REPRODUCTIVE SUCCESS OF THE PROVIDENCE PETREL *PTERODROMA SOLANDRI* ON LORD HOWE ISLAND, AUSTRALIA

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SUMMARY

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The only significant breeding locality of the Providence Petrel *Pterodroma solandri* is Lord Howe Island, Australia, where the population is considered Vulnerable. During the 2000 and 2001 breeding seasons, data were collected on hatching, fledging and breeding success, and on egg and chick mortality. Annual breeding success was 34%–36% in burrows that were visited repeatedly and among adults and chicks handled at least once, and 54% in burrows that were visited only twice and contents not handled. The breeding success of individual adults was positively correlated with body condition, the relationship being stronger for males than for females. Egg losses occurred throughout the incubation period, but chick losses were concentrated within the first four weeks from hatching. Egg and chick mortality were strongly correlated with the distance of the nest from the burrow entrance, with more losses occurring in nests close to the entrance. The main causes of breeding failure were inundation of burrows and predation of eggs and chicks by the endemic Lord Howe Woodhen *Gallirallus sylvestris.* Although breeding success was less than that of some other procellariiforms, we were unable to identify any new conservation measures to enhance reproductive output.

Key words: Providence Petrel, *Pterodroma solandri,* breeding success, predation, Lord Howe Woodhen, body condition index (BCI), investigator disturbance

INTRODUCTION

The only significant breeding locality of the Providence Petrel *Pterodroma solandri* is Lord Howe Island, Australia, where about 32 000 pairs currently breed (Bester 2003). The species was once numerous on Norfolk Island, but no longer breeds there. In 1790, H.M.S. *Sirius* sank on its way to resupply the island's newly established penal colony. That year, Norfolk's garrison and convicts avoided starvation by slaughtering more than 171 000 nesting Providence Petrels and their young (Whitley 1934). Further hunting, together with depredations by feral Domestic Pigs *Sus scrofa,* saw the entire population of petrels extirpated by 1800 (Whitley 1934). The species was thought to be extinct within the Norfolk Group until, in 1985, a small population of approximately 20 birds was discovered breeding on Philip Island (Hermes *et al.* 1986).

In view of its restricted breeding distribution, the Providence Petrel is classified as Vulnerable in the 2006 IUCN Red List of Threatened Species (IUCN Species Survival Commission 2007). Because no detailed studies have been conducted on the Providence Petrel, little is known about its breeding ecology or population demography. Without this information, any threatening processes operating on Lord Howe Island are likely to go unidentified and unmitigated, potentially exposing the petrel to the risk of further population decline.

Early settlers introduced pigs to Lord Howe Island as a food resource around 1800 (Miller & Mullette 1985), and feral populations soon established (Hutton 1991). Before they were eradicated from the island in 1981, pigs greatly reduced the lowland colonies of Providence Petrel (Miller 1980, Miller & Mullette 1985). The Ship or Black Rat *Rattus rattus* arrived on the island in 1918 when the supply ship *Makambo* was deliberately beached after sustaining damage from a collision with submerged rocks (Hindwood 1940). Rats are believed to have been responsible for the extinction of five endemic species or races of island songbirds and the decline of several others on Lord Howe (Hindwood 1940). Their impact on the Providence Petrel has never been assessed. Masked Owls *Tyto novaehollandiae* were introduced onto the island in the late 1920s to control the rats (Hindwood 1940). This attempt at biologic control was unsuccessful, and the population of owls that became established now preys upon several species of seabirds, including the Providence Petrel (Miller & Mullette 1985).

Of these introduced predators, only the pigs have been removed. The impact that each of the remaining species has on the Providence Petrel population is unknown. In addition, two endemic and threatened species, the Lord Howe Woodhen *Gallirallus sylvestris* and Lord Howe Pied Currawong *Strepera graculina crissalis,* have been recorded taking Providence Petrel eggs and chicks (Disney 1977, Miller & Mullette 1985, Hutton 1991). The extent of this predation is also unknown.

The present study investigated the hatching, fledging and breeding success of Providence Petrels on Lord Howe Island during two consecutive breeding seasons. The potential adverse effect of investigator disturbance was examined, as was the relationship between adult body condition and breeding success. The causes of land-based mortality were identified and the potential impact of these threats on the petrel population was assessed.

