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Bird odour predicts reproductive success

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Although the importance of chemical communication in birds has long been overlooked or doubted, volatile compounds in avian preen secretions have been shown to covary with traits including species, sex and breeding condition, and thus may be useful mate recognition cues. Here we demonstrate for the first time that these compounds may reliably predict reproductive success in a North American songbird, the dark-eyed junco, *Junco hyemalis*. Several compounds associated with sex differences in this species varied with reproductive success, such that females with a more 'female-like' volatile profile and males with a more 'male-like' profile produced more genetic offspring. A male's preen oil volatile compounds also predicted his success in rearing offspring in his home nest: males with a higher abundance of 'male-like' compounds had more surviving nestlings, including offspring sired by extrapair males. Finally, males with a higher abundance of 'female-like' compounds had more extrapair offspring in their home nests. Our results suggest that odours correlate with reproductive success and thus have qualities that could allow them to serve as reliable mate assessment cues in birds.
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Although birds have long been assumed to rely primarily upon visual and acoustic cues and signals for mate choice, recent studies have begun to reveal a potential role for chemical communication in avian social and reproductive behaviour (Hagelin & Jones 2007; Caro & Balthazart 2010). The uropygial or 'preen' gland is the largest exocrine gland in most birds, secreting oil that birds spread on their feathers while engaging in the self-maintenance behaviour known as preening (Jacob & Ziswiler 1982). This preen oil contains small volatile and semivolatile compounds that vary qualitatively among species and quantitatively within species (Mardon et al. 2010; Whittaker et al. 2010). Previous studies have demonstrated that these compounds change in abundance during the breeding season (Soini et al. 2007; Shaw et al. 2011; Whittaker et al. 2011b) and vary with sex (Mardon et al. 2010; Whittaker et al. 2010; Zhang et al. 2010), population of origin (Whittaker et al. 2010) and relatedness (Leclaire et al. 2012), and that the measurements of relative abundances are repeatable within individuals over short and long time spans (Mardon et al. 2010; Whittaker et al. 2010). One study of odour preferences in male house finches, *Carpodacus mexicanus*, suggests that odour may communicate information about the quality of male rivals (measured by body condition, immunocompetence and plumage coloration), making odour a potentially useful cue in mate and rival assessment (Amo et al. 2012). Preen oil volatile compounds have been suggested to play a role in reproductive behaviour, perhaps as an indicator of fertility (Whittaker et al. 2011b) or genetic compatibility (Leclaire et al. 2012), but these roles have not yet been confirmed. Correlations between avian odours and individual variation suggest that these odours could serve as a conspecific cue that provides information about the individual's health or quality (reviewed in Hagelin & Jones 2007).

Because of the previously described relationships between preen oil volatile compounds and individual variation, these compounds have the qualities required to serve as species recognition cues (they are highly divergent among species: Haribal et al. 2005; Mardon et al. 2010) and as mate recognition cues (the concentration of these compounds differs between the sexes and with breeding condition: Soini et al. 2007; Whittaker et al. 2010, 2011b). Mate assessment cues must advertise the sender's individual identity and quality, and be highly variable among individuals (Johansson &

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Jones 2007). In the present study, we examined whether volatile compounds in preen gland secretions covary with individual quality and thus could serve as reliable mate assessment cues. Definitions of individual quality vary, but are generally based on phenotypic characters that correlate with fitness (Lailvaux & Kasumovic 2011), although some studies imply that quality and fitness are interchangeable (Wilson & Nussey 2010). In this study, we chose to test whether these potential cues correlated with reproductive success, defined as the number of surviving offspring produced.

We tested whether measurements of preen oil volatile compounds collected early in the breeding season predicted genetic and social reproductive success in the same season. Our study organism is the dark-eyed junco, *Junco hyemalis*, a songbird that has recently been the subject of avian chemical communication studies (Soini et al. 2007; Whittaker et al. 2009, 2010, 2011a, b). For comparison, we also tested whether visual cues, including plumage traits and morphological measurements, could predict reproductive success in these birds, or whether chemical signals might be a more reliable predictor.

METHODS

Field Methods

The dark-eyed junco is a widespread North American emberizid sparrow whose behaviour, ecology and physiology are well studied (Nolan et al. 2002). Juncos are socially monogamous, ground-nesting birds, with biparental care and an appreciable level of extrapair fertilizations (~28%: Ketterson et al. 1997; Gerlach et al. 2012a). We conducted this study during the summer of 2008 on a population of juncos breeding at and around Mountain Lake Biological Station near Pembroke, Virginia, U.S.A., which has been the subject of study for 30 years (Ketterson et al. 2001).

