Can foraging birds assess predation risk by scent?

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Olfaction is commonly used by a variety of aquatic and terrestrial taxa to assess predation risk. However, with a few exceptions (e.g. procellariformes and New World vultures), the evidence for the ecological relevance of olfaction in birds is sparse and inconsistent. This is the case even though birds retain the proper anatomical and neurological structures needed to use olfaction. Here, we examined whether a passerine bird responds to the chemical scent of predators in the laboratory. We exposed house finches, *Carpodacus mexicanus*, to the olfactory cues of predatory and nonpredatory mammalian faeces and observed their behavioural response while feeding. Finches responded to both predator and nonpredator faecal cues, but they responded to the predator cues more strongly in some analyses. For example, in response to both faecal treatments, finches delayed their first feeding, spent less time on the feeder as a whole and reduced feeding bout length; the bout length effect was particularly pronounced in the predator treatment. Vigilance did not increase but instead decreased during the faecal treatments, which may have reflected a strategy of minimizing time on the feeder (where the cue was presented). The behavioural effects of faecal cues weakened quickly over time and were most evident during the first 5 min of an observational session. Overall, our results show that finches can detect mammalian faecal cues and associate such cues with possible danger.

Chemosensory systems are ubiquitous among living organisms. Among animals, chemical cues are often used to detect food (Weissburg et al. 2002) or to assess predation risk (see Kats & Dill 1998), especially in aquatic environments (Chivers & Smith 1998; Wisenden 2000). Olfactory predator detection has been observed in many invertebrates (e.g. Thomas et al. 2008), fish (see Chivers & Smith 1998), reptiles and amphibians (e.g. Ferrer & Zimmer 2007) and mammals (see Apfelbach et al. 2005; e.g. Herman & Valone 2000; Borgo et al. 2006). These olfactory abilities can, in fact, be quite sophisticated (see also Lima & Steury 2005). For example, fathead minnows, *Pimephales promelas,* can detect the density, size and

proximity of their predators by chemical cues alone (Kusch et al. 2004; Ferrari et al. 2006). In addition, many prey species can use olfaction to assess their predator's diet (Chivers & Mirza 2001; Mirza & Chivers 2003), thereby determining the threat posed by a given predator.

Relative to all other vertebrate taxa, there has been much less work on the use of olfactory cues by birds to detect predation risk (Roper 1999). The paucity of such research is probably a result of a common assumption that birds have a very weak sense of smell (Kats & Dill 1998).

There are, however, a few birds whose use of olfaction has been studied, precisely because they were originally believed to be exceptional. Such species include the tubenoses (Grubb 1972; Hutchison & Wenzel 1980; Lequette et al. 1989), New World vultures (Stager 1964; Graves 1992; Kirk & Mossman 1998) and kiwis (Wenzel 1968, 1971), all of which have been known for some time to use olfaction, primarily for foraging. Tubenoses in particular have been well studied and may use their sense of smell for navigation (e.g. Grubb 1979; Bonadonna et al. 2003) as well as other ecologically relevant

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tasks such as individual recognition (e.g. Bonadonna et al. 2007). Tube-noses can locate the smell of decaying fish and plankton (dimethyl sulfide) from kilometres away (Hutchison & Wenzel 1980; Nevitt 1999) and can also locate their burrows using smell (e.g. Bonadonna et al. 2003). Kiwis use their sense of smell to locate prey in soil and mud and can do so with olfaction alone (Wenzel 1968). Likewise, New World vultures can detect carrion (via ethyl mercaptan) from a great distance by smell alone (Smith & Palsek 1986).