METHODS

Study sites

Lord Howe Island (31°30′S, 159°05′E) is an oceanic island of 1455 ha, located in the Tasman Sea approximately 580 km east of the Australian mainland. Two large mountains, Mount Gower (875 m) and Mount Lidgbird (777 m), dominate the landscape. Providence Petrels nest predominantly on the summits of these two mountains, although small scattered colonies occur at lower elevations. In 2000, two colonies were sampled: the large colony on the summit of Mount Gower and the much smaller colony at the western foot of Mount Lidgbird (Fig. 1). In 2001, only the colony on Mount Gower was sampled. Both sites are regularly baited for rats to reduce the losses of palm seed, a resource that is commercially harvested and exported. Rainfall data was extracted from the records of the meteorology station on Lord Howe Island.

Breeding biology

The Providence Petrel is a burrow-nesting seabird that breeds during the austral winter, with adults arriving on Lord Howe Island in late February and March (Hindwood 1940, McKean & Hindwood 1965). Observations indicate that breeding occurs at the same time each year (Whitley 1934; Fullagar, P.J., Clark, R. & Bell, R. cited in Marchant & Higgins 1990). Females lay a single egg in mid- to late May (Whitley 1934), which is not replaced if lost. The incubation period is approximately 55 days, and the parents share incubation duties (Bester 2003). Hatching typically starts in mid-July, and most chicks have fledged by November (Marchant & Higgins 1990). No detailed study of the species' breeding biology has been conducted.

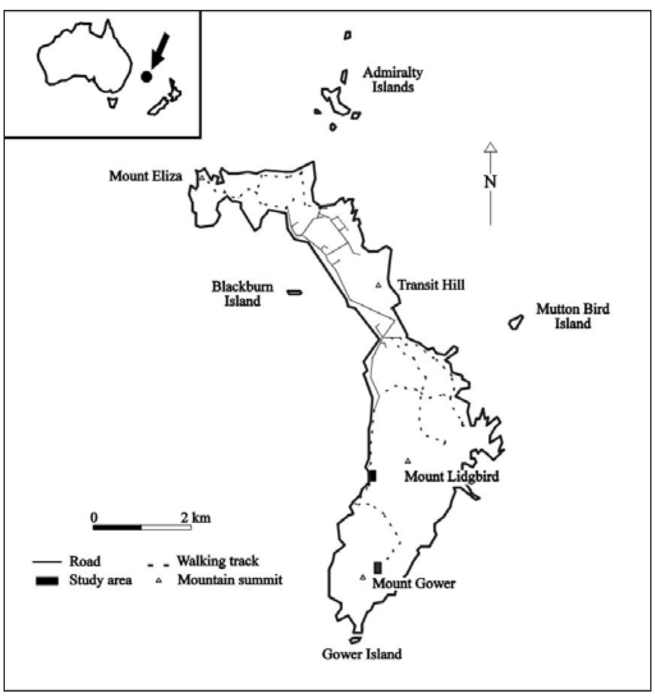

Fig. 1. Location of the two study areas on Lord Howe Island, Australia.

Sampling

Our study was conducted over two consecutive years: 2000 and 2001. In both years, the study commenced shortly after egg-laying and concluded around the time of fledging (22 May to 28 October 2000, 29 May to 14 October 2001). In May of each year, the study area was randomly searched to locate petrel burrows; these were then inspected by hand, and their contents recorded. Each burrow that contained an egg (n = 272 in 2000, n = 171 in 2001) was marked with a numbered plastic tag. During this initial visit, any adult present in the burrow was removed and banded with an individually numbered metal band. Mass, bill length, tarsus length and wing length (maximum flattened straightened wing chord) were measured using techniques described by Lowe (1989). Eggs were also removed from the burrow, measured and weighed. Data on egg size and mass are to be published elsewhere. A graduated flexible probe was used to measure the distance from the centre of the nest to the burrow entrance to the nearest 5 cm. Not all nests were at the rear of the burrow, and so where practicable, the total length of the burrow was also measured. Eggs and adults were then returned to the burrow.

