ANIMAL BEHAVIOUR, 1998, 56, 71–78
Article No. ar980740

A test of sensory bias for long tails in the house finch

MARJORY C. TOBIAS & GEOFFREY E. HILL
Department of Zoology and Wildlife Science, Auburn University

(Received 22 July 1997; initial acceptance 10 September 1997; final acceptance 17 October 1997; MS. number: A7980)

ABSTRACT

The sensory bias model of sexual selection proposes that female preferences for certain male traits result from biases in the female sensory system that existed prior to the evolution of the preferred trait. Phylogenetic tests of the sensory bias hypothesis have provided evidence for pre-existing bias in several species, but the hypothesis has not been tested relative to elongated tail feathers, a widespread sexually selected trait in birds. Elongated tails occur sporadically across avian taxa, including cardueline finches (family Fringillidae), suggesting that long tails evolved independently in many lineages. To determine whether a female preference for longer tails predated the evolution of long tails in cardueline finches, we tested female preferences for artificially lengthened tail feathers in male house finches, *Carpodacus mexicanus*. The house finch is a cardueline finch species with a tail that does not appear to be elongated or sexually selected. In mate choice experiments, females did not demonstrate a preference for lengthened tails over controls. This negative result fails to support the hypothesis that elongation of tail feathers resulted from exploitation of a widespread sensory bias.

© *1998 The Association for the Study of Animal Behaviour*

Several mechanisms have been proposed to explain how female preference can lead to the evolution and maintenance of exaggerated traits (reviewed in Anderson 1994). These mechanisms fall into two general categories: (1) honest advertisement models; and (2) models of arbitrary mate choice, which include runaway processes and sensory bias. Honest advertisement models propose that females choose males with traits that serve as reliable indicators of quality (Zahavi 1975; Andersson 1982b; Kodric-Brown & Brown 1984), thereby gaining resources or genetic benefits for their offspring. The preferred trait may itself contribute to viability or may simply be correlated with other components of viability (Maynard-Smith 1987). Models of aesthetic mate choice explain preferences for arbitrary traits that are not necessarily correlated with viability or quality. According to these models, expression of a male trait and female preference for that trait become genetically linked resulting in a self-reinforcing runaway process in which the trait and the preference coevolve (Fisher 1958; O'Donald 1980; Kirkpatrick 1982). The trait may initially be adaptive, but the runaway process can take it beyond the optimum for survival (Fisher 1958; Maynard-Smith 1991).

The 'sensory bias' or 'sensory exploitation' model proposes that female preferences are due to biases in the species' sensory system. Females are attracted to males with traits that stimulate their sensory systems (Ryan & Keddy-Hector 1992). Such a predisposition to respond to certain sensory stimuli exists in females before the preferred trait appears in males in the population (Kirkpatrick 1987; Ryan & Keddy-Hector 1992; Enquist & Arak 1993) so that, when the trait does arise in the male population, it spreads quickly in response to female preference. A sensory bias mechanism of trait elaboration does not exclude other selective processes; elaboration of ornamental traits may result from the interaction of sensory bias and other mechanisms of sexual selection. For instance, the pre-existing bias may establish a mating preference (a necessary step in all models of sexual selection), but other mechanisms of sexual selection take over to drive the elaboration of the trait.

Studies of several species including the frog *Physalaemus colorodorum* (Ryan & Rand 1990), the platyfish *Xiphophorus maculatus* (Basolo 1990b, 1995a) and the water mite *Neumania distincta* (Proctor 1992), provide evidence that pre-existing biases played a role in the evolution of some ornamental traits. Females of these species demonstrate preference for a male trait that is not expressed by males of their own species. Phylogenetic evidence suggests that the evolution of the preference predated the evolution of the preferred trait in males. Studies of this type have not been conducted with birds.

One group of ornamental traits that has been a focus of work related to sensory bias is elongated tails. Work by

Correspondence: G. E. Hill, Department of Zoology and Wildlife Science, 331 Funchess Hall, Auburn University, Auburn, AL 36849 U.S.A. (email: ghill@acesag.auburn.edu). M. Tobias is at 37 East Palestine Road, Darlington, PA 16115, U.S.A.

0003–3472/98/070071+08 $30.00/0

© *1998 The Association for the Study of Animal Behaviour*

Table 1. Comparisons of tail length in the house finch and cardueline finches with elongated tails

Species	Mean male tail length (mm)	Male tail length relative to body length (%)	Male tail length relative to wing length (%)
Carpodacus mexicanus (I)	61.0	79.7	—
Carpodacus mexicanus (II)	59.6	—	74.9
Carpodacus rubicilloides	88.0	86.3	83.8
Serinus pusillus	59.0	86.1	77.7
Serinus flavigula	50.0	87.0	74.6
Serinus burtoni tanganjicae	70.0	87.5	83.8
Carpodacus rhodopeplus	70.5	88.7	82.0
Uragus sibericus	80.0	88.9	107.4
Serinus koliensis	50.5	88.6	72.9
Eophona migratoria	92.5	90.75	76.6
Carduelis hornemanni	62.0	94.7	79.6
Carpodacus roborowskii	90.0	105.9	73.8
Serinus estherae renatae	58.0	111.5	85.3

Measurements for *C. mexicanus* (II) are from G. E. Hill, unpublished data. All other tail, body and wing measurements were taken from Clement et al. (1993). Where ranges of values were given, the average of the lowest and the highest values was used. To control for size differences, relative tail length was calculated as tail length/body length (total length−tail length) and tail length/wing length.