However, the perception that olfaction is weak or unimportant among most other birds may not be entirely justified (Hagelin 2007; Hagelin & Jones 2007; Steiger et al. 2008). Birds retain the proper anatomical and neurological structures for detecting olfactory cues. All birds have an olfactory bulb, which is similar to that of their reptilian ancestors (Reiner & Karten 1985) and so should be able to use olfaction to some extent. However, birds do lack the accessory olfactory bulb and the neural integrative centre of the vomeronasal system (Bang & Wenzel 1985; Meisami & Bhatnagar 1998). Chemical detection in birds thus is probably restricted to olfaction, taste and trigeminal response (Hagelin 2007). Interestingly, the relative size of the olfactory bulb varies greatly across taxa, and this variation is likely to be adaptive (Bang 1960; Healy & Guilford 1990). Passerines have among the smallest olfactory bulbs of any bird, but nevertheless their olfactory abilities may be roughly equivalent to those of rats and rabbits (Clark et al. 1993). Hence, relative bulb size may not necessarily reflect the quality of olfaction. For a full review and discussion of avian olfaction, see Roper (1999) and Hagelin (2007).

More recently, the ecological relevance of olfaction in birds has gained some much needed attention. In addition to the ongoing work in tubenoses, we now know that other birds can use olfaction to find food. For example, ravens, *Corvus corax*, use olfaction to locate carrion while foraging (Harriman & Berger 1986), and hummingbirds might be able to use olfaction to discriminate among flowers (Ioale & Papi 1989). Similarly, blue tits, *Cyanistes caeruleus*, can be conditioned to the scent of lavender when associated with a food reward (Mennerat et al. 2005). In addition, olfaction is used for nonforaging purposes as well. Pigeons, *Columba livia*, for example, can detect subtle scent cues that may be used during navigation (Wallraff 2004), starlings, *Sturnus vulgaris*, and blue tits use olfaction to select nesting material (Malakoff 1999; Petit et al. 2002), and chickens, *Gallus gallus*, can imprint on scent (Burne & Rogers 1996).

A few studies have addressed olfactory predator detection by birds, but the results are somewhat inconsistent. Fluck et al. (1996) found that chickens do not respond to cat odour when they were young, although they do as they become older. Hagelin et al. (2003) found that crested auklets, *Aethia cristatella*, avoid mammalian musk odours in the laboratory. Godard et al. (2007) saw no response of bluebirds (*Sialia sialis*) to snake or mammal odour cues at nestboxes. Amo et al. (2008) did find a clear behavioural response by blue tits to mammalian scent at nestboxes.

Here, we add to this sparse coverage of antipredator olfaction in birds by examining whether house finches, *Carpodacus mexicanus*, respond to the chemical scent of predatory mammals in the laboratory. We specifically chose the house finch as our model passerine because they are easily captured at feeders, abundant in our study site and respond well to captivity. We exposed finches to the olfactory cues of predatory and nonpredatory mammalian faeces and observed their behavioural response while feeding. We investigated only short-term reactions of birds to these olfactory cues to minimize the effects of habituation. Our expectation, if the birds responded at all to faecal cues, was that the birds would respond more strongly to the predator cue than to the nonpredator and blank control cues.

METHODS

House finches ($N = 51$) were captured at feeders baited with sunflower seeds during the winter of 2006–2007 near Terre Haute, Indiana, U.S.A. Upon capture, finches were immediately taken to an unheated laboratory at Indiana State University and placed singly into experimental enclosures. Six enclosures (approximately $2 \times 1.5 \times 2.5$ m tall) were contained in two adjoining rooms. Enclosures were constructed of standard lumber framing and lined with white opaque plastic (Tyvec-like material) used in home construction. All enclosures contained adlibitum water and a standardized amount of leaf-less deciduous vegetation (tulip poplar, *Liriodendron tulipifera*) as cover.

Each enclosure contained a feeder attached to one wall. This feeder was located on the side of the enclosure opposite cover and consisted of a $30 \times 30 \times 10$ cm tall box mounted approximately 1.5 m off the floor. The top of the feeder box consisted of a set of aluminium vents arranged to restrict the birds' view into the box interior. Sunflower seed kernels were contained in a small cup attached to the top of the feeder box (Fig. 1). The finches had to perch on the edge of the cup to reach the seeds. One-way glass was mounted above the feeder for observation.