Marked burrows were inspected at 10-day intervals, and their contents were recorded. Minor departures from this sampling regime occurred to avoid handling birds when it was raining. Marked burrows on Mount Gower were initially divided into two categories according to the level of investigator disturbance. "High disturbance" burrows (n = 57 in 2000, n = 58 in 2001) were those where, at each inspection, adults and chicks (if present) were removed from the burrow, identified and weighed. At each inspection, chicks were measured (bill, tarsus and wing lengths) in the same way as described above for adults. Data on chick growth rates are to be published elsewhere. "Low disturbance" burrows (n = 215 in 2000, n = 56 in 2001) were also inspected approximately every 10 days. The presence of adults, eggs and chicks was noted, but neither eggs nor birds were removed or unduly disturbed. In 2001, a third category of "minimally disturbed" burrows (n = 57) was added. These burrows were inspected only at the beginning and end of the breeding season. The presence of an egg or fledgling was determined by feel alone, and no egg, adult or chick was removed from the burrow. Because disturbance was the key difference between treatments, burrows with similar disturbance levels were clustered; those disturbed least were sited further from access trails. Burrows in the colony at the foot of Mount Lidgbird were all low-disturbance burrows.

Any marked burrows subsequently found to be empty were searched for the remains of an egg or chick, and were inspected for evidence that could help to identify the cause of egg or chick mortality. Eggs attacked by rats could usually be identified from teeth marks on the shell. Similarly, the remains of chicks attacked by rats often had chew marks and were generally distinguishable from chicks that had been dismembered by avian predators. Digging and other signs of predator activity near the burrow were also noted. In addition, we inspected every burrow after each downpour that occurred while we were present, noting those that had been inundated. Inundated eggs often floated out of the nest or even out of the burrow. Loss of eggs abandoned in sodden burrows or displaced some distance from the nest was attributed to inundation.

Estimation of hatching, fledging and breeding success

Hatching success was calculated as the proportion of eggs laid that hatched successfully. Fledging success was calculated as the proportion of chicks that subsequently fledged successfully. Breeding success was calculated as the proportion of eggs that produced fledglings. No estimate of hatching success or fledging success was possible for the "minimally disturbed" burrows, because these were inspected only at the beginning and end of the breeding season. Chi-square analyses were used to test whether hatching, fledging or breeding success differed between the two study sites or the various levels of disturbance. Where no differences were discernible, data were pooled. Data for each year (2000 and 2001) were analysed separately. Chi-square analyses were used to determine whether hatching, fledging or breeding success differed between years.

Effect of adult body condition on breeding success

To obtain an estimate of the body condition of breeding adults, we investigated the relationship between body mass and body size (measured by tarsus, culmen and wing lengths) using Principal Component Analysis (Tveraa *et al.* 1997). The residuals from the resulting regressions (i.e. the differences between actual and predicted values) provided an adult body condition index (BCI) each time an individual was weighed. Where multiple masses were recorded for the same individual, the median BCI was used in all analyses. To examine whether adult body condition influenced breeding success, breeding individuals were ranked according to their BCI, and successful and unsuccessful breeders were compared using Mann–Whitney U tests.

RESULTS

Hatching, breeding and fledging success

In 2000, the only year that two study sites were sampled, 215 low-disturbance burrows were monitored: 184 on the summit of Mount Gower and 31 at the foot of Mount Lidgbird. For these burrows, the two study sites showed no significant difference in hatching success ($\chi^2_1 = 0.44$, $p = 0.805$), fledging success ($\chi^2_1 = 0.03$, $p = 0.987$) or breeding success ($\chi^2_1 = 0.14$, $p = 0.932$). Thus, the data from the two sites were combined.

