



Red-legged partridges perceive the scent of predators and alarm scents of an avian heterospecific

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A growing body of evidence suggests that birds can use olfactory cues to detect the presence of predators. We predicted that the ability to gather information about predator presence through chemical cues might be particularly important for ground-living and foraging bird species, since their main predators, namely mammals and reptiles, use chemical communication. In this context, we experimentally examined the role of olfaction in the nondomesticated, ground-living red-legged partridge, *Alectoris rufa*, in a natural and context-dependent situation. We tested how individuals responded to three different olfactory stimuli, which were presented in sand bath tubs: (1) a mammalian predator (ferret faeces), (2) an avian alarm scent (alarm secretion of the European hoopoe) and (3) a control (orange oil). As dependent variables we recorded side preferences and dustbathing activity. Red-legged partridges avoided the predator scent to the same extent as the alarm scent of the hoopoe, whereas orange oil scent did not affect side choice or dustbathing behaviour of individuals. Our results indicate that red-legged partridges avoid the scent of a predator as well as the alarm scent of an avian heterospecific. In regard to this, we provide the first indication that, in risk assessment, chemical cues, similar to avian alarm calls, may possibly act as a source of information between avian species.

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Birds have long been regarded as using mainly visual and acoustic rather than chemical stimuli to gather information about their environment (Caro & Balthazart, 2010). However, starting with Bang (1961), a growing number of studies have revealed that in certain bird species a well-developed sense of smell is used in various functional contexts, involving mate choice, foraging, orientation, nest site choice and even kin recognition (Amo, Galvan, Tomas & Sanz, 2008; Amo, Tomás, Parejo & Avilés, 2014; Amo, Visser & Oers, 2011; Buitron & Nuechterlein, 1985; Caro, Balthazart, & Bonadonna, 2015; Caspers & Krause, 2011; Gagliardo et al., 2013; Hirao, Aoyama, & Sugita, 2009; Krause, Krüger, Kohlmeier, & Caspers, 2012; Leclaire, Mulard, Wagner, Hatch, & Danchin, 2009; Papi, Fiore, Fiaschi, & Benvenuti, 1972; Wikelski et al., 2015).

Although the importance of olfaction in predator recognition and risk assessment is generally well understood and accepted in many vertebrate groups (Apfelbach, Blanchard, Blanchard, Hayes, & McGregor, 2005; Schulte, Goodwin, & Ferkin, 2016; Wilson, 1970;

Wyatt, 2014), little is known about whether birds perceive chemical signals as cues to detect and avoid predation (Amo, Visser, & Oers, 2011; Amo et al., 2008; Roth, Cox, & Lima, 2008; Zidar & Løvlie, 2012). Given that their mammalian predators use mainly chemical communication in many behavioural contexts and often have a distinctive smell, the ability to gather information about predator presence through chemical cues might represent an important sensory pathway to gain additional information about environmental risk assessment and might consequently represent an evolutionary advantage (Apfelbach et al., 2005; Schulte et al., 2016; Wilson, 1970; Wyatt, 2014).

Information about a potential threat can be received by the presence of either the predator itself or chemical signals that reflect predator activity or predation events (Apfelbach et al., 2005; Jones & Roper, 1997; Parejo et al., 2013). Interestingly, some birds even produce alarm secretions (Martín-Vivaldi et al., 2010; Parejo et al., 2013), which are suggested to repel predators, but can also signal predation events to conspecifics. Furthermore, birds often increase the level of information received about their environment by eavesdropping. Particularly well known, for instance, is their ability to eavesdrop on the alarm calls of birds and mammals (Magrath, Haff, Fallow, & Radford, 2015; Magrath, Pitcher, & Gardner, 2007). However, in contrast to alarm calls, olfactory cues provide

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information over longer timescales and do not require the immediate presence of a predator. In regard to this, the question arises whether birds are also able to perceive and use chemical cues of heterospecifics to gain information about predation risk. The ability to use a large range of signals for risk assessment and consequently to avoid predation is crucial for survival and should underlie strong evolutionary forces (Caro, 2005).

Most Galliformes are ground living and spend a relatively large amount of time foraging and dustbathing on the ground. Dustbathing behaviour may be crucial for maintaining the plumage and health, for example through removal of ectoparasites, but can also force individuals into a trade-off, since less attention can be paid to predators. Therefore dustbathing should be displayed only when individuals perceive their environment to be safe. Additionally, many ground-living species are flightless or of low flight ability and may consequently face the problem of a restricted view. One might predict that, in such situations, multisensory inputs might be crucial for early predator detection and risk assessment. The olfactory bulbs in Galliformes seem relatively small in comparison to those of other species (Krause, Schrader, & Caspers, 2016), but even domesticated species such as the domestic fowl, *Gallus domesticus*, have a well-developed sense of smell (Bertin et al., 2010; Fluck, Hogg, Mabbutt, & File, 1996; Jones & Roper, 1997; Krause et al., 2016; Zidar & Løvlie, 2012).

