Rollers smell the fear of nestlings

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1. INTRODUCTION

Among other sensory reactions, perception of a threat often triggers the emission of chemical compounds in animals [1,2]. This fear reaction prepares the organism for a sudden escape but may also function in deterring attackers [3], warning conspecifics [4,5] or recruiting them to collectively pursue attackers [6]. Beyond their primary functions, these substances may also be detected and exploited by non-targeted neighbours when assessing predation risk [5–8]. Humans, for instance, increase sweat gland activity when scared, which intensifies their body odour and makes them more detectable by others [9]. Many animals, from insects to mammals [1,6,10–12] produce detectable scents in response to a threat, which we will call ‘the smell of fear’.

Birds are no different and, when threatened, may produce defensive chemicals which help them to discourage predators [8,13]. Northern fulmars Fulmarus glacialis, for instance, propel stomach oils against intruders making them lose their waterproofing [14]. Northern shovelers Anas acuta and common eiders Somateria mollissima, when alarmed during the incubation period, spray faeces on their eggs that deter mammal predators [15]. Surprisingly, the possible role of substances produced during interspecific chemical defence as intraspecific signals has not been investigated in birds [8], although the ecological relevance of avian olfaction is receiving growing interest [16–21].

We explored here whether birds are able to detect the smell of fear, and whether they can evaluate predation risk by relying on chemical cues emitted by conspecifics in response to danger. For this purpose, we performed an experiment with Eurasian rollers Coracias garrulus (roller thereafter), that is a secondary hole-nesting coraciiform in which the use of chemical cues to assess predation risk may be useful, because visual detection of predators may be difficult inside cavities [21]. Furthermore, nestling rollers, when disturbed at nests, vomit an odorous orange liquid (D. Parejo & J. M. Avilés 2005, unpublished data; figure 1a; see electronic supplementary material). The function of this vomit is unknown although it may be defensive, making nestlings distasteful to predators. In addition, this odorous liquid could warn parents of a recent predation attempt on their nests, i.e. signal offspring fear to parents, and hence inform them of the possibility that the predator remained close to the nest. We explored this possibility by assessing in the field whether roller parental behaviour changed in response to the spread of vomit of nestlings at their nest. We expected parents to decrease nest attentiveness if they are able to smell, and are warned, by the substance expelled by nestlings.

2. MATERIAL AND METHODS

(a) Study system

The study was carried out in June–July 2010 in a nest-box breeding population in southeastern Spain (see electronic supplementary material).

(b) Experimental design

Nests with similar hatching date and number of nestlings were randomly assigned to each treatment. When the oldest nestlings in each nest were 10 days old, we measured parental attentiveness in nests randomly assigned to one of the following treatments: (i) vomit (n = 9) and (ii) lemon essence (n = 6). We applied 1 ml of vomit or lemon essence with a paintbrush to the inner part of the entrance hole of the nest-box (see electronic supplementary material). This was done to simulate a situation in which nestlings were scared while parents were far from nests. We are confident that vomit/lemon provided only olfactory cues to adults because they were carefully applied around the inner part of the entrance hole of nest-boxes. Furthermore, colour of nest-boxes was not differently affected by the treatments. Additionally, nest-box design and the early developmental stage of nestlings make nestlings’ vision of the entrance hole unlikely (see electronic supplementary material). We filmed parental provisioning behaviour before and after adding the treatment on the same day. Thus, each nest was first filmed in control odourless conditions and afterwards under experimental conditions.

One observer (D.P.) who was blind to the treatments assigned to nests (i.e. vomiting or lemon) and time (i.e. before or during treatment) extracted from recordings: (i) the time elapsed from the onset of filming until one of the parents entered the nest-box for the first time (latency); (ii) the number of parental provisioning visits; and (iii) total amount of time spent by parents inside nest-boxes. To account for the possible dilution of responses owing to the volatile character of applied treatments, we divided each observation into two consecutive periods of 20 min each after the first parent entered nest-boxes. Differences between during- and pre-treatment periods for a given nest were used for comparison in all analyses.

(c) Statistical analyses

Analyses were carried out using STATISTICA v. 8.0 software. We compared hatching date, brood size at hatching and differences between the during- and pre-treatment periods in nest attentiveness (i.e. latency, provisioning visits to nests, and time spent by parents inside nest-boxes) with Mann–Whitney U-tests.