Table 1 shows hatching, fledging and breeding success for each disturbance regime and each year. In both years, high- and low-disturbance burrows showed no significant difference in hatching success (2000: $\chi^2_1 = 2.989$, $p = 0.084$; 2001: $\chi^2_1 = 0.328$, $p = 0.567$), fledging success ($\chi^2_1 = 1.319$, $p = 0.251$; $\chi^2_1 = 0.010$, $p = 0.920$) or breeding success ($\chi^2_1 = 0.515$, $p = 0.473$; $\chi^2_1 = 0.113$, $p = 0.737$). Therefore, data from high- and low-disturbance burrows were combined and are hereafter referred to as "disturbed burrows." Overall hatching success for disturbed burrows in 2000 (n = 272) was 45.2%, fledging success was 74.8%, and breeding success was 33.8%. Overall hatching success for disturbed burrows in 2001 (n = 114) was 52.6%, fledging success was 68.3%, and breeding success was 36.0%. No discernible difference in any of these three breeding parameters was evident between years ($\chi^2_1 = 1.770$, $p = 0.183$; $\chi^2_1 = 0.848$, $p = 0.357$; $\chi^2_1 = 0.163$, $p = 0.686$ respectively). Breeding success in the minimally disturbed burrows in 2001 was 54.4% (Table 1), the highest breeding success recorded for any disturbance regime in that year. The difference between this and other disturbance regimes in 2001 approached significance at the 5% level of probability ($\chi^2_2 = 5.396$, $p = 0.067$).

Effect of adult body condition on breeding success

The Principal Component Analysis identified culmen length as the best predictor of body mass for both males ($r_s = 0.10$, n = 52, $p = 0.025$) and females ($r_s = 0.20$, n = 52, $p = 0.001$). The residuals from these regressions were used as a BCI.

A significant difference was evident in the BCI of males that successfully fledged chicks as compared with those that did not (Mann–Whitney $U = 595.50$, n = 53, $p < 0.001$). Similarly, females that successfully produced fledglings had a greater BCI than did females that failed, but the relationship ($U = 831.50$, n = 53, $p = 0.058$) was weaker than that seen with males. No significant relationship was evident between the body condition of either male or female parents and hatching success ($U = 313.50$, n = 53, $p = 0.903$; $U = 289.00$, n = 53, $p = 0.452$ respectively).

Effect of burrow length on breeding success

Mean burrow length (data from 2000 and 2001 pooled) was 82 ± 15 cm (range: 40–140 cm; n = 263), and the mean distance from the burrow entrance to the nest was 57 ± 15 cm (range: 20–100 cm; n = 443). No significant difference was discernible between the length of burrows that successfully fledged chicks and those that failed (Student $t_{261} = 0.78$, $p = 0.435$). However, the distance between the nest and the burrow entrance differed significantly between successful and unsuccessful breeding attempts (Mann–Whitney $U = 20038.50$, n = 443, $p = 0.004$), with nests close to the burrow entrance experiencing significantly greater mortality (Fig. 2).

Causes of egg and chick mortality

The reasons for failure were recorded for 72 of the 180 failed nests in 2000 and 27 of the 73 failed nests in 2001 (Table 2). In both years, the two predominant causes of egg and chick loss were inundation of burrows and predation by Lord Howe Woodhens. Inundation accounted for 22.2% of all known losses in 2000 and 40.7% in 2001 (Table 2). Woodhen predation accounted for 23.6% and 33.3% (Table 2). Although abandonment was also recorded as a major cause of egg loss in both years, some eggs were abandoned after having been incubated beyond the normal incubation period. Many

TABLE 1

Hatching, fledging and breeding success of Providence Petrels *Pterodroma solandri* in high-disturbance ("high"), low-disturbance ("low") and minimally disturbed ("min.") burrows on Lord Howe Island during 2000 and 2001

	2000			2001			
	High	**Low**	**Combined**	**High**	**Low**	**Combined**	**Min.**
Eggs (n)	57	215	272	58	56	114	57
Chicks (n)	20	103	123	29	31	60	
Fledglings (n)	17	75	92	20	21	41	31
Hatching success (%)	35.1	47.9	45.2	50.0	55.4	52.6	
Fledging success (%)	85.0	72.8	74.8	69.0	67.7	68.3	
Breeding success (%)	29.8	34.9	33.8	34.5	37.5	36.0	54.4

of these would have been infertile or dead when the adult deserted. Similarly, some of the mortality attributed to predation may also have occurred only after the egg was abandoned. Investigator interference accounted for 15.3% of all recorded mortality in 2000, but none in 2001. Mortality attributable to other causes (Table 2) was relatively minor.

