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Insular bird populations can be saved from rats: a long-term experimental study of white-chinned petrels *Procellaria aequinoctialis* on Ile de la Possession (Crozet archipelago)

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Abstract The white-chinned petrel is a subantarctic seabird that requires urgent implementation of conservation measures for the species. At sea, adults suffer heavy mortality due to fisheries' practices. On land, introduced rats prey on chicks at several localities, and we test here if and how rats can be efficiently controlled. Since 1994, we have conducted an intensive rat-control program during each breeding season in a white-chinned petrel colony on Ile de la Possession (150 km²; Crozet archipelago, southern Indian Ocean), which had been monitored since 1986. On the same island, a control white-chinned petrel colony, where no poisoning occurred, was also monitored, and we assessed the seasonal variations of rat abundance. We compared three situations: high rat-poisoning, low rat-poisoning and control conditions without poisoning. Low-poisoning trials performed in our experimental colony between 1988 and 1991 did not lead to higher chick production than for the previous two control years. However, petrel-breeding success was significantly higher when intensive poisoning occurred (50%) than for the previous years (16%). The duration of our study (8 years before intensive poisoning, plus 8 years afterwards), combined with a comparison of petrel annual breeding success between our experimental and control colonies, allowed us to assess more effectively

the impact of rats. Forty-one per cent of breeding failures occurring in non-poisoned areas were attributed to rats. We conclude that threatened insular bird populations can be conserved and restored in localities even where total rat eradication is not possible. However, only intensive and repeated (long-term) poisoning will control rats sufficiently.

Introduction

After habitat transformation, introductions of alien species represent the second most-important cause of loss of biodiversity (Vitousek et al. 1997). Mammalian predators introduced on islands are known to have severely depleted populations of native species, leading some to extinction (e.g. Veitch 1985). In birds, they pose a real problem, since 25% of the 1,008 currently globally threatened avian species have to cope with alien predators (Stattersfield and Capper 2000). These predators can kill adults or young, depending on their respective body sizes. For example, rats (*Rattus* spp.) prey on the eggs and chicks of several seabird species, and the adults of the smaller species (Atkinson 1985). However, direct observations of rat predation are extremely difficult in the field (Brooke 1995), and previous studies generally failed to assess quantitatively the impact of rodents on eggs and chicks, reporting only anecdotal observations of rats feeding on eggs, chicks, adult birds or carrion, or discoveries of empty nests or chick remains with inferred predation (Kepler 1967; Mougou 1970; Brooke 1995; Seto and Conant 1996). Nonetheless, these studies did show that the risk of predation was greatest for birds whose body mass does not exceed the maximum body mass of the rat species introduced (Moors and Atkinson 1984), even if rats can inflict wounds occasionally resulting in death to species much larger than themselves (Kepler 1967).

For burrowing petrels, the effects of predation can be dramatic for several reasons linked to the biology of these species. Many petrels breed on islands that were

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initially free of mammalian predators, and show very high fidelity, not only to their breeding localities, but also to their nests or burrows (Warham 1990; Bried and Jouventin 2002). Hence, they return to these islands despite new threats from introduced predators. Second, petrels lay only one egg per breeding attempt, without replacement. Third, incubating individuals can desert their egg for a couple of days and, lastly, adults leave their chicks unguarded in burrows at a very young age (Warham 1990).

The high adult life expectancy of petrels (up to several tens of years; Warham 1996) and their low fecundity make these species particularly suitable for both long-term studies in conservation biology and experimental restoration programs. In the smaller petrel species, the impact of introduced rats is most apparent because it is drastic and immediate. In the larger species, however, adults are not attacked by rats, so the decrease becomes apparent several (tens of) years after predation on chicks has started, the renewal of generations being impossible once adults have died from senescence. Furthermore, most petrels have a deferred sexual maturity (Warham 1990), so that the number of young recruited as breeders increases only several years after predator eradication.

