I smell a rat: Can New Zealand birds recognize the odor of an invasive mammalian predator?

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Abstract Although it is well known that birds can assess predation risk through visual and auditory cues, there has been little research into whether similar processes occur with olfactory cues. We examined the role of odor cues in assessing nest predation risk in four species of passerine birds in New Zealand. We compared the ability of two introduced European species (common starling *Sturnus vulgaris* and song thrush *Turdus philomelos*) and two native New Zealand species (rifleman *Acanthisitta chloris* and South Island robin *Petroica australis*) to respond to the scent of rat urine placed in the nest. Rats are an introduced predator in New Zealand and we expected the native birds, which did not co-evolve with any mammalian predators, to lack behavioral adaptations to the scent of rats at their nest. As expected, both riflemen and robins failed to show any change in their behavior at their nest when rat urine was present compared to a control period in which no scent was present. However, a similar lack of response was observed in the introduced song thrush; only the common starling changed its behavior in the presence of the rat urine. Starlings with rat urine at the nest box were more likely to hesitate before entering and they also approached the nest, but refused to enter more often in the presence of rat scent. Both responses suggest they detected the presence of a predator and changed their behavior to minimize risk to themselves. Although based on a small number of species, our results suggest that responses to predator scent may be less common in New Zealand species, and may be a factor contributing to the vulnerability of native birds to introduced mammalian predators [Current Zoology 61 (1): 34–41, 2015].

Keywords Predation risk, Invasive species, Anti-predator adaptations, Predator recognition, Olfactory cues

The use of chemosensory cues has been a neglected area of study in birds (Roper, 1999). The overt use of visual and auditory signals led scientists to believe that olfaction played little role in birds, despite the presence of anatomical and neurological structures for detecting olfactory cues (Wenzel and Sieck, 1972; Kats and Dill, 1998). It is now known birds can use olfactory cues as a means of nest location in petrels (Bonadonna and Bretagnolle, 2002) and finches (Krause and Caspers, 2012), and for foraging in kiwis (*Apteryx* spp.; Cunningham et al., 2009), turkey vultures (*Cathartes aura*; Wenzel and Sieck, 1972), and a variety of seabirds (Cunningham et al., 2008; Nevitt et al., 1995). There is also evidence that birds can use olfaction in identifying their offspring (Cohen, 1981), selecting mates (Hagelin et al., 2003; Zhang et al., 2009), and detecting predators (Amo et al., 2008, 2011; Mason et al., 1991; Roth II et al., 2008; Zidar and Løvlie, 2012). There is also evidence that birds can use olfaction in identifying their offspring (Cohen, 1981), selecting mates (Hagelin et al., 2003; Zhang et al., 2009), and detecting predators (Amo et al., 2008, 2011; Mason et al., 1991; Roth II et al., 2008; Zidar and Løvlie, 2012).

Despite recent investigations into olfaction in birds, only a few studies have dealt with the role of olfaction in predator avoidance (e.g., Amo et al., 2011; Zidar and Løvlie, 2012). For example, Fluck (1996) found that by 7 days of age domestic poultry chicks *Gallus gallus* began to avoid the odor of cats. Similarly, crested auklets *Aethia cristatella* avoided a mixture of mammalian musk odors but not banana odor (a novel odor for this species) (Hagelin et al., 2003). Amo et al. (2008) presented mustelid scent inside the nests of blue tits *Cyanistes caeruleus* and found a significant decrease in the time spent by adults in the nest and the number of times birds approached but failed to enter the nest. These results suggested that blue tits were able to detect the odors of a predator from outside the nest and modified their behavior to reduce the risk to themselves. House finches *Carpodacus mexicanus* were also found to respond more strongly to faeces from predatory cats than non-predatory rabbits (Roth II et al., 2008). However, the ability to recognize predators from their odor cues alone is not ubiquitous, as reptilian and mammalian predator odors applied to nest boxes did not prevent eastern bluebirds *Sialia sialis* from building nests (Godard et al., 2007).

Unlike birds in continental areas, the avifauna of New Zealand evolved in the absence of terrestrial pre-
mammals; the only predators were other birds (Cooper and Millener, 1993). Island birds that evolved in the absence of mammalian predators display a number of different life history traits compared to their continental counterparts (Lima and Dill, 1990). For example, they tend to have low reproductive rates and behave naïvely towards humans and the exotic predators that accompany them (Milberg and Tyrberg, 1993). Defences against mammals prevalent in continental bird species are often absent or reduced in island birds, and instead anti-predator responses are tailored to the visually-hunting avian predators with which they co-evolved. Unfortunately, when humans arrived in New Zealand, they brought with them a variety of predatory mustelids (Mustela furo, M. erminea, and M. nivalis), brushtail possum Trichosurus vulpecula, and feral cats Felis domesticus. All have become widespread on the main islands and are known to prey on birds (Holdaway, 1989; Brown, 1997; Innes et al., 2010). As a result of these introductions, over 40% of the New Zealand avifauna has become extinct (Holdaway, 1989), with many of the remaining species now confined to predator-free islands, or areas on the mainland with predator control.

