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Male quality and conspecific scent preferences in the house finch, *Carpodacus mexicanus*

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There is increasing evidence that birds use chemical cues in different contexts, and this is changing the traditional view that birds are the only largely olfaction-free vertebrates. We performed a choice experiment to examine whether male house finches exhibit any preferences for the sex of conspecifics when only their chemical cues are available. When exposed during the breeding season to the scent of a male and a female, males appeared to respond indiscriminately to both odours. However, when we analysed a posteriori the choices of males in relation to their relative quality, males with worse quality than scent donor males avoided the male-scented area, whereas males with better quality moved towards the male-scented area. Our results suggest that in the context of mate choice/competition for mates, house finches may obtain information via olfaction to assess the quality of rival males.

The role of chemical communication in different contexts of avian life is receiving growing attention (reviewed in Hagelin 2007a; Hagelin & Jones 2007; Caro & Balthazart 2010), and this is changing the traditional view that beyond mechanical interactions, birds mainly respond to visual and acoustic cues in their environment (albeit restricted roles have been recognized for magnetic and thermal cues as well; Hagelin & Jones 2007). However, our understanding of the role of chemical cues in intraspecific relationships is still much scarcer in birds than in other taxa. It has been shown that birds can recognize their nest using chemical cues (e.g. Bonadonna et al. 2004; Caspers & Krause 2011; Krause & Caspers 2012) and discriminate the scent of their partners from the scent of other conspecifics (e.g. Bonadonna & Nevitt 2004), as well as use scent for kin recognition (Bonadonna & Sanz-Aguilar 2012). It has also been shown that chemical signals play a role in the social behaviour of the crested auklet, *Aethia cristatella* (Hagelin 2007b), and Hirao et al. (2009) found that mate preferences in domestic cockerels, *Gallus gallus domesticus*, involve olfactory responsiveness to the female's uropygial secretions.

Birds possess several odour sources, such as feathers, skin or scales, and most have a uropygial gland which secretes both volatile and nonvolatile compounds in the form of waxy fluids that birds collect and spread on their feathers (Jacob & Zisweiler 1982). The amount and composition of this secretion have been shown to vary between seasons (e.g. Reneerkens et al. 2002; Amo et al. 2012), sexes (e.g. Whittaker et al. 2010; Amo et al. 2012), age classes (Amo et al. 2012), diets (e.g. Sandilands et al. 2004a, b), hormone levels (e.g. Whelan et al. 2010) and individuals (Mardon et al. 2010; Whittaker et al. 2010; Leclaire et al. 2011a), suggesting that it may convey potentially useful information during intraspecific interactions such as sex recognition. Furthermore, recent findings show that semiochemical profiles correlate with heterozygosity in both male and female black-legged kittiwakes, *Rissa tridactyla* (Leclaire et al. 2011b), raising the possibility that avian chemical cues may also convey information on genetic compatibility (Leclaire et al. 2011b) which may be useful during kin recognition (Coffin et al. 2011; Krause et al. 2012) and mate choice, as recently demonstrated by Bonadonna & Sanz-Aguilar (2012).

A first step to determine whether chemical signals play a role in pair formation in birds would be to analyse whether they discriminate the sex of conspecifics based on chemical cues only. The first study that examined this hypothesis found no evidence of conspecific sex recognition in the Antarctic prion, *Pachyptila desolata* (Bonadonna et al. 2009), although this species shows olfactory partner recognition (Bonadonna & Nevitt 2004). By contrast, Zhang et al. (2010) demonstrated that female budgerigars, *Melopsittacus undulatus*, can distinguish the odour of male and female

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conspecifics, but reported that males did not make a choice when confronted with the scent of both sexes (Zhang 2011). Whittaker et al. (2011a) exposed male and female dark-eyed juncos, *Junco hyemalis*, to the scent of the uropygial gland secretion of male and female conspecifics and found that both sexes exhibit a preference for the scent of males. Amo et al. (2012) corroborated such preference of males and females for male scent in spotless starlings, *Sturnus unicolor*, using living birds as scent sources. Both studies were performed during the mating period of the focal species, and in both cases, the attraction of males to male scent was explained in terms of intraspecific aggression. While there is no reason to expect that all bird species use the same type of information in social contexts, it is clearly necessary to increase the number of bird species in which chemical sex recognition is investigated, as well as to increase our knowledge of male preferences for the scent of males and females.

In a context of intrasexual aggression, asymmetries between rivals are frequently used to decide whether to get involved in, or to what extent to escalate, a fight (Maynard Smith & Parker 1976). For example, males with better body condition, and hence greater fighting ability, are usually dominant over poorer quality males. Therefore, assessing the quality of the rival is useful for individuals to reduce the costs of aggression. Chemical cues of conspecifics are known to be useful in many species to evaluate the quality of rivals (e.g. Arakawa et al. 2008; Mason & Parker 2010). In birds, it has been recently shown that the chemical composition of the uropygial gland is related to the body size of males (Whittaker et al. 2011a). This evidence raises the possibility that birds may use chemical cues to assess the quality of conspecifics, which may be particularly useful in male–male competition and mate choice.