Basolo (1990a,b; 1995a,b) indicated a role for a pre-existing sensory bias in the elongation of the caudal fin, or sword, in swordtail fish, *Xiphophorus helleri*. Female *X. helleri* prefer males with longer swords (Basolo 1990a). In two species of playfish, *X. maculatus* and *X. variatus*, in which males do not have a sword and for which lack of a sword is the primitive condition, females demonstrate a preference for males with artificial swords (Basolo 1990b, 1995a). The preference is also expressed in the sister genus *Priapella*, as female *Priapella olmacea* prefer tails with artificial swords over swordless tails (Basolo 1995b).

Elongated tail feathers are prevalent among bird species. The sporadic occurrence of long tails within many different families and genera strongly suggests that long tails evolved independently numerous times within the class Aves (Andersson 1994). Some forms of tail elongation may result from natural selective pressures favouring aerodynamically optimal tails (Balmford et al. 1993). However, there is experimental evidence from five avian species in three families that females prefer longer tails (Andersson 1982a; Møller 1988; Andersson 1989, 1991; Barnard 1990; Evans & Hatchwell 1991; Smith & Montgomerie 1991). Extreme sexual dimorphism, a high degree of variability among males, and variation between adult and juvenile males also suggest that the elongated tails seen in many species are ornamental traits that have evolved through sexual selection (Darwin 1874; Alatalo 1988; Andersson 1994; Møller 1994).

Within the cardueline finches (family Fringillidae), males of several species exhibit long tails (Table 1). We plotted as a frequency distribution the relative tail length (tail length/body length) for 111 species of cardueline finches for which measurements were available. We found a bimodal distribution with a natural gap between modes at 86% relative tail length. Thus, we considered a species 'long-tailed' if male tail length was greater than 86% of body length. Two additional natural breaks occurred in the distribution at 90 and 100% relative tail length. Choosing either of these alternative cutoffs for designating species as 'long-tailed' would not have changed the results of our study.

A phylogeny of cardueline finches (Badyaev, 1997 a,b) indicates that lack of tail elongation is the ancestral state for this clade, and that long tails evolved independently several times (Fig. 1). If the appearance of elongated tails in multiple taxa has been promoted by an underlying sensory bias for longer tails, then a preference for longer tails should exist in short-tailed species. Thus, the sensory exploitation hypothesis for the evolution of elongated tails in cardueline finches can be tested by looking for preferences for long tails in a short-tailed species within the clade. Demonstration of a preference for elongated tails in any species that does not exhibit tail elongation would support the sensory exploitation hypothesis, provided that none of the ancestors of the species tested had elongated tails.

In this study, we tested female mating preferences relative to male tail length in the house finch, *Carpodacus mexicanus*. The house finch is a cardueline finch with a tail morphology that does not appear to be elongated or ornamental. House finches also show little sexual dimorphism in tail length compared with species whose tails are thought to be sexually selected (Table 2), and male tail length does not differ between adults and juveniles (G. E. Hill, unpublished data). Variation in tail length among male house finches within a population (coefficient of variation=3.62) is within the typical range of variation for morphological traits that are not sexually selected (Grant & Price 1981; Alatalo 1988).

METHODS

We captured house finches at feeding stations in Lee County, Alabama. Test females included 13 hatching-year females with no previous mating experience, captured between 16 November and 5 December 1995, and 27

