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Anti-predator behaviour in a procellariid seabird: Wedge-tailed shearwaters do not respond to the odour of introduced ship rats

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Abstract Seabirds are particularly vulnerable to introduced alien mammalian predators, especially invasive rats, which are the main contributors to seabird extinction and endangerment in many places worldwide. However, this appears context-dependent because, paradoxically, cases of apparent long-term coexistence between rats and some species of seabird have been reported for centuries, in various locations. Among seabirds, procellariiforms are known to have developed a range of olfactory-driven behaviours, such as partner recognition and homing. Olfaction could be an effective means of recognizing and thereafter avoiding invasive predators. However, the role of olfaction in predation risk assessment has not yet been examined in any procellariiform. Here, we investigated, through a Y-maze experiment, whether the wedge-tailed shearwater (*Puffinus pacificus*) avoided the odour of one of the most damaging alien predators on islands, the ship rat (*Rattus rattus*). The experiment was conducted in different ecological contexts on three neighbouring islets off New Caledonia having different communities of invasive rats. Contrary to our expectations, the wedge-tailed shearwater either did not detect or did not avoid the odour of the ship rat, despite about 175 years of coexistence between rats and shearwaters in New Caledonia. These findings highlight the need for further investigations (across species, across sites) into the factors underpinning the paradox between high vulnerability and the surprising long-term coexistence between procellariid seabirds and alien invasive rats.

Key words: avoidance behaviour, introduced rodent, invasive species, Procellariiformes, Y-maze experiment.

INTRODUCTION

Introduced mammals, especially predators, are known to have severely impacted island birds worldwide, including seabird species (e.g. Owens & Bennett 2000; Courchamp *et al.* 2003; Hervias *et al.* 2013; Spatz *et al.* 2014). Rats (*Rattus* sp.) in particular have colonized about 90% of the world's islands (Atkinson 1985; Towns *et al.* 2006) and are among the main contributors to seabird extinction and endangerment documented worldwide, particularly for small- to medium-sized procellariid seabirds such as petrels and shearwaters (Jones *et al.* 2008; Shiels *et al.* 2014). The vulnerability of petrels and shearwaters to invasive rats is enhanced by their ground- or burrow-nesting habits, which make the eggs, chicks and incubating adults easy prey (e.g. Warham 1996; Jones *et al.* 2008). Like many species having evolved in the absence of predators on isolated islands, petrels and shearwaters gen-

erally exhibit no or ineffective anti-predator behaviour when facing alien predators (Warham 1996; Carthey & Banks 2014).

Nevertheless, several cases of apparent long-term coexistence between rats and seabirds have been reported on many islands around the world (Carty *et al.* 2007; Quillfeldt *et al.* 2008; Ruffino *et al.* 2009). These paradoxical situations suggest that the impact of rats on seabirds could be context dependent, that is, may vary according to the period when seabirds are available as prey (returning to the land) and to the availability of alternative food resources during the year (Rayner *et al.* 2007). Alternatively, some seabirds may sometimes manage to chase away rats through aggression or nest defence behaviour (Warham 1996). Procellariid seabirds may also have locally developed indirect, cryptic anti-predator behaviours so as to reduce the impact of rats (e.g. Ruffino *et al.* 2009; Bourgeois *et al.* 2013). Interestingly, the extent and the rapidity of some seabird population recovery after rat eradication (Bourgeois *et al.* 2013) suggest that rats had previously prevented birds from breeding, and points to an as yet unidentified behavioural process

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enabling shearwaters to detect and avoid rat-infested islands, and to rapidly (re)colonize islands when rats are removed.

The use of olfaction to assess predation risk is common across species of vertebrates (Kats & Dill 1998), and it has recently been suggested that olfaction and chemical communication in birds may be more important than previously thought (Steiger *et al.* 2008; Bonadonna & Mardon 2013). Procellariid seabirds in particular use chemical communication and their sense of smell for many purposes, including identification of foraging areas (Nevitt 2000; Nevitt & Bonadonna 2005), homing and nest recognition (Bonadonna *et al.* 2003a,b; Bonadonna *et al.* 2004), or partner recognition (Bonadonna & Nevitt 2004). The ability to use chemical cues to ascertain predator presence and assess predation risk could be crucial for species nesting in cavities, that is, habitats where visual detection of predators is not easy (Amo *et al.* 2008). This has recently been tested for hole-nesting songbirds (e.g. Godard *et al.* 2007; Amo *et al.* 2008; Roth *et al.* 2008; Amo *et al.* 2011) with positive and negative results. In fact, three of these studies showed that songbird species detected predator odours and showed anti-predator behaviour to cope with the risk of predation (Amo *et al.* 2008, 2011; Roth *et al.* 2008), whereas the last one showed that the presence of chemical cues of nest predators does not ultimately influence selection of nest site by eastern bluebird (*Sialia sialis*) (Godard *et al.* 2007). However, to the best of our knowledge, the use of chemical cues to detect predators has never been investigated in procellariid seabirds.

