Quantifying stochastic and deterministic threats to island seabirds: last endemic prions face extinction from falcon peregrinations

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Abstract

Understanding how anthropically induced interacting factors may compromise the viability of a particular species or population necessitates expressing them in terms of quantitative effects on population dynamics. The use of mechanistic models to assess these effects is especially helpful to management plans when the causes of species decline are multi-factorial and potentially interacting. Here, we took the opportunity of observed predation by a vagrant falcon on a rare and endemic seabird to develop a population dynamics model encompassing multiple deterministic and stochastic threats. The Macgillivray's prion *Pachyptila macgillivrayi*, with a world breeding population of *c.* 540 individuals confined to one rat-free islet off Saint-Paul Island (Southern Indian Ocean), faces high extinction risk from vagrant falcon predation. Extinction is predicted to occur within 200 years if one falcon preys on prions every 5 years, with predation occurring either on breeders only or also on non-breeders. The minimum initial prion population size ensuring a low extinction risk increased linearly with the annual probability of predator occurrence. Therefore, increasing the initial population size is a useful management option to help the prion face stochastic predation. Recent rat eradication on Saint-Paul Island helps the prion to face this threat as it released the carrying capacity of the colony, but the earlier population size might never be recovered if falcons carry on preying on prions frequently. This rare burrowing petrel provides a remarkable case study of an endemic insular species threatened with predation by alien mammals, which reduced historical population size dramatically, and by genuine vagrants as catastrophic events that reduce population growth and increase its temporal variance, and might cause the extinction.

Introduction

Extinction over the past six centuries has largely been dominated by insular species, with non-native mammals being responsible for the majority. Hundreds of bird species on oceanic islands have become extinct since the arrival of humans (Blackburn *et al.*, 2004), while the devastation of island faunas by alien species has been instrumental in raising concerns about the global threat to biological diversity. Besides the consequences of invasion by alien species, insular bird species and populations may be exposed to other anthropogenic threats, such as habitat alteration or direct overexploitation or persecution. These different kinds of threat have been well categorized (Diamond, 1989) and are often well documented for particular species. However, to understand how these ultimate factors may compromise the viability of a particular species or population necessitates expressing them in terms of deterministic and stochas-

tic effects on population dynamics. In particular, it is essential to examine how these factors may affect the ability of a population to grow (mean and spatiotemporal variance of population growth) and to reach a size (carrying capacity) that is compatible with long-term persistence. Population viability analysis has become an extensively used tool for assessing the combined impacts of such deterministic and stochastic factors on population or species dynamics (Coulson *et al.*, 2001), and for providing estimates of the risk of extinction (Beissinger & McCullough, 2002; Morris & Doak, 2002). Among the various mechanisms impairing population viability, environmental stochasticity (i.e. variation in birth and death rates from one season to the next in response to environmental factors) is frequently invoked as one of the most important causes of extinction in both small and large populations (Shaffer, 1987; Lande, 1993; Holsinger, 2000). In particular, rare bouts of extreme environmental perturbations (generally referred to as

catastrophes) have a major influence on extinction risk (Doak *et al.*, 2005); yet, very little information is available on their frequency and severity (Young, 1994; Ludwig, 1999; Reed *et al.*, 2003; Taylor, Scott & Gibbons, 2006). In very small populations (few 10s–100s of individuals), such variations may exacerbate the negative effects of demographic stochasticity, caused by chance realizations of individual probability of death and reproduction events. Here, we used a projective modelling approach to examine the viability of an endemic insular seabird population threatened by several exogenous factors.

Saint-Paul Island, in the Southern Indian Ocean, was discovered in 1559, although the first human landing there occurred in 1696 (Micol & Jouventin, 2002). Transient sealers and fishermen almost exterminated local fur seals by 1810 and decimated original flora and fauna through repeated fires and introductions of alien species, including mammals such as mice, rats, rabbits, cats, goats and pigs (Micol & Jouventin, 2002). The island originally yielded various seabird species, especially a 'blue petrel', with hundreds of thousands of breeding pairs reported (Péron, 1824; Velain, 1878). By the late 1990s, established black rats *Rattus rattus* had extirpated all seabird colonies from Saint-Paul mainland, while only six of the 13 originally breeding species (Worthy & Jouventin, 1999) were represented by only a few individuals confined to a rocky islet free of introduced mammals (Micol & Jouventin, 2002). This rock, the 'Roche Quille', is located 150 m from the main island and is only 1 ha in size. Among these seabirds, the Macgillivray's prion *Pachyptila macgillivrayi* is endemic, with a worldwide population of only 150 pairs all breeding on the Quille (Jouventin *et al.*, 1984), although pairs numbered originally over 200 000 when they used to breed on the Saint-Paul mainland (Micol & Jouventin, 2002).

