

Department of Biology, University of New Mexico, Albuquerque

Female Choice for Male Morphological Traits in House Sparrows, *Passer domesticus*

REBECCA T. KIMBALL

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Abstract

Female mate choice for male morphological traits was examined in captive house sparrows in New Mexico, USA. A study of house sparrows in Denmark indicated that male bib size is important in female choice (MOLLER 1988, 1989). To examine this issue further, and to compare the selective pressures on male morphological traits between the two populations, bibs of males were manipulated to one of four standard sizes and females were allowed to choose from four males, one of each bib size. The amount of time the female spent with each male was recorded for 40 trials. Males were then ranked in each trial, with a rank of 4 given to the male the female spent the most time with. The ranks a male obtained were then averaged to provide an indication of a male's attractiveness to females. Data from 23 different males indicated that bib size was not correlated with a male's average rank, even when the effects of other traits were controlled statistically. In addition, the size of the original (unaltered) bib was not correlated with male average rank. Bill depth was the only trait significantly correlated with a male's average rank. Differences in the populations studied or the methodologies used may have led to differences between the results obtained in this study and that of MOLLER (1988).

Corresponding author: R. T. KIMBALL, Department of Biology, The University of New Mexico, Albuquerque, NM 87131, USA.

Introduction

Female choice for male morphological traits is a well-studied phenomenon (reviews: RYAN & KEDDY-HECTOR 1992; ANDERSSON 1994). The goal of much of this research has been to distinguish among the different models for the evolution of female choice. Good-genes models assert that females choose males of high genetic quality. Under Fisherian or runaway sexual selection, female choice is arbitrary with respect to male quality. Recently, researchers have also examined whether preferred male traits exploit the pre-existing sensory biases of females (BASOLO 1990; RYAN et al. 1990), a mechanism compatible with other models. As a result of those studies, it is now known that females in a wide variety of species actively choose males using traits such as

coloration, ornamentation, body size, and behavior (review: RYAN & KEDDY-HECTOR 1992).

Several studies of sexual selection have focussed on house sparrows. Those studies have established that bib size of male house sparrows is sexually selected (MOLLER 1987a,b, 1988, 1989; VEIGA 1993; KIMBALL 1995). While MOLLER (1987a,b) showed that bib size is involved in male-male competition and female mate choice (MOLLER 1988), other studies have been unable to distinguish whether sexual selection is due to male-male competition, female mate choice, or both.

MOLLER's (1988) mate-choice studies showed that female house sparrows treated with estradiol solicited copulations from taxidermic mounts of large-bibbed males faster than from mounts with small or medium sized bibs. Unlike MOLLER's (1988) laboratory studies, which looked at a single male trait (bib size), I examined female choice using a variety of male morphological traits. These included body size, bill size and color, and bib size. Using live males, and females with natural hormone levels, I conducted controlled laboratory studies of house sparrows to further investigate which morphological traits of males may be important in female choice. In addition, comparison of my results with those of MOLLER (1988) may provide insight into interpopulation variation of female preferences.

Methods

Subjects

In Jan. 1991, 48 female house sparrows were captured north of Albuquerque, NM, USA, and 42 males were captured in Albuquerque and south of Albuquerque. Males and females came from populations separated by at least 14 km, so it is unlikely that they had had any previous contact. The age of the birds and their previous breeding experience were not known. Birds were maintained in single-sex aviaries at least 3 mo prior to the mate-choice trials, so new pair bonds were not being formed.

Maintenance of the Birds

The birds were housed outside at the University of New Mexico, Albuquerque, New Mexico in single-sex aviaries (7.3 × 7.3 × 2.4 m) with no visual contact between the sexes. Each bird was individually marked with a numbered aluminum band. Sparrows were fed ad libitum with a mixture of millet, canary, and thistle seed to which liquid vitamins had been added. Three times a week, they were provided with meal worms and fresh fruit or lettuce. In May 1991, all birds were released to the wild.

About 1 mo after the last birds were captured, I began acclimating them to the test apparatus. Groups of males and females were placed in the appropriate portion of the test apparatus for one week, after which birds were returned to the aviaries until used in a trial. Males and females were visually, but not aurally, isolated while acclimating in the test apparatus. The acclimation period was critical so that birds used in a mate-choice trial would remain calm and responsive to members of the opposite sex.

