Breeding biology of morepork (*Ninox novaeseelandiae*) on Mokoia Island, Lake Rotorua, New Zealand

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Abstract We studied the New Zealand morepork (*Ninox novaeseelandiae*) over 2 breeding seasons on Mokoia I, Lake Rotorua, North Island, New Zealand. Ten pairs were monitored in the 1995/96 breeding season and 8 in the 1996/97 season. Nest sites included tree cavities, hollows amongst tree fern fronds, nest boxes provided for saddleback (*Philesturnus carunculatus*), and scrapes on the ground. Nest cavities were 0-5.2 m agl. Clutch size was 1-3 eggs; egg dimensions averaged 39.0 mm × 32.9 mm. The incubation period for 1 clutch was at least 24 days. Only females were observed to incubate eggs and brood nestlings; males roosted nearby. Two chicks were weighed and measured throughout their development and the nestling period was determined for 1 chick. Nestling development is described. Breeding success was lower in the year after a poisoning operation to eradicate mice from the island. Juvenile mortality was high after fledging. The dispersal of 4 juveniles was monitored, and females appeared to move earlier and disperse farther than males.

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INTRODUCTION

Small (c. 200-300 g), forest-dwelling owls of the genus *Ninox*, are well represented throughout much of Australasia, the south-west Pacific, and the Indonesian Archipelago (Schodde & Mason 1980). One of these species is listed as critically endangered, 1 as vulnerable, and 3 as near-threatened (Birdlife International 2000), while at least 1 island form is extinct and another persists only as a hybrid population (Garnett & Crowley 2000). The morepork (*Ninox novaeseelandiae novaeseelandiae*) is restricted to New Zealand, where it is the sole representative of the genus. It is considered to be conspecific with the boobook (N. novaeseelandiae boobook) found throughout Australia (Higgins 1999). Despite its

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being common and widely distributed throughout forested areas of New Zealand, there have been few detailed studies of morepork's ecology or breeding biology.

Most information on morepork breeding biology is based on anecdotal observations and infrequent nest visits, including 26 cards (from 1927 onwards) from the Ornithological Society of New Zealand's Nest Record Scheme, a handful of short papers on nests discovered on offshore islands (Chambers et al. 1955; Ramsay & Watt 1971; Anderson 1992), and a note on a pair of moreporks using a nest box (Hogg & Skegg 1961).

As a result, knowledge of the breeding biology of moreporks is scant. The breeding season is said to start with an increase in calling activity in the 2nd half of Aug (Imboden 1985). The only report of copulation is for 1 Sep (Imboden 1975), and egg laying is thought to begin in early Oct, reaching a peak in Nov (Imboden 1985). The typical clutch is 2, with a laying interval of *c*. 2 days (Imboden 1985). Imboden (1985) and Heather & Robertson (1996) both state that only the female incubates, and that she is fed by the male on the nest. However, there have been no breeding studies of banded birds, and it can be difficult to sex moreporks using external morphology alone (BMS, unpubl. data). The incubation period has been reported as 30–31 days (Imboden 1985), although Heather & Robertson (1996) suggest 20–30 days. As incubation starts with the laying of the 1st egg, hatching is asynchronous (Imboden 1985). Chicks fledge at 34–35 days (Imboden 1985, Heather & Robertson 1996).

Most nests are in tree-hollows, but nests have been recorded also in thick clusters of epiphytes, in cabbage trees (*Cordyline australis*), in piles of pine needles in tree-forks, in caves (Imboden 1985), in nest boxes (Hogg & Skegg 1961), and on the ground, either in sheltered situations (Anderson 1992) or in burrows (Ramsay & Watt 1971). The nest is a depression formed in the material at the site (Imboden 1985). We have found no published information on the development of morepork chicks, nor quantitative data on fledging rates or breeding success.

Again, almost nothing appears to be known about habits of juveniles after they fledge or about dispersal from the natal territory once the young are independent. A limited study of boobooks in Australia showed that young birds roosted close to the male for 40-50 days after fledging (Olsen & Trost 1998).

We undertook a study of the breeding biology of a **population of individually marked moreporks** to obtain information on nesting habits, clutch size, incubation length, nestling duration, breeding success, chick development, juvenile dispersal, and survival.

METHODS

The study was conducted on Mokoia I (38° 05' S 176° 17' E), an uninhabited 135 ha island in Lake Rotorua in the central North Island, New Zealand. Most of the island is covered in low regenerating forest, composed mainly of understorey species such as five-finger (*Pseudopanax arboreus*), kawakawa (*Macropiper excelsum*), mahoe (*Melicytis ramiflorus*), and rangiora (*Brachyglottis repanda*). The composition and age of the vegetation on Mokoia I mean that there are very few natural cavities.

