Can cat predation help competitors coexist in seabird communities?

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ABSTRACT

On oceanic islands, nest site availability can be an important factor regulating seabird population dynamics. The potential for birds to secure a nest to reproduce can be an important component of their life histories. The dates at which different seabird species arrive at colonies to breed will have important consequences for their relative chances of success. Early arrival on the island allows birds to obtain nests more easily and have higher reproductive success. However, the presence of an introduced predator may reverse this situation. For instance, in the sub-Antarctic Kerguelen archipelago, early arriving birds suffer heavy predation from introduced cats. Cats progressively switch from seabirds to rabbits, since the local rabbit population starts to peak after early arriving seabird species have already returned to the colony. When late-arriving birds arrive, cat predation pressure on seabirds is thus weaker. In this paper, we investigate the assumption that the advantage of early nest mnopolization conferred to early arriving birds may be counterbalanced by the cost resulting from predation. We develop a mathematical model representing a simplified situation in which two insular seabird species differ only in their arrival date at the colony site and compete for nesting sites. We conclude that predation may ensure the coexistence of the two bird species or favor the late-arriving species, but only when seasonal variations in predation pressure are large. Interestingly, we conclude that arriving early is only favorable until a given level where high reproductive success no longer compensates for the long exposure to strong predation pressure. Our work suggests that predation can help to maintain the balance between species of different phenologies.

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1. Introduction

Nests are fundamental resources for many species. In seasonally breeding species, competition for nesting sites may depend on the date at which individuals arrive at the site, with early arriving individuals theoretically able to secure higher quality territories than later-arriving ones (Pulliam and Danielson, 1991; Kokko, 1999). Several studies on different taxa that face strong competition for breeding territories—including insects (e.g., Wang et al., 1990), birds (e.g., Rowan, 1965; Greenwood and Harvey, 1982) and mammals (Bried et al., 2009)—have supported this hypothesis. Such competition can be inter-species (e.g., Quintana and Yorio, 1998), intra-species (e.g., Rowan, 1965; Candolin and Voigt, 2001), or both intra- and inter-species (e.g., Ramos et al., 1997).

In seasonal seabirds, the date of arrival at the breeding grounds and the laying date tend to vary among species due to exogenous (photoperiod) and endogenous factors (e.g., individual hormonal status, circadian rhythm) that elicit migratory and breeding behavior,

and/or to differences in feeding ecology (Both and Visser, 2001; Le Corre, 2001; Brooke, 2004; Lehikoinen et al., 2004). Early breeding is generally advantageous in terms of breeding success (Nelson, 1980; Daan et al., 1988; see also Ollason and Dunnet, 1988; Barba et al., 1995; Sydeman and Eddy, 1995). However, if the breeding locality harbors a predatory species that faces a food shortage during the period when birds are absent, the earliest-arriving individuals are also the most likely to suffer mortality due to predation. The critical question here is: can predation counterbalance the benefit of arriving early and/or the cost of arriving later at the breeding grounds?

To address this question, insular seabird species represent especially suitable models. On most oceanic islands, seabirds have evolved without terrestrial mammalian predators until recently, when rats (*Rattus* spp.) and cats (*Felis silvestris catus*) were introduced by humans on several islands (Atkinson, 1985; Johnstone, 1985; Veitch, 1985). Many seabird species lack the behavioral and ecological adaptations that would enable them to cope successfully with mammalian predators (Lack, 1968; Warham, 1990). Consequently, the impact of introduced predators on insular seabird populations has been catastrophic in most cases (Atkinson, 1985; Veitch, 1985; Pontier et al., 2002; Blackburn et al., 2004).

Pontier et al. (2008) studied certain aspects of competition for nesting sites in a seabird species that faces predation from cats.

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They concluded that, surprisingly, limited nest site availability could favor the long-term persistence of the seabird population by creating a large pool of non-breeding birds that can buffer the demographic impacts of factors such as bad climatic conditions on land. However, their model was a predator–prey model that included only one prey species and prey breeding limitation. The potential existence of several species competing for nest sites was neglected. The present paper aims to determine whether and how the outcome of this competition is affected by predation.

There are several mechanisms through which predators can alter the strength and direction of competition between prey species (Chase et al., 2002). It is widely acknowledged that alien predators are a major factor in biodiversity loss (Courchamp et al., 2003). Indeed, the first direct effect of predation is a reduced abundance of native prey and hence an increased risk of extinction. Moreover, predation can generate indirect competition between two otherwise independent prey species, which can potentially lead to the extinction of one of the two prey species (Courchamp et al., 1999). This is because increasing the abundance of one prey species leads to an increase in predator numbers and hence a decline in the other prey population. However, some mechanisms may allow predation to promote coexistence between prey species. This is the case, for example, if prey that are the best competitors for resources are the most vulnerable to predation (Armstrong, 1979; Abrams, 1999; Leibold, 1996), when different prey species occupy different shelters to avoid predation (Jeffries and Lawton, 1984; Holt and Lawton, 1994) or when the intensity of predation depends on prey density (Roughgarden and Feldman, 1975; Gendron, 1987; Huntly, 1991).