Timing of egg and chick mortality

Table 3 shows the number of eggs and chicks lost during each 10-day period. Mortality was not uniform throughout the breeding season (2000: $\chi^2_{15} = 306.4$, $p < 0.001$; 2001: $\chi^2_{13} = 115.5$, $p < 0.001$). In both years, egg losses occurred throughout incubation (periods 1–5), and peaked around the time of hatching (periods 5–6), the result of many (presumably non-viable) eggs being abandoned. Chick losses were concentrated in the early part of chick rearing (periods 6–7). Deaths of chicks older than 30 days were uncommon.

Despite inundation being a major cause of egg and chick mortality, the number of deaths in each 10-day period was not significantly correlated with total rainfall during that time (2000: $r_s = 0.07$, n = 16, $p = 0.790$; 2001: $r_s = 0.22$, n = 13, $p = 0.474$). Neither was any correlation evident between Woodhen predation and rainfall (2000: $r_s = -0.02$, n = 16, $p = 0.954$; 2001: $r_s = 0.136$, n = 13, $p = 0.659$).

DISCUSSION

Disturbance effects

Breeding success within minimally disturbed burrows was higher than that within high- or low-disturbance burrows, the difference approaching statistical significance at the 5% level of probability. However, no difference in breeding success was evident between low- and high-disturbance burrows. Together, these results indicate that the level of disturbance associated with inspecting the burrow contents every 10 days and handling the adult and chick once may have caused a reduction in breeding success. However, further disturbance, to repeatedly extract and replace adults and chicks, did not lead to a further decrease in breeding success.

Disturbance effects have been reported for other procellariiforms. For example, Sooty Shearwaters *Puffinus griseus* and Flesh-footed Shearwaters *P. carneipes* are particularly prone to disturbance, and a high proportion of adults will desert their egg if handled during incubation (Warham 1990; DP pers. obs.). Weekly handling of

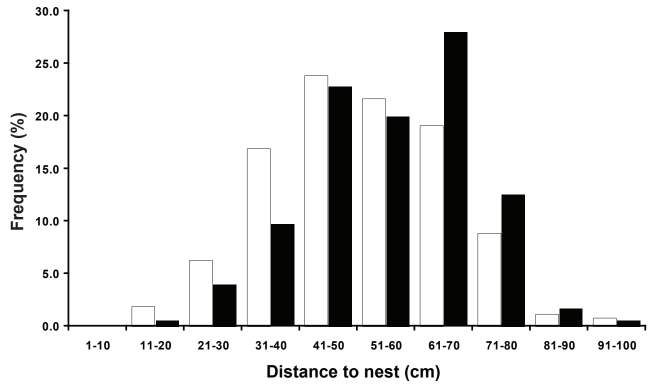

Fig. 2. Frequency distribution (%) of distance from Providence Petrel *Pterodroma solandri* nests to the burrow entrance for successful (solid bars, n = 164) and unsuccessful (open bars, n = 279) breeding attempts on Lord Howe Island during 2000 and 2001.

TABLE 2
Causes of egg and chick mortality of Providence Petrels *Pterodroma solandri* on Lord Howe Island during 2000 and 2001

Cause of mortality	2000						2001					
	Eggs		Chicks		Combined		Eggs		Chicks		Combined	
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)
Inundation	8	21.1	8	23.5	16	22.2	3	23.1	8	57.1	11	40.7
Woodhen *Gallirallus sylvestris* predations	6	15.8	11	32.4	17	23.6	4	30.8	5	35.7	9	33.3
Abandonment	11	28.9	4	11.8	15	20.8	6	46.2	0	0.0	6	22.2
Investigator interference	7	18.4	4	11.8	11	15.3	0	0.0	0	0.0	0	0.0
Burrow collapse	4	10.5	2	5.9	6	8.3	0	0.0	0	0.0	0	0.0
Rat predation	2	5.3	2	5.9	4	5.6	0	0.0	1	7.1	1	3.7
Died on hatching	0	0.0	3	8.8	3	4.2	0	0.0	0	0.0	0	0.0
TOTAL	38	100.0	34	100.0	72	100.0	13	100.0	14	100.0	27	100.0

TABLE 3
Timing of loss of Providence Petrel *Pterodroma solandri* eggs and chicks on Lord Howe Island during 2000 and 2001 [a]

	10-Day period																
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**TOTAL**
2000	9	10	25	18	36	51	12	8	4	0	3	0	0	2	1	1	180
2001	—	11	6	4	8	20	21	2	0	1	0	0	0	0	—	—	73
TOTAL	9	21	31	22	44	71	33	10	4	1	3	0	0	2	1	1	253

[a] The first 10-day period corresponds to 22–31 May 2000 and 19–28 May 2001. In 2001, the study did not commence until Period 2, and it concluded at the end of Period 14.