Eleven morepork nests were located, by using several techniques. Three nests were found by searching likely areas and trees with cavities; 1 more was located by checking known nest sites. Saddleback (*Philesturnus carunculatus*) nestboxes were checked every 2 weeks and 2 morepork nests were discovered in these. Finally, 5 nests were found by following incubating or brooding females carrying radio transmitters as part of a concurrent study (Stephenson *et al.* 1999).

Nest characteristics, including tree species, height above ground, and the internal dimensions of the cavity were recorded. Nests were checked every 2-3 days, and daily as chicks approached fledging, in the 1995/96 season. In the 1996/97 season, nests were checked every 3-4 weeks. Dates of hatching and chick fledging were determined and, where possible, eggs and chicks at various stages of development were measured.

All adults (n = 24) and nestlings (n = 6) were banded, and 17 adults ($7 \Diamond \Diamond$; $10 \heartsuit \heartsuit$) and 4 fledglings ($2 \Diamond \Diamond$; $2 \heartsuit \heartsuit$) were fitted with transmitters, following the techniques described by Stephenson *et al.* (1998). The dispersal of 3 radio-tagged fledglings that survived longer than 1 month post-fledging ($2 \Diamond \Diamond$, $1 \heartsuit$), and 1 un-tagged individual ($1 \heartsuit$ located during the 1996-97 breeding season), was monitored. Blood samples were collected from birds at the time of banding to allow accurate sex determination using PCR-based molecular techniques (Stephenson 1998).

An automatic monitoring system was set up at 1 nest in the 1995/96 breeding season, to investigate nesting habits and identify prey. Using a Super-8 cine camera connected to a flashgun and a photoelectric beam, a single frame was taken every time a bird arrived or left. A small clock positioned in the background allowed the time of each visit to be determined. The camera was run on 6 nights, starting when the chick was 26 days old; the final night of filming captured the chick's fledging from the nest.

RESULTS

Ten pairs were monitored in the 1995/96 breeding season, and 8 pairs in the 1996/97 season. Three pairs were monitored in both seasons, and at least 1 member of each of 3 other pairs was monitored in both seasons. Despite this, only 1 nest site was used during both breeding seasons. Included in the monitored pairs were several (4 in 1995/96; 2 in 1996/97) whose nests were not located, but which were assumed to have attempted to breed. We believe this was justified because successful pairs could be identified by the presence of chicks roosting with them at the end of the breeding season (Jan), when other successful pairs roosted close to their dependent young. The absence of chicks with a pair late in the season therefore indicated that it had not raised young, either because of a failed attempt or because they had **not attempted to breed**.

Timing of breeding

The 2 breeding seasons followed a similar pattern, with pairs beginning to roost together in late Sep.

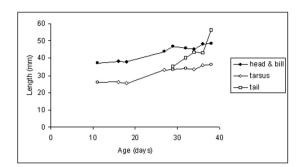


Fig. 1 Head and bill, tail, and tarsus lengths (mm) of 1 morepork (*Ninox novaeseelandiae*) chick from 1 nest in the 1995/96 season. Open circles (○), tarsus; closed circles (●), head and bill; open squares (□), tail.

After this time, females moved from traditional roosts to the nest.

The exact time of laying was not determined for any nest. One nest in a saddleback nest box was empty on 30 Sep 1995, but the female was incubating 1 egg on 18 Oct. On 17 Oct 1995, another female was found to be incubating eggs, the 1st of which hatched on 11 Nov. The 2nd egg hatched the next day when more eggshell was present in the nest cavity. Two nests, with incubating females in attendance, were discovered in mid-late Oct 1996.

The earliest fledging date was 8 Dec 1995 when 2 male siblings fledged. The nestling period on Mokoia is c. 39 days (Chick development, below), so these chicks hatched c. 1 Nov. All of 8 other chicks for which fledging dates were determined (1995/96 7; 1996/97, 1), fledged from mid-Dec to early Jan. However, a chick that died in its nest in the 1995/96 season would have fledged in mid to late Jan had it survived.

Nest sites

Of the 11 nests located, 2 were in nest boxes, 1 was in a cabbage tree cavity, 1 was in a cavity in a mahoe, and 1 was in a hole in an earth bank. The remaining 6 were all associated with tree ferns (*Cyathea medullaris*): 2 in hollow broken trunks, 2 in piles of fronds in the forks of tree ferns, and 2 on the ground at the base of tree ferns.

