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Smelling out predators is innate in birds

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The role of olfaction for predation risk assessment remains barely explored in birds, although predator chemical cues could be useful in predator detection under low visibility conditions for many bird species. We examine whether Great Tits *Parus major* are able to use the odour of mustelids to assess predation risk when selecting cavities for roosting. We analysed whether the response to predator chemical cues is innate and assessed whether the anti-predatory response is associated with exploratory behaviour, a proxy for the personality of birds. In a choice experiment in aviaries, we offered naïve adult Great Tits of known personality two nest-boxes, one control and one experimental. The experimental nest-box had the odour of a mustelid predator or a strong new odour without biological significance, the control nest-box contained no odour. When one of the cavities contained the odour of a predator, birds avoided the use of either of the two offered nest-boxes, whereas there was no avoidance of boxes when one of the nest-boxes contained a control odour. There was no relationship with exploratory behaviour. We show that the ability to use the chemical cues of predators is innate in birds, but individual differences in the response to predator chemical cues cannot be explained by the personality of the bird.

Key words: avian olfaction, chemical ecology, innate, *Parus major*, personality, predation risk assessment

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The importance of chemical communication in different contexts of an organism's life has been extensively studied for a great number of taxa, including invertebrates (Dicke & Grostal 2001) and vertebrates such as reptiles or mammals (Kats & Dill 1998). However, in the case of birds it has been historically neglected (Kats & Dill 1998). Nowadays, it has been shown that olfaction may be a more important sense in birds than was traditionally believed (Steiger *et al.* 2008). Recent evidence suggests that birds can use odours in several ecological contexts and with different functions (Roper 1999, Hagelin 2007, Hagelin & Jones 2007, Rajchard 2007, 2008, Balthazart & Taziaux 2009, Caro & Balthazart 2010). At the intra-specific level, they are known to emit chemical compounds, which are important in several aspects of avian life histories (Caro & Balthazart 2010). For example, birds can recognize

their nest using chemical cues (Mínguez 1997, O'Dwyer *et al.* 2008, Bonadonna & Bretagnolle 2002, Bonadonna *et al.* 2003a,b, 2004, de León *et al.* 2003, Caspers & Krause 2011) and they are able to discriminate the scent of their partners from the scent of other conspecifics (Bonadonna & Nevitt 2004, Jouventin *et al.* 2007). Therefore, chemical cues may play a role in social behaviour (Hagelin 2007). Chemical cues appear to also be useful in the relationship between birds and their environment. For example, birds can use the sense of smell to discriminate aromatic plants (Petit *et al.* 2002, Mennerat *et al.* 2005, Gwinner & Berger 2008), to orientate and navigate (Bonadonna *et al.* 2004, Wallraff 2004, Nevitt & Bonadonna 2005) and to forage (Hutchison & Wenzel 1980, Nevitt *et al.* 1995, Marples & Roper 1996, Kelly & Marples 2004, Cunningham *et al.* 2008).

The ability to use chemical cues to ascertain predator presence has been documented in a great number of taxa (Apfelbach *et al.* 2005), but scarcely in birds (Kats & Dill 1998, Hagelin 2007, but see Amo *et al.* 2008, Roth *et al.* 2008). However, using chemical cues to assess predation risk could be important in birds, especially in species that use habitats where visual detection of predators is impaired (Amo *et al.* 2008). This is the case in hole-nesting birds such as the Great Tit *Parus major*, that use cavities for breeding and roosting, where they may encounter predators such as mustelids. The chemical cues of predators provide a first assessment of predation risk. This may be especially important when survival depends on ascertaining predator presence and avoiding an encounter with a predator. In this case, natural selection may favour the innate detection of predator chemical cues. Animals may also have the ability to learn to detect and recognize chemical cues of predators, since this ability may be important when confronted with new predators. Naïve animals of several species are known to discriminate the chemical cues of their predators (van Damme *et al.* 1995, Dalesman *et al.* 2007, Sundermann *et al.* 2008). However, whether the recognition of predator chemical cues in birds is innate or learned remains unknown. To our knowledge, the only contexts where the ability to recognize and respond to chemical cues has been proved to be innate in birds is in a foraging context (Bonadonna *et al.* 2006) and in the discrimination of the aromatic plants that some species introduce in the nests (Gwinner & Berger 2008).

