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Bird odour predicts reproductive success

Danielle J. Whittaker [a,b,*], Nicole M. Gerlach [b], Helena A. Soini [c], Milos V. Novotny [c], Ellen D. Ketterson [b]

[a] BEACON Center for the Study of Evolution in Action, Michigan State University, East Lansing, MI, U.S.A.
[b] Department of Biology, Indiana University, Bloomington, IN, U.S.A.
[c] Institute for Pheromone Research and Department of Chemistry, Indiana University, Bloomington, IN, U.S.A.

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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.

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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* Correspondence: D. J. Whittaker, BEACON Center for the Study of Evolution in Action, Michigan State University, 567 Wilson Road, Room 1441, East Lansing, MI 48824, U.S.A.

E-mail address: djwhitta@msu.edu (D. J. Whittaker).

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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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volatile compounds in preen oil changes seasonally, increasing during the breeding season (Soini et al. 2007; Whittaker et al. 2011b), suggesting that the amount produced by an individual may also convey information, so we also defined ‘abundance scores’ to reflect the absolute amounts of each compound produced. The difference between these two types of measures is illustrated with a simplified example in Fig. 1 using four compounds found in junco preen oil.

To reduce the number of variables used in analysis, we conducted principal components analyses (PCA) with varimax rotation, once using relative proportions and once using absolute concentrations, retaining PCs with an eigenvalue greater than one. We describe the PC scores from relative proportions as ‘proportion scores’, and the PC scores from absolute concentrations as ‘abundance scores’.

The two separate principal component analyses resulted in four PCs based on relative proportions of volatile compounds (proportion scores), which explained 88.9% of the variance, and four PCs based on absolute measurements of volatile compounds (abundance scores), which together explained 90.1% of the variance (Table 1). In a one-way ANOVA, abundance scores 2 and 3 differed significantly between the sexes ($P < 0.01$, both comparisons), as did proportion scores 1, 2 and 3 (proportion scores 1, 2: $P < 0.01$; proportion score 3: $P = 0.046$). Because of these significantly different patterns, we analysed the sexes separately for subsequent analyses.

We ran forward stepwise linear regressions to test the influence of both abundance and proportion scores on the following dependent variables: number of offspring produced by females, number of genetic offspring sired by males (including within-pair and extrapair offspring, WPO and EPO, respectively), number of social offspring successfully fledged by males (number of surviving nestlings present on day 11 or 12, including EPO in their home nests), and number of extrapair offspring in males’ nests. For all measures except number of social offspring successfully fledged by males, we used the number of nestlings present on day 6 as a measure of male reproductive success (instead of the number of eggs laid or hatched), as day 6 was the earliest day we could get a blood sample from the nestlings, and thus paternity data, to determine reproductive success for males. For females, social reproductive success and genetic reproductive success are the same measure, as females do not lay eggs in others’ nests (Gerlach et al. 2012b). Predation was the primary cause of nest failure in this population. Results did not change whether depredated nests were included or excluded from the analysis (data not shown), and so we chose to retain them. We also included Julian date of preen oil sample collection as an independent variable, but date was found to have no effect on the models. Each stepwise regression returned only a single significant variable. We examined the standardized residuals for normality. We observed significant kurtosis and skewness in only one case: the effect of proportion score 3 on male genetic reproductive success. A Box–Cox transformation to correct for kurtosis and skewness in the dependent variable yielded substantively identical results ($r^2_{\text{adj}} = 0.40$, $P = 0.001$). All analyses were conducted with SPSS 20.0 and all statistics were two tailed.

Juncos exhibit varying amounts of white in their outer tail feathers, and captive females have been shown to prefer males with experimentally increased amounts of tail white (Hill et al. 1999). Because this trait is correlated with the ability to elevate testosterone levels in response to a physiological challenge, which is in turn correlated with short-term increases in testosterone during male–male competition, tail white has been suggested to function as an honest signal of male quality (McGlothlin et al. 2008). We tested for correlations between measures of reproductive success