Cavity entrances had a maximum width of 200 mm, except for the cabbage tree nest which had a large (c. 450 mm × 500 mm) top opening. The cavity size was typically c. 450 mm deep × 450 mm wide, except for the 2 nests in broken tree fern trunks, which were no more than of 200 mm in internal diameter. One of these nests was c. 300 mm below the entrance; the other was 1.5 m below the entrance. The mean height of the nest cavity above ground was 1.9 m (SD = 1.7, range = 0-5.2, n = 11). Nests

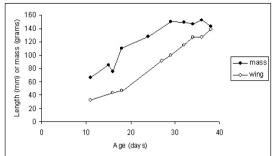


Fig. 2 Weight (5) and wing length (mm) of 1 morepork (*Ninox novaeseelandiae*) chick from 1 nest in the 1995/96 season. Open circles (\circ), wing length; filled circles (\bullet), mass.

were a simple a scrape in the base of the cavity or ground, and did not to contain materials brought from outside the site. Eggs were typically incubated on a layer of leaf litter, or wood dust, or both.

Eggs and incubation

The full clutch size was determined for 9 nests at different stages (from both seasons). Of these, 4 had 1 egg, 4 had 2, and 1 had 3 eggs. It was assumed that eggs had not been lost already, and that the clutch was complete. This was tested by searching the nest for egg fragments before hatching.

Mean egg length was 39.0 mm (SD = 1.4, range 36.3–41.1, n = 9), mean width 32.9 mm (SD = 1.3, range 31.2–35.2, n = 9), and mean weight was 22.5 g (SD = 1.6, range 21.0–24.1, n = 3;, age of eggs unknown). The shell was dull, chalky white, and rough.

The incubation period was not determined, but it was at least 24 days at 1 nest in the 1995/96 breeding season, and probably nearer 30. Only female moreporks were observed to incubate eggs.

Chick rearing and development

Only female moreporks were observed to brood the nestlings. Chick development was investigated at 1 nest (Fig. 1, 2). The chick was weighed and measured for the 1st time on 22 Nov, 11 days after it hatched. At this stage it weighed 66 g and its eyes were open. A smaller (presumably younger by 1 day) chick weighed 56 g and its eyes were still partly closed. On 25 Nov, the smaller chick was found dead and partly consumed in the nest.

Chicks hatched with light, whitish down, which was replaced gradually by darker grey down by day 15. At about day 16, pin feathers started to erupt through the dark grey down, which became a brown fluff; and the bristles around the chick's beak were emerging. Wing feathers grew linearly throughout their development (Fig. 2). By day 25, the chick clacked its bill when removed from the

nest, and the feathers on its back and secondaries had developed white spots. There were still traces of light grey down on the rear half of its head and fluffy brown down on the sides of the head. The rest of the body was still covered in traces of brown and dark grey down. The talons were noticeably stronger. On 8 Dec 1995, when the chick was 27 days old, the light grey down had almost gone, but the body was still covered in dark grey down. However, there was no down around the eyes and beak, just pin feathers, giving the chick a "masked" appearance. By day 30, rectrices had erupted about 10 mm. The chick had lost most of the dark grey down by the time it fledged on day 39, but it still had traces of dark down on the breast, around the head, and on its back.

Two male chicks from another nest, found about 10 days after hatching, followed a similar pattern of growth. Initially, one was noticeably smaller than the other, but 3 days before fledging the smaller chick weighed only 16 g (9%) less than the larger. Four other chicks were weighed within a week of fledging: their mean weight was 162 g (SD = 12.6, range 43–178, n = 6).

Females at 3 nests stopped brooding chicks 5, 7, and 10 days before fledging. Females nesting in smaller cavities stopped brooding earlier. Females were subsequently found roosting within 5–10 m of the nest.

Camera monitoring of nests

The monitoring cine camera produced low resolution images. It was operated on 6 nights, when the nestlings were 25-38 days old, but on 1 night it stopped working after 1.5 h. After the monitoring was over it was found that the birds had been using a 2nd entrance to the nest cavity, so it is possible that not all visits were filmed. However, if the nest entrances were used randomly, the male visited the nest twice as often as the female. The visitation rate for both adults peaked during the 2 h following sunset, with a maximum of 6 visits recorded in the 1st hour after dark. There were usually 2 or 3 visits h⁻¹ after that, with no detectable increase before sunrise. Mean number of visits to the nest each night (determined from arrival and/ or departure of an adult) was 16.2 for the nights on which the camera operated all night (SD = 6.4, range 0-27, n = 5). Nestling age and number of visits to the nest night⁻¹ were not correlated ($r^2 = 0.14$, P = 0.53). Images were obtained of 52 arrivals at the nest, but prey could be identified in only 26 (50%); all prey identified were invertebrates, mainly large weta and moths.