3. RESULTS

Differences in latency between the pre- and during-treatment period varied with applied treatments

increased in nests treated with nestling vomit, whereas parents of nests treated with lemon essence (Z periods in number of parental visits in the first 20 min after arrival to the nest-box in relation to the scent applied to the nest. (a) Nestling roller regurgitating the orange vomit during its handling. (b) Differences in latency (mean ± s.e.) between the pre- and during-treatment period in relation to the scent applied to nests (vomit, n = 9; lemon, n = 6). (c) Differences in the number of parental provisioning visits to nests (mean ± s.e.) between the pre- and during-treatment period in the first 20 min after arrival to the nest-box in relation to the scent applied to the nest.

(Z = -2.30, p = 0.02, Nv = 9, Nl = 6). Latency increased in nests treated with nestling vomit, while it decreased in nests treated with lemon scent (figure 1b).

Differences between pre- and during-treatment periods in number of parental visits in the first 20 min period varied with the treatment (Z = 2.47, p = 0.01, Nv = 9, Nl = 6). Parents of nests treated with nestling vomit decreased their provisioning, whereas parents of nests treated with lemon essence increased it (figure 1c). The effect of treatment on parental provisioning diluted in the course of time, i.e. in the next 20 min period (Z = 0.47, p = 0.64, Nv = 9, Nl = 6).

Differences in the time spent by parents inside nests between the pre- and during-treatment periods did not vary with the treatment, either in the first 20 min (Z = 0.35, p = 0.72, N = 9,6) or thereafter (Z = 1.35, p = 0.15, Nv = 9, Nl = 6).

4. DISCUSSION
We showed that provisioning rollers can smell the fear of offspring and respond to it by approaching their nests more cautiously. As far as we are aware, our study demonstrates for the first time in birds that a likely defensive substance produced during an interspecific challenge may also have a role in an intraspecific scenario. Indeed, the supposedly defensive liquid which nestling rollers vomit when disturbed is smelled by parents so that they can adjust their behaviour to avoid predation. Therefore, the expelling of vomit may act as a cue informing parents of a recent danger at their nests. Interestingly too, our results add to the growing body of evidence showing that birds are not anosmic and that they may rely on olfaction for important tasks [22].

Breeding rollers detected the scent cues and delayed their entrance to nests and decreased provisioning when their nests were treated with the vomit of conspecific nestlings. In addition, as previously shown in other birds [21], rollers detected these cues before entering their nest-boxes, probably owing to the volatile nature of substances. Our results might be attributed to the aversion of birds to unknown odours (review in [23]). However, neophobia is unlikely, because latency did not increase, and parental provisioning during the first 20 min did not decrease in response to lemon essence, which is also an unknown scent for rollers. Alternatively, because we used vomit from foreign nestlings in the experiment, results might be explained by parents’ capacity to recognize kin vomits. Indeed, there is growing evidence of odour-based kin recognition in colonial birds [24–26]. However, kin recognition based on vomit odour is unlikely to occur in rollers because parents are never challenged at their nests to tell their nestlings apart from foreign ones, as may be the case in colonial birds or in species suffering from brood parasitism. It is still possible that a change in nestling behaviour, due to the application of the treatment, mediated parent behaviour, which would be the case if nestlings inside nest-boxes can either see or smell the scents. However, the colour of nest-boxes was not differently affected by the treatments, ruling out the first possibility (electronic supplementary material). Also, a pilot study in which we recorded nestlings’ behaviour revealed that nestling behaved similarly before and after treatment application (electronic supplementary material), which discards the second possibility. Therefore, our results can be solely explained by the detection of a threat through olfaction of nestling vomit scents by parents. Moreover, in response to lemon essence, latency time decreased and number of parental provisioning visits during the first 20 min increased instead. This can be explained by the habituation of rollers to a researcher’s visit to apply the treatment to nests (as in [21]) in a harmless odorous environment. The lack of habituation in nests assigned to the vomit treatment, however, would be an effect of the detection of nestling fear by parents. Therefore, by delaying their first approach to nests after perceiving the fear of offspring and by decreasing provisioning rate, rollers may minimize predation risk. Furthermore, our results show...
that birds are able to change their anti-predator behaviour according to the risk of predation, with birds decreasing their defensive behaviour in the course of time (see also [27]).

The vomit expelled by nestling rollers could be of major importance during breeding, as it seems to warn parents of threats occurred at nests during their feeding trips. Also, if this vomit had a defensive function deterring nest predators by making nestlings unpleasant to predators, it might not only increase parental survival, but also it would increase survival of the brood. This scenario opens a promising research topic about the role of avian compounds used as defensive substances in an intraspecific context.

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