The subantarctic white-chinned petrel (*Procellaria aequinoctialis*) is the largest burrow-nesting petrel (mean adult mass 1,300 g). On land, its chicks are preyed on by introduced black rats (*Rattus rattus*) and Norway rats (*R. norvegicus*) at several of its main breeding localities (Atkinson 1985). At sea, the white-chinned petrel is the predominant Procellariiforme accidentally caught by fisheries which have been operating in the southern hemisphere since the late 1980s (Vaske 1991; Williams and Capdeville 1996; Stattersfield and Capper 2000). In the Kerguelen area of the southern Indian Ocean, white-chinned petrels represent more than 92% of seabirds accidentally killed by longliners (Weimerskirch et al. 2000). Because population trends of long-lived species like the white-chinned petrel (some individuals can reach 34 years, data from this study) depend predominantly on the variations of adult survival rate (see Jouventin and Weimerskirch 1988), a slight increase in adult mortality in petrels should result in a more rapid decrease in population size than in shorter-lived species (see Weimerskirch et al. 1987). For the larger and long-lived petrels, mitigation measures were implemented at sea to reduce adult mortality, but they are ineffective since large numbers of illegal fishing boats are present in the area (CCAMLR 1997; Weimerskirch et al. 1999). As a result, the current mortality rate cannot be sustained for the white-chinned petrel populations from the Indian Ocean (Weimerskirch et al. 2000). Because fishery mortality and predation due to alien mammals are likely to continue, the white-chinned petrel has been classified as Vulnerable, according to the IUCN Red List criteria (Stattersfield and Capper 2000). Consequently, fishery-based conservation measures need to

be supplemented by measures taken on land at breeding sites. Given the remoteness of the land concerned, this should be relatively easy to implement.

As breeding success of many burrowing petrels seems to be negatively correlated with rat density in the localities where these rodents have been introduced, the most obvious solution to restore current petrel populations would be to eradicate rats wherever and whenever possible. Previous experiments conducted on other burrowing petrel populations showed that birds experienced higher breeding success in colonies where rats were poisoned than in control colonies situated on the same island (Thibault 1995; Seto and Conant 1996). However, experimental colonies were only poisoned during one or two successive years, which is insufficient given that the life-history strategies of petrels are very slow, several years being necessary for a population that had declined to resume growing (Stearns 1992). Here, we investigated the efficacy and potential of this experimental method for the recovery of insular avifauna through a 16-year experimental study, using white-chinned petrels as a test species. Whereas rats can be successfully eradicated on small (up to 31 km²) islands (Taylor et al. 2000; Micol and Jouventin 2003), we tested the efficacy of rat control on a larger island where total eradication currently remains impossible. We also sought to monitor white-chinned petrel vulnerability to predation (this species is highly affected by rat predation, but only the youngest chicks are taken, not the adults).

We conducted our experiment on two white-chinned petrel colonies. Intensive rat-poisoning in the breeding area of one colony was undertaken in the last 8 years. We evaluated the impact of rats by comparing petrel breeding success before and after poisoning, and also between the two colonies ("poisoned" and "control"). The duration of our study enabled us to create three levels of experimental manipulation: (1) "control" years with absence of poisoning (4 austral summers: 1986, 1987, 1992, 1993; to simplify, we use only the last year when designing austral summers: for example, the austral summer of 1986, in fact extends from December 1985 to February 1986), (2) "low intensity" poisoning years (4 summers, from 1988 to 1991), and (3) "intensive poisoning" years (8 summers, from 1994 to 2001), so that we could determine the role of poisoning intensity (see Tomkins 1985) by comparing the effects of low and intensive poisoning of rats on petrel breeding success. Additionally, we monitored relative rat abundance and we determined whether factors other than fluctuations of rat numbers affected the breeding success in white-chinned petrels. Through these spatial (inter-colony) and temporal comparisons, it was possible to extend the earlier studies of Thibault (1995) and Seto and Conant (1996), and take into account the long-term effects of rat-poisoning on the demography of the prey species. Our ultimate aim was to establish a conservation protocol suitable for other threatened insular bird populations.

Materials and methods

Effect of rats on petrels

Field work was carried out at Ile de la Possession, Crozet archipelago (46°25'S, 51°45'E), in the southern Indian Ocean. White-chinned petrels from this island are known to interact with fisheries operations when foraging at sea during the breeding period (Weimerskirch et al. 1999; Catard et al. 2000).