We performed an experiment aimed at examining the ability of male house finches to use chemical cues in sex recognition. The house finch is a small socially monogamous and sexually dichromatic passerine that breeds in both cavities and open nests (Thompson 1960). We offered males the choice between the scents of a male and a female during their mating period. If they were able to discriminate between sexes by scent, we would expect them to be either attracted to the scent of conspecific females, or, as previously observed, to move towards the scent of other males because of intrasexual aggression. In the event of males not making a consistent selection on the basis of sex, we decided to analyse the intrasexual aspect of male choice behaviour by exploring a posteriori whether differences in quality between the focal male and the scent donor male affected the choice made by the birds. We expected that differences in quality between males would determine the response of focal males to the female and male scents, with focal males of superior quality moving towards the scent of the lower quality male, and males of worse quality moving away from the scent of the superior male.

METHODS

Study Species

We used 31 adult house finches (24 males and seven females) captured with nets by professional bird catchers authorized by Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT). Birds were captured at the State of San Luis Potosí, México in February 2009, outside the breeding period, but when they normally begin to search for mates. Birds were taken by car in cages to the Instituto de Ecología, Universidad Nacional Autónoma de México (UNAM; México City), where they were housed individually in mesh cages (33 × 27 cm and 31 cm high) containing three perches that they readily used to roost. Bird cages were located inside an aviary with a roof to protect them from the sun and the rain, but they were otherwise maintained in outdoor conditions, at ambient temperature and under a natural photoperiod. Between adjacent cages, dense polycarbonate barriers reduced visual and chemical communication between neighbours. A total of 59 house finches were held in the aviary in individual cages and experimental birds were randomly located within the aviary. The rest of the birds (24 males and four females) were used in other studies and therefore were not available for our tests. Although birds were kept in individual cages, they were maintained inside the same aviary and thus we could not completely prevent some visual or acoustic communication between them. Consequently we assumed that all birds were similarly familiar to each other in terms of visual and acoustic cues. Birds were provided with a commercial dry mixture of seeds for granivorous birds and water ad libitum. The experiments were performed after 2 months of acclimatization.

As a standard procedure, 1 week before the experiment, birds were weighed with a Pesola spring balance to the nearest 0.05 g. We measured the tarsus length with a digital calliper to the nearest 0.01 mm and calculated body condition as the ratio weight/tarsus length. We also measured the T-cell mediated immune response of birds by injecting 0.02 mg of phytohaemagglutinin (PHA) dissolved in 0.04 ml of phosphate-buffered saline (PBS) in the web (patagium) of the right wing. We measured the patagium thickness before and 24 h after the injection with a pressure-sensitive spessimeter with an accuracy of 0.01 mm. The cellular immune response index was calculated as the difference between the pre- and postinjection measures (Smits et al. 1999). No adverse effects of the PHA injection were observed.

Colour was measured using a MINOLTA handheld spectrophotometer (MINOLTA CR-200, Minolta Co. Ltd, Osaka, Japan) that measures the reflectance from 360 to 700 nm in intervals of 10 nm. Although it does not measure across the whole UV spectrum available to birds (some birds are sensitive down to 320 nm), this limitation may not be a problem because the house finch has little plumage reflectance below 400 nm (Hill 2002). Reference calibrations against zero and a white standard tablet associated with the apparatus were performed according to the instructions provided by the maker. Reflectance spectra for each individual were automatically obtained by means of three sequential measurements per individual, each taken at a slightly different place on the bird's breast. The SPECTRAMAGIC software (Minolta Co. Ltd) was used to analyse spectra. We calculated the yellow–red chroma saturation (YRC) as the proportion of total reflectance traceable to the yellow–red region (R560–700/R360–700) of the spectrum. We used YRC to describe feather reflectance because this region corresponds to the colour range that is subject to mate choice in this species (Hill 2002).

On completion of each trial, birds were returned to their cages where they were seen to resume their normal behaviour. Birds were healthy during the tests and did not exhibit signs of stress from the manipulation. After the experiment, the birds were placed in large aviaries for 2 weeks before being released at their capture site. Aviaries were located indoors, with mesh in the open windows to protect them from the sun and the rain, and they were kept at ambient temperature under a natural photoperiod. Aviaries contained several tree branches 1.5–2 m long to provide perches and places to roost. They also contained food and water ad libitum. We did not observe any overt aggression among the birds in these facilities and all were healthy during their stay in the aviaries. Birds were kept in captivity 3 months in total, and then released at their capture location at the beginning of May. The night before the release, birds were put in small individual, specifically designed cardboard boxes. Inside these boxes, birds were in darkness to keep them quiet and we did not observe any sign of stress during the trip. They were transported by car during the night and released