monogamy break down as males and females try to get the best deal for themselves. In all mating systems males and females try to maximise the number of offspring that carry their respective genes into the next generation. In many birds and other animals, the male contribution to reproduction can be very small. Once fertilised, a female is left holding the eggs but a male has the opportunity to fertilise the eggs of other females, thereby increasing the number of offspring carrying his genes. However, selection will operate against this tendency in situations where both parents are required to successfully rear a single clutch. The breeding system that arises in any given situation therefore results from a process of evolutionary optimisation, although it often appears that some individuals or one sex get(s) a raw deal.

The Kakapo is especially interesting from this point of view. Even in the years of fruit abundance when breeding is initiated, females barely manage to rear young on their own. Of the breeding events that we have observed, female Kakapo have generally failed to fledge chicks or have struggled to rear even a single offspring. This is despite the strenuous efforts of the New Zealand Department of Conservation (providing supplementary feed) and the female Kakapo which work throughout the night and even into the day to feed the chicks. Females will spend three months provisioning chicks in the nest, literally running between food sources and the nest. During this time chicks normally end up being heavier than their mother was at the start of breeding, while the female's own weight drops by as much as 80 per cent. This contrast was documented by New Zealand's pioneer Kakapo conservationist, Richard Henry, at the turn of the century: ". . . the mother's feathers are draggled and worn, and I have often wondered how she could tramp away and carry home sufficient food to keep two or three young ones like balls of fat. The males are also very fat, while the mother is like skin-and-bone . . .".

When lekking, male Kakapo will fight (sometimes to the death) for track-and-bowl sites and thus benefit from being big, strong and aggressive.

The differences in activities of males and females may explain a further peculiarity of Kakapo—that of sexual dimorphism. In most parrot species, the sexes are very similar in size but in Kakapo, the male is significantly bigger and typically weighs 2–3.5 kilograms to the female's 1–2 kilograms.

When lekking, male Kakapo will fight (sometimes to the death) for track-and-bowl sites and thus benefit from being big, strong and aggressive. Females seem to prefer the biggest males as mates but different selection pressures are operating on themselves. Whereas large male size seems to have been fashioned mainly by sexual selection, females have apparently been honed by

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In addition to calling from their track-and-bowl arenas, male Kakapo perform a display dance. Although the display has never been observed in the presence of a female Kakapo, this dance presumably acts as a visual stimulus to prospective mates attracted by calling.

natural selection. With the sole responsibility for rearing chicks, female Kakapo have to be exceptionally good at supplying plenty of high-quality food. Being smaller and having a relatively large wing area for their body weight may enable females to forage more quickly, higher up fruiting trees and even to leap or parachute from one tree to another or to the ground. This latter behaviour has been observed in the wild, even though nocturnal activity and rarity reduce the likelihood of such sightings.

Accompanying sexual dimorphism in Kakapo is yet another peculiarity. Instead of the normal one-to-one sex ratio present in most birds, Kakapo have more than twice as many males. This was initially assumed to be an artefact associated with human-induced changes in the environment. In particular, it was thought that predation by introduced Cats, Pigs and Stoats might

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Male Kakapo expand an air chamber in their chest to produce their low-frequency 'booming' call. Booms can be heard for up to one kilometre away but are not directional. A higher frequency, and thus directional, 'ching' call is produced intermittently, and this may help females locate individual males at close quarters.

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Kakapo are usually solitary but occupy large overlapping home ranges. Without the stress of breeding they have little trouble maintaining themselves on a diverse vegetarian diet. Their tails, however, are often bedraggled from contact with the ground and use of the thickly quilled feathers as additional support when climbing and perching.

somehow have a greater effect on female Kakapo than males. I recently had the opportunity to test whether the skewed sex ratio had existed prior to the arrival of humans, by examining fossilised bones that had accumulated in caves 2,000–5,000 years ago. The bones amassed as flightless birds, including Kakapo, fell or wandered into cave systems and died there. Because the size dimorphism of Kakapo is reflected in the size of their bones, I was able to use the numbers of leg bones of different lengths to estimate the prehistoric sex ratio. This turned out to be nearly three males to each female, indicating that the unusual excess of males has persisted for many generations. Although predation by introduced mammals has brought the Kakapo to the brink of extinction, the skewed sex ratio in the surviving population is evidently not the result of any predation-bias toward females.