Black rats were inadvertently introduced on Ile de la Possession during the nineteenth century (Atkinson 1985; Johnstone 1985). However, the large area of this island (150 km²) precludes rat eradication using current protocols (Taylor et al. 2000; Micol and Jouventin 2003). Therefore, we decided to assess the effect of rat-poisoning on the reproductive performance of white-chinned petrels by controlling rodents on a 70-burrow colony, using 2 levels of poisoning intensity. This petrel colony (colony A) was monitored from the austral summers of 1986 to 2001 (inclusive). A numbered wooden peg was planted near the entrance of each burrow, enabling fieldworkers to locate and identify burrows over the 16 years. Adults and chicks were banded with Monel rings, allowing individual identification. Pairs were monitored in their burrows annually, at the beginning of the incubating period in late November/early December. Eggs were checked for hatching in mid-January. If no chicks were found in burrows, breeding attempts were considered to have failed during incubation (egg failures). Burrows were inspected again in mid-March, 3–4 weeks before chicks normally fledge (Jouventin et al. 1985). All chicks found were banded. If a burrow containing a chick in mid-January was found to be empty or to contain chick remains at this time, the chick was considered to have died before fledging (chick failure). Chick mortality between banding and fledging was negligible, enabling us to define breeding success as the total number of chicks banded divided by the total number of eggs laid. Because white-chinned petrels are summer breeders, dates (years) of breeding seasons were expressed in the same manner as for austral summers (i.e. 1990 for the 1989–1990 breeding season).

Rats were not poisoned in the 1986 and 1987 breeding seasons. We defined this period as “control-1” period. From 1988 to 1991, low-intensity poisoning trials were conducted by introducing a handful (ca. 40 g) of poisoned baits into the burrows, but only once or twice between late incubation and early chick-rearing. Poisoned baits consisted of oat seeds containing 0.05 g bromadiolone per kg (Supercad Avoine, Liphatech, Lyon, France). Bromadiolone is an anticoagulant rodenticide that has been used effectively against rats on other islands (Moors et al. 1992). This “low poisoning” period was followed by 2 control years (“control-2” period, 1992 and 1993) with no poisoning. The “control-2” period enabled us to separate the “low poisoning” period and the following “intensive poisoning” period and to compare their respective effects on rats and petrels.

Intensive poisoning was carried out over 8 years, beginning in the 1994 breeding season (see Fig. 1, for a timeline of the rat-poisoning events). Three main sessions took place each year, the first one at the beginning of incubation in late November, the second in mid-December and the last in mid-January (i.e. when checking for hatchlings). During each session, 40 g of poisoned bait was put into PVC tubes near (<20 cm) the entrance of each burrow, to prevent trampling by petrels and consumption by indigenous birds (since the bait was now put outside burrows). Bait consumption by rats was checked weekly during late incubation and early chick-rearing periods. Into early February, poison (40 g) was added into each PVC tube that was found to be empty.

To distinguish between the effect of rats and that of short-term phenomena—such as interannual fluctuations in food availability—that could affect reproductive performance, breeding performance of a second white-chinned petrel colony in which no poisoning occurred (colony B, 37 burrows) was also monitored