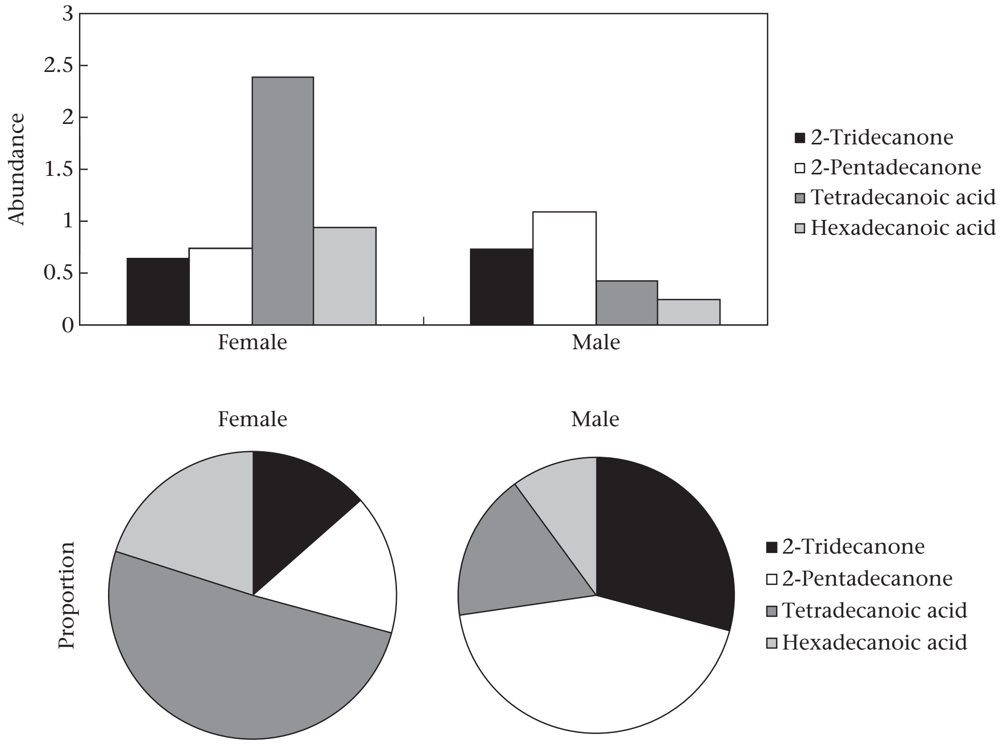

Figure 1. An illustration of abundance and proportion, using male and female junco average measurements. Males and females have roughly the same abundance of 2-tridecanone, but males have a higher proportion of 2-tridecanone relative to the total blend of compounds present in a given individual’s preen oil sample. In females, both the abundance and the proportion of tetradecanoic acid and hexadecanoic acid are higher than in males.

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Table 1
Eigenvalues, percentage variance explained and variable loadings for principal components analysis based on the relative proportion and absolute abundance of each volatile compound

	Proportion score				Abundance score			
	1	2	3	4	1	2	3	4
Eigenvalue	4.923	3.317	2.655	2.443	4.769	3.613	2.915	2.212
% Variance explained	32.817	22.114	17.700	16.285	31.791	24.090	19.433	14.747
1-Decanol	0.131	**0.927**	−0.078	−0.142	0.201	**0.941**	0.213	−0.027
1-Undecanol	0.257	**0.925**	−0.081	−0.138	0.297	**0.921**	0.196	0.013
1-Dodecanol	0.630	**0.663**	−0.251	0.100	0.512	**0.819**	0.128	0.045
1-Tridecanol	**0.805**	0.123	0.115	0.015	**0.692**	0.663	0.079	0.020
1-Tetradecanol	**0.663**	−0.548	−0.292	−0.078	**0.847**	0.293	0.062	−0.016
1-Pentadecanol	0.486	−0.402	0.425	−0.140	**0.855**	0.302	0.006	−0.029
1-Hexadecanol	0.494	−0.801	0.016	−0.010	**0.925**	0.024	−0.012	0.075
2-Undecanone	−0.043	−0.081	0.066	**0.971**	0.083	−0.062	0.036	**0.967**
2-Dodecanone	−0.112	−0.075	0.156	**0.960**	0.107	0.076	0.147	**0.956**
2-Tridecanone	0.147	0.009	**0.890**	0.284	**0.685**	0.454	−0.189	0.336
2-Tetradecanone	−0.008	−0.016	**0.727**	0.618	**0.665**	0.497	−0.096	0.395
2-Pentadecanone	0.193	−0.162	**0.935**	−0.049	**0.811**	0.267	−0.231	0.160
Dodecanoic acid	**−0.955**	−0.050	−0.156	0.187	−0.030	0.196	**0.918**	0.239
Tetradecanoic acid	**−0.980**	−0.041	−0.147	0.029	−0.075	0.099	**0.963**	−0.020
Hexadecanoic acid	**−0.964**	−0.036	−0.172	0.029	−0.041	0.097	**0.956**	−0.003

Bold text indicates volatile compounds strongly associated with each score.

and tail white, as well as with wing length, a trait that has previously been found to correlate with reproductive success in juncos (McGlothlin et al. 2005).