Although recognition of the chemical cues of predators may confer an advantage to prey as it allows an early assessment of predation risk, it can also lead to an overestimation of risk if the animal continues to avoid an area when the predator is no longer present (Kats & Dill 1998). Therefore, once an animal has detected predator chemical cues, it should evaluate the 'real' risk of predation that these cues are signalling, to perform an adequate anti-predatory response. Furthermore, the response to predator chemical cues may be the result of the trade-off between the anti-predator responses appropriate to the risk perceived and other requirements such as foraging, reproduction (Lima & Dill 1990, Sih 1992) or the avoidance of costs of the anti-predatory response itself (Ydenberg & Dill 1986, Sih 1997). Changes in cost-benefits may explain variation in the anti-predatory response of the same individual, as well as differences between individuals differing in sexes or ages that may have a different solution to the trade off between avoiding predation and other requirements (Lima & Dill 1990). However, individual

animals often behave in a way that distinguishes them from other members of their species of the same sex, state and age class, and understanding the source of this variation is fundamental to evolutionary studies (Bennett 1987, Wilson 1998).

Individuals of many animal species are known to differ consistently in several aspects of their behaviour, such as aggressiveness, activity, exploration, risk-taking, fearfulness and reactivity (Wilson *et al.* 1994, Gosling & John 1999, Réale *et al.* 2007). Suites of these consistent traits are also referred to as animal personality, behavioural syndromes, coping styles or temperament (Koolhaas *et al.* 1999, Sih *et al.* 2004, Groothuis & Carere 2005, Réale *et al.* 2007) and are comparable to how humans differ in personality.

Here, we explore the use of chemical cues of predators for predation risk assessment when selecting cavities for roosting by a hole-nesting songbird, the Great Tit. Firstly, we aimed to determine whether the ability to detect predator chemical cues for roosting selection is innate in birds. Roosting may be an important behaviour for overwinter survival, as one of the benefits of sleeping in a cavity is a decrease in energetic costs during cold nights (Walsberg 1986, Webb & Rogers 1988). Birds actively select warmer and thermally more stable roosting places (Veľký *et al.* 2010). Furthermore, birds also avoid roosting in cavities containing the signals of predators (mammal fur and mangled feathers) (Ekner & Tryjanowski 2008). Roosts also help to decrease the risk of predation by owls, but increase the risk of predation by mammals such as mustelids (Dhondt *et al.* 2010). Differences in the costs and benefits of roosting in different populations may have exerted different selection pressures that have led to population differences in the use of cavities during the night (Dhondt *et al.* 2010). Dhondt *et al.* (2010) showed that Blue Tits *Cyanistes caeruleus* from populations where owls are scarce and mammals abundant did not use cavities for roosting, while birds from populations where the relative abundances of predators is the opposite did. Therefore, if natural selection favours the use of cavities while the costs of this behaviour are lower than its benefits, it may also favour the ability to assess the costs of roosting, such as the innate detection of chemical cues of predators. Thus, we hypothesized that the response to predator chemical cues may be innate in birds, as it may be subjected to strong selection. We expect this because mustelid predators can be hidden in cavities where visual detection is difficult, and once the bird has entered a cavity containing a predator survival is unlikely. Secondly, we aimed to examine whether the personality of individuals influ-

