

Short communication

Can Kittiwakes smell? Experimental evidence in a Larid species

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Birds have long been thought to have a poor sense of smell, although they have the proper anatomical and neurological structures for detecting olfactory cues (Roper 1999). However, in the past decade several bird species have been shown to use smell in various contexts, such as foraging (Nevitt *et al.* 1995), navigation (Wallraff 2004), selection of nest materials (Petit *et al.* 2002, Gwinner & Berger 2008), nest location (Bonadonna & Bretagnolle 2002), predator avoidance (Amo *et al.* 2008, Roth *et al.* 2008) and recognition of conspecifics (Hagelin *et al.* 2003) or mates (Bonadonna & Nevitt 2004, for reviews see Roper 1999, Hagelin & Jones 2007, Nevitt 2008).

The evidence, however, mainly concerns the Procellariiformes (petrels, shearwaters and albatrosses), a group that has long been suspected of using olfaction because of their strong body odour, highly developed olfactory bulb, nocturnal habits and burrow-nesting (Nevitt & Bonadonna 2005, Nevitt 2008). Evidence of olfactory ability is scarce in other avian taxa. Exceptions include, for instance, Turkey Vulture *Cathartes aura* (Smith & Paselk 1986), Brown Kiwi *Apteryx australis* (Wenzel 1968), Homing Pigeon *Columba livia* (Wallraff 2004), Blue Tit *Cyanistes caeruleus* (Petit *et al.* 2002, Amo *et al.* 2008), Domestic Fowl *Gallus domesticus* (McKeegan *et al.* 2005), Kakapo *Strigops habroptilus* (Hagelin 2004), Yellow-backed Chattering Lory *Lorius garrulus flavopalli-*

atus (Roper 2003), African Penguin *Spheniscus demersus* (Cunningham *et al.* 2008) and Crested Auklets *Aethia cristatella* (Hagelin *et al.* 2003).

The Laridae, including Black-legged Kittiwakes *Rissa tridactyla*, are diurnal, have relatively small olfactory bulbs (Bang & Cobb 1968) and do not appear to use olfaction to locate food (Frings *et al.* 1955, Lequette *et al.* 1989, Verheyden & Jouventin 1994). Kittiwakes use vocal cues in mate and parent/offspring recognition (Wooller 1978, Mulard & Danchin 2008), suggesting that olfaction may be at best secondary in those contexts. However, mates commonly allopreen, potentially exposing them to their mate's chemical compounds. Moreover, the relative size of the olfactory bulb may be a poor predictor of olfactory abilities (Hagelin 2004, Mennenat *et al.* 2005). The aim of this experimental study was to assess whether Black-legged Kittiwakes are able to detect odours added to the nest.

METHODS

Study site

The study was conducted in June 2008 during the incubation period (median laying date: 1 June) on an abandoned U.S. Air Force radar tower on Middleton Island, Alaska (59°26'N, 146°20'W). Nests on artificial ledges were visible from inside the building through sliding one-way glass windows (Gill & Hatch 2002).

Experimental design

We assessed Kittiwake response to odours present on a fresh salmonberry *Rubus spectabilis* leaf added to the nest (Experiment 1). In this experiment, we used a blend of mammalian musk oils with a strong skunk-like scent (Gusto™, Caven's Lures & Baits). This odour has been shown to elicit avoidance in Crested Auklets (Hagelin *et al.* 2003). The experiment comprised two treatments in which the underside of the leaf was either untreated (Control group, $n = 21$) or spread with the mammalian musk (Skunk group, $n = 26$). This experiment was carried out during the first half of the incubation period (5–8 June).

The second experiment was similar to Experiment 1 except that it comprised three treatments in which the underside of the leaf was spread with banana essence (Cock brand™; Banana group, $n = 27$), meltwater from frozen Capelin *Mallotus villosus* (Fish group, $n = 26$), or fresh water (Control group, $n = 27$). This experiment was carried out during the second half of the incubation period (14–20 June).

