

Male House Finches with Elaborate Songs have Higher Reproductive Performance

Daniel J. Mennill*, Alexander V. Badyaev†, Leslie M. Jonart‡ & Geoffrey E. Hill‡

* Department of Biological Sciences, University of Windsor, Windsor, ON, Canada

† Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ

‡ Department of Biological Sciences, Auburn University, Auburn, AL, USA

Correspondence

Daniel J. Mennill, 401 Sunset Avenue,
Department of Biological Sciences, University
of Windsor, Windsor, Ontario, Canada
N9B3P4. E-mail: dmennill@windsor.ca

Received: February 24, 2005

Initial acceptance: March 29, 2005

Final acceptance: June 2, 2005 (S. Forbes)

Abstract

The elaborate songs of male animals are thought to function in either territory defense (male–male communication) or mate attraction (male–female communication). In non-territorial animals, male vocalizations are expected to function primarily in mate attraction, yet the reproductive consequences of male vocalizations in non-territorial animals are poorly described. Here we explore the relationship between male song and male reproductive performance in a free-living population of house finches, *Carpodacus mexicanus*, a non-migratory, non-territorial songbird. Based on recordings of 20 males, we analyzed three song features (song length, number of unique syllables per song, and song rate) and compared male song with two measures of within-pair reproductive performance (nest initiation date and clutch size) and one measure of extra-pair reproductive performance (whether males sired extra-pair young). We demonstrate a positive association between male song and within-pair reproductive performance; males that sang long songs initiated their first clutch significantly earlier and males that sang songs at a faster rate had larger clutches. Despite the fact that only one of our recorded males sired extra-pair young in the nest of another male, this male's songs were the most elaborate for two of three song features measured, anecdotally suggesting that male song may play a role in both within-pair and extra-pair partner choice. These results suggest that male song is a sexually selected trait in non-territorial house finches.

Introduction

For territorial animals, vocal signals can play an important role in both territory defense and mate attraction. The elaborate songs of many male songbirds (order: Passeriformes) serve these dual functions (Catchpole & Slater 1995; Collins 2004). In non-territorial songbirds, however, the adaptive significance of song is poorly understood. Sexual selection through female choice is expected to be the primary force driving the elaboration of male songs in non-territorial animals, but studies exploring male song characteristics and male reproductive

performance in wild, non-territorial songbirds are scarce.

House finches, *Carpodacus mexicanus*, defend no resources other than their mates and thus are considered to be non-territorial (Hill 1993, 2002). Each male house finch has a repertoire of syllables (Munding 1975; Bitterbaum & Baptista 1979; Pytte 1997) which are combined to produce impressive songs described as rambling, hoarse warbles (Thompson 1960; Hill 1993). Male song structure varies between eastern and western populations: eastern house finch males have repertoires of song types composed of syllables sung in a stereotyped order

(Mundinger 1975), while western males drop and add syllables and sing with subtle variation between consecutive songs (Bitterbaum & Baptista 1979; Pytte 1997). The songs of male house finches have been explored with particular attention to song learning (Miller 1921), vocal imitation (Baptista 1972; Payne et al. 1988), and song dialects (Mundinger 1975; Bitterbaum & Baptista 1979; Pytte 1997; Tracy & Baker 1999). Three lines of evidence suggest that male house finch song may operate in inter-sexual signaling but not intra-sexual signaling: males sing at higher rates when they are near females (Bitterbaum & Baptista 1979), male house finches do not engage in vocal countersinging interactions with other males (Thompson 1960; Bitterbaum & Baptista 1979), and males do not respond to conspecific playback (Bitterbaum & Baptista 1979). An aviary-based experiment suggests that elaborate features of male house finch songs are attractive to females (Nolan & Hill 2004). Whether male song is important for females in choice of social partners or extra-pair partners in free-living birds is unknown.

Here we evaluate the relationship between male song and reproductive performance in house finches. Nolan & Hill's (2004) aviary-based phonotaxis experiment demonstrated that female house finches are attracted to long songs and songs given at a high rate. In many birds, females also prefer males with large song repertoires (Searcy & Yasukawa 1996), although Nolan & Hill (2004) did not detect a female preference for male repertoire size in house finches in their aviary experiment. The experimental procedure used by Nolan & Hill (2004) involved estrogen-implanted females, surgically muted males, and playback of manipulated songs. Our goal was to evaluate whether natural variation in male songs is associated with reproductive performance in free-living non-territorial birds. We investigate male singing and reproductive behavior in a population of color-banded house finches in western Montana by comparing male song features to male nest initiation date, clutch size, and extra-pair mating success.