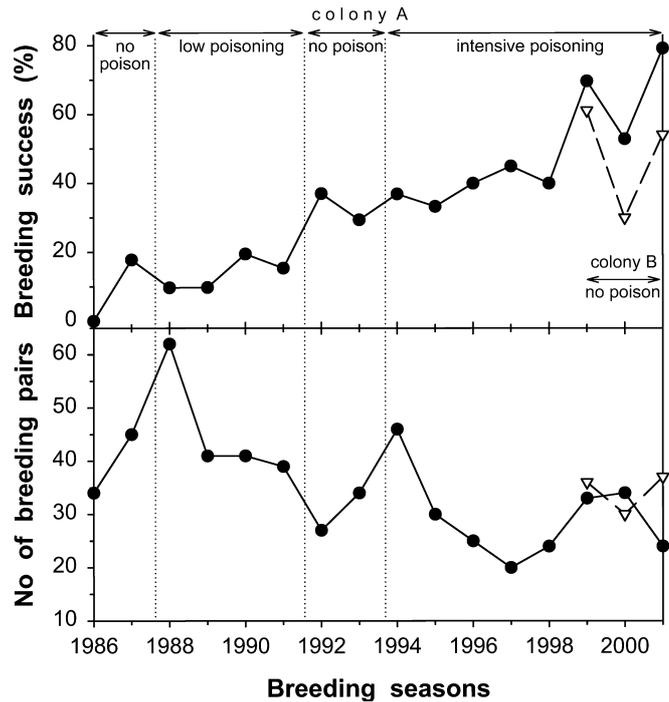


Fig. 1 Interannual variations of breeding success (*top*) and occupancy rate (*bottom*) in our study colonies of white-chinned petrels on Ile de la Possession; *circles*: colony A (experimental), *triangles*: colony B (control). We considered only burrows that were monitored throughout the study. Vertical dashed lines delineate the different periods; chronologically: “control-1” period, “low poisoning” period, “control-2” period, “intensive poisoning” period. During the last period, intensive poisoning occurred in colony A and no poisoning occurred in colony B. Breeding success is the total number of chicks ringed divided by the total number of eggs laid (or the total number of breeding pairs, since petrels lay only one egg)

between 1999 and 2001 (Fig. 1). Hence, we were able to make within-year comparisons of the effects of poisoning on petrel breeding success.

Monitoring of rats

We examined seasonal variations in rat abundance from the austral summer of 1997 to that of 1999 (inclusive), by using 42 snap traps (6 lines of 7 traps spaced 7–10 m) placed on a square grid when conducting our capture sessions. Traps (15×8 cm) were baited with sausage, fish or fruits. Snaptrapping was conducted for 3–9 consecutive nights during each session and trapping sessions were performed monthly. Therefore, three sessions occurred per season (summer: December to February; autumn: March to May; winter: June to August; spring: September to November). Traps were checked once or twice daily (morning and/or evening). Although all sessions took place on Ile de la Possession, we did not conduct them within our white-chinned petrel colonies, because there was a risk of increasing rat densities by using attractive and non-toxic baits.

Rats were frozen after capture and autopsied at our laboratories. They were sexed after examining their genital tract. Females were considered to be in breeding condition if their uterus contained embryos or had placental scars, or if their mammary glands were functional. We defined an index of abundance as the number of individuals captured per session×100 divided by the number of trap-nights.

Results

Consumption of poison and fluctuations of rat abundance

Between 1988 and 1991 (“low poisoning” years), all baits were eaten between two consecutive visits at colony A. During the period of intensive poisoning (from 1994 onward), all poisoned seeds were eaten between two monitorings in most cases. Consumption decreased slightly after late January. On Ile de la Possession, the non-target species likely to consume poisoned bait or poisoned rats (dead or alive) are giant petrels (*Macronectes* spp.), Kerguelen pintails (*Anas eatoni*), black-faced sheathbills (*Chionis minor*), brown skuas [*Catharacta (antarctica) lönnerbergi*] and kelp gulls (*Larus dominicanus*). However, bird mortality on Ile de la Possession did not increase once intensive poisoning began; in addition almost all the rats found dead in the white-chinned petrel colony were found in burrows.

The index of rat abundance varied among years (3.5% in 1997, $N=3,315$ trap-nights, and 2.4% in 1998, $N=2,236$; G -test, $G_1=5.44$, $P=0.02$), but also among trapping sessions ($\chi^2_8=34.17$, $P<0.0001$; see Table 1). When controlling for season, interannual variations of rat abundance were significant in summer, autumn and winter, but not in spring (Table 1). Rat abundance also varied seasonally in the course of the year, but these variations were significant only in 1998 (Table 1). Relative to the total number of trapped rats, the proportion of females in breeding condition was almost 5 times higher in summer and autumn than in winter and spring (6.4%, $N=157$, vs 1.3%, $N=148$; $G_1=5.56$, $P=0.018$), spring being the only season when no females in breeding condition and no young were captured.

Impact of black rats on white-chinned petrels

In our experimental colony (colony A), overall breeding success varied significantly among the four periods of our study (i.e. “control-1”, “low poisoning”, “control-2” and “intensive poisoning”; $\chi^2_3=85.6$, $P<0.0001$; see Table 2 and Fig. 1). When pooling the data from 1986 to 1993 together, overall breeding success was significantly lower during this period (16.1%, $N=323$ eggs laid) than during the “intensive poisoning” period ($\chi^2_1=75.5$, $P<0.0001$).