Leaves were used as the method of odour delivery because being common on Middleton they were less likely to elicit a reaction relative to an entirely novel object. Cotton swabs used to spread the scent on leaves

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were used only once. We manipulated nests with incubating colour-banded Kittiwakes. Each bird was used only once for each experiment. Leaves were placed, underside down, on the edge of the nest bowl, just under the beak of the incubating bird. After placing a leaf on the nest, we recorded breeder behaviours after the first landing: (i) the time taken to resume incubation (Resettling Time) and the time when the breeder (ii) pecked at the leaf for the first time and/or (iii) removed the leaf from its nest. Observations ended when the experimental leaf was removed by the incubating bird, when the nest mate landed on the nest or after 15 min. Observations could not be blind to treatment as the odour was perceptible to the observer. However, recorded behaviours were objective measurements (time, removed the leaf, etc.) that were unlikely to be biased. In particular, the effect of the person observing behaviour was non-significant in all the analyses that we performed ($P > 0.4$ in all analyses). This was tested by checking whether the observer effect on the number of behavioural events detected (or the resettling time) was significant. To limit habituation, leaves were removed immediately after a test and successive tests were performed on distant nests.

Data analyses

Data were analysed with SAS software (SAS Institute 1999). Chi-squared or Fisher exact tests were used to assess the overall effect of treatments on the proportion of birds that pecked at or removed the treated leaf, followed by pairwise comparisons with Bonferroni corrections. In all analyses, only the first peck was taken into account to avoid the potential confounding role of taste. Because resettling time was not normally distributed, we used non-parametric tests to compare that variable across treatments. All statistical tests are two-tailed.

RESULTS

Experiment 1: skunk odour

One bird resumed incubation after removing the leaf and one bird resumed incubation after its partner had landed on the nest. These two nests were therefore removed from the analysis of resettling time. Resettling time was more than twice as long for birds in the Skunk-group as for those in the Control-group (Skunk-group: median 43 s, $n = 24$, Control-group: median 19 s, $n = 21$; Mann-Whitney test: $T_{21,24} = 386$, $P = 0.028$). In two other nests, observation ended because the breeder inadvertently moved the leaf while rolling its eggs or because its partner landed on the nest before the leaf was touched. It was thus impossible to record pecking or removing behaviours. Breeders of remaining nests pecked the treat-

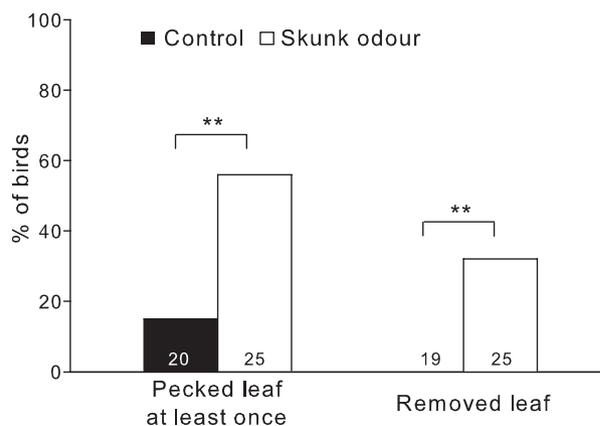


Figure 1. Percentage of Black-legged Kittiwakes that pecked at least once or removed a treated leaf placed in the nest according to the odour added to the leaf in Experiment 1. Whereas leaf removal may have involved taste, this cannot be the case for first pecks. Sample sizes (number of trials) are given in the bars. $**P < 0.01$.

ted leaf 1.6 ± 0.3 times before removing it ($n = 9$). Leaves with skunk odour were pecked ($\chi^2_1 = 6.30$, $P = 0.012$) and removed (Fisher exact test: $P = 0.007$) significantly more often than control leaves (Fig. 1).

Experiment 2: banana or fish odour

Four birds resumed incubation only after removing leaves so that their resettling time could not be recorded. All other birds resumed incubation before pecking leaves. Incubating birds did not delay incubation after the addition of a scented leaf compared to control birds (Banana-group: median 35 s, $n = 24$; Fish-group: median 32 s, $n = 25$; Control-group: median 47 s, $n = 27$; Kruskal-Wallis $H_2 = 2.4$, $P = 0.3$). In two nests, nest mates landed on the nest before leaf pecking or removing could be recorded. Birds pecked leaves 1.2 ± 0.4 times before removing them ($n = 19$), and in the fish odour treatment, two birds tried to swallow the fish-scented leaf. The odour treatment affected the percentage of birds that either pecked at ($\chi^2_2 = 7.2$, $P = 0.027$) or removed the leaf ($\chi^2_2 = 7.8$, $P = 0.020$; Fig. 2). Pairwise comparisons showed that leaves with banana odour tended to be pecked ($\chi^2_1 = 4.4$, $P = 0.036$, $\alpha = 0.017$) and were removed ($\chi^2_1 = 7.8$, $P = 0.0052$, $\alpha = 0.017$) more often than control leaves. Leaves with fish odour were pecked significantly more often than control leaves ($\chi^2_1 = 6.3$, $P = 0.012$, $\alpha = 0.017$) but were not removed more often ($\chi^2_1 = 2.8$, $P = 0.092$, $\alpha = 0.017$).