In 1999, a vagrant peregrine falcon *Falco peregrinus* lingered on Saint-Paul, and predated at least 27 breeding prions. Migratory vagrants reach the Indian Ocean subantarctic islands when displaced by tropical storms (Gauthier-Clerc, Jiguet & Lambert, 2002), which should become more frequent following climate change (Gable, Aubrey & Gentile, 1991; Knutson & Tuleya, 1999; Easterling *et al.*, 2000). Witness four of the five falcons known to have reached the area in the last 55 years have been sighted after 1990. If the occurrence of such vagrant predators increases in the next decades, they might bring the endemic prion to extinction. In order to explore the prion population viability, we developed individual-based stochastic demographic models (Beissinger & McCullough, 2002), accounting for population regulation (carrying capacity of the colony fixed to 150 pairs on the Quille, as rat predation prevented breeding on the main island) and demographic and environmental stochasticities. The effect that catastrophic events can have on extinction risk of the endemic prion was modelled by varying the annual probability of vagrant predator occurrence. As a global restoration initiative, rats and rabbits were eradicated from the Saint-Paul mainland in 1997 (Micol & Jouventin, 2002). We further modelled the effect of rat eradication as having released the carrying capacity of

the colony, and estimated new extinction risk for the prion with varying occurrence of vagrant predator. Our work was motivated by fundamental and applied questions: (1) what is the maximal level of predation tolerable by the prion population, depending on population size limitation and the components of the species life cycle affected by predation?; (2) do rat and falcon threats act synergistically on prion population dynamics and extinction risk?; (3) what are the best management options to minimize the species extinction risk?; and (4) how long would it take for the prion to recover earlier population size after the rat eradication.

Methods

Saint-Paul Island and the Macgillivray's prion

Saint-Paul Island, in the Indian Ocean (38°43′S, 77°32′E), is one of the most isolated islands in the world, being 3000 km away from any continent, located between Africa, Australia and Antarctica (Fig. 1). The island covers 8 km^2, with a maximum height of 268 m at Crête de la Novara. Just out of Saint-Paul's crater lies the small Roche Quille, 150 m from the mainland and only 1 ha in size. In the early 1990s, this rock was the only predator-free islet where Macgillivray's prions were breeding before the rat eradication on Saint-Paul in 1997. Established mammals on the island were rats, rabbits and mice, the two former having been eradicated in 1997.

There is only one breeding population of this burrowing petrel in the world, located on the Roche Quille off Saint-Paul (Tollu, 1984), where 150 pairs breed. Models developed in this study suggest that the total population size is about 540 birds (adults and immatures). The specific status of this taxon has been debated, as it has been considered a subspecies of the broad-billed prion *Pachyptila vittata* (Harper, 1980) or of the Salvin's prion *Pachyptila salvini* (Roux & Martinez, 1986), the latter because of some blue colour on the bill (*vittata* is thus the only prion taxon with an all-black
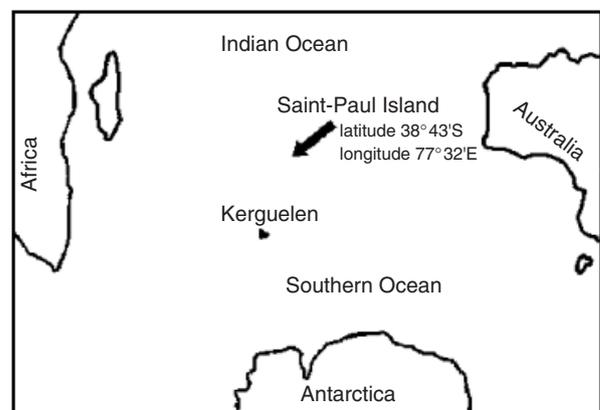

Figure 1 Location of Saint-Paul Island, in the Indian Ocean (38°43′S, 77°32′E).

bill), while bill measurements of *macgillivrayi* are closer to *vittata*. Recent published works on seabirds suggest that *macgillivrayi* is best treated as a separate species, phenotypically intermediate between *salvini* and *vittata*, while all three constitute a group of allospecies (Shirihai & Jarrett, 2002).

Falcon vagrancy and prey casualties

On 27 January 1999, a peregrine falcon was discovered on Saint-Paul. The falcon was then seen almost daily when searched for, in late afternoon and at twilight, actively hunting petrels close to the Roche Quille. The Peregrine hung over the rock, waiting for prions to come back to their colony. Prions gather offshore before attending their burrows at night, and were captured over the water as soon as they approached the rock. Active hunting was observed each time the falcon was seen, for example 20 attacks in 15 min on 4 February. It was last observed on 15 February 1999. There were four more observations of falcon around Saint-Paul and Amsterdam (just 85 km to the North) Islands since 1950, the year when scientific expeditions became annual on Amsterdam Island. An Eleonora's falcon *Falco eleonorae* was on Amsterdam Island on 7 January 1982; probably the same bird was observed offshore 17 days later (Roux & Martinez, 1986); an unidentified falcon was observed from a boat off Amsterdam in the early 1990s (T. Micol, pers. obs.); a European hobby *Falco subbuteo* was photographed on a boat off Amsterdam in January 1998 (J. Bried, pers. comm.); and finally, a sooty falcon *Falco concolor* was captured on the Marion-Dufresne boat while it was sailing to Amsterdam in 2002. Given that vagrant falcons reached the area five times in 20 years, and that the observation pressure is very low on Saint-Paul, as scientific expeditions seldom went there before 1995 and for only a few days each time, it seems conceivable that the annual probability of falcon occurrence on Saint-Paul can reach up to 0.2 (on average one every 5 years). We, however, acknowledge that the evidence for increased falcon vagrancy is theoretical as it is not corrected for the frequency of scientific expeditions to these islands, although human scientific presence on Amsterdam has been permanent in the last three decades.

Observers visited the Roche Quille twice on 7 and 18 February 1999, in order to collect all dead seabirds they found. All petrel remains found on the main island were also collected from 27 January to 21 February. A total of 61 predated petrels were collected; 54 were Macgillivray's prions. Among the prion corpses, 27 presented a broken breast bone typical of predation by falconiforms (Cramp & Simmons, 1980); 19 had an unbroken breast bone as usual for skua (*Catharacta* sp.) casualties (Mougeot, Genevois & Bretagnolle, 1998). Classical biometrics did not differ between predated prions with broken or unbroken breast bone (ANOVA), for those collected prion corpses with available data: wing length ($F_{1,44} = 2.72$, $P > 0.1$), bill length ($F_{1,12} = 0.06$, $P > 0.8$), bill width ($F_{1,12} = 0.26$, $P > 0.6$) and tarsus length ($F_{1,26} = 0.10$, $P > 0.7$). Brown Skuas *Catharacta lonnbergi* are present on Saint-Paul (5–20 individuals), and prey on seabirds and introduced mammals.