To fill this gap, we experimentally tested whether the wedge-tailed shearwater (*Puffinus pacificus*) could detect and respond to the odour of the ship rat. Experiments were conducted in the southern lagoon of New Caledonia, which hosts what is probably one of the world's largest colonies of *P. pacificus* (Benoit & Bretagnolle 2002). The ship rat can dramatically reduce the breeding success of *P. pacificus*, as documented on two Hawaiian islands, where the breeding success of birds sharply increased following rat eradication (Smith *et al.* 2006; Marie *et al.* 2014).

METHODS

Study system

This study was conducted on breeding colonies of *P. pacificus* on three islets off Isle of Pines (22°37'S, 167°29'E), New Caledonia (South Pacific Ocean) in 2012. These islets, hereafter called islets A, B and C, are protected areas with restricted access for non-scientific activities. Their surface areas are respectively 33.6, 10.0 and 19.3 ha. The islets are formed of uplifted coral blocks, with

typical coastal forest on limestone substrate and sandy beaches housing shearwater colonies. Tests were performed between 11 November and 6 December, that is, the period when *P. pacificus* returns to the colonies searching for mates, refurbishing existing burrows or digging new ones. We hypothesized that birds are particularly sensitive to predators' odours at this crucial stage of the breeding cycle. *Puffinus pacificus* weigh an average of 389 ± 31 g ($N = 113$, Brooke 2004), spend most of their lives at sea, with intermittent returns to the islands during the breeding period (October to April).

The ship rat was introduced into New Caledonia by European settlers around 1850, whereas the smaller Pacific rat was introduced into New Caledonia much earlier, about 3000 years ago by Melanesian colonizers (Pascal *et al.* 2006). Our study islets A and B hosted the ship rat but were free of the Pacific rat, whereas islet C was free of the ship rat but hosted the Pacific rat. The presence/absence of the two rat species was confirmed by a total of 700 trap-nights conducted on the islets.

Olfactory experiment setting

The experiment consisted of a standard binary choice test using a portable Y-maze involving the choice between two exit arms (Grubb 1974; Bonadonna *et al.* 2003a; Bonadonna & Nevitt 2004). The Y-maze was built from a single opaque Polyvinyl chloride (PVC) tube (16 cm of diameter) divided into three sections (Fig. 1), to avoid any difference between arms that might influence the bird's choice. The start arm had a temporary bird-holding compartment at its entrance.

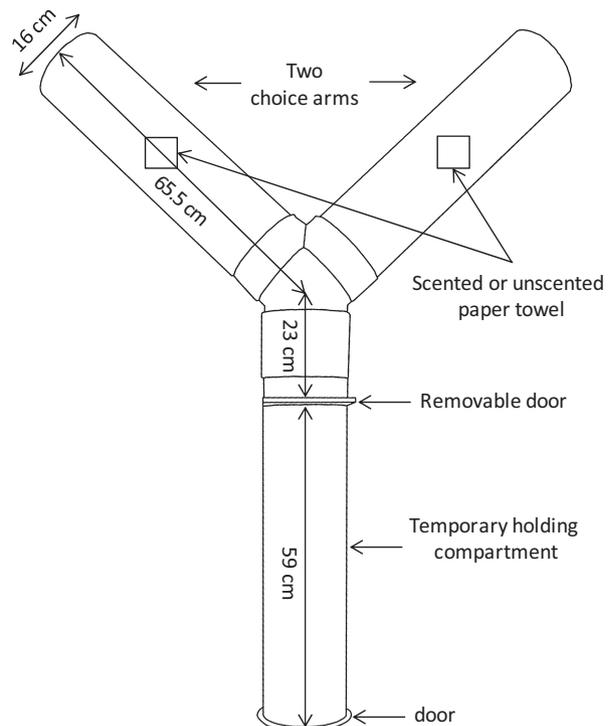


Fig. 1. Diagram of the Y-maze used for experiments.

