



Scent of the enemy: behavioural responses to predator faecal odour in the fowl

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Chemical communication is used by diverse organisms in a variety of contexts and can have strong fitness consequences for the individuals involved. However, despite the extensive use of birds as models for many research areas in biology, avian olfaction has been poorly investigated. Studies on bird species that lack well-developed olfactory organs and those investigating responses to predator odours are particularly scarce. We investigated behavioural responses of the domestic fowl, *Gallus gallus domesticus*, a ground-living species with intermediate olfactory bulb size, to several predator and nonpredator faecal odours. We found that the birds spent less time foraging and were more vigilant when exposed to predator faecal odour compared with nonpredator faecal odour. Individuals showed a similar response when exposed to increased amounts of faeces. Taken together, our results demonstrate that domestic fowl can distinguish between herbivore and predator faecal odour, and respond to predator olfactory cues alone, without prior experience. Our results have implications for the understanding of predator–prey interactions and responses to olfactory cues in general, and for chemical communication in avian species more specifically.

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Chemical communication has been extensively studied in a range of organisms, from invertebrates to humans, and its importance is recognized in multiple ecological contexts. For example, the ability of an individual to register chemical stimuli can greatly improve fitness through location of food, mate choice and predator detection (e.g. Weissburg et al. 2002; Apfelbach et al. 2005; Johansson & Jones 2007). In predator–prey interactions, early detection is often key to success for both parties. Thus, olfaction can be particularly advantageous in instances where odour pre-empted auditory or visual signals. Chemical cues can reveal a predator's proximity to the prey, and even indicate the diet of the predator (Kats & Dill 1998; Mirza & Chivers 2003). Furthermore, registration of olfactory cues can enhance perception and thus predator detection, and detectability is higher and reaction time shorter with multiple rather than single sensory inputs (Gielen et al. 1983). For example, human subjects receiving an olfactory cue were more perceptive during a vigilance task than when exposed to odourless air controls (Warm et al. 1991).

As a response to predator detection, prey animals can alter their behaviour to reduce the risk of predation, for example by decreasing movement, increasing vigilance or relocating to a safer location (see Lima 1998; Apfelbach et al. 2005). Responses to predator odour by prey animals have been demonstrated in several

taxa (e.g. invertebrates: Thomas et al. 2008; vertebrates such as fishes: Ylönen et al. 2007; reptiles and amphibians: Ireland et al. 2007; mammals: Apfelbach et al. 2005), and can be intense and long lasting (e.g. Dielenberg & McGregor 2001).

Although predator detection by olfaction is well studied in a diverse range of animals, its adaptive value has rarely been investigated in avian species. Indeed, birds have long been considered to rely only on visual and auditory signals when perceiving the world (see references in Stager 1967; Jones & Roper 1997; Hagelin & Jones 2007; Balthazart & Taziaux 2009). Furthermore, the use of olfaction in birds has been neglected and even questioned (see references in Kats & Dill 1998; Roper 1999; Balthazart & Taziaux 2009).

Previously, only very few bird species were considered to possess the ability to perceive olfactory stimuli (e.g. petrels, Procellariiformes: Hutchison & Wenzel 1980; kiwis, Struthioniformes: Wenzel 1971; vultures, Cathartiformes: Houston 1986). The belief that these birds were capable of olfactory perception was based either on the impressive structural design of their nasal cavity and olfactory bulb or on the fact that they were nocturnal and so expected to have poor vision, or even on the observation that the birds themselves smelled strongly (Stager 1967; Bang 1971; Wenzel 2007). Studies showed that olfaction was used for foraging (e.g. kiwis: Wenzel 1971; Cunningham et al. 2009; petrels: Hutchison & Wenzel 1980; turkey vultures, *Cathartes aura*: Houston 1986) and for navigation (e.g. Leach's storm petrel, *Oceanodroma leucorhoa*: Grubb 1979). More recent studies, primarily on seabirds, reveal a more diverse dependency, in which olfaction is also used for

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conspecific recognition (crested auklet, *Aethia cristatella*: Hagelin et al. 2003), nest recognition (Antarctic prion, *Pachyptila desolata*: Bonadonna et al. 2003, 2004) and partner and individual recognition (Antarctic prion: Bonadonna & Nevitt 2004; Bonadonna et al. 2007). Evidence of olfactory abilities in other avian species with normal-sized olfactory morphology and diurnal lifestyles is also beginning to accumulate (e.g. ravens, *Corvus corax*: Harriman & Berger 1986; blue tits, *Cyanistes caeruleus*: Petit et al. 2002; homing pigeons, *Columba livia*: Wallraff 2004; zebra finches, *Taeniopygia guttata*: Caspers & Krause 2011).

Despite an increasing interest in avian olfaction, only a handful of studies have investigated predator odour detection, and with varying results. In domestic fowl, *Gallus gallus domesticus*, 7-day-old chicks avoided a cloth marked with odour derived from domestic cat, *Felis catus*, fur (Fluck et al. 1996); crested auklets (Hagelin et al. 2003) and kittiwakes, *Rissa tridactyla* (LeClair et al. 2009) showed aversive behaviour when presented with a blend of mammalian musk; house finches, *Carpodacus mexicanus*, reduced their feeding activity when exposed to faecal odour from domestic cats while foraging (Roth et al. 2008); blue tits delayed their entry to and reduced their time in nestboxes scented with urine and anal secretions from the domestic ferret, *Mustela putorius furo* (Amo et al. 2008); and naïve adult great tits, *Parus major*, avoided roosting in nestboxes in a test aviary scented with ferret urine (Amo et al. 2011b). On the other hand, eastern bluebirds, *Sialia sialis*, showed no evidence of detection of odours from skin of the black rat snake, *Elaphe obsoleta*, or fur from the deer mouse, *Peromyscus maniculatus*, when selecting nestboxes (Godard et al. 2007). Similarly, Johnson et al. (2011) found no response in house wrens, *Troglodytes aedon*, to nestboxes scented with urine and anal secretions from the American mink, *Neovison vison*. Furthermore, Amo et al. (2011a) found no evidence of predator detection in sleeping great tits when exposed to fresh urine from a male ferret. Therefore, to clarify the observed variation and to understand the function and evolution of avian olfaction, responses to predatory odours in birds requires further investigation. Additionally, the studies cited above typically investigated only one distinct predator scent against one nonpredator scent, making it difficult to distinguish whether the results showed actual avoidance of a predator odour or simply aversion to a strong scent (but see Amo et al. 2008).