Test Apparatus

The test apparatus and associated methods were similar to those used in other studies of mate choice (BURLEY et al. 1982; HILL 1990), where the time a female spends with a male is assumed to indicate her mate choice. The female portion consisted of a wooden central portion (45.7 × 45.7 × 61.0 cm) with four arms, one extending from each side of the cage. In the central portion, perches were symmetrically arranged along all sides of the cage. The arms (35.6 × 35.6 × 45.7 cm) had wood on the sides and plexiglass at the end facing away from the central cage. Wire covered the top of the entire cage. The female could enter each arm through a 22.9 × 22.9 cm opening at the bottom of the central cage. The openings were constructed so the female could see the male only if she were in an opening or arm of the cage.

A cage (35.6 × 35.6 × 45.7 cm) containing one male bird was located at the end of each arm. These wire cages had plywood on one side to prevent males from seeing each other. White sheets surrounded the test apparatus, making the walls uniform in shape and color. An incandescent light above each male's cage was adjusted so that light levels were the same in all male cages.

Measurements of Male Traits

Using calipers, male bibs were measured before being altered. After the pre-basic molt in the fall, the black bib feathers of the male house sparrow have variable amounts of buff-colored tips, particularly along the edges of the bib (KECK 1934; MOLLER & ERRITZOE 1992). I measured the maximum size of the bib, as though all tips had worn off, as well as the apparent size of the bib, which is the size the bib appears to be with tips present. I measured chin width, maximum and apparent length of the unaltered bib, and maximum and apparent width of the altered bib. Maximum and apparent bib length, as well as maximum and apparent bib width, were highly and significantly associated ($r = 0.67$, $n = 34$, $p < 0.001$; $r = 0.44$, $n = 34$, $p = 0.009$, respectively). Therefore, I only used maximum length and width of the unaltered bib in the analyses, as MOLLER (1987a) did.

Tarsus length, wing chord, bill length (from nostril to tip), bill depth (height of the bill at the base), and bill width (distance from the right to the left side at the base) were also measured. Because bill color depends on testosterone levels (KECK 1934), bill color was scored for each male immediately after a trial. A score of 1 represented completely black bills, 2 represented bills with a light patch on either the top or bottom, 3 represented bills with a light patch on both the top and bottom, and 4 represented bills that were mostly light.

A photograph showing the original bib size and symmetry was taken of each male prior to bib alteration. Birds were held by the legs and allowed to fluff their feathers while the camera was being set. Just prior to taking the photograph, the bill of the bird was grabbed and held up to insure the bib was fully displayed. This allowed birds a chance to briefly rearrange their feathers after handling. Camera angle and distance from the bird were standardized.

The photograph was digitized and the maximum bib area was measured using NIH Image (developed at the US National Institutes of Health, available from the Internet by anonymous FTP from zippy.nimh.nih.gov). A ruler was included in each photograph to convert measurements into mm².

To experimentally assess female choice for bib size, bibs were altered using templates based on skins of house sparrows in the Museum of Southwestern Biology at the University of New Mexico. The bib sizes I

Table 1: Means and SD for all measured traits

| Trait | \bar{X} ($n = 23$) | SD |
|--|---------------------------|------|
| Unaltered bib measurements | | |
| bib area (mm ²) | 417.4 | 61.9 |
| chin width (mm) | 8.38 | 0.92 |
| maximum bib length (mm) | 15.55 | 2.05 |
| apparent bib length (mm) | 10.03 | 2.17 |
| maximum bib width (mm) | 25.40 | 1.76 |
| apparent bib width (mm) | 17.03 | 2.99 |
| Wing chord (mm) | 76.51 | 1.83 |
| Tarsus length (mm) | 18.27 | 0.62 |
| Bill depth (mm) | 7.78 | 0.25 |
| Bill width (mm) | 7.26 | 0.13 |
| Bill length (mm) | 9.72 | 0.37 |
| Male activity (movements/min) ¹ | 7.72 | 4.44 |

¹ A movement was defined as a change in location within the test apparatus

used in trials were small (117 mm²), medium (230 mm²), large (389 mm²), and extra-large (619 mm²). Bib area of the templates was measured as described above. These sizes are comparable to those used by MOLLER (1988) in mate-choice trials (170 mm², 408 mm², and 646 mm²).