Population dynamics parameters

As the Roche Quille is highly inaccessible, there is no long-term study of population dynamics of the Macgillivray's prion. We used the demographic parameters obtained in two phylogenetically closely related species (Bretagnolle, Zotier & Jouventin, 1990), the thin-billed prion *Pachyptila belcheri* (Nevoux & Barbraud, 2005) and the blue petrel *Halobaena caerulea* (Barbraud & Weimerskirch, 2003). In seabirds, the juvenile survival rate is hardly accessible as immatures do not attend breeding colonies, and various methods have been proposed to obtain estimates (Spendelow *et al.*, 2002; Oro *et al.*, 2004). Here, we applied a 5% decrease from adult survival for each year of immaturity (Oro *et al.*, 2004), giving a 0.728 juvenile survival rate. The demographic parameters used in this study are presented in Table 1. Seasonal field workers assessed recolonization of the main island by prions. In models, the effect of the release of the colony carrying capacity was modelled as a younger age at first breeding, according to the results obtained in another petrel species (Brooke, 1990).

Deterministic matrix model (DMM)

In a first step, a one-sex, age-structured DMM was developed to infer equilibrium intrinsic population properties (in the absence of predation, environmental stochasticity and population regulation). The model was implemented using the ULM software (Legendre & Clobert, 1995; Ferrière *et al.*, 1996). The set of parameters used are presented in Table 1.

Table 1 Annual parameters used for modelling the prion population dynamics

Parameter	Mean	SD[a]	References
Juvenile survival $s_{(0)}$[b]	0.728	0.033	Barbraud & Weimerskirch (2003), Oro *et al.* (2004)
Immature survival $s_{(1)}$, $s_{(2)}$, $s_{(3)}$[b]	0.894	0.033	Barbraud & Weimerskirch (2003)
Adult survival $s_{(\geq 4)}$[b]	0.894	0.033	Barbraud & Weimerskirch (2003)
Age at maturity	4	–	Warham (1990), Oro *et al.* (2004)
Female breeding success	0.519	0.027	Nevoux & Barbraud (2005)
Number of predation events	30	–	This study

[a]SD refers to the standard deviations of β distributions used for modelling environmental stochasticity (if applicable).
[b]$s_{(x)}$ is the annual survival rate between age x and $x+1$.

Individual-based population models (IBM)

In order to examine the joint effect of population regulation (limited number of suitable nesting sites), temporal environmental variations (environmental stochasticity and sporadic falcon predation) and demographic stochasticity, we developed a stochastic two-sex IBM. The IBM allowed a complete description of all individuals in terms of sex, age and reproductive status (breeding vs. non-breeding). At each time step (year), adult individuals paired randomly according to a monogamous mating system. The number of nesting pairs (Np) at time t Np_t was given by $Np_t = \text{Min}$ (Nam_t, Naf_t, N_{site}), where Nam_t and Naf_t were, respectively, the numbers of adult males and females present at time t, and N_{site} was the number of available burrows. The reproductive success of each pair was determined according to a Bernoulli's drawing (parameter F). The sex of each newborn individual was randomly determined according to a 1:1 mean sex ratio. Reproduction was followed by the differential mortality of individuals according to age-specific annual survival rates. Each individual survival event was drawn from a Bernoulli's function. The details of the parameters used are presented in Table 1.

Environmental stochasticity was modelled by drawing survival and fecundity rates at age x in each year from a β distribution with expectation and variance, respectively, given by the mean and process variance of these demographic rates (see Table 1 for values and references).

The occurrence of predator for a given year was modelled as a random process (Bernoulli's trial, with probability Vf). As examples, $Vf = 0.1$ if one falcon predates P prions on average once every 10 years; $Vf = 0.2$ if one falcon predates P prions every 5 years. Different scenarios regarding predation were examined. It was assumed to occur either on all adults (Na), or only on breeders (Nn). The number of predation events P was computed either as a rate r_p (i.e. P was drawn from a Binomial distribution with parameters r_p and Na or Nn), or depending on a fixed value n_p independent from population size and Poisson distributed. When predation occurred on a given individual, its survival probability and the reproductive success of its nest (if any) dropped to zero. We did not consider that predation could occur preferentially on non-breeders, because in 1999, the falcon occurred late in the breeding season, when only chick-rearing adults were attending the colony.

Different scenarios regarding the annual probability of falcon occurrence Vf were investigated in order to extrapolate the effects of different management strategies on population dynamics and viability. In each case, $N_{(0)}$ individuals were present in the population at time zero. In simulation aiming at comparing different management options, the number and age structure of the initial population were derived from the long-term equilibrium values obtained for the set of parameters investigated. Extinction occurred when the population size was equal to zero. Changes in population size and extinction risk were investigated by using Monte Carlo simulations in which 2500 population trajectories were drawn over a fixed time horizon

(100–500 years). In some scenarios, we considered a delay in the first flacon occurrence after the rat eradication, which could be achieved by two means: either catching or shooting (after considering legal and ethical concerns) any falcon reaching the island (falcons benefit from a protected status on French oversea territories).