All data are available in the Supplementary material.

RESULTS

Seven of the males were social mates of seven of the females, so the reproductive success of males and females in this study was not independent. Individuals (or pairs, when both individuals were included) had one to three nesting attempts during the 2008 season (mean: 1.6), zero to eight social offspring that survived to day 6 (mean: 3.1), zero to seven social offspring that survived to fledging (mean: 2.29), and zero to five extra-pair offspring in the nest (mean: 0.86, for an average EPO rate of 28%).

Genetic reproductive success (including both within-pair and extrapair offspring) was predicted by proportion score 3 in both sexes, which explained 17.7% of the variance in odour profiles. In males, the number of offspring sired was positively associated with this score (stepwise linear regression: $r^2_{\text{adj}} = 0.163$, $F = 5.095$, ß = 0.451, $t = 2.257$, $N = 22$, $P = 0.035$). In females, the relationship between this proportion score and total number of offspring produced was reversed (stepwise linear regression: $r^2_{\text{adj}} = 0.271$, $F = 5.079$, ß = −0.580, $t = -2.254$, $N = 12$, $P = 0.048$; Fig. 2). This proportion score was most heavily influenced by the relative proportions of three methyl ketones: 2-tridecanone, 2-tetradecanone and 2-pentadecanone. The proportions of these volatile compounds have been previously shown to be strongly associated with sex differences in juncos, and male juncos have significantly higher proportions of these compounds in their overall volatile profiles than do female juncos (Fig. 3) (Soini et al. 2007; Whittaker et al. 2010). Thus, females with a more ‘female-like’ volatile blend and males with a more ‘male-like’ volatile blend had higher genetic reproductive success.

Male social reproductive success, or the number of offspring present in a male’s home nest(s) that survived to fledging, was predicted by abundance score 1, which explained 31.79% of the variance in absolute concentration of volatile compounds (stepwise linear regression: $r^2_{\text{adj}} = 0.225$, $F = 7.102$, ß = 0.512, $t = 2.665$, $N = 22$, $P = 0.015$; Fig. 4). In particular, this abundance score was strongly influenced by the three methyl ketones present in higher proportions in males (see above) as well as four linear alcohols (1-tridecanol, 1-tetradecanol, 1-pentadecanol and 1-hexadecanol) that increase during the breeding season in both sexes (Soini et al. 2007; Whittaker et al. 2011b) but do not differ between the sexes (Whittaker et al. 2010).

Finally, a male junco’s loss of paternity, measured as the number of offspring in his home nest(s) sired by extrapair males, was predicted by abundance score 3, which explained 19.43% of the variance in absolute concentrations of volatile compounds (stepwise linear regression: $r^2_{\text{adj}} = 0.262$, $F = 6.322$, ß = 0.558, $t = 2.514$, $N = 16$, $P = 0.025$; Fig. 5). This score reflected the concentrations of three carboxylic acids (dodecanoic acid, tetradecanoic acid and hexadecanoic acid), which are found in significantly higher

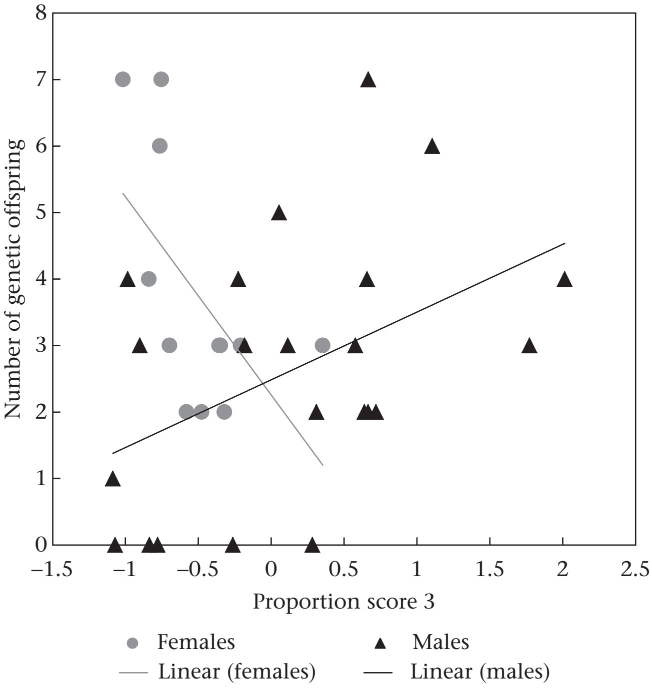

Figure 2. Relation between the number of genetic offspring produced by dark-eyed juncos (including both within-pair and extrapair offspring) and proportion score 3 (relative proportions of volatile compounds in preen oil samples).

