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Trophic roles of black rats and seabird impacts on tropical islands: Mesopredator release or hyperpredation?

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ABSTRACT

Rats contribute to the decline of tropical seabird populations by affecting their breeding success through direct predation of eggs and chicks. When they coexist with other predators, invasive rats may also generate indirect interactions via the changes they impose on the structure of communities and trophic interactions following invasion ('hyperpredation process'), or when apex predators are eradicated from the ecosystem ('mesopredator release effect'). Understanding these effects is necessary to implement restoration operations that actually benefit threatened seabird populations. We investigated these processes on two French tropical seabird islands of the western Indian Ocean, Europa and Juan de Nova, where black rats coexist with two different apex predator species (introduced cats and potentially native barn owls). The parallel use of several methods (diet analysis, stable isotopes, seabird monitoring) to identify trophic roles of rats revealed that the direct impact of rats on seabirds was particularly high on Europa where only rats and owls occur, with high consumption of chicks resulting in low breeding success for several seabird species. We also suggested that hyperpredation associated with top-down regulation of cats is occurring on Juan de Nova, although territoriality of cats may buffer this process. Conversely we found evidence that mesopredator release effect is unlikely, irrespective of the apex predator identity. Considering the most likely effects on both islands we provided recommendations on eradication priorities to mitigate the risk of local extinction that seabirds are currently facing.

1. Introduction

The introduction of rats on islands has been identified as one of the main threats to seabird breeding populations (Croxall et al., 2012). There is an extensive literature documenting the negative direct impacts of rats on seabirds. Jones et al. (2008) identified 94 studies showing a direct impact of invasive rats (*Rattus rattus*, *Rattus exulans*, *Rattus norvegicus*) on seabirds (115 cases of predation on 61 islands, involving 75 species of seabirds). Rats can prey upon eggs and chicks of many families of seabirds as well as adults of some species of small size (e.g. storm petrels) (Jones et al., 2008; Pickup, 1999; Seto and Conant, 1996; Tomkins, 1985).

Invasive rats may also generate negative indirect impacts via the changes they impose on the structure of communities and trophic interactions following invasion, or when apex predators are eradicated from the ecosystem (Fig. 1). In particular mesopredator release effect (a specific case of intraguild predation) and hyperpredation process may occur depending on the functional role of rats in the invaded ecosystem. Intraguild predation occurs when two predators are simultaneously involved in a predatory relationship while competing for a shared prey (Holt and Polis, 1997; Polis and Holt, 1992). Generally one predator (i.e. apex predator) preys upon the other (i.e. mesopredator) through an asymmetrical intraguild predation (Holt and Polis, 1997). In this configuration both predators have an important impact on the common prey and mesopredator release (e.g. release of rats) may occur after removal of the apex predator (e.g. cats) resulting in an increase of the negative impact on native species (Fig. 1) (Courchamp et al., 1999). Hence mesopredator release effect requires two conditions: (1) the negative effect of rats on seabird population growth rate after the removal of the apex predator must outweigh the initial cumulative impacts of both predators, and (2) mesopredator population dynamics must be regulated by the apex predator (i.e. top-down regulation) (Courchamp et al., 1999). Although mesopredator release effect has often been discussed in the field of conservation, there are few documented examples (Nishijima et al., 2014). On Little Barrier Island (New Zealand), cats and rats preyed upon petrels and cats also preyed upon rats. After the eradication of cats, breeding success of petrels considerably decreased, and improved

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only after the eradication of rats (Rayner et al., 2007). Rats are likely to have caused this decrease in breeding success of petrels, although no evidence of simultaneous increase in the rat population could be made (Girardet et al., 2001). In addition, although the breeding success decreased indirectly due to the elimination of cats, an increase in survival of adult birds and population growth rate probably also concomitantly occurred (Le Corre, 2008). Alternatively, rats may act as alternative prey for the apex predator and indirectly impact native seabirds through apparent competition (Bate and Hilker, 2012; Courchamp et al., 2000). Apparent competition applies to those situations in which two prey species have a negative indirect effect on one another resulting from interactions with a common predator (Holt, 1977; Holt and Lawton, 1994). Thus, as in the case of a 'real' competition between the two prey species, the increase of the size of one population causes the decrease of the other, while these two species are not necessarily exploiting the same resource (hence the term "apparent" competition). Apparent competition on islands has been studied in the particular case where the main prey species is native and the secondary prey is an introduced species (Courchamp, 1999), a process called hyperpredation (Smith and Quin, 1996) (Fig. 1). In this process, an introduced prey adapted to predation (e.g. rats) and with high growth rate and behavioural anti-predator strategies, promotes apex predator numbers (e.g. cats), which in turn increases the impact on native prey (e.g. seabirds). Therefore, the possibility of complex and indirect interactions resulting from the introduction or removal of a predator must be the subject of special attention when planning the eradication of invasive rodents.