We captured juncos using baited mist nets and traps from 15 April to 15 May as part of the annual early season population census. We collected preen oil from every adult captured during the 2008 census by gently rubbing the uropygial gland with a 100 μl glass capillary tube (Drummond Scientific, Broomall, PA, U.S.A.), which stimulates the gland to secrete 1–3 mg of preen oil (Whittaker et al. 2010). We stored preen oil at −20 °C within 10 min of collection until it was analysed by gas chromatography–mass spectrometry (GC–MS, see below). We determined sex by the presence of a brood patch (female) or cloacal protuberance (males) as well as by plumage and wing length (Nolan et al. 2002). We took morphological measurements of each bird, including wing length (flattened), and an estimate of the proportion of the tail that is white ('tail white'), a plumage trait that varies with sex, age and size and is attractive to females (McGlothlin et al. 2008). For paternity testing, we collected a small blood sample (50–100 μl) from the alar vein of each bird and stored it in Longmire's solution, a lysis buffer (Longmire et al. 1992). Birds were released at the site where they were captured, typically less than 1 h after capture. Twenty-two adult males and 12 adult females were included in this study.

From 15 May to 15 July, we intensively searched for nests. Once a nest was located, we monitored it every other day until hatching occurred (day 0). We then checked the nest and weighed the nestlings on day 3 and day 6 after hatching; on day 6 we banded the nestlings and took a small blood sample for paternity testing. On day 11–12 (the time at which nestlings leave the nest or 'fledge'), we captured the nestlings to collect additional measurements for the long-term study. On that day we also captured both adults at all nests to verify the identity of the social father and to collect morphological measurements and blood and preen oil samples if they had not been previously obtained (preen oil samples were collected from only one male and one female on this day). All work was conducted in compliance with the Bloomington Institutional Animal Care and Use Committee guidelines (BIACUC protocol 06-242).

Paternity Testing

We extracted DNA from blood samples using standard phenol-chloroform techniques (Sambrook et al. 1989) and IBI Scientific MINI Genomic DNA kits. Birds and nestlings were genotyped at eight microsatellite loci (Gerlach et al. 2012a), and paternity was determined using the program CERVUS 3.0 (Kalinowski et al. 2007).

GC–MS Analysis of Preen Samples

For a previous study (Whittaker et al. 2011b), we analysed preen oil samples from 16 females and 35 males, all of which had been sampled on at least three different days during the first 4 weeks of the field season (15 April–15 May 2008), a time when the adults are undergoing the physiological changes necessary for full breeding condition. For the current study, we examined the same birds and focused on individuals for which annual reproductive success was known in 2008 ($N = 12$ females and 22 males). We measured GC–MS peak areas for 15 volatile compounds, the results of which have been previously published (Whittaker et al. 2011b). Briefly, we extracted volatile compounds from the preen oil samples using a Twister® stir bar and performed quantitative analysis with an Agilent 6890N gas chromatograph connected to a 5973i MSD mass spectrometer (Agilent Technologies, Inc.) with a Thermal Desorption Autosampler and Cooled Injection System (TSDA-CIS 4 from Gerstel). All major compounds were identified by comparison to standards from Sigma–Aldrich, using mass spectra and retention times. Peak areas of the compounds of interest were normalized by dividing each peak area by that of the internal standard (7-tridecanone) in corresponding runs, yielding relative concentrations (i.e. relative amounts per 100 μl of preen oil) (see Whittaker et al. 2011b for full GC–MS methods).

The compounds of interest include linear alcohols, carboxylic acids and methyl ketones. This particular group of compounds was deemed relevant due to the observed increase in levels during the breeding season (Soini et al. 2007). Abundance of preen oil volatile compounds changes significantly over the course of the early breeding season, and we have previously hypothesized that an individual's peak in abundance may signal readiness to mate (Whittaker et al. 2011b). Thus, rather than taking the mean of multiple samples from one individual (which would have a high variance), we chose to analyse the sample with the maximum abundance observed from that individual. For 28 of these individuals (83%), the sample with the maximum abundance was also the sample closest in time to the start of incubation for that individual's first or second nest of the season; for the remaining six individuals, there was very little difference in volatile compound measurements between the sample chosen and the sample closest to incubation start time. The mean preen oil sampling date was 8 May 2008 (standard deviation: 6 days), which is during the population's peak week for egg laying (Whittaker et al. 2011b).

Statistical Analysis

Perception of odour mixtures can be strongly affected by small changes in the ratio, or proportion, of individual components of that mixture (Laing & Willcox 1983; Livermore & Laing 1998). To consider how the relative abundance of compounds in an individual's overall mixture may provide a chemical cue, we defined 'proportion scores' as a measure of how much of an individual's unique odour is made up of each compound. The total abundance of

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