Table 1 Variations in the index of relative rat abundance on Ile de la Possession (rows: interannual variations after controlling for season; columns: seasonal variations in the course of the year; N represents the number of trap-nights)

	1997	1998	1999	Significance
Summer	4.1%, $N=343$	1.8%, $N=546$	1.3%, $N=546$	$\chi^2_2=8.26$, $P=0.016$
Autumn	3.1%, $N=804$	6.1%, $N=294$	–	$G_1=4.76$, $P=0.03$
Winter	4.3%, $N=1056$	1.4%, $N=588$	–	$G_1=12.22$, $P=0.0005$
Spring	2.8%, $N=1112$	2.2%, $N=808$	–	$G_1=0.60$, $P=0.44$
Significance	$\chi^2_3=4.67$, $P=0.19$	$\chi^2_3=20.35$, $P=0.0001$	–	–

Table 2 Variations in white-chinned petrel breeding success in colony A, with respect to the intensity level of rat-poisoning (N indicates the number of eggs laid)

“Control-1” (no poisoning)	“Low poisoning”	“Control-2” (no poisoning)	“Intensive poisoning”
10.1%, $N=79$	13.1%, $N=183$	32.8%, $N=61$	50.2%, $N=241$

However, breeding success in colony A showed an upward trend in the course of our study (Spearman rank correlation, $r_s=0.95$, $N=16$, $P<0.001$). Correlations remained significant if we distinguished the “before intensive poisoning” and “intensive poisoning” periods (Spearman rank correlation, $r_s=0.79$ and 0.91 , respectively; both $N=8$ and $P<0.05$; Fig. 1). During the former period, however, breeding success was highest during the last 2 years despite the absence of rat-poisoning (“control-2” period; Fig. 1). If we excluded these 2 years, we found no more correlation between breeding success and year (Spearman rank correlation, $r_s=0.54$, $N=6$, $P>0.2$). This phenomenon was confirmed by the similar values of breeding success during the “low poisoning” and the “control-1” periods ($\chi^2_1=0.46$, $P=0.50$; Table 2), whereas breeding success was significantly higher during the “control-2” period than during the previous 6 years ($\chi^2_1=15.50$, $P=0.0001$; Table 2, Fig. 1).

To control for potentially confounding effects of other phenomena that could affect rat density (cold winter, higher plant food availability in spring; Mougin 1969; Atkinson 1985) and/or petrel breeding success (variations of food availability at sea; Bried and Jouvantin 2002), we compared breeding success in colony A with that in colony B. Breeding success was higher in colony A, the difference being significant in 2 years out of 3 (Table 3).

Table 3 Comparison of annual breeding success in our two study colonies of white-chinned petrels, between 1999 and 2001; rats were poisoned in colony A only (see text) (N indicates the number of eggs laid)

Breeding season	Colony A	Colony B	G test
1999	72.2%, $N=36$	61.1%, $N=36$	$G_{1W}=0.98$, $P=0.32$
2000	55.5%, $N=36$	30.0%, $N=30$	$G_{1W}=4.31$, $P=0.038$
2001	79.2%, $N=24$	54.1%, $N=37$	$G_{1W}=4.03$, $P=0.045$

The impact of rats on petrel reproductive performance could therefore be assessed. Assuming that overall breeding success in colony A between 1986 and 1993 would have been equal to that between 1994 and 2001 if there had been no rats, the presence of the rats could account for 40.6% of breeding failures ($N=271$). This estimate, however, needed to be refined by controlling for the annual variations in breeding success. To do this, we assumed that annual breeding success in colony A and colony B would have been identical if rats had been poisoned in colony B. The proportion of breeding failures attributable to rats in colony B was dependent on year, although values (28.6% in 1999, 38.1% in 2000, 52.9% in 2001) were not significantly different from each other ($\chi^2_2=1.97$, $P=0.37$). Overall, 40.4% (22 out of 52) of the breeding failures that occurred in colony B during the last 3 years were attributable to rats, this second estimate being very similar to that obtained for colony A during the first 8 years of our study.

The stage at which failures occurred in colony A (i.e. during incubation or chick-rearing, irrespective of whether rat predation occurred or not) was known for 99.2% ($N=391$) of failures. Considering these failures only, the proportion of egg failures was not significantly higher between 1986 and 1993 than during the "intensive poisoning" period (64% of failures at a known stage, $N=269$, vs 55%, $N=119$; $G_1=2.26$, $P=0.13$). Similarly, the proportion of egg failures in colony B did not differ significantly from that in colony A in any of the 3 years during which colony B was monitored (Fisher's exact test, all $P>0.05$).

