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Zebra Finch Females Avoided the Scent of Males with Greater Body Condition

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Simple Summary: Many animals use olfaction to assess potential partners or rivals. However, in the case of birds, the role of olfaction in assessing potential partners is still scarce. We performed a study to analyse whether Zebra Finch females use olfaction to detect male body condition. We used an olfactory chamber to offer females the scent of two males differing in body condition, and we recorded female choice. Our results show that females can detect the body condition of males, but contrary to what should be expected in a reproductive context, females chose the scent of males with a poorer body condition. Therefore, our results suggest that females performed their choice in a non-reproductive social context, avoiding potential conflict with males with better body condition.

Abstract: The role of chemical communication in the social relationships of birds is receiving growing attention, but our knowledge is still scarce compared to that of other taxa. Previous evidence suggests that chemical cues emitted by birds may carry information about their characteristics, which may be useful in the context of sexual selection. However, experimental studies are needed to investigate the role of bird chemical cues in signalling the quality of potential partners. We performed an experimental study aimed at disentangling whether the female Zebra Finches (*Taeniopygia guttata*), use chemical cues to assess the body condition of potential partners. We offered focal females (N = 28) the scent of two males differing in body condition (body mass/tarsus length ratio) (N = 28 scent donor males). Our results showed that females can assess the body condition of potential partners using olfaction. However, contrary to what should be expected in a mate choice context, females avoided the scent of males with greater body condition. Our results, therefore, suggest that, despite performing the study during the breeding period, social interactions may be mediating the avoidance of the scent of the male in better condition in this gregarious species, probably to avoid a conspecific competitor with better body condition.

Keywords: avian olfaction; sexual selection; social selection; chemical cues; partner quality

1. Introduction

Sexual selection promotes the evolution of male traits that honestly reflect genetic quality or condition [1] and increase reproductive success [2]. Mating preferences based on such traits may confer females with direct benefits from parental care and territorial resources [3] and/or indirect benefits such as offspring inheritance of good genes for attractiveness [4] and viability [5], thus influencing mating patterns [6].

According to the idea that sexually selected traits may facilitate female evaluation of variation in male quality [5,7], females should prefer characters that better reflect the quality of males. In birds, the most studied sexually selected trait is plumage coloration [8]. However, because birds grow feathers during moulting, and moulting usually occurs

between breeding seasons, plumage coloration may reflect the condition of birds during moulting [9,10]. However, it may not provide a good measure of current condition at the time of mating. Under this scenario, it would be advantageous for females to base their mate choice on other traits that signal current quality more accurately than plumage coloration alone.

Continuously produced traits, such as chemical compounds, can reflect more recent physiological events, thus allowing individuals to evaluate the current status of their mates. Indeed, chemical cues are accurate indicators of individual current quality because they respond rapidly to changes in condition [11,12] and thus provide females with more actualized information on the condition of prospective mates. For example, the uropygial gland considered the main odour source in birds, secretes both volatile and non-volatile compounds [13] that birds spread on their feathers and play a role in updating the signal value of feathers [14,15], not only by enhancing the visual sexual signal but also by providing additional information about the individual. For instance, the amount and composition of this secretion has been shown to vary among seasons [16–18], sexes [17,19], age classes [17], diets [20,21], hormone levels [22,23], parasite infection [11,24], body condition and immune status [25,26], polymorphisms [27], and individuals [28–30], suggesting that it may convey potentially useful information during social interactions (see [31] for a review). Furthermore, recent findings have shown that semiochemical profiles correlate with genetic heterozygosity [12,32–35]. Therefore, uropygial gland secretions play a role in kin recognition [36–39] and mate choice [38,40].

Also, it has been shown that the chemical composition of the uropygial gland is related to the body size of males [19], suggesting that birds may use these chemical cues to assess the quality of conspecifics, which may be particularly useful in mate choice or intrasexual competition. A study in House Finch (*Carpodacus mexicanus*) showed that when males were offered the scent of a female and a male, the difference in quality between focal and scent donor males influenced the choice of focal males: unpaired males with better body condition and immune response than scent donor males approached rival males, whereas focal males in worse condition avoided the rival male scent and preferred female scent [41]. From these results, it can be deduced that chemical cues emitted by birds may carry information about the characteristics of birds in terms of body condition and health state that may be useful not only in assessing rivals [41] but also in a sexual selection context.