Methods

Sound Recording and Measurement

Between Apr. 27, 2000 and Jul. 6, 2000, we recorded songs from 20 male house finches in a study population in Missoula, Montana (for detailed description of study site see Badyaev & Martin 2000). Birds were color banded to facilitate individual identification. Male house finches do

not defend territories (Hill 1993, 2002), so recordings were made by moving around the study site and recording birds opportunistically. Recordings were made using a cassette recorder (model: Marantz PMD-222, Marantz, Itasca, IL, USA) and a directional microphone (model: Sennheiser MKH-70, Sennheiser, Old Lyme, CT, USA). Most recordings (82%) were collected during the morning, although opportunistic recordings were also collected in the early or late afternoon (18%). All 20 males were resident at the study site throughout the 2000 breeding season and were recorded repeatedly throughout the breeding season.

Recordings were digitized and measured using Syrinx-PC sound analysis software (J. Burt, Seattle, WA, USA). We isolated 555 songs that were not heavily masked by ambient noise. We measured three features of each song (following methods established by Mundinger 1975 and Bitterbaum & Baptista 1979): (1) the length of each song (the number of syllables in each song), and (2) number of unique syllable types in each song. Owing to the masking effects of traffic noise, we rarely had long continuous recording bouts from which we could calculate song rate. Accordingly, we calculated song rate as (3) the interval between consecutive songs of an individual. Birds sometimes stopped singing for brief periods during recording sessions. We ignored inter-song intervals >25 s to avoid including these extended breaks in song rate measurements. All song measurements were collected and analyzed blind to the reproductive data of the singers.

House finch songs may be divided into two categories: songs that contain a buzz syllable (usually as the terminal syllable) and songs that do not contain a buzz syllable (Fig. 1). Non-buzz songs are given throughout the year whereas buzz songs are given primarily during the breeding season (Thompson 1960; Hill 1993) and non-buzz songs are given during flight whereas buzz songs are given from exposed perches (Bitterbaum & Baptista 1979). Of 555 songs we recorded, 375 were buzz songs and 180 were non-buzz songs. In our recordings, buzz songs were longer (buzz songs: 14.0 ± 0.5 syllables; non-buzz songs: 10.5 ± 0.5 syllables; $t_{18} = 6.5$, $p < 0.0001$), and buzz songs had more unique syllable types (buzz songs: 12.1 ± 0.4 ; non-buzz songs: 9.4 ± 0.4 ; $t_{18} = 6.3$, $p < 0.0001$), although there were no differences in the delay between consecutive buzz and non-buzz songs (buzz songs: 12.0 ± 1.4 s; non-buzz songs: 9.8 ± 0.4 ; $t_{18} = 1.9$, $p = 0.07$; paired t-tests for $n = 19$ males for which both buzz and non-buzz songs were recorded). The

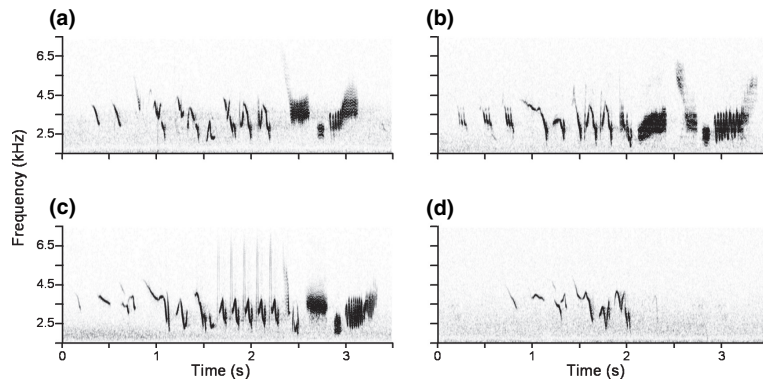


Fig. 1: Sound spectrograms showing male house finch songs from Missoula, Montana. Songs from four different males are shown, demonstrating variation in song length and number of unique syllable types per song. We analyzed songs containing buzz syllables (a–c), which are given primarily during the breeding season. We omitted songs that did not contain buzzes (d), which are given throughout the year and during flight

differences in both the context and structure of buzz vs. non-buzz songs suggest that buzz songs are specifically associated with sexual display. Therefore we include only buzz songs in our analyses of male song and male reproductive performance (analyses include 18.8 ± 4.8 buzz songs from each of the 20 males).