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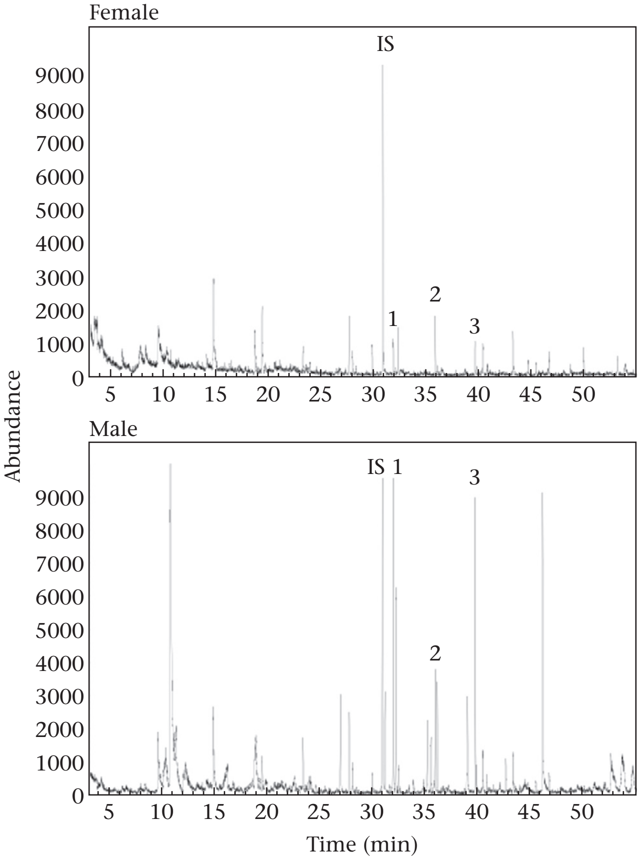

Figure 3. Comparison of preen oil profiles of female and male dark-eyed juncos in the ion m/z 58 chromatograms. IS: internal standard (7-tridecanone); 1: 2-tridecanone; 2: 2-tetradecanone; 3: 2-pentadecanone.

concentrations in female juncos (Whittaker et al. 2010). The relationship between number of extrapair offspring in the nest and the concentration of these compounds was positive, suggesting that male juncos that have a more ‘female-like’ odour lose more paternity in their home nests.

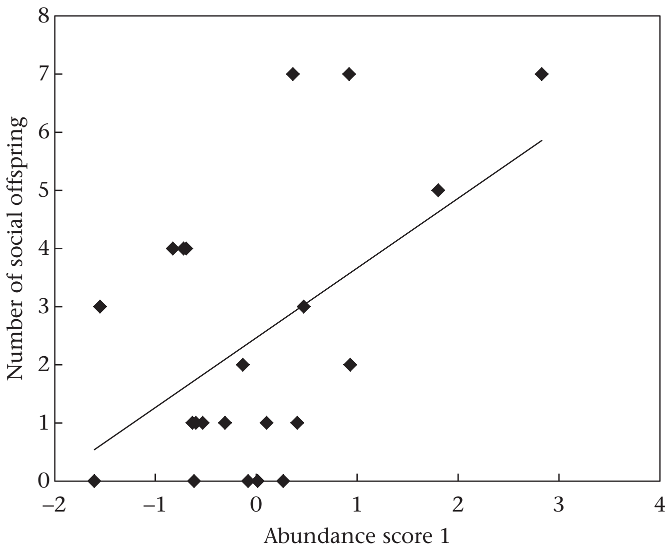

Figure 4. Relation between the number of offspring present in a male junco’s home nest(s) that survived to fledging (social reproductive success) and abundance score 1 (absolute amounts of volatile compounds in preen oil samples).