Chemical cues have been demonstrated to play a role in mate choice in other vertebrate taxa [42,43], indicating variations between individuals and reflecting aspects such as body condition, health state, parasite load, and even genetic compatibility [42,43]. However, the role of chemical cues emitted by conspecifics in assessing the quality of potential partners remains unclear in birds. Here, we report the results of an experimental study on the Zebra Finch (*Taeniopygia guttata*) aimed at examining whether females use olfactory cues during the breeding period to assess the quality of potential partners in terms of body condition (body mass/tarsus length ratio). We hypothesized that Zebra Finches may be able to discriminate the body condition of conspecifics using olfaction. Therefore, we expect a female preference for a specific male scent. Two mutually exclusive preferences might demonstrate that females are able to assess the quality of males using olfaction. One may occur in the context of sexual selection, in which females may prefer the scent of a potential partner of greater quality. Alternatively, in a social competition context, females may choose the scent of a potential competitor with lower quality to avoid a high-quality conspecific competitor. Because our experiment was conducted with unmated females during the breeding period, we expect that females were inclined to make choices in the context of sexual selection, thus preferring males with a better body condition. However, because other social interactions rather than reproduction take place during the mating period in gregarious species such as Zebra Finches, we cannot discard the possibility that females choose in a competitive context, thus preferring males with lower body condition.

2. Methods

2.1. Study Species

The Zebra Finch offers a good model for studying the role of olfaction in assessing potential partners because the olfactory capability of this species has been previously demonstrated in social contexts [44–50]. Experimental birds were obtained from a captive breed population located at the Foundation for Research and the Study of Ethology and Biodiversity (Casarrubios del Monte, Toledo). Birds (N = 56) were housed, separated by sex, in outdoor aviaries (2.5 ×2.5 × 2.5 m). Aviaries contained bamboo branches as perches and grass and sand on the ground. Commercial food and water for granivorous passerines were provided ad libitum. Two weeks before the beginning of the experiments, the birds were individually housed in cages (60 × 40 × 40 cm) inside the aviaries. Therefore, the birds were maintained at outdoor temperature (mean temperature: 18.6 °C, mean maximum temperature: 26.4 °C, mean minimum temperature: 11.8 °C) and natural photoperiod (14:10) throughout the experiment. We measured birds with a digital calliper to the nearest 0.01 cm, and birds were weighed with a spring balance to the nearest 0.1 g. All birds were individually banded with numbered aluminium and PVC rings. Birds were released again in the aviaries after the behavioural tests were completed. Birds were maintained healthy throughout the experiments.

2.2. Classification of Scent-Donour Males

We calculated the body condition of the scent donor birds as the body mass/tarsus length ratio. To create pairs of scent donor birds, we ranked birds according to their body condition, beginning with birds with a higher body condition ratio (body mass/tarsus length). We obtained the same ranking if we sorted birds according only to body mass or tarsus length. We classified the half of males as "good body condition" or "good quality males" (body condition ratio mean $\pm$ SE = 1.18 $\pm$ 0.02) and the other half as "bad body condition" or "bad quality males" (body condition ratio mean $\pm$ SE = 0.94 $\pm$ 0.01). We created pairs of scent donor birds by selecting the first male with a higher body condition ratio between the "good quality males" and the male with a higher condition ratio between the "bad quality males". Therefore, we ensured significant differences in the body condition of both scent donor males in a pair (see Section 3).

2.3. Behavioural Experiments

The experiments were performed in May 2017, during the breeding period, in an olfactometry chamber under indoor conditions (temperature maintained at 23 °C, natural light provided by a window). The device was T-shaped (Figure 1) and built with PVC tubes (40 m diameter). It was composed of a central tube (25 cm in length) where the experimental bird was introduced. The central tube had a door located 15 cm from the entrance. The door was built with methacrylate and had small holes to allow airflow. The central tube was connected to two lateral tubes (25 cm in length), referred to as the choice chambers. The choice tubes were connected to plastic opaque boxes (30 × 25 × 25 cm) that contained two little cages (13.4 × 23.5 × 19.8 cm) where the scent donor birds were situated. Overall, the device was sealed, and only openings at the farthest walls of the plastic boxes allowed airflow. The central tube contained a small 12 V PC fan at the entrance door that extracted the air from the device, creating a controlled low-noise airflow. The fan created two constant airflows, each entering across the openings located at the farthest walls of each plastic box containing the scent donor birds, passing by the donor birds, crossing the central tube, and going outside from the device through the fan. Thus, the focal bird received two separate airflows, each carrying the scent of the corresponding donor bird. Donor birds were kept in darkness in opaque boxes for the entire trial duration and housed in reduced space (scent donor cages), restricting movement and vocalizations; thus, scent donor birds did not emit any noise. Therefore, the experimental birds only perceived the scent of the donor birds, without visual or acoustic contact. The experimental room was sealed from exterior noise, enabling the experimenter to perceive any acoustic signals from the focal