Results

Intrinsic population properties

In the absence of regulation and inter-annual variation of demographic rates (DMM), the population was intrinsically growing (asymptotic growth rate $\lambda = 1.021$). The growth rate was highly sensitive to variations in adult survival (elasticity = 0.91). As juvenile survival rate is the less reliable demographic estimate, we performed an analysis of sensitivity of all results to changes in juvenile survival rates s_0, which indicated that the population remained intrinsically growing when considering realistic values of juvenile survival, comprised between 0.6 and 0.85: λ varies from 1.004 with $s_0 = 0.6$–1.036, with $s_0 = 0.85$.

Overall, the DMM suggested that joint decreases of adult survival and reproductive success would have a huge impact on population growth (the population growth rate became intrinsically constant when applying a 2% reduction in both reproductive success and adult survival), which suggested that even low predation rates on nesting adults would strongly affect population dynamics.

Equilibrium population properties in the absence of predation

In the absence of falcon predation, our simulations showed that a maximum capacity of 150 breeding pairs was sufficient to ensure long-term population persistence (zero probability of extinction over 500 years, based on 2500 iterations, starting from $N_{(0)} = 500$ adult individuals). The overall population size stabilized at 540, with individuals older than 3 years representing the majority of the population (equilibrium pre-reproductive proportions of individuals of age 1, 2, 3 and ≥ 4 are, respectively, 10, 9, 8 and 73%). All subsequent simulations were conducted using this initial age distribution.

Type of falcon predation

The effect of the type of falcon predation on the prion population dynamics was examined by comparing the effect of predation modelled as a fixed number of prions depredated (n_p) versus a proportion of population size, on the one hand, and comparing predation occurring on all adults versus predation occurring on breeders only, on the other. Simulations aiming at comparing the effect of predation modelled as a fixed number versus a proportion of population size indicated that predation modelled as a fixed number had the most deleterious effect on extinction risk, although it did not qualitatively affect the results presented

below. Similarly, different values of the number of prions depredated (n_p) were investigated. The deleterious impact of predation obviously increases with n_p. However, as no effect of n_p on the qualitative conclusion was found, all subsequent results are presented for $n_p = 30$. As a single predator can only have limited absolute impact on the prey population, we consider a fixed number of birds predated in all subsequent results. When comparing the effect of predation on all adults versus predation on effective breeders only, results indicated that predation on breeders was the only situation having the highest deleterious effect on population dynamics and extinction risk in the long run, while the reverse was true at a short time scale (Fig. 2; see 'Discussion'). As vagrant falcons occurred in the summer time when prions are rearing their chicks, and as only breeding birds are attending the colony at that time of the breeding cycle, we assumed that predation occurs only on effectively reproducing individuals in all subsequent results.

Minimal viable population size

When starting from the current population size (150 pairs, 540 individuals), our simulations indicated that the risk of extinction is primarily driven by the occurrence frequency of the predator (predation risk Vf). However, for a fixed value of Vf, short- and long-term viability was substantially improved by increasing the initial population size, revealing a strong synergy between size limitation and predation on extinction risk. We studied the minimum initial population size required to ensure population persistence under different predation risks (Fig. 3), which indicated that the current population size of the Macgillivray's prion, with 150 breeding pairs, was able to ensure short-term species persistence (100-year extinction risk below 5%) as long as falcon
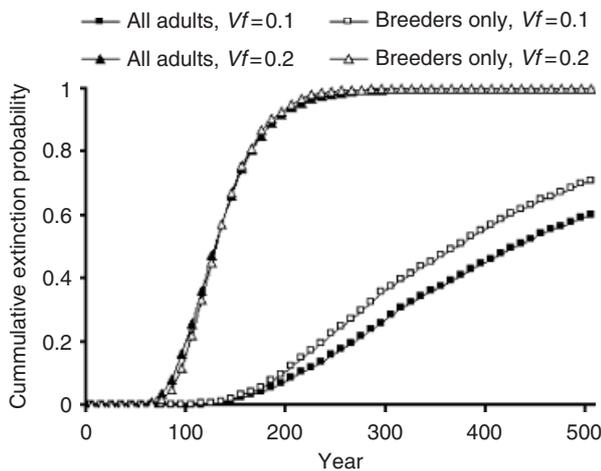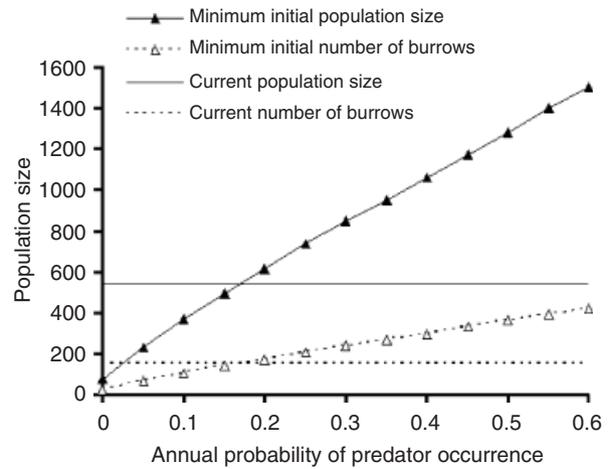

Figure 3 Minimum initial population size required to ensure a less than 5% extinction probability within 100 years, as a function of predation pressure. Solid triangles, overall minimum population sizes; open triangles, numbers of nesting sites necessary to obtain these populations sizes at equilibrium. The horizontal lines represent estimates of current number of suitable nesting sites and overall population size.

occurrence frequency was below 0.17. When considering long-term species persistence (500-year extinction risk), the falcon occurrence probability should not overstep 0.05. As the predator occurrence increased, the minimal population size enabling species persistence increased linearly, and for a falcon occurrence probability of 0.2 (a value close to the potential rate within the last 20 years), a population of 1000 birds or 280 breeding pairs would be necessary to ensure a less than 5% extinction risk over 500 years.