In species where males and females are monogamous a ratio of one to one is generally expected and found. In most lekking species the sex ratio is also usually about one to one, although the operational ratio favours females because few males actually get to mate at all and therefore do not contribute to the next generation. Certainly it is hard to see why having more males would be favoured in an evolutionary context. It is a cruel irony that, given the effort required to raise a chick, a female Kakapo will often be wasting her time when her offspring are male. This is because, even if her sons carry genes for being big and loud (that is, good lekkers), they may not get a chance to express them, as achieving large adult size is dependent on the size achieved in the nest. Due to the way avian skeletons develop, bone length and thus overall skeletal size are fixed by the time a bird fledges. If food is poor, then male Kakapo chicks will be small despite their genes. In good years of course, male chicks will be big because their fathers' 'big' genes can be fully expressed. Female chicks, however, have genes for small skeletons; their reproductive potential is not limited by size.

Observations of nesting Kakapo reveal that, even in the absence of predators, many breeding attempts fail. Success is dependent on the continued availability of good-quality food throughout the growth of the chicks. When food at the nest becomes scarce (because the mother is having trouble finding enough) some or all chicks will go hungry. As with most birds, the largest chicks dominate the food supply until they are sated. In Kakapo nests the largest chicks are usually going to be males because they have greater potential growth rates than females. In addition, aggressive traits (favoured in successful lekking adult males) may also be expressed in male chicks. These features may combine to give male Kakapo chicks competitive advantages over female siblings to the extent that females may suffer higher nest mortality. This would lead to a greater proportion of males in the adult population.

HOW COULD ALL THESE EXTRAORDINARY features have come together to make a viable species? Whatever the reasons that led to Kakapo evolving a lek breeding system in the first place, it is likely that the environment in which

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Female Kakapo are solely responsible for the care of eggs and chicks. The nest generally consists of a hollow in a decayed log, among tree roots or other vegetation. The eggs are small (five centimetres long), and the hatching and survival of the chicks depend on the quality of food available to the mother. The longer she is away from the nest foraging, the greater the chance of eggs or chicks chilling. In conditions of abundant food, chicks rapidly gain weight and are soon heavier than their mother.

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Kakapo are inquisitive and, despite their large size, are capable climbers. The typical parrot beak and zygodactylous feet (two toes forward and two back) are put to good use when foraging on the forest floor and in trees.

they did so differed from that in which they live today. I believe that the most profound change that has occurred in New Zealand's recent biological time (excepting human interference) was climate cooling. This was most extreme during the period of glaciation that ended about 15,000 years ago, although temperatures remain lower than before the ice age. During the warmer climates that existed for most of New Zealand's prehistory, plant diversity was higher and abundant fruiting may well have been more frequent. In such conditions Kakapo would have produced successful broods more often and chicks would not have been in competition for food.

If Kakapo evolved lekking in such conditions, they may now be maladapted and have limited evolutionary opportunities because of the nature of their breeding system. This is not to say they cannot