Here we experimentally examined whether a nondomesticated galliform species, the red-legged partridge, *Alectoris rufa*, has the capacity to eavesdrop on direct as well as indirect olfactory predator cues. We chose three olfactory stimuli in ecologically relevant concentrations. All three scents occur naturally and frequently in the partridge's environment and the birds should hence be familiar with the scents (see Methods). We designed a noninvasive, context-dependent experiment, in which individuals had to choose between two dustbathing substrates. As birds only start dustbathing when they perceive the environment to be safe, possible effects of stress-associated behaviours on the birds' choice were thus likely to be minimal. Finally, we also excluded effects of distraction by other internal factors such as hunger, given that food was offered ad libitum.

To achieve the study aims we used (1) predator faeces as a direct olfactory predator stimulus, (2) the alarm scent produced by the sympatric European hoopoe, *Upupa epops*, in response to a predator attack (Hagelin & Jones, 2007) as an indirect cue and (3) orange fragrances produced by a common tree in their habitat as the nonpredator control. Stimuli were presented separately in a choice test and we compared the response to these stimuli with that to a neutral scent.

METHODS

Ethical Note

Our research on red-legged partridges was carried out in 2008 in compliance with the Austrian welfare law (Tierversuchsgesetz–TVG, StF: BGBl. Nr. 501/1989) and the institutional guidelines of the Austrian Academy of Sciences. Housing conditions of the birds were in accordance with the Austrian law for animal keeping and animal protection regulations. Permission to sample scents from European hoopoes was provided by the government of Lower Austria under the licence number RU5-BE-7/010-2011; BD2-N-200/057-2005. The partridges, at 1 year old, were purchased from a farm owned by the Government of Andalusia (Junta de Andalucía Medioambiente y Ordenación del Territorio, Caza y Pesca, Jaén, Spain) and transported to Austria by air and car. The birds were transported in four specially designed wooden boxes (50 × 80 cm and 30 cm high) with two opposite slots (80 × 10 cm) covered with

wire mesh to guarantee enough airflow. Sufficient familiar food (commercial partridge food) and fruits (apples and oranges) were provided during the flight. The total time from the farm to the institute was less than 7 h. The birds were transported under the supervision of a Spanish and an Austrian governmental veterinary medical officer. After the experiments the birds were released back into their original aviary; we checked that they successfully reintegrated into the flock.

Study Species and Housing Conditions

Red-legged partridges are ideal for an experimental approach focusing on the use of olfactory cues to estimate predation risk. They live, forage and breed on the ground, and rest and dustbathe in shallow hollows in dry earth and sand. During the breeding season they form monogamous long-term pair bonds, with the male building the nest and both parents caring for the offspring (Cramp, Simmons, & Perrins, 1982–1994). Red-legged partridges do not cover the eggs with vegetation during the laying and incubation period and therefore suffer from higher predation than related species (e.g. grey partridges, *Perdix perdix*) in the same environment (Potts, 1980; Rands, 1988). We tested 74 individuals (37 males and 37 females). The birds were 2 years old at the time of the study and born and raised in captivity, but originated from wild-caught individuals. The sex of all birds was determined by the cloacal protuberance; plumage coloration and behaviour were used to confirm the sex. All individuals were banded with a unique colour combination of aluminium and plastic rings. Prior to the experiment all birds were kept in a mixed-sex flock of approximately 40 individuals in an indoor aviary (16 × 5 m and 3 m high), under a natural light regime. The aviary was equipped with perches, shelters and dustbathing opportunities, and the ground was covered in a layer of wood-chips. The birds were provided ad libitum with water and commercial grain-based poultry food, salad leaves and insectivorous food (protein-based mash).

Red-legged partridges are social birds and spend most of the time in pairs or flocks (Cramp et al., 1982–1994). Isolation and separation from conspecifics would lead to unnatural behaviour and panic (K. Mahr & H. Hoi, personal observations). Thus, for the birds to behave naturally during experiments it was essential to use mixed-sex pairs. We minimized the possibility of behaviours such as aggression and mating interfering with the experimental procedure by performing the three experiments, testing the scent of a predator, an alarm scent produced during a predation event and a nonpredator control scent, respectively, outside the breeding season (January, February and August 2009) with the trials for each scent category approximately equally distributed over the experimental period.

For each trial, we randomly chose one male and one female from the original flock. The birds were not identified as a territorial pair but were familiar with each other. Each scent was tested in a separate trial, with a minimum of 1 month between experiments. Therefore the composition of the pairs varied with each type of olfactory stimulus presented to the birds. Each bird was used only once per olfactory treatment.

The experiments were carried out in an isolated experimental indoor enclosure (3 × 4 m and 2.5 m high) provided with shelters, water and food ad libitum and under natural light conditions (Fig. 1). There was no visual or acoustic contact with any other birds in the surroundings. Individuals entering the experimental procedure were provided with the same diet as in the housing aviary. Prior to the trials, the pair was housed in the experimental aviary for 3 days without dustbathing opportunities and the timeframe of separate housing never exceeded 7 days. Individuals were monitored on a daily basis to habituate them to the observer.

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