Extinction risk when facing falcon predation

Given the impossibility of controlling predation risk in the long run, and the strong interaction between predation risk and initial population size on both short- and long-term viability, most feasible conservation actions may consist in an intensive short-term management of the population, aiming at obtaining a rapid population size recovery. Such management may allow the species resilience to falcon predation in the long run to improve substantially. For different predation risks, we examined projected species viability obtained under different management scenarios: (1) no rat removal or predation control (carrying capacity constrained to 150 breeding sites); (2) rat removal (carrying capacity released to 200 000 burrows); (3) rat removal and predator control for 10 years (i.e. no predation can occur during the first 10 years); and (4) rat removal and predator control for 25 years. The results of such models are presented as the 100-year (Fig. 4a) or 500-year (Fig. 4b) extinction risk. Simulations revealed that rat eradication, having released the carrying capacity of the colony, significantly reduced the prion extinction risk for moderate falcon occurrence probability, with a significant gain for long-term dynamics (Fig. 4b): for example extinction risk decreased from 73.9 to 6.9% for a falcon occurrence probability of 0.1.
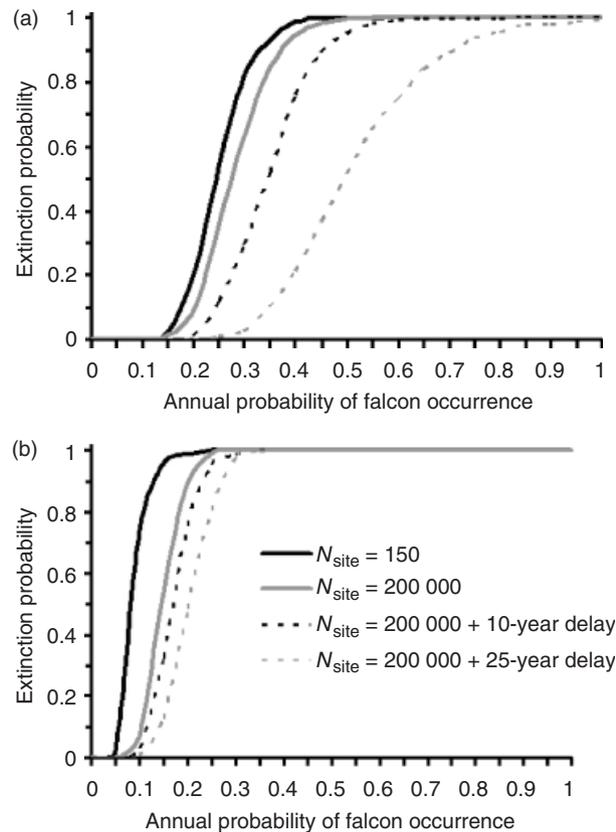

Figure 2 Extinction risk when predation occurred on all adults versus breeders only, with varying annual occurrence probability of vagrant predator Vf (one falcon predating 30 prions on average once every 10 years for $Vf = 0.1$, every 5 years for $Vf = 0.2$, etc.) The number of breeding sites is fixed to 150; the demographic parameters are presented in Table 1.

Figure 5 Increase in population size following the release of the carrying capacity of the colony (N_{site} from 150 to 200 000 as a consequence of rat eradication on the Saint-Paul mainland). Initial populations are implemented with the size and age structure obtained at equilibrium using the current actual number of nesting sites and no predation ($N_{site} = 150$; $Vf = 0$). In this simulation set, only 150 population trajectories could be drawn and averaged because of time-consuming individual-based population model running when population sizes are large. Results are shown for models with varying frequency of falcon occurrence and two values for age at first breeding (optimistic scenario with first reproduction at 3-years of age instead of four).

Figure 4 Extinction probability of the Macgillivray's prion *Pachyptila macgillivrayi* as a function of vagrant predator occurrence probability. Initial populations are implemented with the size and age structure obtained at equilibrium in two-sex individual-based stochastic models using the current number of nesting sites ($N_{site} = 150$) and no predation. 100 years (a) and 500 years (b) extinction rates are shown, for the situation in the 1990s with 150 burrows on the Roche Quille and rats *Rattus rattus* preventing breeding on the main island ($N_{site} = 150$), released carrying capacity of the colony after rat removal ($N_{site} = 200 000$), released carrying capacity and further delay in first falcon occurrence ($N_{site} = 200 000$; 10 or 25-year delay).

Considering further a delay in the first falcon occurrence after the eradication also reduced the extinction risk, with a gain increasing with the length of the delay: extinction risk was only 0.8% for a 25-year delay after 500 years for a falcon occurrence of 0.1, which means one falcon predating 30 breeding adults on average once in 10 years. If a falcon occurred every 5 years (0.2 occurrence probability), the extinction risk was still estimated at the high value of 48.1% after 500 years for a 25-year delay.