Males were randomly assigned to bib-size categories, so all bibs needed to be altered. Bibs were reduced by clipping the black portion of the feathers until the bib fitted within the template. The base of the black bib feathers is grey, similar in color to the non-black breast feathers. Bibs were enlarged by coloring feathers outside of the bib template with a black marker (Carter's permanent Marks-A-Lot) until the bib was the desired size. To ensure even coloration, the bibs of all birds were covered with black marker. The marker did not appear to affect the texture of the feathers. As the marker faded over long periods, birds were re-colored to the correct bib size prior to each trial. There was no loss of coloration during trials. Buff-colored tips on the bib were either removed or colored black and so were not influencing results.

Means and standard deviations of all measured traits are presented in Table 1. Since males were randomly assigned to bib-size categories, there were no significant differences in any measured trait among males in the four bib-size categories (R. T. KIMBALL unpubl. data).

Preliminary Trials

In 1990, I ran preliminary trials during early and late Jul. All five females tested in early Jul. (when the last clutches were laid in the wild) investigated and spent time near the males. In late Jul. (when no new clutches were being laid), six of 11 females appeared uninterested in any male, spending almost the entire time in the central portion of the cage, even though the males were active and singing. The following results report on experiments which were conducted in the spring, when females were motivated to pair. In all cases, they moved around the cage and spent much of the time near one or more of the males, confirming that the females were interested in pairing.

Trial Methodology

Trials were run between Apr. 6 and May 12, 1991, between 0730 and 1130 h. In the wild, this was the time when many birds were beginning to pair and build nests. Birds were maintained under natural light and temperature conditions and were fed a high-quality diet. Trials were run during the pairing season. Each female was used only once. Males used in the analyses were used between five and nine times. Four males, one of each bib size, were used in each trial. Each female viewed a unique combination of males with no more than two of the four males having been used together previously.

Males were placed into the test apparatus first, with males of different bib sizes randomly assigned to compartments. Females did not prefer one compartment over the others ($\chi^2 = 3.6$, $df = 3$, $p = 0.308$). The female was released into the central portion from an opening at the top. The direction she faced when released was rotated between trials, preventing a bias toward a particular direction. Females did not prefer the first male they saw ($\chi^2 = 1.4$, $df = 3$, $p = 0.706$).

A video camera hung from the ceiling to record the trials. The location of all birds could be determined from the video tapes. Trials lasted 90 min, after which the birds were returned to the aviary. If the female did not visit all four males during the first hour, the trial was discarded. The time a female spent in each arm was recorded. Males were then ranked by the amount of time the female spent with the male during the 30 min after she had seen each male. For some trials, I also measured the amount of time a female spent with a male for an hour after she had seen each male, and this did not change results, so I only analyzed the first 30 min.

During the 30 min. in which I collected data on female behavior, I measured the amount of time each male was actively moving around the cage, either moving about on the perch or moving about the floor or on the wires of the cage. Specific male behavior, such as courtship displays or singing, could not be reliably identified from the videos and were not thus recorded.

Statistical Analysis

In each of the 40 trials, males were ranked by the amount of time the female spent with them (4 was the male with which the female spent the most time, i.e. the chosen male, while 1 was the male with which the

Table 2: Time in minutes spent by females with males. Data was collected for 30 min

| Male rank | All trials \bar{X} (range) 40 trials | Subset 1 ¹ \bar{X} (range) 13 trials | Subset 2 ² \bar{X} (range) 27 trials | Subset 3 ³ \bar{X} (range) 27 trials |
|----------------|--|---|---|---|
| 4 ⁴ | 12.9 (1.6–25.4) | 19.8 (15.1–25.4) | 15.5 (6.3–25.4) | 15.0 (1.6–25.4) |
| 3 | 4.5 (0.2–10.4) | 4.5 (2.3–7.8) | 4.4 (0.8–8.6) | 4.0 (0.2–8.6) |
| 2 | 2.4 (0.0–6.9) | 1.5 (0.0–4.4) | 1.8 (0.0–4.9) | 1.6 (0.0–4.4) |
| 1 | 1.3 (0.0–4.5) | 0.9 (0.0–3.8) | 1.1 (0.0–4.5) | 0.8 (0.0–3.8) |

¹ Females spent more than 15 of 30 min with the preferred male

² Females spent at least 5 more min with the preferred male than with any other male

³ Of the time spent with males, more than 50% of the time was with the preferred male

⁴ 4 is the male the female spent the most time with

female spent the least time). Only one tie occurred, and the tied males were given a rank of 1.5, since they were the two least-preferred males. Ranks were then averaged for each male. The resulting variable was normally distributed and provided an indicator of a male's attractiveness to females.