ences the response to predator chemical cues in order to understand individual variability in anti-predatory behaviour. In the Great Tit, birds from wild populations can be placed along an axis ranging from slow to fast explorers in a novel environment (Verbeek *et al.* 1994, Drent *et al.* 2003). This is correlated with differences in their reaction to novel objects (Verbeek *et al.* 1994), aggressiveness (Verbeek *et al.* 1996), recovery time and behaviour after lost contests (Verbeek *et al.* 1999), foraging behaviour (Drent & Marchetti 1999, Marchetti & Drent 2000) and reactions to stress (Carere & van Oers 2004, Fucikova *et al.* 2009). Artificial selection combined with cross fostering resulted in clear evidence for a genetic basis of these traits (heritabilities between 20 and 50%; Drent *et al.* 2003, van Oers *et al.* 2004b) and in natural populations variation in personality was found to be under natural (Dingemanse & Réal 2005) and sexual selection (van Oers *et al.* 2008). The personality of birds is also related to the response of birds to a risky situation, with fast Great Tits being more prone to return to a risky feeding place than slow individuals (van Oers *et al.* 2004a). Therefore, we hypothesize that birds of different personality types may also differ in their anti-predatory behaviour when exposed to predator chemical cues, with slow birds exhibiting a greater anti-predatory response than fast birds.

METHODS

Study species

We used 20 hand reared captive Great Tits (8 females and 12 males) belonging to the 4th generation of a bidirectional artificial selection program for fast and slow (7 fast and 13 slow) exploratory behaviour (for details see Drent *et al.* 2003). All birds were 1 year old. Birds used in the experiments were naïve to predator odour, as they were maintained in captivity since 10 days after hatching. Furthermore, nestboxes where nestlings were reared during the first 10 days of their life were frequently inspected and neither predation events nor signals of predator visits were detected.

Birds were housed individually in cages of 0.9 m (L) × 0.4 m (W) × 0.5 m (H), with wooden bottom, top, side, and rear walls, a wire-mesh front, and three perches. The bottom was covered with sawdust. They were kept under natural winter daylight augmented with fluorescent light tubes and provided with *ad libitum* water, sunflower seeds, a commercial dry mixture (proteins, trace elements, minerals, and vitamins), a fresh mixture of raw heart and live mealworms. A week

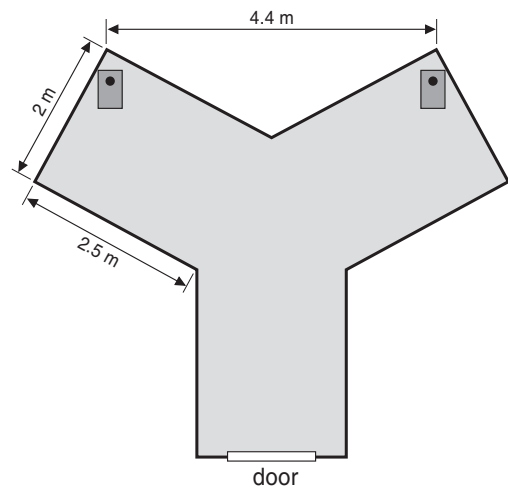


Figure 1. The aviary where the experiment was carried out.

before the experiment, the Great Tits were released into the experimental aviary individually for one hour to decrease stress due to novelty of the environment during the experiment. Birds did not exhibit any sign of stress and were healthy during the experiment.

Experimental set up

The experiment was carried out during February and March 2007. We performed the experiment in two outdoor Y-shaped aviaries (Fig. 1). Aviaries were built with mesh screens (mesh size 1.3 cm), with each branch of the aviary measuring 2.5 × 2 × 2 m. The central branch was closed 72 cm from the intersection with the other two branches. Each aviary contained food and water and two perches, one near each nestbox. The perches were branches of trees, of similar shape and number of small branches. One nestbox was placed at the end of each of the branches of the aviary, separated 4.4 m from each other (Fig. 1). One of the nestboxes was a control and the other the experimental nestbox. The control nestbox contained an 'odourless control' (water). The experimental nestbox had one of the following treatments impregnated in absorbent papers: a) 'predator' (ferret scent) (see Amo *et al.* 2008) or b) 'cologne' (Eau de Cologne from Hema).