Recovering earlier population size

Overall, our simulations suggested that even when considering optimal conditions (removal of the rat and falcon threats, earlier age at first breeding due to reduced competition), the prion population would need several centuries to recover initial population levels (i.e. before rat invasion).
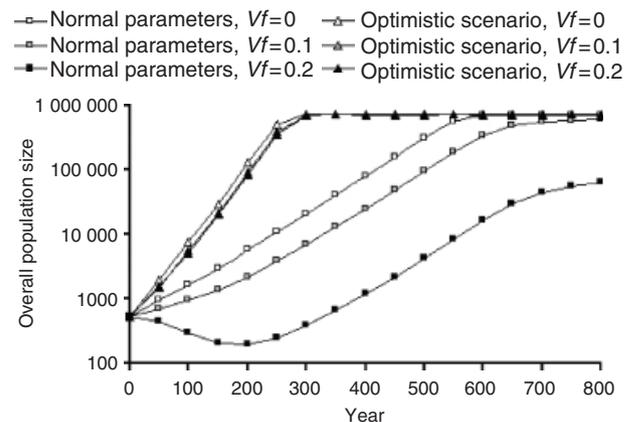
Once considering that the carrying capacity of the colony has been released, population size increased until reaching an equilibrium (fixed to 200 000 breeding pairs here; Fig. 5). This equilibrium was reached after about 250 years with early age at first breeding (three instead of 4 years), whatever the falcon occurrence probability. With normal, non-improved demographic parameters, the time necessary to recover initial population size is 600 years with no falcon predation, while moderate to high-falcon occurrence did not allow the population size to reach the equilibrium even after 800 years.

Discussion

Macgillivray's prion conservation

For the situation in the early 1990, with 150 breeding pairs on the Quille, we estimated a population size of 540 individuals for this rare and endemic burrowing petrel. There are only 205 bird species around the world with known population number less than 500 individuals (BirdLife International's World Bird Database WBDB, May 2006; information provided by Ian Burfield, Birdlife International), which makes the Macgillivray's prion one of 2% of bird species with the smallest population sizes in the world (if considered as a species on its own). As a rare, localized petrel that has encountered a huge population decrease in the last century, the Macgillivray's prion is certainly a taxon of high-conservation concern, while the occurrence of a vagrant falcon on its unique breeding site led

to a high-predation rate on breeding adults. Field observations suggested that predation by falcon on prions is extremely efficient and occurred on effective breeders because of time-concurring falcon migration and prion reproductive cycle, which motivated our choice to model predation as acting on breeders only by removing a fixed number of individuals. Predation by local native predators such as skuas is probably stronger on non-breeders, as they are more conspicuous at the colony while looking for a mate and a burrrow (Mougeot *et al.*, 1998; Mougeot & Bretagnolle, 2000) earlier in the breeding season, while non-breeder prions do not attend breeding colonies during the chick-rearing period (Warham, 1990).

When modelled as a fixed number of events, the effect of predation on extinction risk was extremely severe, because the proportion of killed individuals became more important when the prey population size decreased, engendering an Allee effect (Courchamp, Clutton-Brock & Grenfell, 1999). As a consequence, falcon predation acts in synergy with the effect of rats, which constrain the population to low densities (Fig. 4). Moreover, when occurring on breeders only, predation had a maximum deterministic effect on population growth (Fig. 2). As a consequence, it appeared that even a low-predation risk (i.e. on average one falcon occurrence every 10 years) may strongly influence population dynamics and extinction risk. In agreement with theoretical expectations (Palmqvist & Lundberg, 1998), other simulations indicate that considering a temporal autocorrelation in predation occurrence further increases the negative effect of predation, as it increases the probability that predation occurs in 2 consecutive years.

However, although our quantitative results varied according to predation modelling assumptions and parameter values, all scenarios provided consistent conclusions suggesting that the effect of predation was exacerbated for small population sizes, emphasizing the necessity of releasing the carrying capacity of nesting sites on Saint-Paul Island. On the Quille, prions were using all available 150 burrows, and the adjacent Saint-Paul Island was unfavourable as long as it held rats. However, rats were eradicated from the Saint-Paul mainland in 1997, and hence the carrying capacity of the colony suddenly increased dramatically: 8 km^2 of rat-free island could be recolonized (Micol & Jouventin, 2002). Indeed, observations on the main island revealed that at least 10 burrows were occupied in 2000 (Micol & Jouventin, 2002), 14 pairs succeeded in raising a chick in March 2005 and at least 34 burrows were frequented by prions in 2006. By modelling the effect of this capacity release on the petrel extinction risk, we showed that rat eradication, as a global restoration initiative, appears to be an efficient conservation measure for the prion to face falcon predation, for moderate falcon occurrence frequency, although it was not originally dedicated to face this threat. A further option to increase the initial prion population size is to prevent predation by falcons during the first years after rat removal. Models associating a released carrying capacity with a time delay in the first falcon occurrence reduced the extinction risk significantly. If this delay was extended to 25 years after the rat eradication, extinction risk for the prion was nil as long as falcons occurred thereafter on average less than once every 5 years. Despite the potential positive effects of present and future conservation efforts, the Macgillivray's prion is a typical illustration of a species strongly affected and threatened by anthropogenic causes. Our results showed that the species decline was not an irreversible phenomenon (from a purely demographic viewpoint), although complete population recovery may be extremely long. We estimated how long it would take for the species to recover early population numbers, that is, at least 400 000 breeding birds, according to various scenarios of predator vagrancy and demographic parameters. It took 100 years to decimate the population down to 150 pairs (Micol & Jouventin, 2002), and models predicted that 600 years would be necessary for the population to recover the earlier size in the absence of falcon predation. An optimistic scenario, with earlier age at first breeding (from 4- to 3- year-old) after the release of the colony carrying capacity (Brooke, 1990), gave shorter delays (250 years), but pessimistic scenarios with even low falcon occurrence led to the conclusion that the prion would never recover the original numbers.