The interior of the feeder box was accessible from outside an enclosure via a small door. This external access
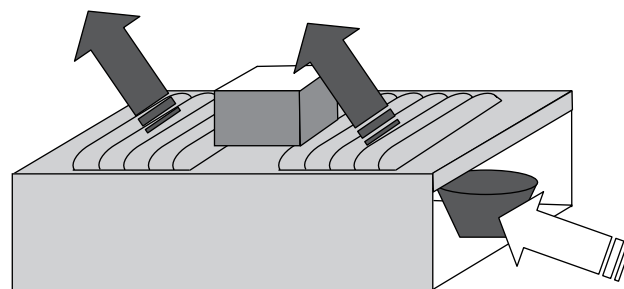
Figure 1. Illustration of feeder/scent delivery mechanism. Airflow follows the direction of the arrows. Light arrow indicates clean air; dark arrow indicates treatment air. Birds were unable to see the contents of the stimulus cup, and they responded only to the volatiles delivered via the air passing over the stimulus and through the vents.

allowed us to quietly introduce scent stimuli into the feeder box, and thereby into the enclosure, without being seen by and without disturbing the birds. In addition, birds could not see the scent stimuli, and thus could only react to the volatile chemicals rising through the vents in the top of the feeder box. Minimal positive air flow through the box, held constant throughout the experiment, ensured a uniform delivery of scent cues into an enclosure. Air flow was generated with a large pump, cleaned with a carbon and mechanical filter, and then delivered to the enclosures.

Scent Cues

Cat faeces were used as a predator cue, rabbit faeces as a nonpredator cue, and water as a control cue. The cat faeces were collected from five house cats, which were fed a variety of commercial canned and dried diets that contained animal products, including poultry. Rabbit faeces were collected from multiple laboratory rabbits in the Indiana State University laboratory animal facility. These rabbits were not involved in any experiments before or during the collection of the faeces. Rabbits were fed a commercial rabbit formula (Graham Feed Rabbit Pellets No. 701, Terre Haute, IN, U.S.A.), which contained no animal products.

Faeces were homogenized in a blender to create a slurry. Reverse osmosis water was added to the slurry when necessary to achieve a pourable and similar consistency between the two treatments. Faecal samples were then distributed in approximately 20 ml aliquots in plastic cups and frozen at $-80°$ C until the day before use, when they were allowed to thaw at room temperature. Reverse osmosis water was used as the control cue.

Scent Presentation and Behavioural Observations

Each bird was held in captivity for 4 days. Immediately after capture, a finch was introduced into an enclosure and given 2 full days to acclimate to its new surroundings. On the third day, a water control was introduced into the feeder boxes to measure baseline behaviour, then removed following approximately 30 min of observation. On the following treatment day, either cat faeces, rabbit faeces, or a water control was placed into the feeder box. A given bird received only one of these treatments during its time in captivity, yielding a sample size of 17 birds per group. The experimental trials were performed in groups of three birds and staggered between the six enclosures so that at any given time three birds (in three separate enclosures) were involved in trials while the other three (newer) birds were being acclimated to their enclosures. Treatment was randomized among the three active enclosures for each trial.

On both baseline and treatment days, the stimulus cup was deposited into the feeder box 5 min before lights on. After the lights had turned on, the behaviour of the birds was recorded for 25 min with Sony camcorders. After recording, the stimulus was removed. Immediately after

the treatment observation period, the three birds were removed from the enclosures, banded and released at their site of capture. The feeder areas and boxes were then cleaned with 95% isopropynol.

Observations from video tapes were recorded by T.C.R. and J.G.C. blind to treatment (cat, rabbit or control) and day (i.e. baseline or treatment). We recorded the total amount of time spent on the feeder platform, on the cup, and feeding (handling and consuming food), as well as the mean length of a feeding bout (time spent consecutively on the cup feeding with no more than a 10 s delay between pecks), the delay to first feeding from lights on, and vigilance (frequency of alert postures consisting of a vertical elongation of the body, extension of the legs and raising of the head) to the nearest second using JWatcher (Blumstein et al. 2006). The difference in a given individual's behaviour between the baseline measurement day and the following treatment day was used as the metric for comparison in all analysis. We analysed the data using ANOVA with least significant difference (LSD) post hoc comparisons. Because the direction of the difference between the predator and control treatments was predicted, our results were interpreted with $\alpha = 0.10$, although the interpretations do not change greatly when $\alpha = 0.05$. To examine a possible decline in response over time, we used repeated measures ANOVA to examine an effect of time on vigilance and feeding behaviour.