In addition to predatory mammals, a number of exotic bird species have also been introduced to New Zealand in the last 150 years (Oliver, 1930). Unlike native New Zealand birds, introduced birds originate from continental areas where they co-evolved with mammalian predators, and thus are likely to have retained adaptations to detect such predators and adopt behaviors to reduce the risk of predation to themselves or their nests. The ability to detect and respond appropriately to a predator or a predatory cue is critical to a bird’s reproductive success, as nest predation is the major cause of failure and mortality in birds (Ricklefs, 1969). Native New Zealand birds in particular, appear to suffer high rates of nest predation from introduced mammalian predators (Brown, 1997; Innes et al., 2010; Starling-Windhof et al., 2011). Thus introduced birds provide an opportunity to investigate the role of olfactory communication pathways in both native birds (which did not evolve with predatory mammals) and continental birds (which did evolve with mammals).

Previous studies have shown that continental species hesitate before entering their nest after the introduction of a predator’s odor, suggesting they recognize the danger and alter their behavior accordingly (Amo et al., 2008; Mennerat, 2008; Whittaker et al., 2009). Given their different evolutionary histories, we expected that native New Zealand species would lack this ability. Thus, our objective was to examine whether birds can detect the presence of a predator at the nest using odor cues alone, and if this differs between native and introduced species. We tested the response of birds to rat R. rattus odor as this species is a major predator of birds in New Zealand (Atkinson, 1973; Brown, 1997; Innes et al., 2010). As both native and continental species of birds now occur in New Zealand, we were able to compare responses to rat odors between the two groups of birds living in the same locality, but possessing different evolutionary histories. If native birds fail to respond to the scent of a rat at the nest, this may help explain why they appear so vulnerable to exotic predators.

1 Materials and Methods

1.1 Study site

The study was carried out in two forest areas near the town of Kaikoura, New Zealand (42°20' S, 173°40’ E). The first site, Kowhai Bush, was a 240 ha low-elevation native forest dominated by kanuka Leptospermum ericoides with an understory of small shrubs. Most mammalian predators that have established in New Zealand are present at this site (see Hunt and Gill 1979 for description of study area) although some predator control occurs along the margins. The second site, Waimangarara Bush, was located ~5 km away and has a similar vegetation structure and avifauna, and is connected to the first site by a band of montane forest. More extensive control of mammalian predators was carried out at the second site, although studies of nest success (Starling-Windhof et al., 2011) suggest predators were still present albeit at lower levels.

1.2 Study species

The native species studied were rifleman Acanthisitta chloris and South Island robin Petroica australis. The introduced species studied were common starling Sturnus vulgaris and song thrush Turdus philomelos. Both starlings and song thrushes were introduced from Britain in the 19th century (Oliver, 1930), and are now widespread and abundant across New Zealand (Robertson et al., 2007). Rifleman and starlings are cavity-nesters and readily used artificial nest boxes we had set up in the first study area. South Island robins and song thrush both build open-cup nests and we searched for nests of these two species by following parents during building, incubation or nesting stages. Biparental care occurs in all four species, although rifleman sometimes have helpers at the nest (Preston et al., 2013). We con-
ducted our study during the austral breeding season from November to December 2008 (rifleman only) and September 2009 to January 2010 (all species including rifleman).

All rifleman and robin pairs used in this study were color banded, which ensured we did not test any individuals more than once. However, only a few starlings and song thrushes were banded and it is possible we re-sampled the same birds twice. We minimized this risk in several ways. First, we did not use a song thrush nest if it was found within 15 m of a nest used previously, on the assumption that the proximity increased the likelihood the two nests were built by the same pair. Secondly, the high degree of breeding synchrony among starlings (all nests were active within 3 weeks of each other) reduced the chance that we re-sampled a pair tested earlier in the season. Finally, as all starling, song thrush and robin nests were filmed during a single breeding season, we did not run the risk of sampling the same birds in two years. All nests of starling, song thrush and rifleman were filmed only on the Kowhai Bush study site, but due to low numbers of robins, this species was only studied at the Waimangarara Bush study site.