We prepared the odourless control treatment by adding several drops of water to a clean absorbent paper. We did this to resemble the level of humidity of the papers containing the two other treatments, and water has been widely employed as an odourless control stimulus in studies on chemical detection (e.g. Cooper & Burghardt 1990, Cooper 1998, Amo *et al.* 2004, 2008). We obtained predator odour by placing

clean absorbent papers inside the cage of a male Ferret *Mustela furo*. Even though Ferrets are not natural predators of Great Tits, the scent (especially that produced by an anal sac secretion used to mark the territory) is very similar to those of other mustelids (Brinck *et al.* 1983) as Stoat *Mustela erminea* and European Polecat *Mustela putorius* that include birds in their diets. This similarity in odour may explain why ferret scent is recognized and avoided by other species that are not a natural prey of this mustelid, including birds (e.g. Zhang *et al.* 2007, Amo *et al.* 2008). In our study area, European Pine Marten *Martes martes* is present, and predares Great Tits (pers. obs.).

The Ferret was housed in a 100 × 60 × 50 cm cage. It had water and food (dry pellets for Ferrets) *ad libitum*. We placed papers in the Ferret cage three days before the experiment, to ensure odour collection. When collecting papers daily for the experiment, we selected wet papers containing fresh urine. This method of odour collection has proven successful in previous studies with hole-breeding passerines (Amo *et al.* 2008). The cologne treatment was obtained by placing some drops of 50% diluted Eau de Cologne on clean absorbent papers. We used cologne as an odorous control that allows us to compare the behaviour of birds when they find the odour of a predator inside the nestbox or a new pungent odour without biological significance.

We added the corresponding treatment to the nestboxes by introducing an absorbent paper (12 × 7 cm) soiled with the corresponding odour in a plastic-mesh cage completely covering the bottom of the nestbox. In this way, the birds could not touch the paper. Furthermore, to avoid birds visually detecting the paper with the treatment, we placed a clean absorbent paper on this mesh cage. On each test day, we used new papers and clean nestboxes. We cleaned the nestboxes with water and soap. The location of treatments (control vs. experimental) in the nestboxes of an aviary was balanced, as well as the treatments in the aviaries (cologne vs. predator). To control for a possible effect of ambient conditions in the behaviour of birds, every test day one of the aviaries contained the cologne treatment and the other aviary contained the predator treatment.

Birds were released in the aviary one and a half hours before sunset to allow them to inspect the aviary and the nestboxes before choosing one to spend the night in. We filmed the behaviour of birds during one hour with a video camera located 5 m in front of each aviary. We recorded the nestbox visited for the first time and the proportion of visits to the experimental nest-

box in each treatment. We defined a visit as when a bird perched on the entry hole of the nestbox. We could not record the behaviour of three birds due to problems with the video camera. We determined which nestbox the bird spent the night in by examining the presence of faeces inside the nestboxes. This is a reliable method to assess the use of a nestbox, since results of another study, in which we forced birds to sleep in cavities containing different scents, including predator scent, show that birds always defecate during the night (L. Amo, S.P. Caro and M.E. Visser, unpubl. data). We thereby noted whether the birds used the control nestbox, the experimental nestbox or whether they spent the night outside any nestbox. We performed a repeated measures design: all birds were tested in the two treatments (predator and cologne) in a balanced order. The following morning, birds were captured and returned to their cages. Only one trial was conducted per bird per day, and there was at least one week between trials with the same bird.

Statistical analyses

We analysed whether there were differences between treatments and personality types in the nestbox of the aviary visited first, as well as in the proportion of visits to the experimental nestbox by using generalized linear mixed models (GLMM; lmer in R package lme4) with binomial errors and a logit link function. In order to analyse the location where the bird spent the night, we distinguished two dependent variables: (1) whether the bird slept inside any nestbox or outside; (2) when the bird used a nestbox, whether the bird slept inside the control or the experimental nestbox. We analysed whether both variables were affected by treatment and personality with GLMM with binomial errors and a logit link function. We included the interaction in the models to test whether the response to the treatments differed between fast and slow birds. We also included the individual as a random factor. We used the software package R 2.7.2 and STATISTICA for statistical analysis. We calculated the power of a McNemar's test analysing the proportion of birds that slept outside or inside the nestbox without including the personality (Power = 0.87), and separately for each personality type (Power: for slow birds = 0.74, for fast = 0.02).