RESULTS

Finches responded to both rabbit and cat faecal cues, but they responded to cat cues more strongly in some analyses. Finches significantly delayed their first feeding in both rabbit and cat treatments ($F_{2,43} = 4.59$, $P = 0.016$; Fig. 2a). This significant effect reflected (in part) the fact that the finches experiencing the control cue were much less reluctant to approach the feeder during the treatment day than they were on the previous baseline day (leading to a negative response, Fig. 2a); this suggests that these finches continued to habituate to their enclosures on the second day of observations. The finches in the faecal treatments remained relatively reluctant to approach the feeder during the treatment day, hence the overall significant result. During the treatment day, finches in both faecal treatments also spent less time on the feeder as a whole ($F_{2,46} = 3.64$, $P = 0.034$; Fig. 2b), while birds experiencing the control cue increased time on the feeder. Time spent on the food cup itself decreased during the treatment day in the faecal treatments, especially in the cat treatment (Fig. 2c), although the overall model was not significant ($F_{2,46} = 1.53$, $P = 0.227$; Fig. 2c).

Odour treatment did not affect changes in feeding bout length from baseline to treatment days ($F_{2,50} = 0.270$, $P = 0.765$; Fig. 3) in the repeated measures analysis. There was a significant effect of time ($F_{2,50} = 6.244$, $P = 0.016$) in the model, with birds in the rabbit treatment having significantly longer feeding bouts in the second time block (paired t test $t_{16} = 2.76$, $P = 0.014$). There was no significant interaction between treatment and time ($F_{2,50} = 1.849$, $P = 0.168$; Fig. 3). However, when
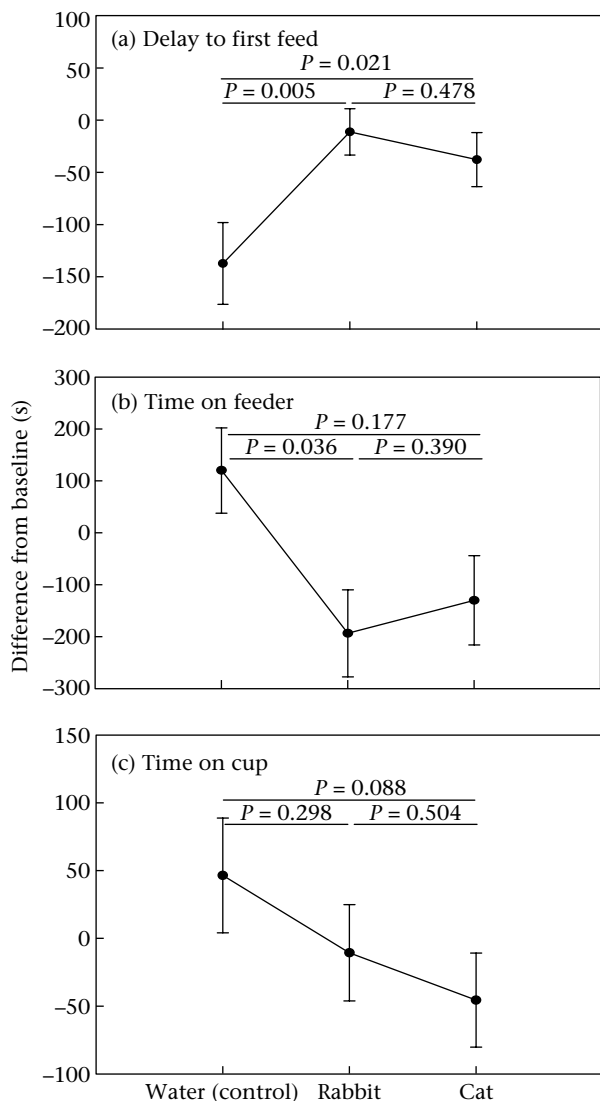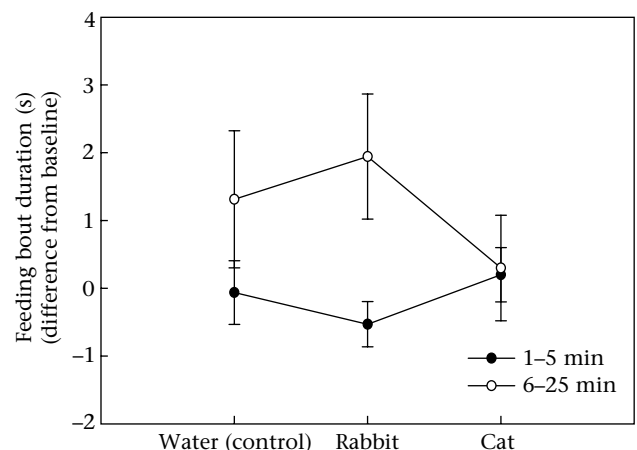
Figure 2. Mean difference in behavioural responses (in seconds) between treatment and baseline days for the (a) delay from lights-on to first feeding, (b) amount of time spent on the feeder and (c) the amount of time spent on the cup. *P* values represent post hoc Fisher's LSD comparisons. Error bars = SE.