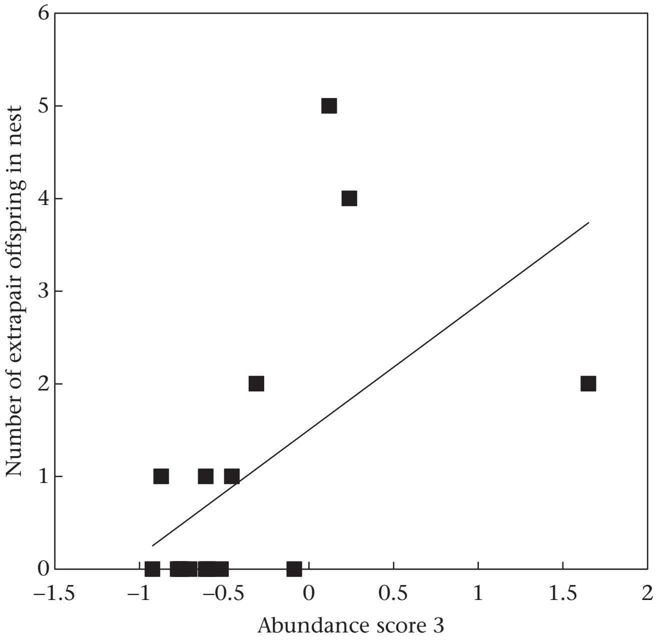

Figure 5. Relation between a male junco’s loss of paternity, measured as the number of offspring in the home nest sired by extrapair males, and abundance score 3 (absolute amounts of volatile compounds in preen oil samples).

We found no significant relationship between any measure of male or female reproductive success and wing length (Table 2). Tail white was correlated with the number of extrapair offspring in a male’s nest: the less tail white a male had, the more paternity he lost (Table 2). Tail white was not correlated with any other measure of reproductive success or with any measure of odour.

DISCUSSION

Our results show that the abundance and relative proportion of the volatile compounds that make up bird odour may predict genetic and social reproductive success in dark-eyed juncos. The proportion score reflecting differences between the sexes in the relative proportions of volatile compounds was associated with genetic reproductive success in both sexes: males with a more ‘male-like’ volatile profile and females with a more ‘female-like’ volatile profile had higher reproductive success. These compounds were 2-tridecanone, 2-tetradecanone and 2-pentadecanone, which were typically found in higher proportions in males. The abundance score that reflected differences between the sexes in these same three compounds, plus 1-tridecanol, 1-tetradecanol, 1-pentadecanol and 1-hexadecanol, which were also present in higher proportions in males and have not been previously found to covary with other traits, was related to number of social offspring

Table 2
Pearson correlations between measures of reproductive success (RS) and morphological traits in male and female juncos

	Wing length			Tail white		
	r	*df*	*P*	*r*	*df*	*P*
Male genetic RS	−0.165	20	0.44	0.364	20	0.096
Male social offspring fledged	−0.250	20	0.262	−0.004	20	0.984
Male number of extrapair offspring in nest	0.116	14	0.670	−0.508	14	**0.044**
Female RS	0.074	10	0.819	0.091	10	0.779

Significant *P* values are shown in bold.

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that a male successfully reared to fledging. Finally, the abundance score that reflected the concentration of compounds that were typically higher in females (dodecanoic acid, tetradecanoic acid and hexadecanoic acid) was correlated with the paternity that a male lost to extrapair fertilizations; thus, males that had a more 'female-like' odour lost paternity to other males more often. Although it is not yet known whether other aspects of individual quality are associated with these compounds, the significant relationship between early season odour and reproductive success in the same season suggests that odour might be a reliable signal of quality in songbirds.

In this study, an individual's odour during the early season was correlated with reproductive success in that year, but visual cues such as size and plumage were less reliable predictors. In larger studies on the Mountain Lake population, wing length is the strongest morphological predictor of male success: males with longer wings have higher mating success (McGlothlin et al. 2005) and sire more offspring (N. M. Gerlach, J. W. McGlothlin, P. G. Parker & E. D. Ketterson, unpublished data). We detected no relationship between wing length and reproductive success in the current study, although this may be due to our smaller sample size. In a previous study in a different subspecies (*J. h. thurberi*), we found a significant relationship between the proportion of volatile compounds (specifically, a principal component driven by 1-decanol, 1-undecanol and the five methyl ketones 2-undecanone through 2-pentadecanone) and wing length but not tail white (Whittaker et al. 2011a). In the present study, the principal components were not exactly comparable to those in the previous study, but when we attempted to replicate the analysis, we did not get the same results. When both males and females were included, there was a significant negative correlation between proportion score 2 and wing length (Pearson correlation: $r_{44} = -0.438$, $P = 0.002$), but not when males were analysed alone ($r_{31} = -0.025$, $P = 0.891$), suggesting that the correlation was driven entirely by sex differences. Proportion score 2 in the current study was most heavily influenced by the linear alcohols 1-decanol, 1-undecanol and 1-dodecanol, and females had significantly higher scores than males; thus, higher scores were more 'female-like' and were associated with shorter wings. In the previous study, female juncos from multiple subspecies preferred the odour of males with shorter wings (Whittaker et al. 2011a), the opposite of what would be expected given the well-documented relationship between longer wings and mating success in the Mountain Lake population (McGlothlin et al. 2005). This result could suggest a possible olfactory ornament (Whittaker et al. 2011a), but another explanation is that the context of the odour preference test (a two-way choice test in a Y-maze) does not represent the context of mate choice in a natural population. Females may exhibit different preferences when choosing a social mate and when choosing between potential males in a competition context.