In this study, we aimed to investigate further the ability of avian species to respond to predator odour by experimentally testing behavioural responses in domestic fowl to a range of predator and nonpredator faecal odours.

METHODS

Eighty domestic fowl ($N_{\text{females}} = 40$, $N_{\text{males}} = 40$) from a population of an old Swedish game breed (Harrison 1987) kept at Tovetorp Zoological research station (Department of Zoology, Stockholm University, Sweden), were used in this study (population size = 125, $N_{\text{females}} = 65$, $N_{\text{males}} = 60$). The population is kept under seminatural conditions, and has been randomly bred. As a consequence, birds from the population are very similar to the red junglefowl, *Gallus gallus gallus*, the wild ancestor of all domesticated chickens (Fumihito et al. 1994), in both morphology and behaviour (Schütz & Jensen 2001; see references in Løvlie & Pizzari 2007). The birds used in this study are habituated to humans and are regularly used for behavioural studies, allowing close observations of natural behaviours (e.g. Pizzari et al. 2003; Løvlie et al. 2005; Løvlie & Pizzari 2007; Lisney et al. 2011). Birds were kept in mixed-sex, mixed-age (1–10 years) groups in several outdoor enclosures (ca. 5×10 m) with ad libitum access to water, commercial poultry feed, perches and dust baths. The enclosures had double nets (ca. 50 cm between the outer and the inner net)

keeping predators away from the birds. However, we cannot rule out the possibility that birds may have had some previous visual or olfactory interaction with predators (e.g. foxes, *Vulpes vulpes*, domestic cats and dogs, *Canis lupus familiaris*) through the nets. All individuals were marked with leg bands with individual identity numbers facilitating recognition. Experiments were conducted according to ethical requirements in Sweden (Linköping Ethical committee, ethical permission number 60-10).

The study was conducted between 8 July 2011 and 18 September 2011. Data were collected during hours when the birds are most active, from 0530 to 1900 hours with a break during the warmest part of the day around 1100–1500 hours local time (see references in Løvlie & Pizzari 2007).

All individuals were tested singly in one of two similar indoor experimental rooms (ca. $3 \times 3 \times 2$ m) with no visual contact with other birds or the surroundings. Birds were tested singly to prevent responses being influenced by social interactions or behaviour of other birds. Although the fowl is a social species, individuals have been observed foraging away from the group for short periods (Collias & Collias 1967). Isolation and separation from the flock for the short test period (20 min) are therefore not expected to result in unnatural behaviours (see e.g. Lisney et al. 2011 for an example of meaningful behavioural responses of fowl during short periods of isolation). Both rooms contained ad libitum water, but lacked food to prevent any potential reduction in response to test odours caused by increased motivation for foraging. However, the floors had a marbled surface encouraging some food-searching behaviour. The temperature in the test room was kept within a similar range throughout treatments (the thermostat was set to 19 °C) and treatments were presented at random for each group on successive days with the aim to keep temperature changes to a minimum. An observer sat on a chair in one corner of the room. In the opposite corner a plain, white bucket (ca. 10 litres) was placed containing (1) predator faeces, (2) nonpredator (herbivore) faeces or (3) nothing, as a control (see below). The same bucket was used throughout the experiment for each bird. The buckets were thoroughly cleaned between treatments with warm water and detergent and air-dried between test days.

After each trial, any bird faeces present in the test room were removed to avoid any potential influence that conspecific faeces could have on the behaviour of the next bird to be tested (e.g. faeces of scared birds differ in smell and consistency from faeces of relaxed birds, see Jones & Roper 1997). Because birds were tested 10–60 min apart and the test room was not cleaned and aired between birds tested on the same day, we recorded the order in which a bird was tested and added the term 'position in testing sequence within a day' in the statistical analyses. Between each treatment day, both rooms were flushed clean with warm water and aired out during the night to remove any residual odour before birds were exposed to the next treatment.

Olfactory Cues Employed

For predator cues, we used faecal samples from two of the natural predators of red junglefowl. Red junglefowl are native to southern and southeastern Asia (Collias & Collias 1967; Collias & Saichuae 1967; Peterson & Brisbin 1999) and their main predators are felids, canids and birds of prey (Collias & Collias 1967; Collias & Saichuae 1967). In this study we used faecal odour from tigers, *Panthera tigris*, and dholes, *Cuon alpinus*. Tigers are known to pursue red junglefowl and feed on them opportunistically (Schaller 1984) and faecal analyses have revealed that red junglefowl are part of the diet of dholes (Borah et al. 2009). As nonpredator cues, we used two herbivore inhabitants of the Asian tropical forests: the Asian elephant, *Elephas maximus*, and the nilgai antelope, *Boselaphus tragocamelus*. Faeces used in this study came from several individuals

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