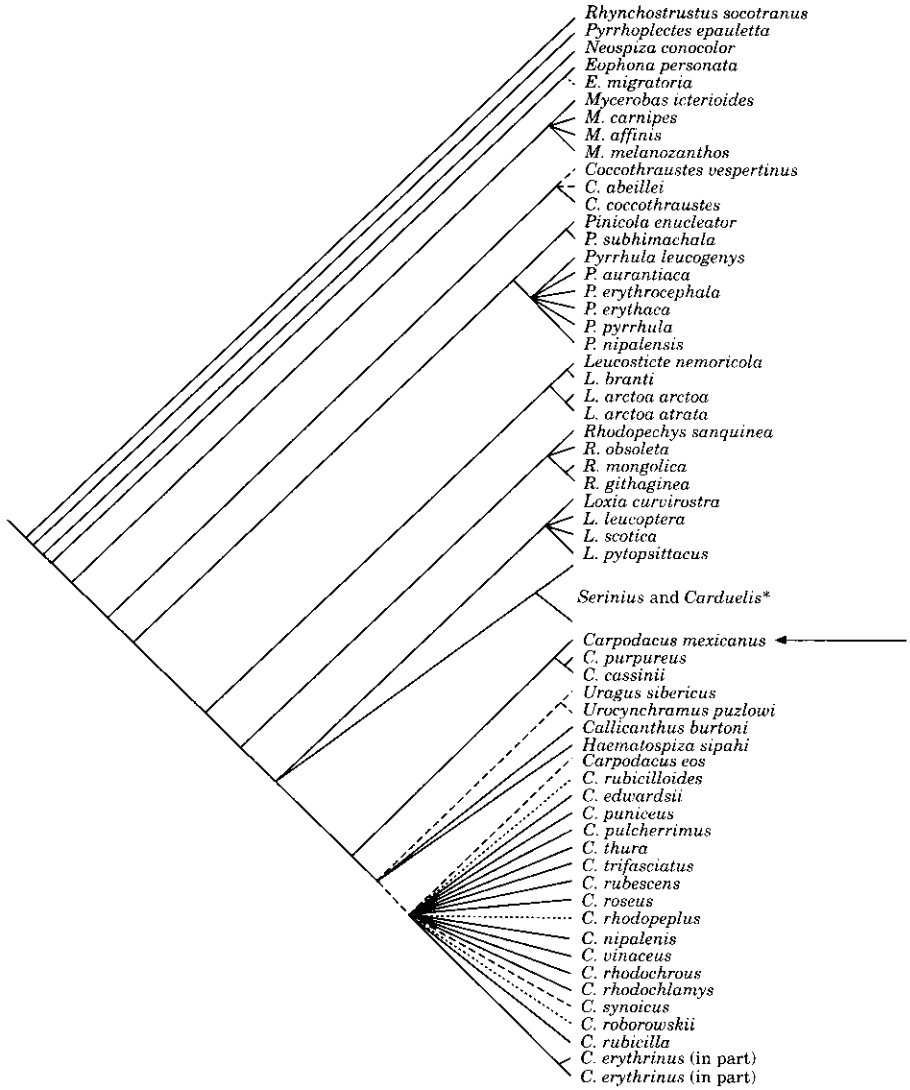

Figure 1. A phylogeny of cardueline finches (Badyaev, 1997a,b). Dotted branches indicate elongated tails (relative tail length of males >86%). Dashed branches indicate unknown relative tail length. *Indicates a clade of 70 species including *Linurgus olivaceus* and members of the genera *Serinus* and *Carduelis*. Six species within this clade exhibit tail elongation. An arrow indicates the position of the house finch in this phylogeny.

females of unknown age captured between 4 February and 1 May 1996. All males were adults captured between 7 February and 27 March 1996. To ensure that males and females had no previous exposure to each other, we captured males and females at different sites and housed them in separate outdoor flight cages (1.5 × 3.7 × 2.4 m) at the Auburn University aviary. Males and females were visually, but not acoustically, isolated from each other. Each cage housed up to 25 birds. Finches received an ad libitum diet of bird seed (wild bird seed mix and sunflower seed) supplemented weekly with sliced apples and lettuce. All birds were released into the wild upon completion of mate-choice experiments.

Experimental Design

The ideal experimental design would have been to use a different male to represent each of the four tail-treatment groups in each of the trials. This would have entailed capturing and housing a minimum of 160 males, and cutting and pasting nearly 2000 tail feathers. Such an experimental design was beyond our means, so we devised an experimental design that permitted us to house and manipulate a much smaller number of males while at the same time reducing (but not eliminating) pseudoreplication resulting from using the same males as stimulus males in multiple trials (see Hill 1990, 1994). We chose 16 males in our captive flock that were similar in size, plumage coloration and extent of ventral plumage coloration (patch size) (see Hill 1990, 1992 for plumage scoring techniques, and Hill 1993a for natural variation in size, plumage coloration and patch size in house finch populations). All 16 males had identical plumage hue (redness) but there were small differences among the males in plumage saturation and tone. To avoid assigning more brightly coloured males to a particular

Table 2. Comparisons of tail length in the house finch and selected species with elongated tails

Species	Male tail length (mm)	Male relative tail length (%)	Dimorphism	Coefficient of variation	References
Carpodacus mexicanus	59.6	75*	1.03	3.6	G. E. Hill, unpublished data
	—	80†	—	—	Clement et al. 1993
Vidua regia	235	200 approx.†	—	5.7	Barnard 1990
Euplectes progne	496	—	7.14	9.4	Andersson 1982a
Euplectes jacksoni	200 approx.	—	—	—	Andersson 1989
Nectarinia johnstoni	178	—	—	8.2	Evans & Hatchwell 1991
Hirundo rustica	105	130†	1.16	9.6	Møller 1988; Balmford et al. 1993

Dimorphism was calculated as male tail length/female tail length. Coefficient of variation is an index of variation in tail length among males.
*Tail length/wing length.
†Tail length/body length.

tail-manipulation group, we first separated the males into four sets of very similar plumage coloration. Within each of these four sets of males, we randomly assigned one male to each of the four tail-treatment groups. For each trial, we randomly selected a set of four males, one from each tail-manipulation treatment group. Thus, each female was presented with a unique combination of four males.

We used these 16 birds in 34 of 40 trials. In the remaining six trials we substituted one of two additional males (not included in the original set of 16) for a male that had died. One of these substitute males had plumage scores close to the mean of the scores of the original 16. The second substitute male had a lower hue score than other stimulus males, but this male was used in only one trial.