In this paper, we investigated the trophic roles of black rats (*R. rattus*) on tropical islands. In particular we compared direct and indirect effects they generate on breeding populations of seabirds. Trophic roles of rats and their consequences on seabirds were studied with a combination of methods (diet analysis, stable isotopes, seabird monitoring) on two contrasted French tropical islands lying in the Indian Ocean. These data also meet the current need of documenting the effects of invasive rats on native communities on tropical islands (Towns et al., 2006; Varnham, 2010). The results may inform local stakeholders on eradication priorities for the restoration of these islands. The understanding of these interactions also has a global scope in terms of conservation, as the predator associations described here are relatively common on islands.

2. Material and methods

2.1. Study sites

Europa (2223 ha; 22°210S, 40°210E) and Juan de Nova (561 ha; 17°030S, 42°450E) are two tropical islands lying in the Mozambique Channel (between the East African coast and Madagascar), administered since 2007 by TAAF (Terres Australes et Antarctiques Françaises) (Fig. 2). The climate is characterized by the alternation of a warm and wet season (austral summer, between November and March) and a dry and cooler season (austral winter between April and October). Black rats have been introduced to both islands before the mid-19th century (Russell et al., 2011b). Europa supports high rat densities (10–80 rats ha^{-1}) whereas rat densities are intermediate on Juan de Nova (10–35 rats ha^{-1}) (Russell et al., 2011a). On Europa, the large lagoon supports an additional 3-ha islet at the northern entrance, where rats are also present. Cats (*Felis catus*,<80 individuals in 2006) and mice (*Mus musculus*) have also been introduced on Juan de Nova and a small population of barn owls (*Tyto alba*,<15 pairs) breeds on Europa but their status (native or introduced) is uncertain (Russell and Le Corre, 2009). Cats were heavily controlled on Juan de Nova between 2006 and 2011 but not eradicated (123 cats removed and less than 10 cats left in 2011). These islands are major breeding sites for seabirds (Table 1) and turtles (*Chelonia mydas*, *Eretmochelys imbricata*) (Le Corre and Jaquemet, 2005). In particular, very large colonies of sooty terns (*Onychoprion fuscatus*) breed during summer on Juan de Nova (450,000 pairs) and during winter on Europa (760,000 pairs). They are also home to several other native species, including reptiles, songbirds and shorebirds, and are stopping points for many migratory species. Fieldwork consisted of 1 or 2 months long visits (at least once a year between 2006 and 2013) to these remote islands occupied year-round by military detachments (15 people).

2.2. Diet of black rats

Black rats were trapped in summer and winter between 2006 and 2013 on both islands. On each island trapping sessions were carried out inside and outside sooty tern colonies (within 1 km of the colony) when terns were breeding (during summer on Juan de Nova and during winter on Europa), and only outside tern colonies when terns were absent. No other seabird bred inside and outside tern colonies on Juan de Nova but a few breeding pairs of

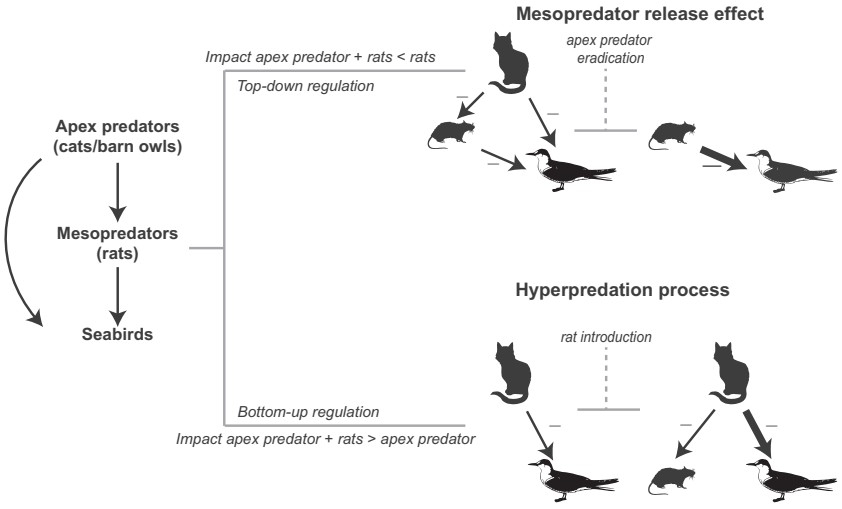

Fig. 1. Schematic representations of mesopredator release effect and hyperpredation process. In a bottom-up driven system (hyperpredation process) rat population is regulated by trophic resources whereas in a top-down driven system (mesopredator release effect) abundance of rats is regulated by apex predators.