Monitoring Reproductive Activities

We monitored the reproductive activities of all birds at the study site by observing pairs on a daily basis (see detailed methods in Badyaev & Martin 2000). To assess within-pair reproductive performance, we recorded nest initiation date and clutch size for all males that paired with a female that laid at least one clutch ($n = 13$). Nest initiation date is the best predictor of overall reproductive success in house finches (Badyaev et al. 2000, 2001b). As part of another study of house finch paternity, we used minisatellite DNA fingerprinting to assess extra-pair reproductive performance of birds in this population (detailed methods are presented in Badyaev et al. 2001a). Briefly, we used minisatellite fingerprinting methods to test whether offspring showed novel fragments relative to their social mother and father. The 20 males that we recorded were genotyped as potential extra-pair sires and evaluated as possible sires of extra-pair young in the broods of other birds in the population. None of the recorded males lost paternity in its own nest.

Statistical Approach

Based on the results of aviary-based female choice experiments with house finches (Nolan & Hill 2004), we predicted a positive association between reproductive performance and both song length and song rate (measurements 1 and 2, above). Based on the widespread pattern of female preference for males

with high song output and large repertoires (Searcy & Yasukawa 1996), we predicted a positive association between reproductive performance and the number of unique syllable types per song and song rate (measurements 2 and 3, above). Because of these directional predictions, we use one-tailed statistical analyses. All analyses were conducted in JMP 5.0 (SAS Institute, Cary, NC, USA). All values are presented as $\bar{x} \pm SE$.

Results

Song and Within-Pair Reproductive Performance

Male house finches that sang long songs initiated their first nest significantly earlier (Fig. 2). We found no significant relationships between nest initiation

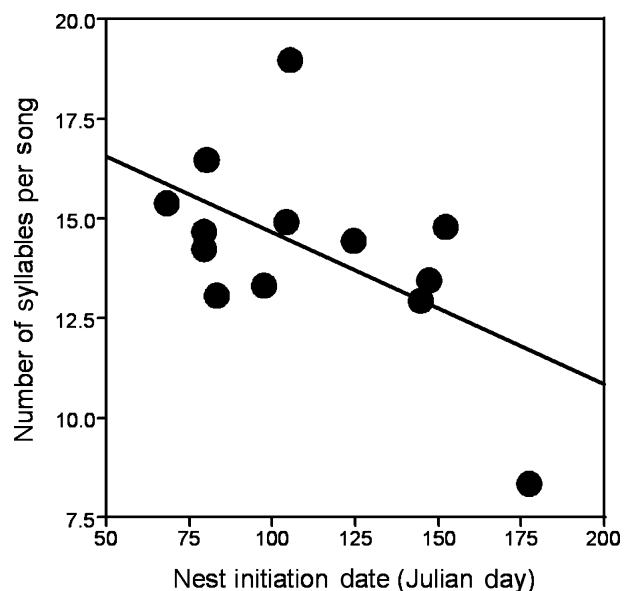


Fig. 2: Relationship between song length (number of syllables per song) and date of first nest initiation for male house finches ($r = 0.55$, $n = 13$, $p = 0.03$)

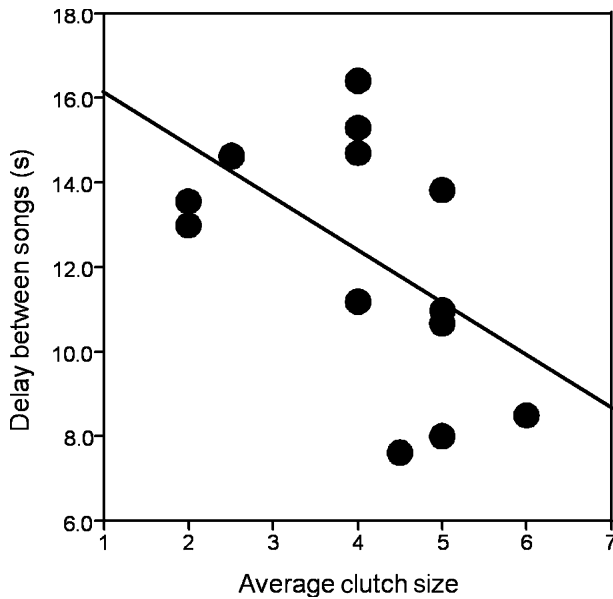


Fig. 3: Relationship between song rate (delay between consecutive songs) and average clutch size for male house finches ($r = 0.53$, $n = 13$, $p = 0.03$)

date and the other two song measures, although both of these relationships were in the predicted direction (number of unique syllable types: $r = 0.45$, $n = 13$, $p = 0.06$; song rate: $r = 0.30$, $n = 13$, $p = 0.17$).