and scent donor birds in the device. The experimenter was present during the entire trial period but was not visible/audible to the focal bird. Similar devices and methodologies have been successfully used in social context studies [17,39,41,50–52].
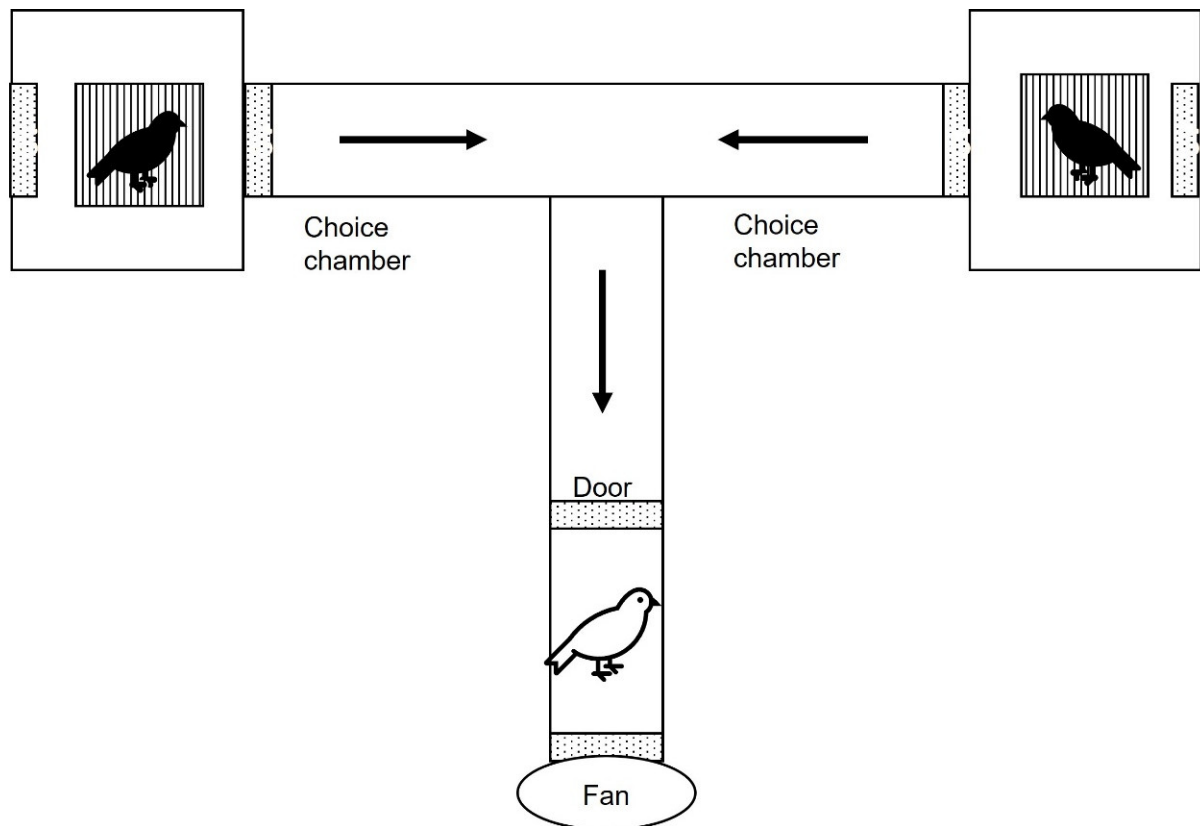

Figure 1. Olfactometry chamber. The solid arrows indicate the direction of airflow within the chamber. Scent donor birds (black) were located at the farthest parts of the choice chambers inside cages. The focal bird (white) was introduced into the chamber and kept at the entrance for 5 min. After that time, the door was opened, and the focal bird was allowed to move to one of the two choice chambers.

In each test, a female was introduced into the central tube, maintained in the dark for 5 min and exposed to the scent of two males differing in quality. After 5 min, the door was opened by the experimenter. We noted the choice tube that was first approached by each tested focal bird after opening the central tube. Because the device was opaque and the experimental room was maintained in darkness and silence, the experimenter relied on hearing to score the choice of the focal bird. Immediately after hearing the movement of the bird, the experimenter opened the tubes to ensure the bird was in the choice tube where it was heard.

We used 28 females as focal individuals and 28 different scent donor males distributed in 14 pairs of scent donor birds. Pairs were used twice. The location of the scent donor birds within the olfactometry device was randomized between trials (14 times the good-quality male was on the left side and 14 times on the right side). As soon as the birds were tested, they were returned to their cages. The olfactometry device was cleaned with alcohol between trials.