Tail white was not correlated with paternity lost to extrapair males in this study. Tail white has been suggested to be an honest indicator of quality in male juncos (McGlothlin et al. 2008). Our result matches well with the hypothesis that females choose a social mate that is most likely to provide parental care, but they may seek extrapair mates to ensure higher fitness for their offspring (Gerlach et al. 2012a). However, we observed no correlation between tail white and genetic reproductive success in either sex. Tail white also was not correlated with any measure of odour.

The linear alcohols, carboxylic acids and methyl ketones in junco preen oil are well-known lipid metabolism products found in the secretions of many taxa (e.g. on human skin: Zeng et al. 1996; Bernier et al. 1999; Penn et al. 2007; on facial areas of large felines: Soini et al. 2012). Previous studies in juncos have identified sex differences in the abundance and proportion of many of the same compounds that were related to reproductive success in the present study (Soini et al. 2007; Whittaker et al. 2010). However, four of the linear alcohols related to a male's success at fledging social offspring are less understood; experimentally elevating testosterone levels leads to a significant increase in 1-tridecanol levels in both sexes in juncos (Whittaker et al. 2011b), but it is not currently known whether the other linear alcohols may be influenced by hormones related to reproduction or parental care. Ongoing research is examining the potential relationship between these compounds and a male's ability or tendency to provide parental care, possibly mediated by hormones.

The relationship between odour and reproductive success in songbirds suggests that the volatile compounds present in preen secretions could serve as a cue for mate assessment. In socially monogamous species with appreciable rates of extrapair paternity, females may use different criteria to evaluate potential social mates versus potential genetic sires (Jennions & Petrie 2000; Mays & Hill 2004). Indicators of parental care are likely to be more important in social mate choice, while genetic quality or compatibility may be more important in extrapair mate choice. Odour profiles covaried with different aspects of male fitness, including offspring survival and increased genetic siring success, which suggests, all else being equal, that individuals selecting mates based on odour would be selecting high-quality mates and would be favoured by natural selection.

These preen oil volatile compounds probably function over short distances since they are only moderately volatile (Soini et al. 2007), and thus, could be important during courtship, when the male and female are relatively close to each other. These cues would probably be most useful as mate assessment cues rather than as mate attractants, and would probably be assessed in conjunction with other traits, including visual cues. Correlational selection in wing length and tail white suggests that males that fare well in female choice (large plumage ornaments) as well as in male–male competition (larger body size, as measured by wing length) will be most successful (McGlothlin et al. 2005). Because tail white is correlated with the ability to elevate testosterone levels in response to a physiological challenge, which is in turn correlated with short-term increases in testosterone during male–male competition, this trait has been suggested to function as an honest signal of male quality (McGlothlin et al. 2008). However, in the current study, we did not detect increased reproductive success for males with longer wings or whiter tails.

This study shows that odour from avian preen secretions may have the potential to serve as a cue for mate assessment, and that females may be able to use different aspects of odour to choose males for social mates versus extrapair mates. These observed correlations are likely caused by underlying, unmeasured factors such as hormone levels, condition and genotype. We do not yet know all of the individual traits that affect a bird's chemical signals, but given the observed correlation between odour and reproductive success, we argue that these chemical signals likely function as indicators of underlying quality. Until more is known about the mechanisms of odour production in birds, these correlative results should be interpreted with caution. Future research should continue to investigate the influence of physiological traits on avian chemical signals, as well as the role of sexual selection in the evolution of chemical cues in birds (Andersson 1994), and how birds may integrate information from multiple sensory channels.

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Supplementary Material

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