To investigate how predation by introduced cats (hereafter referred to as predation) can modify the benefit-cost balance of arriving early at the nesting sites and hence alter seabird community structure, we built a mathematical model considering two seabird species that differ only in their date of arrival on a hypothetical remote island. These species both face predation and share the same nesting sites. One fundamental model assumption is that the impact of cat predation may differ between seabird species according to their date of arrival. Indeed, early arriving birds arrive before a surge in the rabbit population and therefore constitute the main prey of cats during this period. Late-arriving birds suffer weaker predation because they return to the island at the moment when rabbits become abundant and are again an important target for cats. Here we determine whether predation can help late-arriving birds—which here are always disadvantaged in the absence of predation—to obtain nest sites and to breed as successfully as their early arriving counterparts.

2. Materials and methods

2.1. The mathematical model

Our mathematical model extends classical Lotka–Volterra Competition equations (see Murray, 2003, for a review). It is parameterized to represent two typical colonial burrow-nesting seabird species on an island (or a group of islands) that is home to both cats and rabbits, as in the Kerguelen archipelago, southern Indian ocean (Pontier et al., 2002), or on the Canary Islands, subtropical north-eastern Atlantic (Nogales and Medina, 2009). The first species of birds breeds early (early breeders, species 1), while the second species starts breeding later (late breeders, species 2). In our model, superscript labels 1 and 2 represent early and late breeders, respectively. The two seabird species are assumed to be otherwise identical. Given this framework, we can be sure that the outcome of the competition between the two
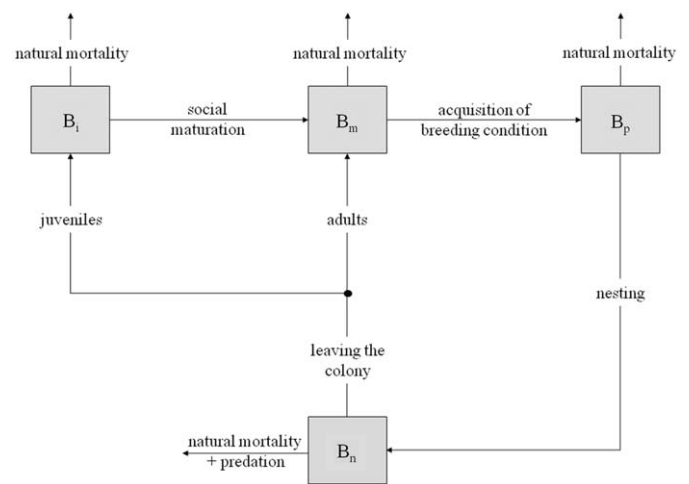

Fig. 1. Schematic life cycle of seabirds, where B_i is the number of immature birds, B_m the number of socially mature birds, B_p the number of prospectors and B_n the number of occupied nests.

seabird species will be the result of the selective advantage and disadvantage conferred by their dates of arrival on the island.

Our model is a simplified version of that proposed by Pontier et al. (2008). We consider two seabird species with a balanced sex ratio, such that the model only represents the changes in the number of females. The birds' life cycle is illustrated in Fig. 1. We use K_n to denote the number of available nesting sites on the island, with $B_n(t)$ being the number of nests occupied at time t. To simplify, we assume that all the birds occupying a nest behave in the same manner: all birds leave the colony at the same time at the end of the breeding season, and if one individual in a nest dies, then all the individuals from this nest will die. Given the extended incubation period in seabirds (between 18 and 83 days, depending on the species; see Appendix 2 in Schreiber and Burger, 2002), the bulk of predation occurs before the eggs hatch (especially in the early arriving species) and hence mainly affects adults. This pattern results in a very high rate of breeding failure: without biparental care, chicks die along with their parents (see Lack, 1968).

At time t_1 (t_2), all the individuals of species 1 (species 2) leave the nest, leading to a number $bB_n^1(bB_n^2)$ of immature individuals, where b is the average number of juveniles in each occupied nest. The 'immature' class (B_i) includes all individuals between fledging and the age when they will become socially mature (compartment B_m) at a rate γ_1. All the birds that have returned to the colony at least once since fledging and the birds that will return ashore for the first time in their lives during the current breeding season are considered 'socially mature'. Socially mature birds become prospectors at a rate $\gamma_2^1(t)$ for early breeders and $\gamma_2^2(t)$ for late breeders. Prospectors (class B_p) are those individuals that come ashore during the current breeding season. This class includes both former breeders that are ready to breed again and individuals that are now ready to breed for the first time. During the appropriate period of the year that depends on seabird species (the seasonal behavior of the two seabird species as modeled here is represented in Fig. 2), prospecting birds start colonizing vacant nests (at a rate $\mu^1(t)$ for early breeders and $\mu^2(t)$ for late breeders). All the birds face a natural mortality (i.e., mortality due to any cause other than predation) at rate m.

We introduce a saturating term to model the rate at which socially mature birds become prospectors: we assume that the number of breeding and prospecting birds is limited to a certain quantity, K_b, due to limited resources at sea. Indeed, the distribution and abundance of marine organisms (Waluda et al.,