Rats also seemed to affect the size of the breeding population in colony A. Burrow occupation by breeders continued decreasing until 1998, then resumed increasing; however, the overall trend was a decline (Spearman rank correlation, $r_s=-0.76$, $N=16$, $P<0.002$; Fig. 1). Regardless of whether poisoning was conducted or not, breeding success in colony A was negatively correlated with the number of breeding pairs throughout our study, as well as with the number of occupied burrows, including those occupied by non-breeders (Spearman rank correlation, $N=16$, both $P<0.005$; see also Fig. 1).

Discussion

Effect of poison on rats and non-target species

In most cases, poisoned baits were totally consumed between two consecutive visits, even during the "intensive poisoning" period when PVC tubes were checked weekly. Thus, poisoning did not lead to total rodent eradication in colony A, strongly suggesting that some of the rats that died from poisoning (corpses were observed within the colony area) were replaced quickly, probably by neighbours. Furthermore, our experimental and control colonies were situated on adjacent slopes, suggesting that rat density in colony B might be slightly

lower than it would have been if no poisoning had occurred in colony A. Ideally, it would have been better to find a more distant colony than colony B as a control. However, (1) Thibault (1995) and Seto and Conant (1996) have already shown that "poisoned" colonies experienced higher breeding success than distant control colonies, (2) colony A and colony B were surrounded by distinct areas harbouring both white-chinned petrels and rats, so that they only partly shared their populations of rats. Despite methodological differences between these studies and ours, our comparisons of reproductive performance in colony A with that in colony B also allow us to conclude that rat-poisoning in colony A resulted in a strong decrease in rat densities and in higher breeding success for white-chinned petrels, confirming the conclusions of Bried and Jouventin (1999). In addition, breeding success in colony A, once intensive rat-poisoning was carried out, was similar to that in other petrel colonies where nest-preying rats were controlled (Cruz and Cruz 1987; Thibault 1995). Finally, the results from our 3-year comparison confirm those of Thibault (1995) which were based on 1 year only for each of his experimental colonies, and those of the 2-year study of Seto and Conant (1996), but in which data from the 2 years were pooled.

Besides, the apparent absence of negative effects on the native avifauna suggests that putting bait into PVC tubes represents an efficient means of preventing Kerguelen pintails and black-faced sheathbills from consuming poison. Although the discovery of almost all the dead rats in burrows does not mean that the bulk of rat mortality occurred in burrows, making corpses inaccessible to skuas, gulls, sheathbills and giant petrels, such a phenomenon, however, was most likely to occur. Indeed, the effect of bromadiolone is delayed, so that poisoned rats have sufficient time to find a shelter before dying. Therefore, we are confident about the negligible impact (if any) of our rat-poisoning technique on the avifauna, which represents an important aspect for the conservation of native species.

Direct impact of black rats on white-chinned petrels

We found that about 41% of breeding failures in white-chinned petrels were attributable to nest predation by rats. When considering other studies on burrowing petrels, our estimates are lower than those found for the Bonin petrel (*Pterodroma hypoleuca*) (79%, Seto and Conant 1996), but they are similar to the percentages observed for the dark-rumped petrel (*Pterodroma phaeopygia*) on some of the Galapagos islands (Tomkins 1985). However, because rats were not totally eradicated, we consider our estimates to represent minimal values.

Our results also indicate that rats seemed to have a similar impact on both eggs and chicks, whereas Mougín (1970) found that they were responsible for chick mortality only. Because direct observation of rats preying on

petrel eggs or chicks is very difficult (Brooke 1995; this study), conducting a long-term study appeared to us as the most practical means to assess the impact of these rodents accurately. Nevertheless, our latter conclusion is supported by our observations of rats in burrows where eggs were left unattended, and by our discoveries of recently broken eggs that had been rolled out of burrows and that contained a partially eaten embryo. The absence of breeding females and young amongst the rats that were captured in spring strongly suggests that predation by these rodents on white-chinned petrels' eggs is unlikely to be the consequence of increasing rodent numbers during this period (see also Table 1), and that spring might be the least favourable season for rats on Ile de la Possession. Several phenomena support this hypothesis. First, king-penguin chicks that have survived their winter fast are fed again by their parents (Jouventin and Lagarde 1995), becoming increasingly healthy and providing no more carrion. Second, most other seabirds are still at sea or have just started to incubate their eggs (which they defend against conspecifics or predators) and, third, plants have only just started resuming growing. Under these conditions, unattended petrel eggs may represent an alternative food resource for the rats from Ile de la Possession, as they do for the rats from Midway Atoll (Seto and Conant 1996). In summer, although the presence of breeding females and young individuals suggests that rat densities have increased, predation on white-chinned petrel chicks ceases when nestlings reach 200–300 g (Mougin 1970). This threshold, which corresponds to the body mass of an adult black rat on Ile de la Possession (mean 246 g, maximum 339 g; D. Aurès, unpublished data), confirms that rats become reluctant to attack prey heavier than themselves (see references in Introduction), but it may also be a result of the increasing aggressiveness of white-chinned petrel chicks as they grow older (J. Bried, personal observations).