The two exit arms each contained a paper towel either scented with ship rat odour (obtained from seven wild-trapped ship rats and by placing paper towels on the floor of cages containing rats to collect urine and faeces) or unscented (soaked with distilled water). To avoid human scent contamination, the paper towels were prepared with latex gloves and handled with metal pliers (one pair of pliers to handle the unscented paper towels and another pair for the paper towels carrying the ship rat odour). For each test, new gloves were used, and the pliers were cleaned with 95% ethanol. The paper towels were placed on the lower surface of the tube, half way along each exit arm. The bird therefore had to walk over one of the paper towels before leaving the maze. New paper towels, either scented or unscented, were used for each test. The entire maze was cleaned with 95% ethanol after each test to remove any odour (i.e. rat and shearwater). The same arm contained the ship rat odour in each test, to avoid potential bias due to any presence of residual rat odour (after cleaning) in the arm considered as the control arm. This involved disassembling and interchanging the arms between bird trials so that the odour was sequentially located on the left and on the right, allowing time (about 10 min) for the ethanol to evaporate before the next test.

Birds were caught early at night on the ground, when they landed at the colony. There is unfortunately no ringing programme on *P. pacificus* in the study area, so age or reproductive status of individuals (prospecting or breeding bird) could not be determined. Each bird was then placed individually in a new cotton bag (i.e. with no residual odour of other birds), transported to the maze and placed in the holding compartment for a 5-min acclimation period (Bonadonna *et al.* 2003a,b; Bonadonna & Nevitt 2004; Bonadonna *et al.* 2004). The maze was placed outside the colony (approximately 50–100 m) to reduce possible interference from birds flying and calling in the vicinity. Both exit arms were oriented toward the edge of the forest habitat, that is, toward a similar dark and uniform area, to avoid a possible visual effect on exit choice. The entrance of the maze faced the sea to avoid (i) the wind entering the two exit arms and potentially intensifying odour diffusion disproportionately in one arm, and (ii) odours from outside entering the two exit arms.

After the trap door was raised, we recorded the bird's choice between scented/control arms to escape the maze. No individual visited the two arms before exiting. Total handling time (from capture to exit) did not exceed 25 min: 10 min between capture and acclimation period, 5 min of acclimation, and 5–10 min to exit the maze. Only a few birds left the maze without prompting. If the bird did not leave the holding compartment after 5 min, we gently knocked on the door to rouse it from its quiescent state and prompt it to move. This procedure has previously been found not to affect birds' choice between two chambers (Amo *et al.* 2012). In our experiments, no individual left the maze immediately following our 'knocking'; all the birds took time (5–10 min) choosing between the scented and unscented arms before exiting. This indicates that the birds' choice of exit was not affected by prompting, and a response was recorded for all birds tested. As the birds left the experimental device, they were recaptured and then released at their initial capture location. Each bird was marked with a dash on the palm of its foot by a permanent marker, so as to avoid birds being tested several times.

Overall, a total of 100 different birds were tested (45 on islet A, 15 on islet B and 40 on islet C). The binary response variable (0: scented arm; 1: unscented arm) was modelled according to the ecological conditions on the islets (a three-level factor for islets A, B, C), using a generalized linear model with a binomial distribution of error and a logit link (implemented in R 2.15.0; R Development Core Team 2012). We assessed whether the bird avoidance rating (proportion of birds choosing the unscented/control arm) differed from a random choice (intercept fixed at 50%). A power analysis, based on a binomial process with a threshold set at 80%, indicated an avoidance rating of 0.65, 0.70 and 0.72 respectively for a sample size of 100, 60 and 40.

RESULTS

For each islet, the number of choices of right arm *versus* left arm showed no lateral preference ($P > 0.46$).

Selection by *P. pacificus* of rat-scented/unscented arms to exit the plastic Y-maze did not differ from random (Fig. 2; Table 1). On islet A, 23 out of 45 birds left through the unscented arm, 7 out of 15 on islet B, and 23 out of 40 on islet C. Pooling the islets with ship rats (A and B) *versus* the islet without ship rats (islet C) gave a similar result (Table 1). The avoidance rate was therefore very close to 50% whatever the islet (51%, 47% and 57% respectively for islets A, B and C), and irrespective of the presence or absence of the ship rat (50% for islets A and B with ship rats present and 57% for islet C with no ship rats).