Treatment Groups

Tail-manipulation treatment groups were as follows. (1) Shortened tail group: we cut a 1.0-cm section from the middle of each male's 12 rectrices, then reattached the apical piece of each feather by inserting a minutien pin into the shaft of the two sections of feather and gluing it in place with Duro Quick Gel® super glue. (2) Lengthened tail group: we inserted a 1.0-cm piece of feather (cut from the rectrices of a shortened tail male) into the middle of each male's 12 rectrices, then attached the feather sections in the same manner as above. (3) Control group 1: to control for the effects of tail manipulation, we cut the 12 rectrices of each male 3.0 cm from the tip and reattached the 3.0-cm apical piece as above. Tail length was not altered. (4) Control group 2: to control for effects of possible differences in spectral quality between the insert and the feather being lengthened, we cut the 12 rectrices of each male 3.0 cm from the tip and replaced the 3.0-cm apical piece with a piece of the same length from another bird. Tail length was not altered. Elongated and shortened tails were 5 mm longer and shorter, respectively, than the extreme tail lengths observed in wild house finches. This change in tail length was obvious to a human observer viewing a finch perched 5 m away.

Mate Choice Trials

We conducted mate choice trials at the beginning of the spring breeding season (between 20 February and 2 May), when female finches in the local wild populations are seeking males and forming pair bonds (Hill 1993b). We ran trials in an outdoor aviary (Fig. 2) between 0630 and 1300 hours. Stimulus males (one from each of the four treatment groups) were held in four parallel flight cages (1.5 × 3.7 × 2.4 m) separated by solid walls so that males were visually isolated from each other. The test female was held in an adjoining cage that was divided into two chambers by a partition that extended from a height of 1.2 m to the ceiling. The female could choose to remain in the outer chamber where she had access to food and water but could not view the males. If she chose to associate with the males, she could move to the inner chamber by flying under the partition. In the inner chamber the female was able to view males individually

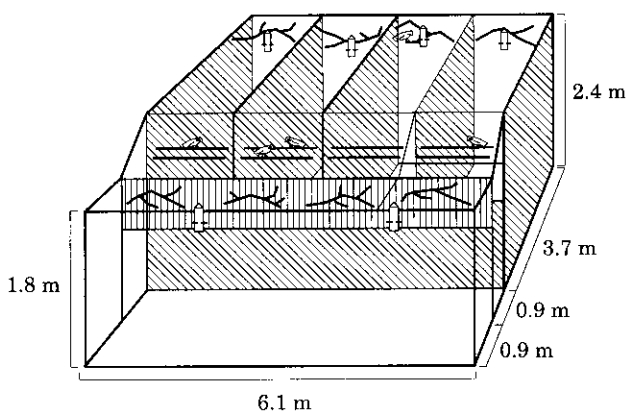

Figure 2. Design of aviary used for mate choice trials. Shading indicates solid walls. Stimulus males in four parallel flight cages were visually isolated from each other. The female cage extended across the width of all four male cages, allowing the test female to associate with males from perches in front of each male's cage. The female could choose not to associate with males by remaining behind the partition (dark shading) that divided the female cage into two compartments. The slanted roof of the inner compartment allowed for better viewing from the observation platform.

from perches in front of each of the adjoining cages. Hardware cloth separating the males from the female allowed limited interaction between them, but did not permit copulation.

Before the beginning of each trial, we gave the finches 10 min to adjust to the experimental cages. A trial began only after the female had visited each male at least once after the initial 10-min period. If, after 30 min, the female had not yet visited all of the males, we removed her from the cage and used another female for that trial. The original female could be used again on a different day with different stimulus males. Each trial lasted 50 min. We used a video camera mounted on a pole above the cages to make a permanent recording of each trial. We also observed some of the trials from behind a blind. We recorded the amount of time that the female spent in front of each of the four cages during the trial period. A trial was considered successful if the female spent at least 25 min associating with males or directing courtship behaviour (billing or clinging to the cage close to the male) towards at least one of the males. To control for position effects, we rotated treatment groups among the four cages so that males from each treatment group were placed in the end and centre cages approximately an equal number of times. Each male was used in 5–12 trials, except for one male that was used only once. A different female was tested in each of the 40 trials.

After each trial, we ranked males from one to four (least to most preferred) according to the relative amount of time the female spent with each during the 50-min trial period (ranking system A). We also applied a second ranking system (ranking system B) in which we totalled only periods of association time greater than or equal to 20 s. If the time spent with any two males varied by less than 60 s, we assigned the same rank to the two males. As a third means of assessing female preference for stimulus males, we ranked males according to the amount of courtship billing or close association (clinging to the cage close to the male) that the female directed towards each male. Males with which the female initiated only close association received lower ranks than males with which the female also billed.

Statistical Analysis

We performed a Friedman's test, correcting for tied ranks, to determine whether the distribution of preference ranks among the treatment groups differed from a random distribution. We also tested whether the distribution of ranks varied among cage positions. Where significant differences were found, we performed a multiple comparisons test (Gibbons 1976) to determine which pairs of ranks differed significantly.

To test for effects of plumage colour on female choice, we ranked males in each trial from one to four according to colour intensity and patch size. Similar Friedman's tests were performed to identify differences in preference ranks relative to colour intensity and patch size. Trials in which two or more males had the same patch size scores or intensity scores were omitted from this analysis because these males could not be assigned different ranks.