Although no poisoning occurred in 1992 and 1993 (i.e. during the "control-2" period), breeding success was high during these 2 years (Fig. 1). The most likely explanation for this phenomenon is interannual variations of the impact of rats caused by variations in availability of plant food and/or rat abundance (Mougin 1969; Thibault 1995). Temperatures on Ile de la Possession during the austral winters of 1991 and 1992 were lower than average (Météo-France, personal communication), which may have caused exceptionally high levels of rat mortality, resulting in lower rodent densities the next spring and summer.

Another consequence of the presence of alien predators may be a progressive desertion of the colony site (Austin 1940; Møller 1982). Indeed, disturbance and breeding failures make the colony less active and less attractive for prospecting birds (Thibault 1995), which no longer consider it as a suitable place for breeding. For instance, the breeding population of Zino's petrels (*Pterodroma madeira*) continued to decline during the first 2 years of rat-poisoning on Madeira Island (Buckle

and Zino 1989), and Corsican Cory's shearwater (*Calonectris diomedea*) colonies with low reproductive success were visited by fewer prospectors than were thriving ones (Thibault 1995). Because petrels show quasi-absolute fidelity to their breeding colonies (Warham 1990), the most likely explanation for these two phenomena is that chick mortality reduced the recruitment at these localities. Furthermore, most petrels, like many seabirds, start breeding only when several years old (Warham 1990; Weimerskirch 2002), so that population recovery consequent to rat-poisoning is delayed, as was the case for Zino's petrel. The fact that the breeding population of white-chinned petrels in colony A continued to decline after intensive poisoning started suggests that such a weak renewal of generations and such a delayed response were also occurring in our study.

Disturbance caused by rats

If we exclude man-induced mortality at sea, alien mammalian predators represent the main threat to birds breeding on subantarctic islands (Johnstone 1985). Within the Crozet archipelago, only 10 burrowing-petrel species breed on Ile de la Possession, versus 16 on the nearby (18 km distant) Ile de l'Est, which has similar topography and area but is free of rats. Moreover, Ile de la Possession harbours the same species as Ile de l'Est in areas where rats do not occur. Jouventin et al. (1984) hypothesised that these rodents were responsible for the difference observed between the two islands, the species absent from Ile de la Possession not being affected by fisheries.

Although intensive poisoning considerably diminished the effects of rat predation in our study colony from 1994 onward, rats are still present and may be responsible for some breeding failures, even if their impact is very low (see Cruz and Cruz 1987; Bried and Jouventin 1999), and for a lower rate of recruitment (Buckle and Zino 1989; Thibault 1995; probably this study). In addition, the disturbance caused by these rodents has been shown to result in higher incidence of divorce and burrow switching in our white-chinned petrel population, which may result in missed breeding years (Bried and Jouventin 1999, 2002). For the species whose smaller size makes them more vulnerable to predation, rats might also be indirectly responsible for a decrease in adult survival rate in the long term, by increasing the level of predation on the adults prospecting for a new site/mate by native predators such as brown skuas (see Bried and Jouventin 2002). At sea, the level of adult mortality due to fisheries is no longer sustainable for the Indian Ocean population of white-chinned petrels (Weimerskirch et al. 2000). Given the importance of adult survival for the population dynamics of long-lived species (see Introduction), fishery-induced mortality is likely to have replaced low recruitment of young resulting from egg and chick predation by rats as the main cause of the decrease of the breeding population of white-chinned petrels, not

only in colony A, but also on the entire Ile de la Possession (P. Jouventin personal observation). This hypothesis is supported by a recent study, which predicts that the white-chinned petrel population from the Crozet archipelago should keep declining as long as fisheries operate, even if breeding success is high (A. Catard, unpublished data).