RESULTS

There were no differences in the behaviour of males and females in any of the variables considered ($P > 0.05$ in all cases), or in the number of males and females

that slept outside the nestbox or inside any nestbox in the cologne (Chi-squared test: $\chi^2_1 = 1.20$, $P = 0.27$) and predator treatments ($\chi^2_1 = 0.59$, $P = 0.44$). The sexes did not differ in their choice of nestbox in the cologne ($\chi^2_1 = 0.03$, $P = 0.86$) and predator treatments ($\chi^2_1 = 1.89$, $P = 0.17$). Therefore, we did not include the sex of birds in subsequent analyses.

During the first hour of observed behaviour, all birds visited at least one of the nestboxes. More birds approached the experimental nestbox before the control nestbox when the experimental box contained predator scent (12 vs. 5) compared to when the experimental box contained cologne scent (7 vs. 13) (lmer: $\chi^2_1 = 4.65$, $P = 0.03$). There were no significant differences between personality types (lmer: $\chi^2_1 = 0.54$, $P = 0.46$), and also the interaction was not significant (lmer: $\chi^2_1 = 1.98$, $P = 0.16$). The proportion of visits to the experimental nestbox did not differ between treatments (lmer: $\chi^2_1 = 1.52$, $P = 0.22$) or personality type (lmer: $\chi^2_1 = 0.14$, $P = 0.71$). The interaction was also not significant (lmer: $\chi^2_1 = 1.69$, $P = 0.19$).

When one of the nestboxes contained predator scent, more birds did not use any nestbox and slept outside than when one of the nestboxes contained cologne (lmer: $\chi^2_1 = 17.86$, $P < 0.0001$; Table 1). There were no differences in this behaviour associated with the personality of the birds (lmer: $\chi^2_1 = 0.02$, $P = 0.90$) and also the interaction between treatment and personality was not significant (lmer: $\chi^2_1 = 0.10$, $P = 0.75$), indicating that birds with different personality types did not react differently to the presence of predator scent.

Within birds that used a nestbox, there was no difference in the number of birds that slept inside the control or the experimental nestbox between treatments (lmer: $\chi^2_1 = 1.18$, $P = 0.28$; Table 1), neither did personality affect this choice (lmer: $\chi^2_1 = 2.81$, $P = 0.09$). The interaction between treatment and personality was not significant (lmer: $\chi^2_1 = 1.35$, $P = 0.25$), indicating that birds of different personality did not differ in their reaction to the treatment.

DISCUSSION

Our results provide evidence that birds can detect the chemical cues of predators and use them to assess the level of predation risk while selecting cavities to roost in. When there was predator scent in one of the nestboxes, more birds slept outside a nestbox. These results agree with the experiment of Ekner & Tryjanowski (2008) in natural conditions that shows that small hole nesting passerines, mainly Great Tits, prefer to roost in control nestboxes compared to nestboxes containing signals of predators and predation (mammal fur and mangled feathers). Our results are also in accordance with previous studies on Blue Tits (Amo *et al.* 2008) and House Finches (Roth *et al.* 2008), which show that birds can detect and use chemical cues of predators in a reproductive and a foraging context, respectively. We did not find any significant effect of the cologne treatment on choosing a nestbox for roosting, despite the fact that birds are known to exhibit aversive responses to unknown odours (Jones *et al.* 2002; reviewed in Roper 1999). Therefore, this suggests that birds are responding to specific predator chemical cues but not to a new scent or a non-biological scent, comparable to previous results using different controls such as bird scent (Amo *et al.* 2008) or non-predatory mammal scent (Roth *et al.* 2008). However, we did not find differences in the use of nestboxes between control and experimental nestboxes, which suggests that birds perceived the whole aviary as a risky area. This result may be explained because the minimum home range of the European Polecat is 60 hectares (Blanco 1998), and therefore, the presence of predator chemical cues in one of the nestboxes may indicate an elevated risk of predation at both boxes inside the aviary. Our results provide the first evidence that the chemical detection of predators is innate in birds, as it has been previously found in other taxa (Turner *et al.* 2006, Sundermann *et al.* 2008).