Since the likelihood a female would spend time with a male might be dependent upon the other males used in the trial, I also analyzed the data by trial, though this meant that samples were not independent. Male ranks within a trial were then correlated with male traits. The distribution of correlation coefficients was then compared with that expected under a random distribution. These analyses gave the same results as those using male average rank, and hence were not included. Only bill color, which changed within an individual over time, was analyzed by trial.

I selected three subsets of trials in which the female appeared highly motivated or decisive about choosing a mate. These were trials in which the female: 1. Spent more than 15 of 30 min with the preferred male; 2. Spent at least 5 more min with the preferred male than with any other male; or 3. Spent more than 50% of the total time spent with males with the preferred male. Male average ranks were then recalculated and the above analyses were re-run. Data on the time females spent with males of different ranks, for all trials as well as for the three subsets of trials, are presented in Table 2.

Table 3: Pearson correlation coefficients of male average rank with male traits. Results significant at $p < 0.05$ before and after performing a sequential Bonferroni are indicated. N is the number of males data was collected from

| Trait | All trials (n = 23) | Subset 1 (n = 10) | Subset 2 (n = 22) | Subset 3 (n = 23) |
|-----------------|------------------------|----------------------|----------------------|----------------------|
| Bib (unaltered) | | | | |
| bib area | -0.02 | 0.06 | -0.11 | -0.09 |
| chin width | 0.01 | -0.21 | -0.24 | -0.08 |
| maximum length | 0.25 | 0.15 | 0.18 | 0.18 |
| maximum width | 0.37 | 0.06 | 0.28 | 0.35 |
| Wing chord | 0.22 | -0.12 | 0.20 | 0.20 |
| Tarsus length | 0.24 | 0.20 | 0.18 | 0.15 |
| Bill depth | 0.65 ** | 0.46 | 0.55 * | 0.53 * |
| Bill width | 0.39 | 0.31 | 0.24 | 0.37 |
| Bill length | 0.36 | 0.38 | 0.27 | 0.26 |
| Male activity | -0.62 ** | -0.73 * | -0.58 ** | -0.54 * |

* Before performing a sequential Bonferroni, significant at $p \leq 0.05$

** After performing a sequential Bonferroni, significant at $p \leq 0.05$

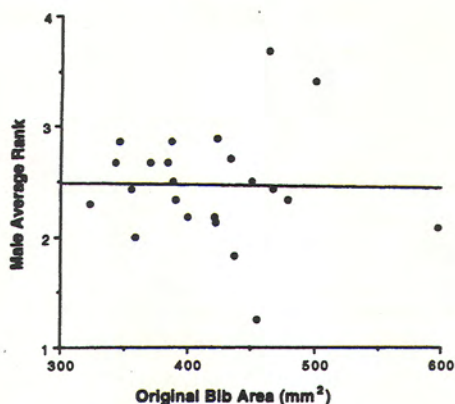


Fig. 1: Relationship between male average rank and original bib size. Data from all trials is included. Statistical information can be found in Table 3

Variables were analyzed using parametric tests. Two-tailed tests were used throughout. To prevent type-I error, without greatly increasing the chances of type-II error, I performed a sequential Bonferroni (RICE 1989) on each column of analyses within Table 3. Correlations significant at $p \leq 0.05$ before performing a sequential Bonferroni were also noted in the tables.

Results

I expected bib size to be important in female choice, based on MOLLER's (1988) findings. However, I found no differences in male average rank among males in different bib-size categories (ANOVA $F = 0.82$, $df = 3, 19$, $p = 0.501$). Male bib size before alteration was not correlated with male average rank (Fig. 1), indicating that females were not choosing mates based upon traits correlated with original bib size.