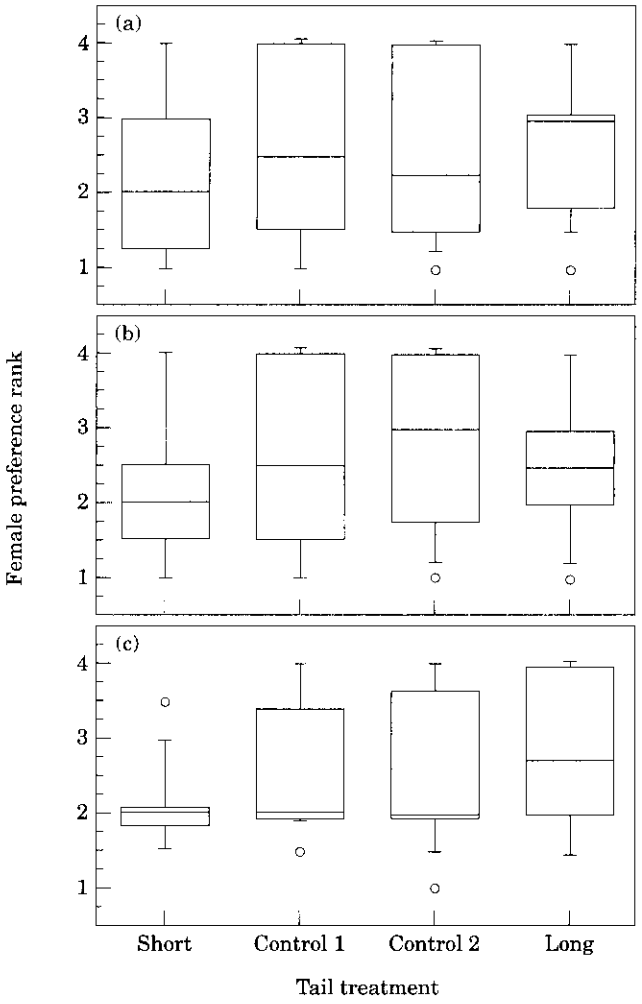

Figure 3. Female response to males of different tail-treatment groups for all trials as measured by (a) total association time (N=40), (b) association time counting only time periods of 20 s or more (N=40), and (c) courtship behaviours directed towards males (N=20). Horizontal bars in box plots indicate the 10th, 25th, 50th, 75th and 90th percentiles; open circles show data outside this range.

RESULTS

Females displayed no significant preference for any tail length when trials were analysed by association time using ranking system A, counting total association time (χ^2=4.18, N=40, P=0.24), or ranking system B, counting only time periods of at least 20 s (χ^2=6.00, N=40, P=0.11; Fig. 3). Similarly, female behaviour initiated towards males did not indicate any significant preferences relative to tail length (χ^2=5.59, N=20, P=0.13; Fig. 3). However, when the analyses involved only those trials in which all four males were in the same set, matched by plumage colour and patch size, the distribution of ranks differed from random for both ranking systems (A: χ^2=7.98, N=15, P<0.05), with females discriminating against short-tailed males (P<0.05; Fig. 4), but not discriminating among the other tail-treatment groups. Ranks based on female behaviour exhibited a similar, but nonsignificant, trend (χ^2=4.88, N=7, P=0.18; Fig. 4).

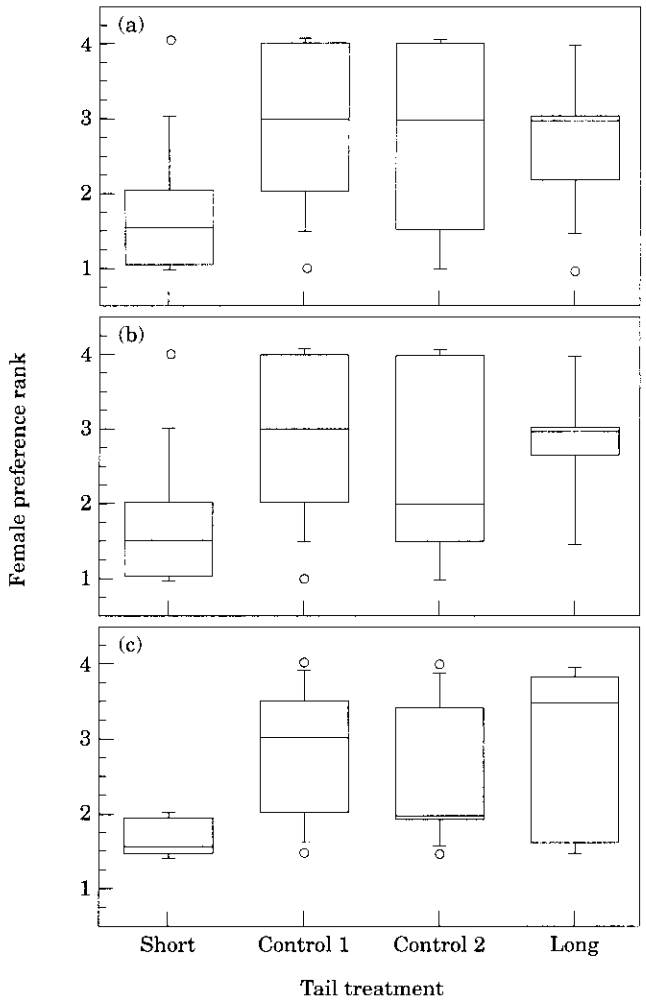

Figure 4. Female response to males of different tail-treatment groups for trials in which all four males were in the same set (matched by plumage colour and patch size) as measured by (a) total association time (N=15), (b) association time counting only time periods greater than or equal to 20 s (N=15), (c) courtship behaviour directed towards males (N=7). Percentiles are as indicated in Fig. 3.