DISCUSSION

The behaviour of Black-legged Kittiwakes was affected detectably and differentially by the introduced odours.

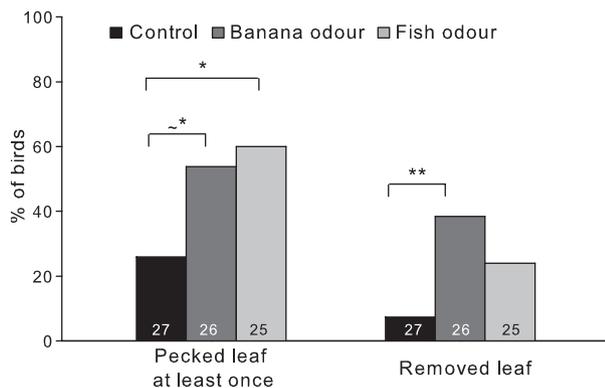


Figure 2. Percentage of Black-legged Kittiwakes that pecked at least once or removed a treated leaf placed in the nest according to the odour added to the leaf in Experiment 2. Whereas leaf removal may have involved taste, this cannot be the case for first pecks. Comparisons marked with asterisks ($*P < 0.05$. $**P < 0.01$) were significant after Bonferroni correction, except that marked with a tilde. All other differences were non-significant. Sample sizes (number of trials) are given in the bars.

Birds pecked at scented leaves more often than at control leaves, regardless of odour treatment. However, they did not remove all types of smelly leaves equally. Breeders removed banana- or skunk-scented leaves more often than control and fish-scented leaves. Furthermore, they took more time to resume incubation when confronted with skunk-scented leaves than when confronted with control leaves.

Birds have three chemosenses: olfaction, taste and the trigeminal system (McKeegan *et al.* 2005). At the first peck, birds may taste scented substances coated on leaves. Thus further pecks and removals may involve taste. However, any behaviour occurring before the first peck (i.e. resettling time behaviour and percentage of birds that pecked at the leaf) could not be influenced by taste. Trigeminal chemoreceptors detect volatile compounds and are responsible for burning and irritating sensations (Laska *et al.* 1997). The skunk odour used in Experiment 1 was highly aversive and caused painful nasal irritations for experimenters. Thus, bird reactions to the skunk treatment may have been mediated through the trigeminal system rather than olfaction. Assessing whether the trigeminal system was involved in our experiments would necessitate the use of invasive methods. In most behavioural studies on olfaction in birds, when authors refer to evidence of sense of smell, they merely mean that a bird has been shown to respond to airborne chemical stimuli (Roper 1999).

Birds exhibit aversive responses to unknown odours (Roper 1999, Jones *et al.* 2002). Removal of banana- and skunk-scented leaves may reveal such an aversive response or nest sanitation, whereas the lower removal

response toward fish-scented leaves (Fig. 2) may be due to the recognition of that treatment as a normal food odour or taste. Breeders confronted with a skunk-like odour took significantly more time to resume incubation than those confronted with a control leaf. Following Hagelin *et al.* (2003), we see two possible explanations; birds found the scent either particularly unpleasant or as revealing of a danger. The skunk odour used in this study is sold as lure for martens and foxes, mammals that have been seen preying upon Kittiwakes breeding on the tops of Breton cliffs (Stone Martens *Martes foina* and Red Foxes *Vulpes vulpes*). This would support the predator-avoidance interpretation of our result, as did the observation that Blue Tits delayed entry into a nestbox when European Ferret *Mustela putorius* odour was added to the nest, relative to unfamiliar odours (Amo *et al.* 2008). In our study, olfactory compounds may have reacted with those of the leaf. The resulting odour may thus have differed from the original one. However, our goal was to demonstrate that Kittiwakes can smell, and their differential reactions to different odours strongly suggest that this is the case.

The question of the natural use of olfaction in that species remains unresolved, however. Kittiwakes have been shown to mate preferentially with genetically dissimilar individuals, raising the question of how such discrimination is achieved (Mulard 2007). Vocal cues probably give little information on individual genetic differences (Mulard 2007). Thus, mate selection may involve olfactory cues as in mammals (Penn & Potts 1998, Wedekind & Penn 2000). Further studies are needed to understand the scope and context of olfaction in Kittiwakes, and for birds in general (Hagelin & Jones 2007).

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