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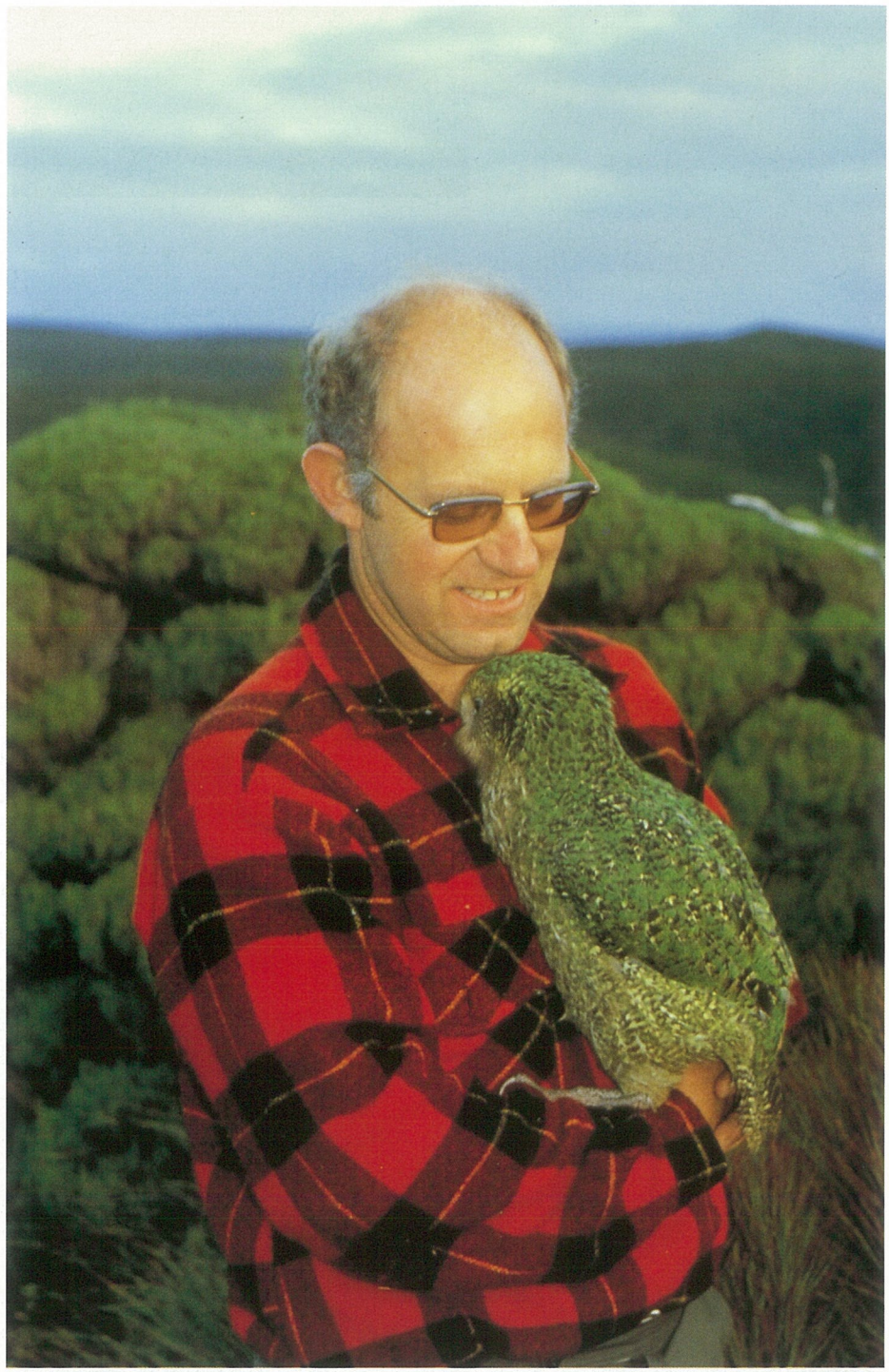
Kakapo spend most of their time on the forest floor among shrubs, mosses and ferns where they are well camouflaged. If disturbed by a potential predator, Kakapo freeze until the danger has passed. This is the only means of defence they have and it is no match for introduced Cats or Stoats.

persist as a species but that they may exist as a biological oddity. Even though failure of fruiting crops at the critical moment of chick rearing leads to increased stress to mothers, sibling rivalry (causing female chick mortality) and the overproduction of undersized males, the species has persisted. In the absence of mammalian predators and blessed with a long life expectancy of at least 50 years, the Kakapo can survive despite its odd sex ratio.

Today conservation efforts are being directed at protecting Kakapo from introduced predators and, in a sense, from themselves. Eradication of introduced mammals on potential island reserves was once an almost untenable prospect, but now appears to be relatively straightforward. On the other hand, ensuring that Kakapo initiate breeding attempts and have sufficient food to successfully rear healthy chicks of both sexes is demanding very special efforts in the way of providing appropriate analogues for masting fruits. This includes the identification of cues that stimulate initiation of breeding, determination of the important nutrient components in the diet, production of suitable supplementary foods, and mimicking the fluctuating abundance of natural foods. There is no way we can alter the sexual behaviour of Kakapo but, by understanding how it evolved, we have the opportunity to alter the outcome of that behaviour.

As I write, one Kakapo receiving supplementary food is tending a nest and caring for two fat chicks, a male and a female. This is only the second surviving female to hatch since 1981. A third (male) chick that hatched last was smaller than its siblings and did not compete well for food. It is now being hand-reared and is also doing well. It is interesting to note that, despite being the first to hatch, the female chick is not the biggest any more, having been outgrown by its slightly younger male sibling. If the food was not as good as it is, we can well imagine that this faster-growing male would have the advantage over his sister, with the dire results that we see represented in the existing population.

Kakapo biologists are very encouraged by these latest results and, although not all individuals have responded in the same way, it could be that, at last, the Kakapo is making a comeback. We can look forward to the continued success of conservation efforts and to having evermore evidence to help us understand the nature of the Kakapo, New Zealand's paradoxical parrot. ■



MARGARET SHEPARD

The trusting nature of Kakapo is one feature that assists their conservation. This 12-week-old fledgling nestles against Don Merton, a key figure in the New Zealand Department of Conservation Kakapo recovery program.

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