1.3 Collection and presentation of rat scent at nests

We used similar methods to present the scent of a potential mammalian predator as Amo et al. (2008) and Godard et al. (2007). We used R. rattus as our predator, as this species was introduced around 200 years ago and, like all introduced rats, is a major nest predator of passerines in New Zealand (Brown, 1997; Empson and Miskelly, 1999). We could not find any studies that measured that rate of rat predation in the native range of the two European bird species in our study, except that starlings have been recorded in the diet of rats in Britain (Feare, 1984). Thus, we assumed that rats in their native range likely prey on bird nests, and this would have consisted of the same size squares of clean paper dampened with water. The papers were housed in 2 × 2 cm² ‘sachets’ of black nylon mesh. Control and scent papers were enclosed in the sachets to reduce the conspicuousness of the paper but without obstructing diffusion of odors. The sachets also provided a rigid frame that could be inserted into nests.

1.4 Experimental procedure

Experiments were conducted 10 to 15 days after hatching at a point when the wing feathers of the nestlings had begun to emerge from the sheaths. The age at which this occurs varies between species but using this criterion ensured young were at approximately the same developmental stage. Each presentation experiment consisted of a control and a scent treatment. Only one presentation trial was conducted per day but we ran the two trials on consecutive days. The order of presentation was alternated between each nest of each species to control for order effects (i.e., if control presented on day one and scent treatment on day two, the order of presentation was reversed in the next nest of the same species to be tested). In cavity-nesting species, a thread was used to secure the scent sachet such that it hung half way down the wall of the nest box. This position was used because nestlings often defecated on sachets hidden on the edge of the nest. For cup-nesting species, the sachet was hidden into the material of the nest wall. In both types of nests, we ensured the sachet was hidden from view and did not provide a visual cue to the parents.

To assess the response of parents to the presence of rat scent at the nest, parental behavior was recorded by a video-camera set up 5 to 10 m from the nest. The camera was put into position an hour before the trial commenced to allow time for parents to habituate to its presence. The trial began once either the control or scent treatment was placed at the nest. Each nest was then filmed for 30 minutes. The control and treatment trials were always conducted 24 hours apart, to ensure that filming occurred at the same time of day. In all cases, the number of nestlings remained the same in both trials. As rain can have a significant effect on incubation and brooding in birds (Beintema and Visser, 1989; Poisbleau et al., 2007), no trials were conducted on rainy days. We only examined the short-term response to rat odor at the nest as previous workers have found anti-predator response to odors start to decrease rapidly after the first 5 minutes (Amo et al., 2008; Mennerat, 2008; Roth Li et al., 2008).

Videos were transcribed to record visits to nests and
time spent at the nest (to nearest second). To describe the response of the parents to the sachets, we measured four behaviors. First, we recorded latency, which was defined as the time from the placement of the sachet to the first visit by one of the parents. Second, we counted the number of visits to the nest that were “aborted”. For nest-box species, this was the number of times parents sat on the box, or within 20 cm of the box but did not enter the box before flying away. For cup-nesting species, this was the number of times parents approached to within 20 cm of the nest, but then left without attending to the nestlings. The duration of aborted visits was also recorded and is referred to as time spent “hesitating.” It was assumed that birds which spent time outside the nest before entering were hesitating (rather than going in directly without stopping), and that the longer the duration of this behavior, the more hesitant the response. Finally, we recorded the total time spent by parents on the nest. This is the time parents did visit the nest during the recording period to attend their offspring, either for feeding or brooding. If parents were able to detect the rat scent, we expected they would change their behavior in order to minimize the risk to themselves. This would involve longer latency times before approaching the nest, more aborted visits, longer periods of time hesitating before entering, and spending less time tending their offspring.

1.5 Data analysis

Data were log-transformed to ensure normality. For comparisons within each species, we used paired t-tests to compare differences in latency, the average time parents spent hesitating, and the time spent on the nest between the control and treatment sachets. For the number of aborted visits, we used a Wilcoxon signed-ranks test to determine differences between control and scent trials.

A critical value of 0.05 was used in all tests but we adjusted the P-values using a Bonferroni correction as we performed several tests on the same data set. Due to the small number of species (two species of native birds and two species of introduced birds), it was not possible to statistically compare the two groups of species. Instead, we present the results as a first step in identifying whether there are any differences in response to predators between native and introduced birds that would be worth investigating further with a larger group of species.