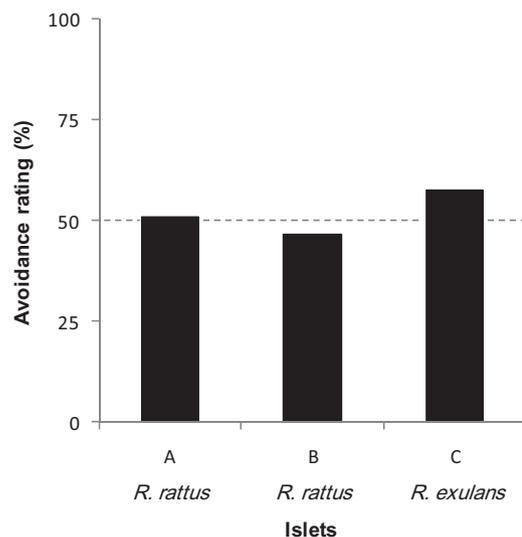


Fig. 2. Avoidance rating (i.e. number of unscented arm choices divided by total number of arm choices) of birds for arm treated with predator (*Rattus rattus*) odour on the three islets of Isle of Pines Archipelago (New Caledonia). The dotted line indicates the rating fixed for no effect of odour, 50%. The species of rat present on the islets is indicated under A, B and C.

Table 1. Results of generalized linear model for avoidance rating of arm treated with predator odour as compared with no effect of odour (avoidance rating 50%) for the three islets and for the two islets with ship rats (i.e. invaded) and the islet without ship rats (i.e. non-invaded)

	Estimate	Standard error	z value	Pr (> z)
Islet A	0.04	0.30	0.15	0.88
Islet B	-0.13	0.52	-0.26	0.80
Islet C	0.30	0.32	0.94	0.34
Invaded (A + B)	0.00	0.26	0.00	1.00
Non-invaded (C)	0.30	0.32	0.94	0.34

DISCUSSION

Our results show that the *P. pacificus* either did not detect the odour of the ship rat or, if they detected it, did not avoid it. This result holds true irrespective of whether ship rats were present on the islet housing the shearwater colony, and is rather surprising given the high vulnerability of *Puffinus* spp. to rats, particularly the ship rat (Lock 2006; Smith *et al.* 2006; Jones *et al.* 2008; Rando & Alcover 2008; Spatz *et al.* 2014). The power analysis indicated that our experimental sample size was adequate to detect a biologically relevant difference.

Even though the possibility that stress following capture impaired the birds' ability to respond to odour cannot entirely be ruled out, great care was taken to avoid this bias. In particular, the experiment was designed to minimize stress for individuals (e.g. short handling time, acclimation period before tests). Moreover, similar experiments testing the odours of partners (Bonadonna & Nevitt 2004) or nests (Bonadonna *et al.* 2003a,b; Bonadonna *et al.* 2004) have been successfully conducted on other procellariid seabirds (Antarctic prion *Pachyptila desolata*, common diving petrel *Pelecanoides urinatrix*, South-Georgian diving petrel *P. georgicus*, blue petrel *Halobaena caerulea*). These studies showed evidences for nest- and partner-odour recognition in procellariid seabirds, which provide an olfactory signature that allows birds to recognize their own burrow. We can therefore be reasonably confident that our results actually reveal that *P. pacificus* can detect but do not avoid the odour of ship rats in our study area.

This absence of avoidance is counter-intuitive, especially in light of the extensive use of olfaction in procellariid seabirds for various purposes (Warham 1996). Although the use of olfaction to assess predation risk has never been tested in procellariid seabirds, recent studies with hole-nesting songbirds have shown some evidence of variation in the ability to detect predators between closely related species (Johnson *et al.* 2011). Naïve great tits (*Parus major*) (i.e. main-

tained in captivity for 10 days after hatching and without predation events or signs of predator visits to nest boxes containing nestlings during the first 10 days of their life) avoided the odour of predators when selecting cavities for roosting (Amo *et al.* 2011). However, eastern bluebirds (*Sialia sialis*), which had evolved with snakes and small mammal predators, were as likely to lay eggs in boxes with predator cues as in boxes with neutral cues (Godard *et al.* 2007); and house wrens (*Troglodytes aedon*), another species which had co-evolved with nest predators, either did not detect or did not respond to nest predator odour (Johnson *et al.* 2011). Two native bird species from New Zealand, the rifleman (*Acanthisitta chloris*) and the South Island robin (*Petroica australis*), which had not co-evolved with any mammalian predators, did not change their behaviour at nests when the odour of the ship rat (also an introduced predator in New Zealand) was present. In the same study area, only one of the two introduced European passerines, which had co-evolved with mammalian predators, altered their behaviour to minimize risk to themselves (Stanbury & Briskie 2015). In our study, the lack of co-evolution with mammalian predators combined with the presence of two different introduced rat species, respectively for about 3000 and 150 years, apparently did not lead to development of, or variation in, anti-predator behaviour in *P. pacificus*.

