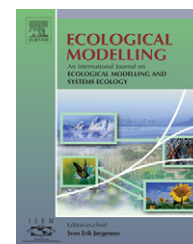


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Limited nest site availability helps seabirds to survive cat predation on islands

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ABSTRACT

Introduced cats *Felis catus* have a high detrimental impact on native seabirds on islands, especially when alien preys, like rabbits *Oryctolagus cuniculus*, co-occur. Seabirds are highly vulnerable because of their long reproductive cycles, slow turn-over of generations and the absence of efficient behaviour against terrestrial predators, especially in some burrow-nesting species. Through a deterministic modelling approach, we explored a neglected mechanism that may explain the resistance of some seabird species to cat predation. It was indeed observed that seabirds may compete for nest sites. As a consequence, part of the breeders foregoes breeding when nest sites are a limiting resource. Our model linked the dynamics of cats with that of seabird species. We showed that the annual impact of cats on seabirds was lower when seabirds faced competition for burrows than when the latter were not a limiting resource. This was due to the fact that limited nest site availability prevents an optimal growth of the cat population. Cats in turn cannot manage to exterminate all the prospecting birds during the same breeding season. The limitation of the number of nest sites generates a mechanism leading the bird population to conserve a large pool of sexually mature individuals while only slightly reducing the production of juveniles in the colony. This pool of floaters may play an important role in natural populations by buffering the decrease in colony size during years with harsh environmental conditions on land. In combination with buffer mechanisms, the limitation of the number of nest sites may greatly improve the chances of survival of bird populations facing predation.

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1. Introduction

Insular ecosystems are extremely sensitive to anthropogenic perturbations (Jarvis, 1979; Byrne, 1980; Dowding and Murphy, 2001). Most of the bird extinctions attributable to introduced predators, if not all, have occurred on islands (Stattersfield and Capper, 2000). Amongst introduced predators, cats *Felis catus* (L.) have played a major role in the extirpation of indigenous seabirds on islands (Moors and Atkinson, 1984; Dowding

and Murphy, 2001). Their impact on the native avifauna was the most dramatic on islands where alien preys co-occur (Atkinson, 1985), like for instance rabbits *Oryctolagus cuniculus* (L.) (Weimerskirch et al., 1989).

Because they evolved in areas inaccessible, or poorly accessible, to mammals (that is, oceanic islands or inaccessible cliffs on mainlands), seabirds generally lack the adaptations, both in their behaviour and their life-history strategies, that would enable them to cope successfully with alien predators (Lack,

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1968; Moors et al., 1992). Moreover, most seabird species show quasi-absolute fidelity to their breeding island (review in Bried and Jouventin, 2002), which will increase the probability of extermination by alien predators. The risk is higher for burrowing petrels which leave their single chick unattended in their burrows when a few days old (Warham, 1990). Seabirds also have a slow turn-over of generations: they generally have a low fecundity, the extreme being a single-egg clutch without replacement (especially in all albatrosses and petrels), a delayed sexual maturity (the minimum age at first breeding ranges from 2 to 8 years) and they can live up to several tens of years (reviews in Warham, 1996; Bried and Jouventin, 2002; Appendix 2 in Schreiber and Burger, 2002). They also have long breeding cycles, that is, long periods of colony attendance: from several weeks to more than one year (review in Bried and Jouventin, 2002). Because seabirds are long-lived, the dynamics of their populations is extremely sensitive to a small increase in adult mortality (Weimerskirch et al., 1987; Cuthbert et al., 2001). In addition, introduced predators have an indirect impact on seabirds by increasing the incidence of nest switching and divorce, which can result in the loss of several breeding years (Bried and Jouventin, 1999).

Studying the impact of introduced predators is of paramount importance for conservation biology, especially on subantarctic islands where the native avifauna shows high levels of endemism and is often made up essentially by seabirds (Marchant and Higgins, 1990; Higgins and Davies, 1996; Shirihai, 2002). The existence of simplified trophic webs on many subantarctic islands but also on tropical and temperate islands free of native mammals where avian communities exhibit similar characteristics makes such islands excellent models to assess the impact of introduced predators on the marine avifauna. Previous theoretical studies, despite increasing accuracy (Courchamp et al., 2000; Gaucel et al., 2005; Zhang et al., 2006), tended to neglect important aspects of seabird population dynamics. In particular, while competition for nest sites is common in seabirds (Burger and Shisler, 1978; Ramos et al., 1997; Quintana and Yorio, 1998), the role of nest site availability in the response of seabirds to predation has never been investigated.