2 Results

There were no significant differences between control and scent treatments in latency time for any of the four species studied (all P > 0.05; Table 1, Fig. 1). The number of aborted visits increased significantly when starlings were presented with the scent treatment, increasing from an average of 0.29 ± 0.18 (mean ± SE) aborted visits with the control sachet to 2.1 ± 0.46 aborted visits with the scent sachet (Table 1; Fig. 1). However, there were no significant differences in the number of aborted visits with treatment in song thrush, South Island robin or rifleman. The amount of time spent hesitating was again significantly higher in the scent treatments for starlings, but there was no significant difference for any of the other species (Table 1; Fig. 1). Starlings spent an average of 8.9 ± 3.4 seconds hesitating in the control trials but this increased to 41.0 ± 7.9 seconds in the rat scent trials. No song thrushes ever hesitated when approaching their nests. Finally, there was no significant difference for any species in the time spent in the nest during the scent treatments compared to the control treatment (Table 1; Fig. 1). All tests remained significant after a Bonferroni correction.

Table 1  Results of paired t-tests (latency, time hesitating and time in nest) and Wilcoxon signed-rank test (number of aborted visits) for differences in the behavioral responses of four species of New Zealand birds to the presence of rat urine at the nest compared to a control. Number of nests tested given in parentheses. For each species the t or z and P values are presented. See text for definitions of behavioral responses.

<table>
<thead>
<tr>
<th>Behavioral response</th>
<th>Introduced species</th>
<th>Native species</th>
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<tbody>
<tr>
<td></td>
<td>Starling (7)</td>
<td>Song thrush (7)</td>
</tr>
<tr>
<td></td>
<td>t or z  P</td>
<td>t or z  P</td>
</tr>
<tr>
<td>Latency</td>
<td>-0.71  0.50</td>
<td>0.42  0.69</td>
</tr>
<tr>
<td>Time hesitating</td>
<td>-7.80 &lt; 0.001</td>
<td>0  1.0</td>
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<tr>
<td>Time in nest</td>
<td>0.67  0.53</td>
<td>-0.09  0.93</td>
</tr>
<tr>
<td>Number aborted visits</td>
<td>-2.20  0.027</td>
<td>-1.00  0.32</td>
</tr>
</tbody>
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Fig. 1  Response of four species of birds to the presence of rat urine in the nest (grey bars) compared to a control (open bars)

Figures show the latency (time in seconds taken for bird to return to nest after treatment added), hesitancy (time in seconds an adult spent by the nest but without entering), time on nest (length of time in seconds adult on the nest), and the number of aborted visits (frequency of visits to nest in which adult bird then fails to enter and instead flies away). For illustration purposes the values are presented as box and whisker plots on a log scale. Asterisks denote comparisons that are significant after a Bonferroni correction.

3 Discussion

Of the four species tested, only common starlings appeared to detect the odor of rats at the nest and exhibited behaviors that could potentially decrease predation risk to adults visiting the nest. Although none of the four species showed any changes in latency to approach the nest or time they spent on the nest once visits resumed, starlings increased the number of aborted visits and the time spent hesitating when the rat odor was present in the nest. As expected from their lack of evolutionary history with mammalian predators, neither the rifleman nor the South Island robin showed any change in behaviors between odor and control treatments. This suggests that either they could not detect the odor of the rat, or if they were able to detect it physiologically, they did not change their behavior as a consequence. However, contrary to expectations, the introduced song thrush also did not display any difference in behaviors at the nest between treatments.

Amo et al. (2008) interpreted the behavior of blue tit parents approaching the nest-box but flying away without entering the box and feeding chicks as ‘refusing to enter the nest’. This is similar to what we termed ‘aborted’ visits in our study. Refusing to enter the nest could be interpreted as an anti-predatory behavior because predation risk would decrease for such individuals in the event of returning to the nest while a predator is still inside or nearby. The amount of time hesitating outside the box, before finally going to the entrance and entering the nest box may reflect how long it takes before birds decide it is safe to enter or approach the nest. This increases the time birds spend listening and examining the nest for signs that a predator may still be present. Perhaps only after being unable to detect any visual or auditory signs of a predator, does the bird then enter the nest. The behavior of the starlings we observed in response to the sachets of rat urine appears similar to that of the blue tits studied by Amo et al. (2008), suggesting the increased number of aborted visits and the increase in time spent hesitating were an adaptive response to minimize predation risk.