Breeding success

Nine chicks were known to have been fledged by 10 breeding pairs (4 fledged none; 3 fledged 1; 3 fledged 2) monitored in the 1995/96 breeding season, giving a mean fledging rate of 0.9 chicks pair⁻¹. However, 3

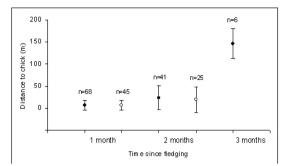


Fig. 3 Distance (mean, SD) of chicks to the roosting male (1) and female (O) adult **morepork** (*Ninox novaeseelandiae*) for the **1st, 2nd, and 3rd months after fledging. Distances** for the **1st, 2nd, and 3rd months are derived from 3 chicks,** 2 chicks, and 1 chick, respectively. Sample sizes are total number of roosting distances plotted. The female parent of the single chick plotted in the **3rd month had died earlier** in the season, so only distances to the male are plotted. Error bars indicate **1** SD.

chicks died within 1 month of fledging, a further 2 were not seen later than 1 month after fledging, and another died about 7 months after fledging. Only 2 are known to have survived at least 9 months after fledging, and only 1 to have survived and attempted to breed in the 1996/97 breeding season.

The cause of death was unknown for most of these fledglings. Bad weather between 20 Dec 1995 and 1 Jan 1996 may have contributed to the losses in that period. **One juvenile's transmitter was found** in an Australasian harrier (*Circus approximans*) nest about 10 days after it fledged. Another juvenile fitted with a transmitter survived for about 7 months, but it may also have been killed by a harrier because, when found, its remains were similar to those found in the harrier nest.

During the 1996/97 breeding season, 8 morepork pairs were monitored, but only 1 chick fledged. All pairs exhibited breeding behaviour, such as roosting together early in the season, then the female disappearing. Although nests were not located for all pairs, the mean fledging rate was 0.125 chicks pair¹. That juvenile was last observed 1 month after fledging.

The number of chicks successfully fledged nest¹ was higher in 1995/96 than in 1996/97 (Mann-Whitney U_{8,10} = 55.5, P < 0.05, 1-tailed). The number of successful versus unsuccessful nests followed a similar pattern (Fisher exact test, P < 0.057, 1-tailed).

Juvenile dispersal

Following their fledging, the female usually roosted within 1 m of the chicks. The male was also usually close by, and was capable of feeding and caring for at least 1 fledgling, as one male did when his mate died shortly after their chicks fledged.

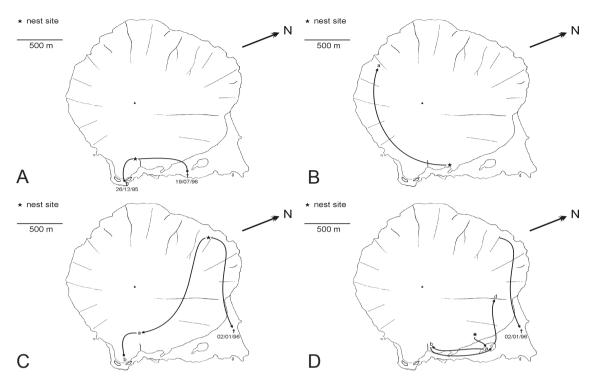


Fig. 4 Dispersal of fledglings. A, movements of 2 male chicks that fledged on 8 Dec 1995 (smaller chick disappeared 26 Dec; feathers found; cause of death unknown; larger chick stayed near the natal territory except for some movements into neighbouring areas; found dead 19 Jul 1996). B, movements of female chick that left nest in mid-Dec 1995, and had left natal territory by Mar 1996; located roosting on other side of the island (a) near a male, and roosted in his territory at least until early Oct 1996 when transmitter ceased operating. C, movements of 2 female siblings captured 1 week after fledging at end of Dec, when 1 was fitted with transmitter. Its remains were found in a harrier's nest 4 days later. The 2nd chick was located on the other side of the island in mid May (a) and then found roosting with the male of that territory in Sep 1996 (b). They may have attempted to breed as she disappeared during the early part of the breeding season. D Dispersal of 2 chicks, 1 (male) of which was banded and fitted with a transmitter (solid line). This chick remained close to the adults until Mar before moving into the bush patch (a). It was then found roosting in a nearby territory (b) in Jun, before returning to the bush island (c) in Jul and Aug. In late Sep it moved in the opposite direction (d), where he was found until the transmitter failed in early Oct. Fate of its sibling of unknown sex unknown.