Figure 3. Mean difference, between treatment and baseline days, in feeding bout duration during minutes 1−5 and 6−25 of observation. Error bars = SE.

considering vigilance (Fig. 4), there was a significant interaction between time and treatment ($F_{2,49} = 3.995$, $P = 0.025$). Finches in the faecal groups significantly reduced the number of vigilance stances relative to the control group in the early time block, but they were relatively more vigilant in the later time block (Fig. 4).

DISCUSSION

Overall, our results clearly show that finches can detect mammalian faecal cues. To our knowledge, this study is the first to find evidence of birds using scent as a possible cue to assess predation risk while foraging, and is further evidence that olfactory cues may be relevant for birds in a variety of ecological settings (see also Roper 1999; e.g., Ioale & Papi 1989; Petit et al. 2002; Wallraff 2004; Mennerat et al. 2005).

Our results are consistent with the idea that finches associated mammalian faecal odours with possible danger. This is especially apparent in the significant delay to initiate feeding and the time on the feeding platform. We believe that this interpretation holds even though the response to the rabbit cue was sometimes similar to that of the cat cue, as such responses are not uncommon in similar experiments. For example, our results are consistent with Amo et al. (2008), who also found some response to the non predator odour cue in blue tits. In addition, comparable mammalian studies sometimes find a response to the non-threatening stimulus (e.g. Caine & Weldon 1989). The observed response to rabbit faeces could simply be the result of encountering a new stimulus (i.e. presence of an unknown mammal scent where there had been none before). Along the same lines, the response to rabbit faeces might be a function of the time required for olfactory sampling of the newly encountered stimulus. A better understanding of why finches might react to rabbit faeces will require additional study. Nevertheless, there are good reasons to expect that cat faeces, with a high concentration of sulfur metabolites resulting from consuming meat, would be indicative of greater predation risk (Nolte et al. 1994; Berton et al. 1998).