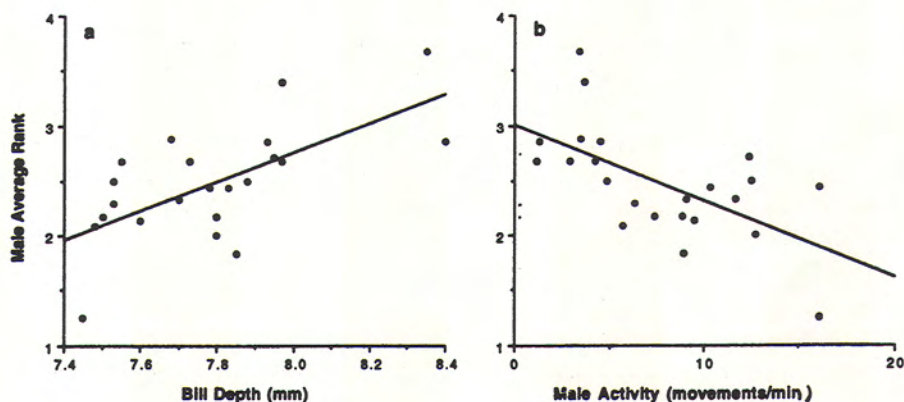


Fig. 2: Relationship between male average rank and bill depth (part a) and male activity levels (part b). Data from all trials is included. Statistical information can be found in Table 3

Bill depth and male activity levels both correlated significantly with a male's average rank (Fig. 2). Females preferred males with deep bills which were less active. No other traits were correlated with male average rank (Table 3).

Females may have avoided males whose bibs had been clipped or greatly enlarged. To test this, I classified each male as either having the bib reduced (clipped) or enlarged (painted only). A *t*-test between the two categories showed that female preference for a male did not differ between the two treatments ($t = -1.11$, $df = 21$, $p = 0.278$). Since the degree of alteration may be more important than the type of alteration, I also calculated the area of the bib that was altered, ignoring whether the bib had been reduced or enlarged. Females did not avoid males with greatly altered bibs ($r = -0.27$, $n = 23$, $p = 0.212$).

Male average rank also did not differ among the different bib-size categories once the effects of bill depth and male activity levels were held constant (ANCOVA $F = 2.17$, $df = 5, 17$, $p = 0.129$). Controlling for body size (tarsus length and wing chord) also did not yield a significant preference for large-bibbed males (ANCOVA $F = 1.12$, $df = 4, 18$, $p = 0.368$). Additional analyses controlling for all combinations of the above variables failed to provide any evidence that females preferred large-bibbed males. Using the unaltered, original bib size and performing a partial correlation controlling for the effects of body size, bill depth, and male activity levels also yielded no high or significant correlations with female preference.

Females that were more motivated to mate or more decisive in their choice may have had stronger preferences than other females (e.g. ZUK et al. 1990a). In analyses involving data from the three subsets of trials in which females may have been more motivated to mate, bill depth was the only morphological trait which correlated highly with male average rank (Table 3).

Since bill color depends on testosterone levels and may reflect male condition, I tested whether females preferred males with dark bills. Male rank within a trial was random with respect to bill color ($\chi^2 = 8.1$, $df = 9$, $p = 0.524$). Females may make a trade-off between bib size and bill color, possibly choosing a light-colored bill if the male had a large bib. A Fisher's exact test, using the altered bib sizes and the four bill-color scores, showed that this was not the case ($n = 40$, $p = 0.225$).

To determine whether females use a suite of traits in mate choice, I performed a multiple regression using all male morphological traits except bill color. This was not a better predictor of male average rank than was bill depth alone (adjusted $r^2 = 0.39$, $df = 8, 14$, $p = 0.045$). I could not find any combination of male morphological traits which explained more variance in male average rank than did bill depth alone. In addition, a principal-components analysis of all male morphological traits did not yield a variable that correlated significantly with male average rank.

Discussion

Previous research in house sparrows indicates that females prefer males with larger bibs (MOLLER 1988). Although I could detect female choice for a male morphological trait, bill depth, the females I studied in New Mexico did not prefer males with large bibs, even when the effects of other traits were controlled statistically. Females also

showed no preference for males with large bibs in preliminary trials run in 1990, where females were allowed to choose among males with unmanipulated bibs (R. T. KIMBALL unpubl. data). Thus, the results I obtained are unlikely to be an artefact of bib manipulation (e.g. BENNETT et al. 1994).