With time, the distance between fledglings and adults increased (Fig. 3). Fledglings began to explore the natal territory and gradually expanded their **movements into neighbouring territories**. Dispersal of 4 fledglings from their natal territories is shown in Fig. 4A-D. The 1st (male) chick fledged along with its younger sibling on 8 Dec 1995. It stayed in its natal territory until it was found dead (possibly killed by a harrier) on 19 Jul 1996 (Fig. 4A). During this time, the bird made 'exploratory' movements, spending several days outside the natal territory, but generally it stayed in, or close to, its natal territory until its death.

The 2nd (female) chick fledged on 16 Dec 1995, and was in its natal territory until 24 Feb 1996 (Fig. 4B). On 30 Mar 1996 it was discovered on the far side of the island, in a gully, roosting near a male morepork. This female was located several times in this area, roosting close to the male, and was last seen in the same area on 1 Oct 1996, when its transmitter failed.

The 3rd (female) chick fledged in late Dec 1995, along with her sibling; neither was fitted with a transmitter. The fledgling was last seen in its natal territory on 30 Dec 1995 (Fig. 4C). On 15 May 1996 she was discovered in the territory of an adult male on the opposite side of the island, where she was seen again on 18 Jun 1996. From then on, the bird was always found in this male's territory. They were seen roosting together in late Sep 1996, and they may have attempted to breed.

The 4th (male) chick fledged with his sibling some time in early Jan 1996 (Fig. 4D). He was found to be still roosting in the natal territory on 16 May 1996, with occasional 'exploratory' movements outside the area. On 17-18 Jun 1996 he was found well outside his natal territory, but on 19 Jul and 8 Aug he had returned. On 26 Sep 1996, he was found roosting well outside the natal territory, and continued to roost in this same area at least until 1 Oct 1996, when the transmitter failed.

Although the sample size is small, the 2 males stayed in or near their natal territories for longer periods than either of the females. Both the females dispersed rapidly, and were subsequently located on opposite sides of the island to where they fledged.

DISCUSSION

General breeding biology

The data presented support Imboden's (1985) observation that moreporks begin laying in early Oct. The nest sites were similar to those found in other studies (Hogg & Skegg 1961; Ramsay & Watt 1971; Imboden 1985; Anderson 1992). The variety of nest sites suggests that moreporks do not have specific requirements for their nest locations. Tree cavities are uncommon on Mokoia, and this may be reflected in the use of tree fern trunks and ground sites. However, pairs nested successfully in both kinds of sites, the latter possibly because there were no mammalian predators.

Clutch size was also similar to that given by Imboden (1985) and Heather & Robertson (1996). The incubation period of at least 24 days recorded in this study accords with the broad span of '20–30 days' given by Heather & Robertson (1996), and the evidence suggested it was *c*. 30 days, again being similar to the 30–31 days given by Imboden (1985). This is close to that of boobooks: 33 days (Fleay 1926); 26-33 days (Schodde & Mason 1980). It was confirmed that only females incubate and brood nestlings, as in other *Ninox* owls, such as powerful owls (*Ninox strenua*), rufous owls (*Ninox rufa*), barking owls (*Ninox connivens*), and boobooks (Fleay 1942; Fleay 1968; Schodde & Mason 1980).

The single chick for which data were obtained had a nestling period of 39 days. This is longer than the 34 days suggested by Imboden (1985) and *c*. 35 days cited by Heather & Robertson (1996). The nestling period for Fleay's (1926) captive boobook pair was 43 days, whereas Schodde & Mason (1980) estimated 5–6 weeks (35-42 days) and Olsen & Trost (1998) 6 weeks (42 days) for boobooks. Further work is needed to determine the fledging period of the New Zealand morepork.

The cause of death for most chicks observed during this study was unknown. One nestling may, however, have been a victim of siblicide, which is common in owls and hawks (Mock 1985), and 2 juveniles may have been eaten by harriers.