Multi-factorial causes of extinction: insights from models

A recurrent problem in population viability analysis is the lack of detailed quantitative data on species ecology (Hamilton & Moller, 1995; Ludwig, 1999; Morris & Doak, 2002), especially concerning isolated seabird species (Oro *et al.*, 2004). Although the precision of our quantitative projections of extinction probabilities and population sizes is directly related to the confidence intervals of input data, the relative comparisons of alternative management strategies certainly provided robust qualitative conclusions useful to decision making (Boyce, 1992). The modelling approach may be especially relevant in cases where the causes of extinction are multi-factorial, as it allows to (1) hierarchize the different types of threats, in terms of the magnitude and time scale of their effects; (2) uncover potential interactions among the effects of different types of threat; and (3) assess the efficiency of different management options to minimize these effects.

For the Macgillivray's prion, the causes of decline are certainly multi-factorial, and derived from the conjunction between local (rat invasion) and global (potential increase of predator vagrancy following climate change; Gable *et al.*, 1991; Knutson & Tuleya, 1999; Easterling *et al.*, 2000; Gauthier-Clerc *et al.*, 2002) anthropically induced phenomena. Although specific conservation measures can only be adopted at a local scale, a reliable assessment of their efficiency necessitates taking into account all potential sources of threat, including global ones. The reasons for species extinction are generally multiple (Pimm, 1996; Gurevitch & Padilla, 2004; Cardillo *et al.*, 2005), and extinction itself can be described as a complex multi-factorial process in which species decline is due to one or several ultimate

factors, followed by other aggravating proximal (stochastic) factors further accelerating the final extinction (Caughley, 1994). Further work aiming at examining potential synergistic interactions among extinction factors is therefore needed to improve the reliability of species viability assessments. In such a context, seabirds, as marine top predators, display potential high susceptibility to the effects of climate change on large-scale oceanographic processes (Barbraud & Weimerskirch, 2001, 2003; Thompson & Ollason, 2001). Changes in sea-surface temperatures might bring further constraints to population dynamics (Weimerskirch *et al.*, 2003; Nevoux & Barbraud, 2005) of the endemic and rare Macgillivray's prion, whether rats and falcons prey on them or not.

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References

Barbraud, C. & Weimerskirch, H. (2001). Emperor penguins and climate change. *Nature* **411**, 183–186.

Barbraud, C. & Weimerskirch, H. (2003). Climate and density shape population dynamics of a marine top predator. *Proc. Roy. Soc. Ser. B* **270**, 2111–2116.

Beissinger, S.R. & McCullough, D.R. (2002). *Population viability analysis*. Chicago: University of Chicago Press.

Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004). Avian extinction and mammalian introductions on oceanic islands. *Science* **305**, 1955–1958.

Boyce, M.S. (1992). Population viability analysis. *Annu. Rev. Ecol. Evol. S.* **23**, 481–506.

Bretagnolle, V., Zotier, R. & Jouventin, P. (1990). Comparative population biology of four prions (genus *Pachyptila*) from the Indian Ocean and consequences for their taxonomic status. *Auk* **107**, 305–316.

Brooke, M. (1990). *The manx shearwater*. London: T&AD Poyser.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L. & Purvis, A. (2005). Multiple causes of high extinction risk in large mammals species. *Science* **309**, 1239–1241.

Caughley, G. (1994). Directions in conservation biology. *J. Anim. Ecol.* **63**, 215–244.

Coulson, T., Mace, G.M., Hudson, E. & Possingham, H. (2001). The use and abuse of population viability analysis. *Trends Ecol. Evol.* **16**, 219–221.

Courchamp, F., Clutton-Brock, T.H. & Grenfell, B. (1999). Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* **14**, 405–410.

Cramp, S. & Simmons, K.E.L. (1980). *Handbook of the birds of Europe, the Middle East and North Africa. Vol II. Hawks to Bustards*. Oxford: Oxford University Press.

Diamond, J. (1989). Overview of recent extinctions. In *Conservation for the twenty-first century*: 37–41. Western, D. & Pearl, M. (Eds). Oxford: Oxford University Press.

Doak, F.D., Morris, W.F., Pfister, C., Kendall, B.E. & Bruna, E.M. (2005). Correctly estimating how environmental stochasticity influences fitness and population growth. *Am. Nat.* **166**, E14–E21.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000). Climate extremes: observations, modeling, and impacts. *Science* **289**, 2068–2074.

Ferrière, R., Sarrazin, F., Legendre, S. & Baron, J.-P. (1996). Matrix population models applied to viability analysis and conservation: theory and practice using the ULM software. *Acta Oecol.* **17**, 629–656.

Gable, F.J., Aubrey, D.G. & Gentile, J.H. (1991). Global environmental change issues in the western Indian Ocean region. *Geoforum* **22**, 401–419.

Gauthier-Clerc, M., Jiguet, F. & Lambert, N. (2002). Vagrant birds at Possession Island, Crozet Islands, and Kerguelen Island from December 1995 to December 1997. *Marine Ornithol.* **30**, 38–39.

Gurevitch, J. & Padilla, D.K. (2004). Are invasive species a major cause of extinctions? *Trends Ecol. Evol.* **19**, 470–474.

Hamilton, S. & Moller, H. (1995). Can PVA models using computer packages offer useful conservation advice? Sooty Shearwaters *Puffinus griseus* in New Zealand as a case study. *Biol. Conserv.* **73**, 107–117.

Harper, P.C. (1980). The field identification and distribution of the prions (genus *Pachyptila*), with particular reference to the identification of stormcast material. *Notornis* **27**, 235–286.