Male house finches that sang songs at a faster rate had larger average clutch sizes (Fig. 3). Clutch size did not show a significant relationship with the other two song measures, although both of these relationships were in the predicted direction (song length: $r = 0.12$, $n = 13$, $p = 0.32$; number of unique syllable types: $r = 0.28$, $n = 13$, $p > 0.17$).

Song and Extra-Pair Reproductive Performance

Among 16 recorded male house finches that were recorded and genotyped as potential extra-pair sires, only one male gained extra-pair paternity in the nest of another male. This male’s songs were longer than all other males’ songs (Fig. 4a), had more unique syllable types than all other males’ songs (Fig. 4b), and showed the third shortest delay between consecutive songs (i.e. the third fastest song rate; Fig. 4c).

Discussion

Our analyses of male house finch songs demonstrate an association between elaborate song features and both nest initiation date and clutch size. Males with more syllables per song initiated their nests significantly earlier, and males that sang at faster rates had larger clutches. Nest initiation date is the best predictor of male reproductive success in house finches, where birds that nest early produce more offspring (Badyaev et al. 2000) and their offspring fledge in better condition and experience lower mortality (Badyaev et al. 2001b). Our analyses anecdotally suggest that song is also important to male extra-pair reproductive performance; the only male to gain extra-pair paternity in our study population sang the most elaborate songs. Our observations of the context in which males sing are consistent with previous studies, which suggest that song plays an important role in intersexual communication; male song was not given in male–male contests but instead in bouts of spontaneous broadcast singing while in the presence of females. Therefore, the elaborate songs of non-territorial male house finches appear to function in mate attraction or mate stimulation.

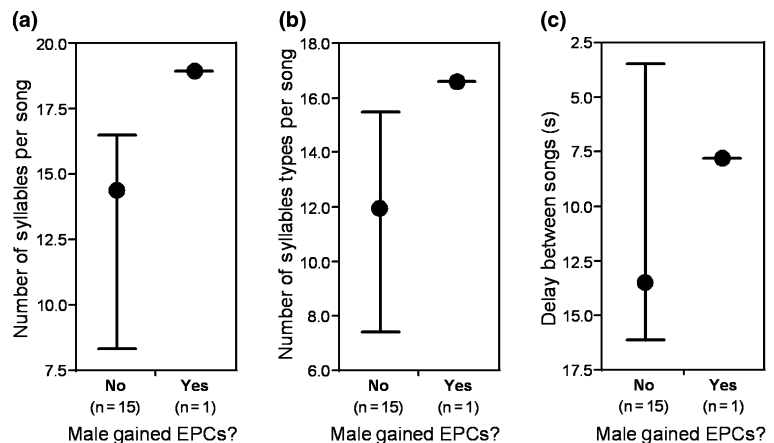


Fig. 4: Of 20 male house finches that were genotyped as potential extra-pair sires, one male gained extra-pair paternity in the nest of another bird in the population. This male sang a longer songs than all other males (a), it sang more unique syllables per song than all other males (b), and it had the third shortest average delay between consecutive songs (c)

Several mechanisms could explain the observed association between male songs and male reproductive performance. (1) Males singing more elaborate songs may attract higher quality females that nest earlier and produce larger clutches. (2) Females paired to males singing more elaborate songs may nest earlier because they perceive they are paired to a high-quality male. (3) Males singing more elaborate songs may stimulate their females to nest earlier or produce larger clutches. Careful investigation of the phenology of singing, pairing, and nesting behavior together with measurements of male and female quality will help to clarify which of these hypotheses best explains the association between male song and male reproductive performance. Under the first explanation, females paired to males that sing elaborate songs should be of higher quality than females paired to males singing less elaborate songs. Under the second and third explanations, there need be no quality differences among females, but under the third explanation there should be an increase in male singing of elaborate songs immediately prior to the onset of female nesting and egg laying.