Our results could be interpreted as an 'antifaeces' response, but several details argue against such an interpretation. The scent of faeces while foraging could indicate that the food is not safe to eat because of contamination or for reasons other than predation. However, our finding that the birds' avoidance reactions weakened more quickly (within 5 min) in the rabbit treatment than in the cat treatment (Figs. 3, 4) suggests that it was an antipredator response that we observed. If the observed responses were due to an avoidance of faeces, then we might expect the birds' avoidance reactions not to attenuate because as long as the smell remains, the potential contaminant remains. On the other hand, if the avoidance responses were antipredator in nature, then we might expect the response to weaken relatively quickly. Olfactory cues contain less temporal precision than do visual cues (Chivers & Smith 1998; Kats & Dill
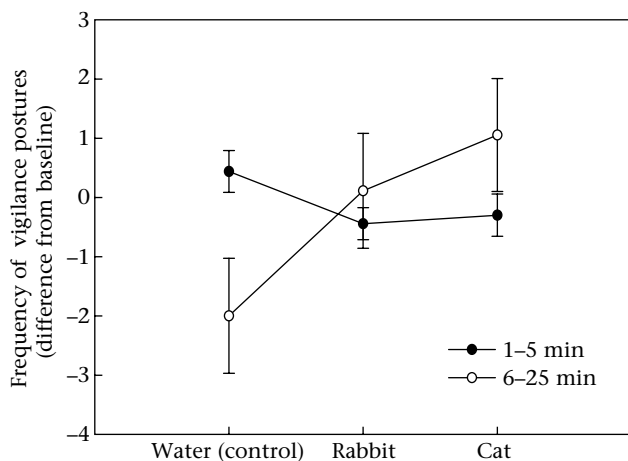
Figure 4. Mean difference between treatment and baseline days in number of vigilant stances during minutes 1–5 and 6–25 of observation. Error bars = SE.

examine this effect in a more natural setting as well as consider the effects of temperature, wind and age of cue, for example. Additionally, we suggest that birds might react differently to an olfactory predator cue presented after their dawn feeding bout, as the relative value of food might change later in the day (McNamara et al. 1994).

In conclusion, we have shown that house finches can detect the faecal cues of mammals while foraging. This by itself is novel, as the ecological relevance of olfaction to birds is still a subject with mixed support in the literature. Our results suggest a general avoidance of feeders in the presence of mammalian scents, and that this avoidance might be done at the expense of vigilance while at the feeder. We found evidence that the finches distinguish between predator and nonpredator scents, although their ability to do so may not be as well developed as in other taxa (e.g. Chivers & Smith 1998; Kats & Dill 1998). Further investigation into the olfactory capabilities of passeriforms should remain a very fruitful direction of study.

1998), thus we might expect a bird to use visual cues (or lack thereof) to verify or refine olfactory information about predators. Smells reveal current or past presence, whereas visual (or auditory) cues reveal current presence. Thus, it is perhaps unsurprising that, after a brief period, the finches may have given precedence to the visual information and continued to feed (see also Parsons & Bondrup-Nielsen 1996; Hartman & Abrahams 2000; Lima & Steury 2005; Belton et al. 2007).

Another point of discussion is the unexpected drop in vigilance observed in the finches in both faecal treatments. Other behavioural measures (delay to begin feeding and time spent on the feeding platform) suggest that the finches were attempting to limit time on the feeder, and this vigilance response might have contributed to their overall avoidance of the feeder. In other words, the finches may have opted to reduce the time exposed on the feeder by reducing their vigilance and feeding very quickly (sensu Lima 1987). This is consistent with the low levels of vigilance relative to controls in both the faecal groups during the first 5 min of the experiment followed by an increase in vigilance behaviour (especially in the predator treatment) after the birds had had an opportunity to eat. We note that much of the delay in initiating feeding (during the faecal treatments) was spent perched and vigilant off the feeder, and during that time the finches may have visually assessed all that they could, and hence did not invest additional time in vigilance once they were on the feeder.

Future directions for this type of research in birds might also consider the importance of multiple predatory stimuli. It is well known that multiple cues from a predator can have compounding effects on the behavioural response of prey (e.g. Parsons & Bondrup-Nielsen 1996; Hartman & Abrahams 2000; Belton et al. 2007). Might visual corroboration strengthen the response to the scent cue, or, vice versa, might olfactory cues strengthen antipredator responses to visual indicators? Given that birds are visually oriented animals, additional visual information might be necessary to allow the finches to distinguish predator from nonpredator cues. Also, field-based research should

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