Holsinger, K.E. (2000). Demography and extinction in small populations. In *Genetics, demography and viability of fragmented populations*: 55–74. Young, A. & Clarke, G. (Eds). Cambridge: Cambridge University Press.

Jouventin, P., Stahl, J.C., Weimerskirch, H. & Mougin, J.L. (1984). The seabirds of the French Subantarctic Islands and Adelie Land, their status and conservation. In *Status and conservation of the world seabirds*: 609–625. Croxall, J.P., Evans, P.G.H. & Schreiber, R.W. (Eds). Cambridge: ICBP Technical Publication.

Knutson, T.R. & Tuleya, R.E. (1999). Increased hurricane intensities with CO_2-induced warming as simulated using the GFDL hurricane prediction system. *Clim. Dynam.* **15**, 503–519.

Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* **142**, 911–927.

Legendre, S. & Clobert, J. (1995). ULM, a software for conservation and evolutionary biologists. *J. Appl. Stat.* **22**, 817–834.

Ludwig, D. (1999). Is it meaningful to estimate a probability of extinction? *Ecology* **80**, 298–310.

Micol, T. & Jouventin, P. (2002). Eradication of rats and rabbits from Saint-Paul Island, French Southern Territories. In *Turning the tide: the eradication of invasive species*: 199–205. Veitch, C.R. & Clout, M.N. (Eds). Gland: IUCN SSC Invasive Species Specialist Group.

Morris, W.F. & Doak, D.F. (2002). *Quantitative conservation biology*. Sunderland, USA: Sinauer.

Mougeot, F. & Bretagnolle, V. (2000). Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach. Using acoustic signals. *Anim. Behav.* **60**, 647–656.

Mougeot, F., Genevois, F. & Bretagnolle, V. (1998). Predation on burrowing petrels by the brown skua (*Catharacta skua lonnbergi*) at Mayes Island, Kerguelen. *J. Zool. (Lond.)* **244**, 429–438.

Nevoux, M. & Barbraud, C. (2005). Relationships between sea ice concentration, sea surface temperature and demographic traits of thin-billed prions. *Polar Biol.* **29**, 445–453.

Oro, D., Aguilar, J.S., Igual, J.M. & Louzao, M. (2004). Modelling demography and extinction risk in the endangered Balearic Shearwater. *Biol. Conserv.* **116**, 93–102.

Palmqvist, E. & Lundberg, P. (1998). Population extinctions in correlated environments. *Oikos* **83**, 359–367.

Pimm, S.L. (1996). Lessons from a kill. *Biodivers. Conserv.* **5**, 1059–1067.

Péron, P. (1824). *Mémoires du Capitaine Péron sur ses voyages*. Vols. I–II. Paris: Brissot-Thivars.

Reed, D.H., O'Grady, J.J., Ballou, J.D. & Frankham, R. (2003). The frequency and severity of catastrophic die-offs in vertebrates. *Anim. Conserv.* **6**, 109–114.

Roux, J.P. & Martinez, J. (1986). Rare, vagrant and introduced birds at Amsterdam and St Paul Islands, Southern Indian Ocean. *Cormorant* **14**, 3–19.

Shaffer, M. (1987). Minimum viable population: coping with uncertainty. In *Viable population for conservation*: 69–86. Soulé, M.E. (Ed.). Cambridge: Cambridge University Press.

Shirihai, H. & Jarrett, B. (2002). *The complete guide to Antarctic wildlife*. Princeton: Princeton University Press.

Spendelow, J.A., Nichols, J.D., Hines, J.E., Lebreton, J.-D. & Pradel, R. (2002). Modelling postfledging survival and age-specific breeding probabilities in species with delayed maturity: a case study of roseate terns at Falkner Island, Connecticut. *J. Appl. Stat.* **29**, 385–405.

Taylor, B.E., Scott, D.E. & Gibbons, J.W. (2006). Catastrophic reproductive failure, terrestrial survival, and presistence of the marbled salamander. *Conserv. Biol.* **20**, 792–801.

Thompson, P.M. & Ollason, J.C. (2001). Lagged effects of ocean climate change on fulmar population dynamics. *Nature* **413**, 417–420.

Tollu, B. (1984). La Quille (Ile Saint-Paul, Océan Indien), sanctuaire de populations relictes. *L'Oiseau & R.F.O.* **54**, 79–85.

Velain, C. (1878). Passage de Vénus sur le soleil (9 décembre 1874). Expédition française aux îles Saint-Paul et Amsterdam. Zoologie: observations générales sur la faune des deux îles suivies d'une description des mollusques. *Arch. of Zool. Exp. Gen.* **6**, 1–44.

Warham, J. (1990). *The petrels. Their ecology and breeding systems*. London: Academic Press.

Weimerskirch, H., Inchausti, P., Guinet, C. & Barbraud, C. (2003). Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarct. Sci.* **15**, 49–256.

Worthy, T.H. & Jouventin, P. (1999). The fossil Avifauna of Amsterdam island, Indian Ocean. *Smithson. Contrib. Paleobiol.* **89**, 39–65.

Young, T.P. (1994). Natural die-offs of large mammals: implications for conservation. *Conserv. Biol.* **8**, 410–418.

Supplementary Material

The following material is available for this article online:

Appendix S1 Saint-Paul Island with the Roche Quille in front of the crater.

Appendix S2 The Roche Quille, the only place in the world where the endemic Macgillivray's prior was breeding before the rat eradication on the adjacent main Island in 1997.

Appendix S3 A recently fledged Macgillivray's prion, and the vagrant peregrine falcon observed in 1999.

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