Leach's Storm-Petrels *Oceanodroma leucorhoa* reduced breeding success by 50% (Blackmer *et al.* 2004), and daily handling of Fork-tailed Storm-Petrels *O. furcata* reduced hatching success from 84% to 58% (Boersma & Wheelwright 1979). Investigator disturbance also increased breeding failures in the Northern Fulmar *Fulmarus glacialis* (Ollason & Dunnet 1986). On the other hand, some species, such as the Gould's Petrel *Pt. leucoptera,* are not prone to disturbance effects (O'Dwyer *et al.* 2006). A number of factors, including body size and nesting behaviour (surface- or burrow-nesting), probably influence a species' susceptibility to disturbance.

In this study, investigator disturbance caused 11 deaths directly. Five eggs were broken while extracting adults from the burrow, and one egg was crushed when the burrow collapsed under the weight of the investigator. On one occasion, disturbance elicited such a violent response by a parent that the bird destroyed its own egg; another disturbed adult attacked and killed its chick. Similar reactions have been reported in other studies (e.g. Gillham & Thomson 1961, Serventy *et al.* 1971, Serventy & Curry 1984, Simeone & Schlatter 1998). Another three chicks died after having regurgitated while being handled during the previous visit; although other causes may have contributed, we attributed these deaths to our interference.

Breeding success

Annual breeding success was 34%–36% in high- and low-disturbance burrows and 54% in minimally disturbed burrows. These estimates were based on egg and chick survival during the interval between the first and last inspection of each burrow. This method slightly overestimates breeding success because it excludes eggs lost before the first inspection and chicks that died after the last inspection but before fledging. No attempt was made to correct for these unknown losses. Allowing for the effects of investigator disturbance and slight differences in methodology between studies, the breeding success of the Providence Petrel on Lord Howe Island falls within the broad range recorded for most stable procellariiform populations (e.g. Brooke 1978, Byrd *et al.* 1983, Floyd & Swanson 1983, Schramm 1983, Tomkins 1985, Green & Johnstone 1986, Fugler *et al.* 1987, Austin & Edmunds 1994, Cooper *et al.* 1995, Priddel & Carlile 1997).

In some situations, it has been possible to increase breeding success of threatened petrels through direct conservation action undertaken to ameliorate threats. For example, the Great-winged Petrel *Pt. macroptera* on Marion Island had a breeding success as low as 0%, but success increased to 60%–64% after the eradication of feral Domestic Cats *Felis catus* (Cooper *et al.* 1995). Similarly, Priddel & Carlile (1997) recorded about 20% breeding success in Gould's Petrel before the removal of entangling plants and avian predators, but up to 59% afterwards. However, we uncovered no anthropogenic impacts or threats (other than disturbance by researchers) that could affect the breeding success of the Providence Petrel on Lord Howe Island. Consequently, beyond maintaining the existing rat control program and minimising disturbance, no conservation measures to enhance reproductive output were identified.

Breeding success was positively correlated with body condition of the parents, although the relationship was much weaker for females than for males. Chastel *et al.* (1995) found a similar relationship for male Blue Petrels *Halobaena caerulea,* but female breeding performance was related to breeding experience, not to condition. No significant relationship was evident between the body condition of Providence Petrels and hatching success, suggesting that body condition had the most influence on breeding success during the chick-rearing period. Bester (2003) found that adult Providence Petrels in poor body condition fed their young smaller-than-average meals and produced chicks with relatively low body mass, which in turn is likely to affect chick survival and thus breeding success. Adult body condition is presumably determined by prey availability, a topic about which we know very little for this species.