The automated camera system proved useful. The male visited the nest twice as often as the female, which agreed with Imboden's (1985) finding that the male feeds the female on the nest, but our results show that the female also delivers prey to the nest. All identifiable prey items delivered to the nest were invertebrates. This is puzzling because prey remains found during day-time nest examinations are usually vertebrate (Chambers *et al.* 1955; Hogg & Skegg 1961; Ramsay & Watt 1971; Anderson 1992; Stephenson 1998; Stephenson, unpubl. data). The importance of invertebrate prey may be underestimated in studies that rely on nest contents only.

The frequency of nest visits was also interesting. The peak in the first few hours after sunset was expected, but the continuous visits during the night and the lack of a peak before sunrise, were not anticipated. A bimodal pattern of nocturnal visits has been found in flammulated owls (Otus flammeolus) (McCallum et al. 1995; Powers et al. 1996), and moreporks appeared to be more active during the hours before sunrise than during the middle of the night (Stephenson, unpubl. data). The number of visits h⁻¹ also appears to be extremely low, but may be an artefact of our having monitored only 1 of 2 nest entrances. The mean of 16.2 visits night⁻¹ recorded is very low in comparison to the means of 81 and 93 night⁻¹ for recorded flammulated owls (< 50% as large and with a similar clutch size) by McCallum et al. (1995) and Powers et al. (1996), respectively. Prey size may be a factor, because flammulated owls often brought lepidopteran larvae and small moths, which are small in comparison to the relatively large weta brought to the nest by moreporks. A camera with higher resolution might have allowed estimates of the biomass of prey delivered. The advent of high quality digital equipment will facilitate such studies.

Comparison of breeding success in 1995/96 and 1996/97 In Sep 1996, Brodifacoum poison was broadcast on Mokoia I to eradicate mice (Mus musculus) (Stephenson et al. 1999). This could have reduced the breeding success of moreporks by reducing mouse numbers, or by sub-lethal secondary poisoning of breeding adult moreporks. Breeding success was indeed lower in the 1996/97 season than in 1995/96. For 1996/97, both the number of fledged chicks and the percentage of successful nests decreased. Mouse numbers decreased after the poisoning operation, and numbers of invertebrates had not yet recovered (Stephenson 1998). Nevertheless, this interpretation should be treated with caution, because the sample sizes were small and factors unrelated to the Brodifacoum poison, such as weather, could have affected the breeding success of moreporks on Mokoia I that season. Further research will be needed to determine the extent of natural annual fluctuations in morepork breeding success

The low nest site fidelity recorded during this study was possibly related to deaths caused by the rodent poisoning operation (Stephenson *et al.* 1999).

The potential relationships between pest eradication operations and nesting behaviour in moreporks also warrant further study.

Juvenile survival and dispersal

Survival of juvenile moreporks on Mokoia I appeared to be low in the study years. The cause of most post-fledging deaths was unknown. Two juveniles do appear to have been killed by harriers. Juvenile survival after the 1995/96 breeding season may have also been affected by the poison operation in Sep 1996, *c*. 9 months after most chicks would have fledged. However, as only 2 of the 9 chicks that fledged that season were known to have survived to Sep, the effect of the poioning operation on fledglings is unknown.

Many species of owl, including spotted owls (*Strix occidentalis*) (Willey 1995), Ural owls (*Strix uralensis*) (Lundberg 1981), tawny owls (*Strix aluco*) (Southern 1970), and eastern screech-owls (*Otus asio*) (Belthoff & Ritchison 1989), experience high mortality rates in the first few months after fledging. This may result from the difficulty of learning to locate and catch prey, and possibly also be both the result of and the reason for the highly territorial behaviour of many owls.

The process of dispersal of juvenile moreporks is protracted. Juveniles generally stayed within their natal territories for the 1st 2-3 months, gradually roosting further from the adults. In Australia, juvenile boobooks may be fed by their parents for a month or so after fledging and may remain in the parents' territory until the following autumn (Schodde & Mason 1980). Olsen & Trost (1998) found that a female boobook stopped feeding the chicks 2–4 weeks after fledging, after which they started to follow the male and to roost with him. We found no evidence of such behaviour, but instead found that fledglings appeared to be dependent for a period of at least 2 months, with juveniles roosting further away from both adults during their 3rd month after fledging, as against *c*.1 month for boobooks (Olsen & Trost 1998). Although sample size was small, juvenile females appeared to disperse earlier and further than males, leaving their natal territories and moving to the far side of the island where they quickly paired with 'bachelor' males. This is consistent with the natal dispersal of most territorial birds, in which the female is generally the dispersing sex (Greenwood 1980).

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Breeding biology of New Zealand morepork 315

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