In contrast to the starling, no song thrushes hesitated during approaches to the nests, and only on one occasion did a New Zealand robin hesitate during an approach. This apparent lack of hesitation may be due to differences in the way birds approach open-cup nests compared to cavity nests. To approach a cavity nest, birds such as the common starling usually first landed nearby, and then later hopped or fluttered towards the entrance in a series of steps. In contrast, the cup-nesting species we monitored appeared to fly directly to the nest or at least near it (within ~5 cm). The difference may be the result of open-cup nesting species being able to see into the nest on approach and assess the situation visually while flying. This could give them enough time to change flight path if danger cues are visible at the
nest. In contrast, cavity-nesting birds have fewer visual cues about the contents of their nest when approaching (as the contents are hidden from view), and instead rely on auditory or olfactory cues. Relying on visual cues alone for cavity-nests may mean a parent risks entering a nest with a predator inside. Although the lack of a response by New Zealand robins to the rat odor could be due to their lack of co-evolutionary history with mammalian predators, the similar lack of a response by song thrushes (a species expected to respond to the rat odor) is consistent with this idea. If thrushes rely primarily on visual and auditory cues to assess predation risk at the nest, the open nature of their nests may allow them assess the risks quickly and without hesitating. Even if they then detect the odor of a predator after landing on the nest, they will have already assessed visually that it is no longer present.

An alternative explanation for the lack of a response by the two open-cup nesting species is that the strength of rat odor was greater within the cavity nests. This could occur if the urine dried out more quickly or the odors dissipated more rapidly in open-cup nests than in the confined space of the cavity nests. Thus, open-cup nesters may have failed to respond simply because the odor was weaker or even absent. Although we cannot rule out this possibility, the lack of a response in the rifleman, despite nesting in nest boxes that were even smaller than starling boxes (and thus would have potentially increased the odor stimulus), suggests that differences in odor strength alone cannot explain the lack of response. We also believe that the treatment used, in which a 2 x 2 cm urine-soaked paper was added to the nest, presents a relatively strong olfactory stimulus to the birds as it seems unlikely that rats urinate at every visit to a the nest. On the other hand, it is possible that the odor of urine alone is not sufficient as a treatment, as a visit by a real rat to a nest would also leave behind other olfactory cues (e.g., hair, feces, skin oils, etc.). It is possible the presentation of multiple olfactory cues might mimic a natural encounter more accurately, although the positive responses we observed in starlings suggest that rat urine alone may be enough to stimulate a response in at least some species.

Although we have interpreted our results to indicate a direct link between the presence of rat odor and a change (or lack of change) in adult response, it is possible that adults were instead responding to changes in the behavior of their nestlings. For example, if the movements or begging of nestlings was subdued or somehow changed in response to the rat odor, then it could have been that the adults were responding only to their nestlings and not to the odor itself. Nevertheless, this interpretation does not rule out the use of olfaction to assess predation risk but instead simply places nestlings in the front line response that then is acted upon by their parents. Unfortunately, we could not record the response of nestlings during our trials and further study would be needed to determine if it is changes in nestling behavior that in turn change adult behavior. Given the benefits to adults of being able to detect predation risk at other times of the nesting cycle (e.g., during incubation), it would seem advantageous for birds of all ages to independently detect and assess odor cues. Testing whether the responses of starlings to rat odor change at different stages of the nesting cycle may be one way to separate adult from nestling behavior.

On average, native New Zealand birds appear to suffer higher rates of nest predation than introduced European species, even within the same habitats (Starling-Windhof et al., 2011). Native birds display a number of different behavioral traits compared to their continental counterparts that might explain this vulnerability. For example, native birds tend to visit their nest more often than continental species, which increases nest conspicuousness to predators (Starling-Windhof et al., 2011). Many native species also appear unusually tame, and do not exhibit as many fear reactions towards humans, even at their nests (Maloney and McLean, 1995). The results of this study indicate another behavior in which New Zealand birds may differ from continental species and that may contribute towards their vulnerability to introduced mammalian predators. Despite the presence of rat odor at their nests, neither robins nor rifleman showed any indication they recognized a threat nor altered their behavior. As robins are open-cup nesters, this might simply be a result of this nest type but rifleman are a cavity-nesting species and particularly vulnerable to mammalian predation. As a consequence, they may face an increased risk of predation due to their inability to react to olfactory cues from introduced mammalian predators. Although we were only able to test a limited sample of species, and further work is needed to test the generality of our findings, it would be valuable to examine whether other native cavity-nesting species such as the stitchbird Notiomysis cincta or South Island saddleback Philesturnus carunculatus also lack the ability to detect rat odors. Both of these species currently only survive in areas free of introduced predators (Armstrong et al., 1999; Hooson and Jamieson, 2003). Given their lack of evolutionary history with mammalian predators,
it seems likely that they also may lack the ability to detect and respond to olfactory cues.

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References