Causes of mortality

Inundation of burrows after heavy rain was the primary cause of egg and chick mortality. By extrapolating the data from failed nests where the cause of mortality was identified to all nests, we estimate that the proportion of nesting attempts that failed because of inundation was 14.7% in 2000 and 26.1% in 2001. Three heavy downpours were witnessed during the 2000 breeding season (daily rainfall: 27 May, 50 mm; 11 July, 45 mm; 21 October, 32 mm), and four during 2001 (daily rainfall: 21 June, 22 mm; 15 July, 23 mm; 27 July, 48 mm; 27 August, 27 mm). Each downpour resulted in numerous burrows being inundated. Inundated eggs rapidly became chilled, seldom hatched and were generally abandoned soon afterwards. Small chicks were also extremely vulnerable to inundation. The down of nestlings, unlike that of adults, is not water repellent and quickly becomes waterlogged (Warham 1996). Saturated young chicks, unable to maintain body temperature, can die from hypothermia. Older chicks are better able to withstand inundation (as was observed after the downpour on 21 October 2000) because by this stage they are homeothermic, protected by a dense layer of subcutaneous fat, and have developed some waterproof feathers. Also, many burrows contained an elevated platform at the rear of the nest chamber. Some older, more-mobile chicks retreated to this platform so as to remain above the floodwater. Inundation also weakened some burrows, causing them to collapse later.

Given the high losses to inundation, the breeding success of the Providence Petrel on Lord Howe Island could be expected to be greater at lower elevations, where rainfall is less than that on Mount Gower. Yet we found no difference between the breeding success on Mount Gower and that at the foot of Mount Lidgbird. However, because of the rarity of burrows at low elevations, the sample size in this study was too small to adequately examine this question.

Predation was another major cause of egg and chick mortality, although some eggs may have been abandoned before they were taken. The proportion of breeding attempts that failed because of predation was estimated to be 19.3% in 2000 and 23.7% in 2001. The Lord Howe Woodhen was the principal predator (or scavenger) responsible, accounting for 24%–33% of all breeding failures (16%–21% of all breeding attempts). Ship Rats accounted for predation in only 3.7% and 2.4% respectively of breeding attempts in those years.

Woodhens preyed predominantly on eggs or on young chicks; only three of the 16 chicks taken were older than four weeks. Adult Providence Petrels are aggressive and capable of repelling potential predators. However, adults generally guard the chick for only 1-4 days after hatching (Bester 2003). After that time, they return to sea to feed, leaving the chick unguarded. Our repeated visits to the nests may have triggered or increased nest predation by Woodhens; however, no direct evidence of any such observer effect was noted. Moreover, other rails routinely prey on the young of ground-nesting birds. For example, Wekas *Gallirallus australis* often take chicks and eggs of the Westland Petrel *Procellaria westlandica* (Taylor 2000).

Nest-site characteristics can influence the susceptibility of eggs and chicks to predators (Hudson 1982, Martin & Roper 1988, Seddon & Davis 1989, Frere *et al.* 1992), and in our study, distance to nest played an important role in breeding success. Woodhens were generally reluctant to venture deep into burrows; they would enter burrows to take petrel eggs or chicks only when the nest was close to the entrance. Woodhens were observed on a number of occasions taking Providence Petrel chicks from within deep burrows by excavating a hole in the roof of the nest chamber and then, through this hole, extracting the chick below. Dyer & Hill (1992) recorded a lower hatching rate in short burrows of the Wedge-tailed Shearwater *Puffinus pacificus,* although whether burrow length was related to predation was not investigated. On Montague Island, where predators are absent, Schultz (2001) found no relationship between burrow length and the breeding success of Wedge-tailed and Short-tailed Shearwaters *Puffinus tenuirostris.*