This ongoing decrease in petrel numbers is likely to have resulted in higher prey availability per capita at sea (density-dependent effect), which might explain: (1) the global increase in breeding success we observed throughout our study in colony A, and (2) the negative correlation we found between breeding success and the occupancy rate in the same colony, although the latter phenomenon may also have been caused by the recruitment lag-time of breeders (white-chinned petrels do not breed until 6 years old, data from this study). Indeed, food availability is known to influence the outcome of breeding attempts in seabirds (Bried and Jouventin 2002). Furthermore, fishing vessels represent an additional source of food for white-chinned petrels, which take baits from hooks during line-setting and feed on the offal dumped at sea as an attempt to decrease seabird by-catch (Catard et al. 2000; Weimerskirch et al. 2000). Observations of parallel variations of breeding success in colonies A and B during the last 3 years (Fig. 1) support this hypothesis of increased food availability. Another possible explanation for this negative correlation between breeding success and occupancy rate, which does not exclude the previous hypotheses, may be that decreasing petrel densities on land result in lower disturbance and incidence of fights (which can be risky for eggs and small chicks) due to competition for burrows (e.g. Mougin 1970). Moreover, an effect of increasing pair experience on reproductive performance is unlikely in the white-chinned petrels breeding in the experimental colony where rat-poisoning was carried out (Bried and Jouventin 1999).

When conducting our experiment, we were aware that rat control alone would probably not enable our study population to fully compensate for the mortality caused by fisheries. Our aim was only to assess the effects of our method on a species with extended demographic parameters, in order to help establish conservation and restoration protocols suitable for other threatened bird populations, including multi-brooded species, whose offspring production can vary in a much more important manner than in procellariiforms. Our results, in both temporal and spatial (colony A vs colony B) planes, allow us to conclude that rat-poisoning led to significantly higher petrel reproductive performance in colony A. This confirms the results of the 2-year study of Seto and Conant (1996) on Bonin petrels, and enables us to eliminate, as long as the poisoning is repeated regularly, an eventually masking effect of external short-term and long-term factors. Furthermore, our study confirms that controlling rat density in a location where total predator eradication is impossible represents an efficient means of increasing seabird breeding success (Buckle

and Zino 1989; Thibault 1995; Seto and Conant 1996). This may act directly or through higher burrow and mate fidelity, which both lead to more frequent breeding (Bried and Jouventin 1999, 2002). Our study also suggested that poisoning once or twice during the breeding period did not suffice to improve significantly the reproductive performances of petrels, contrary to previous hypotheses that predicted that intensive poisoning would not lead to much higher petrel breeding success than “low” poisoning (Tomkins 1985). In our white-chinned petrel colony, intensive predator control (i.e. weekly poisoning throughout the period that young were unable to deter rats) appeared to be necessary to increase petrel reproductive success.

Implications for future seabird studies and conservation

To our knowledge, this study represents the first long-term accurate monitoring of an insular seabird population, both before and after controlling an alien predator. Thibault (1995) poisoned rats in one colony at a time, and for 1 year only, to assess the impact of these rodents on Cory's shearwaters; yet, rat densities fluctuated from year to year (as in our study), so that breeding success in a given colony was sometimes lower when rats were controlled than in the absence of poisoning. Seto and Conant (1996) improved Thibault's (1995) protocol by poisoning rats in three different areas simultaneously and for two consecutive years, and by comparing petrel breeding success in poisoned areas with that in non-poisoned zones in which habitat conditions were similar. However, they did not control for interannual fluctuations when making their comparisons. To overcome these problems, we had to conduct this long-term study on white-chinned petrels, involving rat-poisoning and the monitoring of a control colony for several consecutive breeding seasons. Although our results reveal the importance of the impact of the rats on white-chinned petrels and confirm the efficacy of rat-poisoning for seabird conservation on land, the white-chinned petrel will remain threatened as long as large-scale effective measures are not taken against the illegal fisheries that operate in subantarctic waters. In addition, enlarging the scope of our study would be desirable by conducting similar experiments to ours on other rat/bird associations, including terrestrial birds, provided that the conservation status of the birds makes it possible. This would greatly help in both assessing the impact of introduced predators and in restoring threatened insular bird populations, especially if the latter are endemic to islands where rat eradication remains impossible.

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