In this study, bill depth was the one morphological trait clearly related to female mate choice. This result is found whether analyses are performed on a per-male basis (Table 3) or on a per-trial basis (R. T. KIMBALL, unpubl. data), indicating that this experimental protocol could detect non-random associations between females and males. None of these analyses revealed a strong or significant preference for any other morphological trait. MOLLER (1989) found positive and significant sexual selection (as measured by success in obtaining mates) for bill depth, as well as bib size, in yearling male house sparrows. Although deep bills are important in sexual selection in both populations, it is not known whether bill depth directly reflects any aspect of male quality.

Different methodologies may have led to differences between the results I obtained and those of MOLLER (1988). In MOLLER's (1988) laboratory trials, females were implanted with estradiol and presented with one of three taxidermic mounts which varied in bib size. The time until the female solicited a copulation from the taxidermic mount, usually 1–2 min, was then recorded. This provided a direct measure of a female's desire to mate with a particular male. In this study, female hormone levels were not altered by implantation with estradiol. Instead, females were maintained outdoors under natural light and temperature regimes, fed a high-quality diet, and were tested during the pairing season in New Mexico. Females were then presented with multiple live males and the time during which a female associated with different males was recorded. Both males and females in this study moved freely about the test apparatus and males displayed in ways similar to wild birds.

The different methodologies may have tested different aspects of female choice. MOLLER's study (1988), where females were highly and artificially motivated to mate, may have demonstrated female preferences in selecting males with which to copulate (genetic mates), as house sparrows participate in extra-pair copulations (e.g. KIMBALL 1995; WETTON et al. 1995). In my experiment, females may have been selecting males with which to pair-bond (social mates). In other species, females have been known to seek extra-pair copulations with males morphologically different from their mate (KEMPENAERS et al. 1992). To test this idea, it would be interesting to use MOLLER's (1988) protocol on my population in New Mexico or vice versa.

Differences in the populations studied may have led to differences between the results I obtained and those of MOLLER (1988), as population differences have been found in other species (BREDEEN & STONER 1987). House sparrows were introduced to North America from English and European populations and may have lost traits through genetic drift. However, North American and European populations of house sparrows are similar morphologically (SELANDER & JOHNSTON 1967; JOHNSTON & SELANDER 1971, 1973) and show similar levels of genetic variability (FLEISCHER 1983). The populations may differ in other ways, e.g. in the relative strengths of intra- vs. intersexual selection or in the different natural selective pressures which may have affected female mate choice.

Females may select mates using traits correlated with some aspect(s) of male quality (e.g. HILL 1990, 1991; ZUK et al. 1990a,b). Bill color, which is dependent upon testosterone levels, should reflect male quality. However, this did not appear to be important in female choice. In New Mexico, most pairs form in the spring, when bills of all males are black. Thus, there is no variation for females to choose from.

Male activity levels could also provide information on male condition to females. However, in this study, females spent more time with males that were less active during the trials. I measured male activity levels by recording the time a male actively moved about the cage. Courtship-behavior patterns, such as male singing, are performed while the males are stationary. Males that were actively moving about may have spent little time displaying, and may not therefore have been preferred by females. Alternatively, male activity levels may have been higher in subordinate or frightened males, and females may have avoided these males.

Females also may choose mates using age or dominance status rather than, or in addition to, male morphology. Bib size is larger in older males in some populations (VEIGA 1993; WETTON et al. 1995; but see MOLLER 1987a). Older males have larger bibs in the population I studied (eight adults, nine juveniles; $t = 2.27$, $df = 15$, $p = 0.038$), based upon museum specimens collected in Albuquerque, and aged by skull pneumatization. Males with large bibs also are dominant (MOLLER 1987a,b; VEIGA 1993). Therefore, choice for either older or dominant males may have been expected to yield a correlation between bib size and male average rank. Even if this were not the case, the results of this study provide no evidence for female mate choice on male bib size (cf. MOLLER 1988, 1989).

This study, considered with those of MOLLER (1988, 1989), suggests that female mate choice in house sparrows may involve different male traits and may vary spatially and/or temporally. Since the methods differed from study to study, it would be necessary to repeat each study in the other population to ensure that these differences exist. However, the results presented here indicate that it may be necessary to examine intraspecific variability of female choice, both within and between populations, before drawing firm conclusions on its evolution or its importance in the evolution of male morphology.

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