Using an aviary-based phonotaxis experiment to study song preferences of female house finches in Alabama, Nolan & Hill (2004) controlled for male plumage color and demonstrated that females are attracted to loudspeakers playing long songs and songs given at a fast rate. Our analyses of male song and reproductive performance of house finches in Montana show a corresponding association between song rate and clutch size (Fig. 3). Our results, when taken together with the experimental work of Nolan & Hill (2004), demonstrate that male song in house finches plays an important role in intersexual communication.

Male song is a far-carrying signal that can convey information about male quality to multiple individuals across considerable distances. Consequently, male song may play an especially important role in female choice of extra-pair partners. Male house finches engage in intensive mate-guarding behavior throughout the breeding season (Beck 2003; McGraw & Hill 2003), which may prevent females from assessing potential extra-pair partners in close proximity. Although male plumage color is an important sexual signal in house finches (Hill 2002), there is no relationship between male plumage color and a male's risk of being cuckolded (Hill et al. 1994; Badyaev et al. 2001a). Here we show an anecdotal association between male song and male extra-pair mating success. Despite the fact that only one of our

recorded males sired extra-pair young in the nest of another male, this male's songs were the most elaborate for two of the three features we measured. Although the frequency of extra-pair paternity in house finches (6.5–8.3% of nestlings; Hill et al. 1994; Badyaev et al. 2001a) falls below the average for all birds (11.1% of nestlings; Griffith et al. 2002), mixed matings may nevertheless have important fitness consequences and contribute to the evolution of elaborate song in males. Although male plumage color plays a prominent role in house finch sexual signaling (Hill 2002), male song may be a more salient component of extra-pair partner choice than male plumage color.

In several other songbirds there is a positive association between male song features and male reproductive success. In studies of within-pair reproductive success, males with larger repertoires breed earlier in sedge warblers, *Acrocephalus schoenobaenus* (Catchpole 1980), and males with higher song output breed earlier in willow warblers, *Phylloscopus trochilus* (Radesäter et al. 1987) and are preferred as social mates in pied flycatchers, *Ficedula hypoleuca* (Alatalo et al. 1990) and zebra finches, *Taenopygia guttata* (Collins et al. 1994). In studies of extra-pair mating success, males with larger repertoires are preferred as extra-pair partners in great reed-warblers, *A. arundinaceus* (Hasselquist et al. 1996), males with longer songs are preferred as extra-pair partners in blue tits, *Parus caeruleus* (Kempenaers et al. 1997), and males with high song rates are preferred as extra-pair partners in zebra finches (Houtman 1992). Almost all data linking male song and male reproductive success come from studies of territorial birds. Our investigation of male house finch song makes an important contribution by demonstrating that song is an ornament relevant to reproductive performance in wild, non-territorial songbirds. Our analyses suggest that male song functions in mate choice for non-territorial house finches in much the same way that male song does for territorial songbirds.

The native range of house finches includes the south-western US and Mexico but the species' range has expanded over the past 80 yr to cover most of the US and parts of southern Canada (Hill 2002). Although there is marked variation in several song features between eastern and western populations (Mundinger 1975; Bitterbaum & Baptista 1979; Pytte 1997; Tracy & Baker 1999) all house finches that have been investigated to date demonstrate variation in the song features that we studied here, including variation in song length, number of syllables per

song, and song rate. Consequently, we expect the relationship between elaborate male songs and male reproductive performance will be widespread among populations of house finches.

Acknowledgements

We thank many field assistants for help with data collection and the personnel of the Vigilante MiniStorage of Missoula, Montana, for allowing us to work on their property. We thank S. Doucet, L. Estep, A. King, M. Liu, H. Mays, K. Navara, L. Siefferman, and M. Shawkey for comments on the manuscript. D.J.M. was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) and the University of Windsor. Field data collection was partially supported by NSF grants 0075388 and 0218313 to A.V.B. G.E.H. was supported by NSF grants IBN 0218313 and 9722171.