Females did not show a preference relative to patch size of carotenoid-based coloration (A: χ^2=1.98, N=32, P=0.58; B: χ^2=3.00, N=32, P=0.39) or colour intensity (A: χ^2=5.99, N=24, P=0.11; B: χ^2=5.90, N=24, P=0.12) by either ranking system. Female association relative to cage position was nonrandom (A: χ^2=27.43, N=40, P<0.0001; B: χ^2=14.50, N=40, P<0.002). Females spent more time in front of the two end cages than the two centre cages. To determine whether position effects may have obscured or created female association patterns relative to male tail length, we repeated the analyses using only those trials in which the male with the lengthened tail and the male with the shortened tail were both in end cages or both in centre cages. Results of this test indicated no significant preferences relative to tail length (A: χ^2=0.63, N=13, P=0.70; B: χ^2=1.10, N=13, P=0.78). Differences between ranks of long- and short-tailed males became smaller than in previous tests. Similarly, there were no significant preferences relative to tail length in tests using only those trials in which the lengthened-tail and control 1 males were both in end cages or both in centre cages (A: χ^2=2.75, N=14, P=0.43; B: χ^2=6.18, N=14, P=0.10) or lengthened-tail and control 2 males were both in end cages or both in centre cages (A: χ^2=4.97, N=13, P=0.17; B: χ^2=7.38, N=13, P=0.61). In these tests, the mean rank for long-tailed males was slightly less than the mean rank of the respective control males, or the difference between the mean ranks became smaller than in tests using all 40 trials. The results of these tests indicate that position effects did not obscure preferences relative to tail length.

DISCUSSION

If a male trait results from exploitation of a pre-existing female bias, one should observe that (1) absence of the trait is the ancestral state, (2) in species exhibiting the trait, variation in the trait is used as a criterion in female mate choice, and (3) in species that do not exhibit the trait, females prefer the trait (Basolo 1990b).

With respect to elongated tails, the first condition is met in birds in general and cardueline finches in particular. The sporadic occurrence of elongated rectrices in a small minority of species in at least 50 families of birds (Austin 1985) suggests that tail elongation is a derived character within Aves. More specifically, the available hypotheses for cardueline finch relationships (Badyaev 1997a,b) indicate that tail elongation is a derived character. The second condition is met in several avian species in which females are known to prefer longer tails (Andersson 1982a; Møller 1988; Andersson 1989, 1991; Barnard 1990; Evans & Hatchwell 1991; Smith & Montgomerie 1991). To our knowledge, there is no experimental evidence for female preferences for longer tails within the cardueline finch family. Sexual selection by female choice, however, is a likely explanation for tail elongation within this group, particularly in those species exhibiting sexual dimorphism in tail length.

This study was designed to test the third prediction: preference for longer tails in a species that does not exhibit tail elongation. We found no evidence for such a preference in the house finch. Negative results are only convincing if they are derived from powerful tests with a reasonable expectation of detecting a preference. Johnson et al. (1993) found significant female preferences relative to several male traits in American goldfinches, using a similar aviary and testing a smaller sample of females. In addition, previous studies with house finches in which smaller samples of females were tested (sample sizes of 4–21), revealed a significant association preference for bright plumage and large patches of ornamental coloration (Hill 1990, 1994). In this study, we tested as many females as logistically possible, given the constraints for housing birds and running experiments. By testing preferences of 40 females, we had approximately an 80% chance of detecting a strong mate preference (i.e. a large effect size; Cohen 1992). To our knowledge, this is the most powerful mate-choice experiment with captive wild birds ever published.

The only significant preference that we observed in this study was an aversion by females to shortened tails. Even in tests in which differences were not significant, there was a consistent trend towards aversion to shortened tails. An aversion to shortened tails is not particularly surprising and may be explained without reference to sensory bias. In wild populations, a short tail may be a sign of improper moult, disease, or tail breakage (Smith & Montgomerie 1991; Møller 1994). Thus, a short tail may serve as an honest indicator of poor quality in the same way that Thomas (1993) proposed that degree of tail asymmetry would be an honest signal of poor quality. Therefore, discrimination against unusually short tails would enable females to avoid mates of poor quality.

Although differences in plumage colour and patch size of carotenoid-based coloration have been shown in previous studies of house finches to be important criteria in female mate choice (Hill 1990, 1994), they were not confounding variables in this study. Variation in plumage coloration among stimulus males was low (coefficient of variation=3.7) compared with variation among males in wild populations (coefficient of variation=36.2; G. E. Hill, unpublished data). Hue scores, which appear to be the most meaningful in terms of female preference for male colour (Hill 1994), were uniform among test males, and females did not show significant preferences relative to plumage colour scores or patch size.