2.4. Data Analysis

To test whether there were significant differences in body mass and tarsus length between the two scent donor birds (good quality vs. bad quality), we performed two repeated measures ANOVA, including the pair as a within-measures factor. Both variables followed a normal distribution (Kolmogorov–Smirnov tests; $p > 0.05$ in both cases).

To analyse whether females could detect the quality of potential partners by using chemical cues alone, we performed a generalized linear model with binomial errors and a logit link function (GLMM). We modelled the probability that females chose the side of the chamber containing the good-quality male (as a dichotomous variable: left (yes) vs. right (not)). We included the side of the chamber where the good-quality male was located. Statistical analyses were performed using the Statistica 8.0.

3. Results

There were significant differences in the body mass of scent donor birds (good quality (mean $\pm$ SE = 18.40 $\pm$ 0.35) vs. bad quality (mean $\pm$ SE = 13.64 $\pm$ 0.24), repeated measures ANOVA, $F_{1,13}$ = 229.91, $p < 0.001$) and in the tarsus length (good quality (mean $\pm$ SE = 15.63 $\pm$ 0.22) vs. bad quality (mean $\pm$ SE = 14.55 $\pm$ 0.15), repeated measures ANOVA, $F_{1,13}$ = 25.65, $p = 0.0002$) in relation to the type of donor bird.

The difference in quality between the two scent donor birds influenced the choice of focal birds (Wald stat = 4.84, df = 1, $p = 0.03$, Table S1). Most females (20/28) avoided the scent of a potential partner with higher quality, i.e., with a better body condition (Figure 2). The choice of females was not affected by the side of the chamber where the better male was located (Wald stat = 0.69, df = 1, $p = 0.41$).
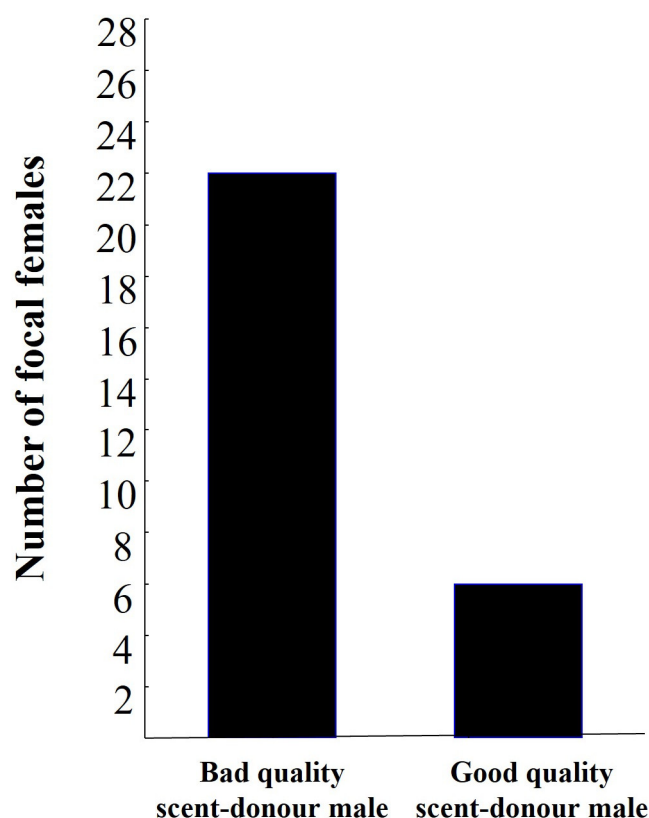

Figure 2. The first choice of focal Zebra Finch females, when exposed to the scent of two males, differed in quality in terms of body condition (body mass/tarsus length ratio). Most females (N = 20/28) chose the side of the chamber containing the scent of the male of worse quality (lower body condition).

4. Discussion

Our results showed that Zebra Finch females used olfaction to assess the quality of conspecific males. However, although the study was performed during the reproductive period of the species, when we would expect a preference for the scent of the best potential partner, our results showed that females avoided the scent of males with a higher body condition, i.e., greater body mass and body size. Our results are difficult to explain in a sexual context because males with better body condition may have greater reproductive

success [53]. Furthermore, previous evidence has found an overall preference of females for males with better body condition and size [54], although other studies have found assortative mating in this species [55,56]. However, interpreting scent preferences in a choice test is challenging because odour preferences may be related to other behaviours that also take place during the mating period, such as competition and aggressive interactions. Zebra Finches are gregarious [57] and are known to establish dominance hierarchies [58], with larger males being more aggressive than smaller ones [59]. The preference for the scent of the potential partner with lower body mass and smaller tarsus length suggests that our results can be interpreted as a social preference rather than a mating preference independent of breeding times.