In this paper, using a modelling approach, we show that the impact of alien predators on seabirds may differ if we account for the limitation in the number of nest sites. We consider a situation similar to that on the main island of the Kerguelen archipelago, southern Indian Ocean, for which there are reliable estimates of cat densities (Say et al., 2002), and because 33 out of the 35 avian species breeding at this locality are seabird species (Weimerskirch et al., 1989). Our model incorporates the cat as a top-level predator and a “theoretical” cavity-nesting seabird species (whose demographic parameters fall within the range of those observed in burrow-nesting seabirds and where breeders show absolute year-to-year fidelity to their colony) that faces variations in nest site availability. We also consider that cats prey on birds only during the breeding period of the latter, and that nests are easily accessible to cats. If too few nest sites are available, all the birds that are in breeding condition cannot breed during a given breeding season and cats suffer from the decrease in prey availability. The growth of the cat population is limited, resulting in a decreased predation pressure on birds. This rather simple mechanism creates

a scenario that may enable seabird species to persist longer than they would if all potential breeders could easily obtain a nest. Finally, we discuss the implications of our results for seabird conservation.

2. Materials and methods

2.1. Considerations and definitions

In our model, and like on the Kerguelen Islands, seabird colony size varies between 10^3 and 10^5 pairs, depending on species (see, e.g., Weimerskirch et al., 1989; Marchant and Higgins, 1990), and cat density varies between 1 and 2 cats/km² (Say et al., 2002). Our model takes the limiting resources for seabirds and the seasonality of reproduction of prey species into account. Birds leave the colony at the end of the breeding season and remain at sea until the onset of the next breeding cycle. Cats prey on birds but also on alien preys, for instance rabbits and mice *Mus musculus* which are present in the same area on the main island of the Kerguelen archipelago (Pontier et al., 2002) and provide feral cats with a primary prey species, helping them to maintain their numbers during the winter and to spread (Moors et al., 1992; Pontier et al., 2002; Gaucel et al., 2005). Because of their opportunistic behaviour, cats take birds at the beginning of the breeding season (i.e., from the pair formation period onwards) and then, the proportion of birds in their diet decreases towards the end of the breeding period (Bloomer and Bester, 1990).

The birds' life cycle is modelled as follows (Fig. 1). Each individual belongs to only one of the following categories: (1) juveniles (B_j) that is, young from hatching until their departure to sea, (2) immatures (B_i) that is, individuals between fledging and the year when they will become socially mature, (3) “socially mature” individuals (B_m) that is, all the birds that have returned to the colony at least once since fledging (some of them will remain at sea without returning ashore during the currently starting breeding season), plus the birds that will return ashore for the first time of their life during the currently starting breeding season, (4) prospectors (B_p), i.e., all the individuals that come ashore during the current breeding season (this category includes the former breeders that have regained breeding condition, the individuals reaching breeding condition for the first time and the individuals that are not physiologically able to breed but that come ashore to secure a nest and/or a mate for the next year; see, e.g., Nelson, 1983; Warham, 1990) and (5) breeders (B_n), that is, the prospectors that effectively attempt to breed (i.e., that lay at least an egg or whose female lays at least an egg). The prospectors that do not attempt to breed during the current breeding season are thereafter referred to as “floaters”. At the end of the breeding season, breeders return to the B_m compartment. Let b_B be the birth rate of birds. We note γ_1 the rate at which immature becomes socially mature. By definition, only prospectors return to the colony and their number is limited by K_B through food availability at sea. Indeed, the distribution and abundance of marine organisms (Waluda et al., 1999), linked to variations in oceanographic conditions (e.g., Deacon, 1977), directly influence the amount of body reserves stored by the individuals, as well as their breeding perfor-

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