The results of this study failed to support the hypothesis that tail elongation among cardueline finches resulted from exploitation of a pre-existing bias that was present in a common ancestor of all the long-tailed cardueline finches. The strength of a phylogenetic test of the sensory bias model depends upon both the hypothesized pattern of evolution of the male ornamental trait and of the female preference for the trait as well as the choice of taxa used for the test. For instance, if one assumes that sensory bias for longer tails arose several times among cardueline finches, then the more closely related the test species and the long-tailed species are, the greater the probability of detecting a pre-existing bias. Evidence of a pre-existing bias at this level, however, does not account for the widespread occurrence of long tails among cardueline finches and within the class Aves. The fact that elongated rectrices have evolved in virtually every family and subfamily of passerines by means of many independent evolutionary events led us to hypothesize that if a pre-existing bias has driven the evolution of elongated tails in passerines, it must be a primitive condition for the group. Therefore, the bias should be widely expressed among passerines, including cardueline finches. However, this study failed to uncover such a widespread pre-existing bias for longer tails.

Failure to provide evidence of a pre-existing sensory bias for longer tails among cardueline finches does not preclude a role of sensory bias in the evolution of ornamental traits. All models of selection by female choice require the existence of a female preference for a trait as an initial condition. Sensory bias provides the neural mechanism underlying the initial female preference for a trait and reveals the 'neural target' of selection on the preference (Ryan & Keddy-Hector 1992). If sensory bias is the mechanism behind the female preference, then the sensory bias necessarily existed prior to the evolution of the trait. One criterion for providing phylogenetic support for the sensory exploitation model requires that the time lapse between the origin of the preference and the evolution of the trait was sufficient to allow speciation. Otherwise, the branching of the phylogenetic tree can not reveal the historical relationship between the preference and the trait. This criterion is not always met. While phylogenetic evidence for a pre-existing preference for a trait suggests a role of sensory bias in the evolution of the trait, absence of such evidence does not indicate that sensory bias is not involved.

The distinction between sensory bias and the sensory exploitation model is an important one. Sensory bias, as a mechanism underlying female preferences, is likely to be crucial in every case of sexual selection by female choice. On the other hand, sensory exploitation of widespread pre-existing sensory biases may not be as prevalent as has been suggested by some authors.

Beyond its role as a mechanism underlying female preferences, the ability of sensory bias to drive the evolution of traits is unclear. The extreme elaboration and complexity seen in many ornaments is unlikely to result from sensory bias alone (Eberhard 1993). Interaction among various models of sexual selection provides a more complete explanation for the evolution of complex ornaments. Sensory biases can become established through natural selective pressures acting in other contexts (Clark & Uetz 1992; Proctor 1992; Ryan & Keddy-Hector 1992). Once established, a sensory bias may determine the direction of evolution of male traits. Other selective forces, however, such as those involved in honest advertisement and runaway process models, may maintain or further drive the evolution of the preference and the trait (Ryan & Keddy-Hector 1992).

Sensory bias is likely to be a critical component underlying female preferences, but at present, sensory bias and its precise role in sexual selection is poorly understood. Further study may lead to a better understanding of the prevalance of pre-existing biases, the ability of sensory biases to drive the evolution of ornamental traits, and the interaction among various models of sexual selection.

Acknowledgments

This research was conducted as partial fulfilment for the degree of Master of Science for M.C.T. We thank Robert Lishak and Craig Guyer for helpful suggestions during this investigation and for comments on the manuscript. We are especially grateful to Alexander Badyaev for permission to use his phylogeny of cardueline finches before it was published. This research was supported by a Faculty Grant-in-aid of research from the Auburn University College of Science and Mathematics, by the Auburn University Department of Zoology and Wildlife Sciences, and by the Alabama Agricultural Research Station.

References

Alatalo, R. V. 1988. Patterns of variation in tail ornament size in birds. *Biological Journal of Linnean Society*, **34**, 363–374.

Andersson, M. B. 1982a. Female choice selects for extreme tail length in a widowbird. *Nature*, **299**, 818–820.

Andersson, M. B. 1982b. Sexual selection, natural selection, and quality advertisement. *Biological Journal of the Linnean Society*, **17**, 375–393.

Andersson, M. B. 1986. Evolution of condition-dependent ornaments and mating preferences: sexual selection based on viability differences. *Evolution*, **40**, 804–820.

Andersson, M. B. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Andersson, S. 1989. Sexual selection and cues for female choice in leks of Jackson's widowbird *Euplectes jacksoni*. *Behavioral Ecology and Sociobiology*, **25**, 403–410.

Andersson, S. 1991. Bowers on the savanna: display courts and mate choice in a lekking widowbird. *Behavioral Ecology*, **2**, 210–218.

Austin, O. L. J. 1985. *Families of Birds*. New York: Golden Press.

Badyaev, A. V. 1997a. Altitudinal variation in sexual dimorphism: a new pattern and possible underlying causes. *Behavioral Ecology*, **8**, 675–690.

Badyaev, A. V. 1997b. Avian life history variation along altitudinal gradients: an example with cardueline finches. *Oikos*, **111**, 365–374.

Balmford, A., Thomas, A. L. R. & Jones, I. L. 1993. Aerodynamics and the evolution of long tails in birds. *Nature*, **361**, 628–631.