Literature Cited

- Alatalo, R. V., Glynn, C. & Lundberg, A. 1990: Singing rate and female attraction in the pied flycatcher: an experiment. *Anim. Behav.* **39**, 601–602.
- Badyaev, A. V. & Martin, T. E. 2000: Sexual dimorphism in relation to current selection in the house finch. *Evolution* **54**, 987–997.
- Badyaev, A. V., Hill, G. E., Stoehr, A. M., Nolan, P. M. & McGraw, K. J. 2000: The evolution of sexual dimorphism in the house finch: II. Population divergence in relation to local selection. *Evolution* **54**, 2134–2144.
- Badyaev, A. V., Hill, G. E., Dunn, P. O. & Glen, J. C. 2001a: Plumage color as a composite trait: developmental and functional integration of sexual ornamentation. *Am. Nat.* **158**, 221–235.
- Badyaev, A. V., Whittingham, L. A. & Hill, G. E. 2001b: The evolution of sexual size dimorphism in the house finch: III. Developmental basis. *Evolution* **55**, 176–189.
- Baptista, L. F. 1972: Wild house finch sings white-crowned sparrow song. *Z. Tierpsychol.* **30**, 266–270.
- Beck, M. L. 2003: The influence of male and female quality on reproductive effort and strategies in the house finch. MSc Thesis, Auburn Univ., Auburn, AL.
- Bitterbaum, E. & Baptista, L. F. 1979: Geographical variation in songs of California House finches (*Carpodacus mexicanus*). *Auk* **96**, 462–474.
- Catchpole, C. K. 1980: Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour* **74**, 149–166.
- Catchpole, C. K. & Slater, P. J. B. 1995: *Bird Songs: Biological Themes and Variations*. Cambridge Univ. Press, New York.
- Collins, S. A. 2004: Vocal fighting and flirting: the functions of bird song. In: *Nature's Music: the Science of Bird Song* (Marler, P. & Slabbekoorn, H., eds). Elsevier, San Diego, CA. pp. 39–79.
- Collins, S. A., Hubbard, C. & Houtman, A. M. 1994: Female mate choice in the zebra finch – the effect of male beak color and male song. *Behav. Ecol. Sociobiol.* **35**, 21–25.
- Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002: Extra-pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.* **11**, 2195–2212.
- Hasselquist, D., Bensch, S. & von Schantz, T. 1996: Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* **381**, 229–232.
- Hill, G. E. 1993: The house finch. In: *Birds of North America*. No. 46 (Poole, A. & Gill, F., eds). Academy of Natural Sciences, Philadelphia, PA; American Ornithologists' Union, Washington, DC.
- Hill, G. E. 2002: *A Red Bird in a Brown Bag: the Function and Evolution of Colorful Plumage in the House Finch*. Oxford Univ. Press, Oxford.
- Hill, G. E., Montgomerie, R., Roeder, C. & Boag, P. 1994: Sexual selection and cuckoldry in a monogamous songbird: implications for theories of sexual selection. *Behav. Ecol. Sociobiol.* **35**, 193–200.
- Houtman, A. M. 1992: Female zebra finches choose extra-pair copulations with genetically attractive mates. *Proc. R. Soc. Lond. B* **249**, 3–6.
- Kempnaers, B., Verheyren, G. R. & Dhondt, A. A. 1997: Extra-pair paternity in the blue tit (*Parus caeruleus*). *Behav. Ecol.* **8**, 481–492.
- McGraw, K. J. & Hill, G. E. 2003: Mate attentiveness, seasonal timing of breeding and long-term pair bonding in the house finch (*Carpodacus mexicanus*). *Behaviour* **141**, 1–13.
- Miller, L. 1921: The biography of nip and tuck. *Condor* **23**, 41–47.
- Mundinger, P. 1975: Song dialects and colonization in the house finch, *Carpodacus mexicanus*, on the east coast. *Condor* **77**, 407–422.
- Nolan, P. M. & Hill, G. E. 2004: Female choice for song characteristics in the house finch. *Anim. Behav.* **67**, 403–410.
- Payne, R. B., Payne, L. L. & Whitesell, S. 1988: Interspecific learning and cultural transmission of song in house finches. *Wilson Bull.* **100**, 667–670.
- Pytte, C. 1997: Song organization of house finches at the edge of an expanding range. *Condor* **99**, 942–954.
- Radesäter, T. S., Jakobsson, S., Andbjør, A. & Nystrom, K. 1987: Song rate and pair formation in the willow warbler, *Phylloscopus trochilus*. *Anim. Behav.* **35**, 1645–1651.

Searcy, W. A. & Yasukawa, K. 1996: Song and female choice. In: *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D. & Miller, E. H., eds). Cornell Univ. Press, Ithaca, NY. pp. 454—473.

Thompson, W. L. 1960: Agonistic behavior in the house finch. I. Annual cycle and display patterns. *Condor* **62**, 245—271.

Tracy, T. T. & Baker, M. C. 1999: Geographic variation in syllables of house finch songs. *Auk* **116**, 666—676.