Many seabird populations on Lord Howe Island have declined markedly since the arrival of humans in 1788 (McAllan *et al.* 2004). Rats undoubtedly contributed to this process, having caused severe declines in numerous seabird populations worldwide. A few examples include the Dark-rumped Petrel *Pt. phaeopygia* on the Galapagos Islands, Bonin Petrel *Pt. hypoleuca* on Midway Island, Kerguelen Petrel *Pt. brevirostris* on Kerguelen Island, and Wilson's Storm-Petrel *Oceanites oceanicus,* Grey-backed Storm-Petrel *Garrodia nereis* and Common Diving Petrel *Pelecanoides urinatrix* on the Falkland Islands (Moors & Atkinson 1984, Woods & Woods 1997). Also, rats have significantly lowered the breeding productivity of many species, including Little Shearwater *P. assimilis* and Pycroft's Petrel *Pt. pycrofti* on Coppermine and Lady Alice Islands in New Zealand (Pierce 2002). Rats prey on the eggs and chicks of smaller seabirds in particular (Booth *et al.* 1996). Within the Lord Howe Island Group, White-bellied Storm-Petrels *Fregetta grallaria* are now restricted to small rat-free islets. Their extirpation from the main island is almost certainly attributable to rats. In contrast to these demonstrated impacts, the effect of rat predation on Providence Petrel breeding success is relatively minor. The reasons are unclear. Providence Petrels are large birds [adults weigh 395–670 g (Bester 2003)] and are probably not as vulnerable to rats as many smaller species are. Alternatively, rat predation on Mount Gower may possibly have been low because of an abundance of alternative food in this particular habitat [gnarled mossy forest (Pickard 1974)]. Fleet (1972) found that Pacific Rats *Rattus exulans* turned to predation only when plant food was in short supply. A third possible explanation is that routine baiting to control rats on parts of Lord Howe Island (including Mount Gower) significantly reduced the potential impact of this introduced pest. Imber *et al.* (2000) reported high rates of rat predation of petrels on Whale Island, New Zealand, in years when no rat control was undertaken, and an appreciable increase in breeding success when rat control measures were implemented.

Incidental observations of predation on Providence Petrel outside the study area involved both the endemic Lord Howe Pied Currawong and the introduced Masked Owl. A group of five currawongs was observed to attack and kill a large petrel chick. Two incidences of an owl attacking a petrel were also observed: one attack on an adult petrel was successful; the other, on a near-fledged chick, failed.

Overall, 11% of Providence Petrel eggs were recorded as having been abandoned. This was less than the percentage reported for some other species such as the Great-winged Petrel [41% (Schramm 1983)], the Soft-plumaged Petrel *Pt. mollis* [40% (Schramm 1983) and the Short-tailed Shearwater [42% (Serventy & Curry 1984)]. However, adult birds abandon eggs for a variety of reasons, including egg infertility, breeding inexperience, death of a mate, inadequate pair-bond strength (Weimerskirch & Jouventin 1987, Brooke 1990, Meathrel *et al.* 1993) and disturbance (Serventy *et al.* 1971). In the present study, eggs were also abandoned after having been inundated. Had we not differentiated the effects of inundation from abandonment, the rate of egg abandonment would have been much higher. On the other hand, many abandoned eggs may have been taken by predators, with the abandonments therefore unrecorded. In view of these confounding effects, the rate of abandonment was not considered further.

CONCLUSIONS

As is the situation for many other species of threatened seabirds, management decisions regarding the conservation of the Providence Petrel on Lord Howe Island must be made in the absence of detailed knowledge of population trends. Although long-term monitoring of population size is fundamental to any informed conservation action (Caughley and Gunn 1996), no such monitoring programme for the Providence Petrel exists. Without it, this study provides the only information available to guide management decisions. It gives the first measures of reproductive success for the Providence Petrel and identifies key factors affecting egg and chick mortality.

Although breeding success for the Providence Petrel was less than that for some other burrowing procellariiforms, we uncovered no anthropogenic impacts or threats (other than perhaps investigator disturbance). Consequently, we see no need for conservation action beyond maintaining the existing rat control programme, particularly on Mount Gower. It should be noted, however, that most long-term studies of petrels have found significant annual and geographic variability in breeding success. Short-term studies like this, although giving an approximate assessment of breeding success, often do not accurately reflect long-term trends nor identify the extent or causes of variation (Strayer *et al.* 1986, Bradley *et al.* 1991, Tiller 2003).

Notwithstanding its limitations, this study provides important benchmarks from which initial judgements can be made and future trends assessed. The study has also shed new light on the interactions between the Providence Petrel and the other threatened endemic species that share its breeding habitat. Such information will be invaluable for determining the conservation actions necessary to conserve the full suite of species present on Lord Howe Island.

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