Barnard, P. 1990. Male tail length, sexual display intensity and female sexual response in a parasitic African finch. *Animal Behaviour*, **39**, 652–656.

Basolo, A. L. 1990a. Female preference for male sword length in the green swordtail (*Xiphophorus helleri*). *Animal Behaviour*, **40**, 332–338.

Basolo, A. L. 1990b. Female preference predates the evolution of the sword in swordtail fish. *Science*, **250**, 808–810.

Basolo, A. L. 1995a. A further examination of a pre-existing bias favouring a sword in the genus *Xiphophorus*. *Animal Behaviour*, **50**, 365–375.

Basolo, A. L. 1995b. Phylogenetic evidence for the role of a pre-existing bias in sexual selection. *Proceedings of the Royal Society of London, Series B*, **259**, 307–311.

Clark, D. L. & Uetz, G. W. 1992. Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behaviour. *Animal Behaviour*, **43**, 247–254.

Clement, P., Harris, A. & Davis, J. 1993. *Finches and Sparrows*. Princeton, New Jersey: Princeton University Press.

Cohen, J. 1992. A power primer. *Psychological Bulletin*, **112**, 155–159.

Darwin, C. 1874. *The Descent of Man, and Selection in Relation to Sex*. 2nd edn. London: John Murray.

Eberhard, W. G. 1993. Evaluating models of sexual selection: genitalia as a test case. *American Naturalist*, **142**, 564–571.

Enquist, M. & Arak, A. 1993. Selection of exaggerated male traits by female aesthetic senses. *Nature*, **361**, 446–448.

Evans, M. R. & Hatchwell, B. J. 1991. An experimental study of male adornment in the scarlet-tufted malachite sunbird: II. The role of the elongated tail in mate choice and experimental evidence for a handicap. *Behavioral Ecology and Sociobiology*, **29**, 421–427.

Fisher, R. A. 1958. *The Genetical Theory of Natural Selection*. 2nd edn. New York: Dover.

Gibbons, J. D. 1976. *Nonparametric Methods for Quantitative Analysis*. Holt, Rinehart & Winston.

Grant, P. R. & Price, T. D. 1981. Population variation in continuously varying traits as an ecological genetics problem. *American Zoologist*, **21**, 795–811.

Hill, G. E. 1990. Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Animal Behaviour*, **40**, 563–572.

Hill, G. E. 1992. Proximate basis of variation in carotenoid pigmentation in male house finches. *Auk*, **109**, 1–12.

Hill, G. E. 1993a. Geographic variation in the carotenoid plumage pigmentation of male house finches (*Carpodacus mexicanus*). *Biological Journal of the Linnean Society*, **49**, 63–86.

Hill, G. E. 1993b. House finch (*Carpodacus mexicanus*). In: *The Birds of North America, No. 46* (Ed. by A. Poole & F. Gill), pp. 1–24. Washington, D.C.: The American Ornithologists' Union.

Hill, G. E. 1994. Geographic variation in male ornamentation and female mate preference in the house finch: a comparative test of models of sexual selection. *Behavioral Ecology*, **5**, 64–73.

Johnson, K., Dalton, R. & Burley, N. 1993. Preferences of female American goldfinches (*Carduelis tristis*) for natural and artificial male traits. *Behavioral Ecology*, **4**, 138–143.

Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. *Evolution*, **36**, 1–12.

Kirkpatrick, M. 1987. The evolutionary forces acting on female mating preferences in polygynous animals. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 67–82. New York: John Wiley.

Kodric-Brown, A. & Brown, J. H. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *American Naturalist*, **124**, 309–323.

Maynard-Smith, J. 1987. Sexual selection: a classification of models. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 9–20. New York: John Wiley.

Maynard-Smith, J. 1991. Theories of sexual selection. *Trends in Ecology and Evolution*, **6**, 146–151.

Møller, A. P. 1988. Female choice selects for male sexual tail ornaments. *Nature*, **332**, 640–642.

Møller, A. P. 1994. *Sexual Selection and the Barn Swallow*. Oxford: Oxford University Press.

O'Donald, P. 1980. *Genetic Models of Sexual Selection*. Cambridge: Cambridge University Press.

Proctor, H. C. 1992. Sensory exploitation and the evolution of male mating behaviour: a cladistic test using water mites (*Acari: Parasitengona*). *Animal Behaviour*, **44**, 745–752.

Ryan, M. J. & Keddy-Hector, A. 1992. Directional patterns of female mate choice and the role of sensory biases. *American Naturalist*, **139** (Suppl.), 4–35.

Ryan, M. J. & Rand, A. S. 1990. The sensory basis of sexual selection for complex calls in the túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution*, **44**, 305–314.

Smith, H. G. & Montgomerie, R. 1991. Sexual selection and the tail ornaments of North American barn swallows. *Behavioral Ecology and Sociobiology*, **28**, 195–201.

Thomas, A. L. R. 1993. The aerodynamic costs of asymmetry in the wings and tail of birds: asymmetric birds can't fly round tight corners. *Proceedings of the Royal Society of London, Series B*, **254**, 187–189.

Zahavi, A. 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology*, **67**, 603–605.