Following the introduction of a new predator in an ecosystem, it has been shown that some species of amphibians and mammals can rapidly develop anti-predator responses (Kiesecker & Blaustein 1997; Russell & Banks 2007). Regarding birds, one study showed that the New Zealand bellbird (*Anthornis melanura*) was able to respond to nest predation risk after a co-existence of about 700 years with introduced predators (i.e. mustelids, rats, cats, possums, hedgehogs) (Massaro *et al.* 2008). No data are available on the time that seabirds need to adapt their behaviour, and the about 150 years of co-existence between shearwaters and ship rats in our system may not be long enough to induce behavioural adaptations. The presence of a predator archetype (i.e. predator species that use similar morphological and behavioural adaptations in obtaining prey) might favour an anti-predator response from island prey (Cox & Lima 2006). Here, however, the roughly 3000-year presence of the Pacific rat, belonging to the same predator archetype as the ship rat and having similar effects on seabirds weighing <300 g (Townsend 2009), did not prepare shearwaters to avoid the odour of the ship rat.

Procellariiforms such as *P. pacificus* are highly philopatric and highly faithful to their breeding site (Warham 1990). These birds form long-term pair bonds, and site fidelity constitutes a means for pairs to reunite (Bried *et al.* 2003). These biological character-

istics may thus strongly constrain breeding site selection and encourage birds to come to breed on the same sites, despite the detection and presence of rats.

Shearwaters may also rely on cues other than smell to ascertain the presence of ship rats. These birds could use visual cues (i.e. direct encounters with rats) to assess the risks of nesting in a colony. Another cue might be conspecific reproductive success (Danchin *et al.* 1998). The long-lived shearwaters typically spend their first 3–5 years as non-breeders but regularly prospect colonies, and in so doing are able to assess average breeding success in different colonies so as to choose the most successful breeding site (Warham 1990, 1996; Danchin *et al.* 1998). Breeding site selection based on an integrative cue such as conspecific reproductive success is likely to be more efficient than direct cues of the presence of predators.

All these factors may well explain the absence of avoidance of the ship rat odour; yet, some observations had led us to believe that *P. pacificus* would respond. In fact, the dramatic increase in some shearwaters' breeding population immediately following rat eradication (Bourgeois *et al.* 2013; Marie *et al.* 2014; VanderWerf *et al.* 2014) suggested that procellariid seabirds may select their breeding sites according to direct cues. However, we hypothesized that this selection could also be at least partially driven by olfaction (avoidance of burrows 'smelling' of rats), with a predation risk assessment based upon predator chemical cues. Moreover, there is growing evidence that some shearwater species select breeding areas based on the absence of introduced predators, like ship rats, at different spatial scales (Bourgeois & Vidal 2007; Ruffino *et al.* 2008, 2009). For example, at the nest scale, the yelkouan shearwater (*Puffinus yelkouan*) avoids cavities frequented by rats and preferentially selects the deepest and most winding cavities for breeding (Bourgeois & Vidal 2007; Ruffino *et al.* 2008). At the colony scale, selection of intra-island refuges (e.g. steep cliffs) less accessible to mammal predators could also partly explain the surprising length of apparent coexistence (about 2000 years) between procellariid seabirds and invasive ship rats on Mediterranean islands (Ruffino *et al.* 2009).

Although Smith *et al.* (2006) has shown that the ship rat could dramatically reduce the breeding success of *P. pacificus*, we suspect that for our three studied New Caledonian islets, the impact (i.e. the level of predation on eggs or chicks) of the ship rat may not actually be great enough to induce avoidance behaviour. In fact, if the costs of anti-predator responses do not outweigh the benefits, natural selection may not favour the detection of predator chemical cues, nor favour individuals that respond to this odour (Amo *et al.* 2011). The limited

impact of ship rats may be explained by the presence of alternative food resources or may reflect the process by which these predators were introduced. On islands, rats are likely to be introduced in an isolated manner, a few individuals at a time, which may result in a population that does not necessarily impact seabirds. Rat density (Iguar *et al.* 2006) and factors intrinsic to rats such as physical-limiting factors (Freeman & Lemen 2008; Williams *et al.* 2009; Zarzoso-Lacoste *et al.* 2011), lack of predation skill or social learning (Grant *et al.* 1981; Booth *et al.* 1996) can alter the magnitude of rat impact on seabirds. Therefore, further experiments should be conducted on a variety of procellariid seabirds, prospecting or breeding birds, and within colonies where the impact of rats is quantified, to determine to what extent ecological factors, bird species characteristics (e.g. body mass, egg size; Bradley & Marzluff 2003; Jones *et al.* 2008; Towns 2009), reproductive status of individuals and intensity of predator's impact influence the onset of anti-predator behaviour in procellariid seabirds.

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