Conspecific chemical cues are known to be useful in many species to evaluate the quality of conspecifics in social contexts [59,60]. In the context of competition, asymmetries between opponents are used to decide whether to get involved or to what extent to escalate a fight [61]. Therefore, the ability to assess the quality of a rival is useful for individuals to reduce the costs of aggression. Previous studies examining avian olfactory capabilities have found evidence that birds use chemical cues to assess the characteristics of their potential rivals in social contexts. For example, Whittaker et al. [19] and Amo et al. [17] exposed male and female Dark-Eyed Juncos (*Junco hyemalis*) and Spotless Starlings (*Sturnus unicolor*), respectively, to the scent of male and female conspecifics and found that both sexes exhibit a preference for the scent of males. In both studies, which were performed during the mating period, the attraction of males to male scent was explained in terms of intraspecific aggression because, during the mating period, other interactions between conspecifics take place, such as intrasexual competition for breeding areas or access to partners. Krause et al. found that Zebra Finch adults preferred the scent of same-sex conspecifics rather than the scent of opposite-sex conspecifics [50]. Therefore, our results are in line with previous evidence, suggesting that inter-and intrasexual relationships may occur during the breeding period and may influence bird response to the scent of conspecifics.

In birds, the chemical composition of the uropygial gland is related to the body size of males [19], and the results of a previous study suggest that House Finches can assess the quality of rivals in terms of body condition and T cell-mediated immune responses thanks to olfactory cues [41]. Our results add new evidence with Zebra Finches that chemical cues seem to be useful in non-reproductive social interactions.

The first choice is a good proxy of the spontaneous interest of an animal in a particular cue [17,39,41,50–52], but time spent close to the stimulus [55] may be related to the behaviour that takes place later in the series of events triggered by the exposure to the scent. Indeed, birds exposed to the scent of two potential conspecifics of the opposite sex differing in body condition in an olfactometer may first avoid an encounter with the bird in better body condition, trying to avoid an aggressive interaction and, only when they realize that the bird is not prone to be involved in an aggressive encounter, they may spend more time close to that potential partner. We used living birds as scent donors; thus, the initial preference test represented a valid measure of the response of birds to scents in our study. However, more studies are needed to assess the subsequent response of birds to the scent of potential partners to analyse whether the preferences for the scent of the potential partner with lower body condition is maintained over time or if it may change and reflect a mate choice instead of a social choice. Furthermore, similar studies with non-gregarious species, where competition during the reproductive period for other resources such as food may be less accurate, may also help to understand the choice of females for the scent of males with lower quality in gregarious species such as Zebra Finches, Spotless Starlings [17], or Dark-Eyed Juncos [19].

Due to expected differences in the volatile profile of feathers and uropygial gland secretions [62], we used live birds as scent sources as opposed to merely uropygial gland secretions to increase the robustness of our study approach. However, our results are in line with the results of a previous study that showed that Dark-Eyed Junco females spent more time with the odour of the uropygial gland secretion of males with smaller

body size [19]. Uropygial gland size, a proxy for gland activity, has been found to differ between Zebra Finch males and females during the reproductive period [63]. Therefore, differences in the secretory activity of the uropygial gland or in the composition of the uropygial gland secretion may signal the body condition to potential partners or rivals. Further research may determine whether uropygial gland composition is related to body condition in Zebra Finches.

Study Limitations

Individual condition can be evaluated in several ways to assess different components of individual health. In this study, we used body condition as a measure of the relative size of energy stores compared with structural components of the body. Given that our study was designed to test whether individuals were able to assess the natural variation in body condition of their conspecifics, we did not manipulate the body condition of scent-donor birds. Therefore, we can not exclude the possibility that, despite we chose males differing in body condition, other factors associated to the body condition of males may have caused the preference of females for the scent of the lower condition males, such as parasite load or stress. For example, more parasitized males or more stressed males may show a lower body condition, and females may be assessing though olfaction not the body condition but the parasite status or stress levels of males. Thus, additional studies modifying the quality of males may help to disentangle the cause of the preference of females for males with lower body condition.

5. Conclusions

In summary, our results suggest that female Zebra Finches can assess the body mass and body size of males. Females avoided the scent of males with a greater body condition. Therefore, despite performing the study during the breeding period, our results suggest that social interactions may be mediating the avoidance of the scent of the conspecific of the opposite sex with greater body mass and body size in this gregarious species.

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