Our results show that individual differences in the response to predator chemical cues could not be

Table 1. Number of birds (by type, 'fast' or 'slow' birds) that spent the night in the control nest-box, experimental nest-box or outside any nest-box in the 'Cologne' or 'Predator' treatments.

Type	Cologne treatment			Predator treatment		
	Control nest-box	Experimental nest-box	Outside	Control nest-box	Experimental nest-box	Outside
Fast	4	2	1	1	4	2
Slow	10	3	0	6	2	5
Total	14	5	1	7	6	7

explained by the personality of the individual. This is despite the results of a previous study that showed that, in a foraging context, the personality of birds helped to explain individual differences in anti-predatory behaviour, with slow Great Tits returning later to a feeding place after being startled than fast individuals (van Oers *et al.* 2004a). Birds were released in the aviary at least one and a half hours before sunset, when they usually explore potential sites for roosting (Velký *et al.* 2010) and therefore, they had time to assess the risk of predation by using chemical cues and to respond to it. Furthermore, more birds approached the experimental nestbox first when it contained predator chemical cues than when it contained a control scent; i.e. they inspected the predator-scented nestboxes before nestboxes containing a control scent. They thereby perched on the hole of the nestbox, looking around and inside. This inspecting behaviour may allow birds to identify the odour source and assess predator presence. This predator inspection behaviour has been described in many prey fish (Brown & Dreier 2002), but birds are also known to approach predators during nest defence (Regelmann & Curio 1983). This result indicates that Great Tits were able to detect the chemical cues of predators from outside the nestbox, in agreement with previous findings (Amo *et al.* 2008). Also, after the first visit, both cologne and predator scented nestboxes were visited similarly. The personality of birds did not influence which nestbox was visited for the first time and the proportion of visits to the experimental nestboxes or the choice between either sleeping inside or outside one of the nestboxes. However, we may have incurred Type II error due to the low sample size of each personality type used in the experiment, therefore, the low power of our test in relation to personality does not allow us to draw strong conclusions. Thus, the factors affecting the anti-predatory behaviour of birds that perceived the chemical cues of predators remain unclear. Further research is needed to try to disentangle the causes of individual variation in the anti-predatory responses of birds to predator chemical cues.

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SAMENVATTING

Er is weinig onderzoek verricht naar de rol die het ruikvermogen bij vogels speelt om de aanwezigheid van roofdieren vast te stellen. Vooral in het donker zouden vogels er veel baat bij kunnen hebben als ze roofdieren kunnen ruiken. De auteurs onderzochten of koolmezen *Parus major* de keuze voor een slaapplek laten beïnvloeden door de geur van marterachtigen. Tevens werd onderzocht of de reactie op de geur van roofdieren aangeboren is. Ook werd nagegaan of exploratief gedrag (een maat voor de persoonlijkheid van de vogels) hierbij een rol speelt. In de experimenten met koolmezen die in gevangenschap waren opgegroeid, bestond de keuze uit twee typen slaapplekken. Het ene type was een sterk ruikende nestkast die of behandeld was met de geur van marterachtigen of met parfum, het andere een niet-behandelde nestkast. Wanneer een van de twee kasten naar een marter rook, vermeden de mezen beide nestkasten. Parfum daarentegen schrikte de mezen niet af. De conclusie wordt getrokken dat het vermogen om gebruik te maken van de geur van roofdieren aangeboren is. De persoonlijkheid van de mezen speelt hierbij volgens de experimenten geen aantoonbare rol. (DH)

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