

# Structure of Social Networks in a Passerine Bird: Consequences for Sexual Selection and the Evolution of Mating Strategies

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**ABSTRACT:** The social environment is a critical determinant of fitness and, in many taxa, is shaped by an individual's behavioral discrimination among social contexts, suggesting that animals can actively influence the selection they experience. In competition to attract females, males may modify sexual selection by choosing social environments in which they are more attractive relative to rivals. Across the population, such behaviors should influence sexual selection patterns by altering the relationship between male mating success and sexual ornament elaboration. Here we use network analysis to examine patterns of male social behavior in relation to plumage ornamentation and mating success in a free-living population of house finches. During the nonbreeding season, less elaborate males changed associations with distinct social groups more frequently, compared to more elaborate males that showed greater fidelity to a single social group. By the onset of pair formation, socially labile males effectively increased their attractiveness relative to other males in the same flocks. Consequently, males that frequently moved between social groups had greater pairing success than less social individuals with equivalent sexual ornamentation. We discuss these results in relation to conditional mating tactics and the role of social behavior in evolutionary change by sexual selection.

**Keywords:** social structure, mate choice, niche construction, *Carpodacus mexicanus*.

## Introduction

Organisms are sometimes portrayed as passive participants in evolutionary processes, subject to sorting and filtering by their environment. Yet there is overwhelming evidence that animals choose, modify, and create their environment and, thus, the selection they experience (Lewontin 1978; Odling-Smee et al. 1996; Laland et al. 1999). Behaviors that allow individuals to preferentially associate with habitats in which they are likely to experience high fitness represent one of the most conspicuous of these processes

(i.e., habitat selection; Lack 1933; Svårdson 1949; Rosenzweig 1981; Cody 1985; Bazzaz 1991; Orians and Wittenberger 1991). Such behaviors have important evolutionary consequences that range from the dampening of evolutionary change when individuals avoid environments in which they would experience low fitness (Bogert 1949; Schmalhausen 1949; Huey et al. 2003; Badyaev 2005) to promoting divergent evolution when organisms are exposed to novel selective environments as a result of habitat selection (Wcislo 1989; Robinson and Dukas 1999; Duckworth 2006). Thus, empirical studies that examine the fitness consequences of individual choice of environment are critical for understanding the role of such behaviors in determining the pace and direction of evolutionary change (Baldwin 1896; Sol et al. 2005; Duckworth 2009).

The social environment is a critical determinant of fitness and, in many taxa, is often shaped by individuals' behavioral discrimination among different social contexts. More specifically, by preferentially interacting with some conspecifics and avoiding others, individuals can effectively modify their social environment and, hence, the selection they experience (Noë 2001; Lewis 2008). In many species, the density, phenotypic characteristics, or demographic composition of interacting individuals within a group may influence a male's mating success (e.g., Farr 1980; Jirotkul 2000), especially when mate attraction involves cooperative courtship displays (Foster 1977; McDonald and Potts 1994; Hall 2004) or territory defense (Sinervo and Clobert 2003) or when females compare potential mates within a local pool (i.e., best-of- $n$  sampling tactic; Wiegmann et al. 1996; Uy et al. 2000; Wagner et al. 2001). For example, when mating success depends on attracting females to clusters of courting males (e.g., in a lek), comparatively unattractive individuals might benefit from close associations with more attractive males because of the increased number of visits by choosy females (Beehler and Foster 1988). Such a tactic, however, is expected to confer fitness benefits only when females mate multiply and there is little interaction between mates outside of mating context (Tarof et al. 2005). An alternative, but

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untested, hypothesis suggests that by preferentially associating with comparatively unattractive conspecifics, males might benefit by increasing their relative attractiveness to prospecting females (Bateson and Healy 2005). However, behaviors that involve searching for preferred contexts are often costly in terms of time or energetic expenditure (e.g., Stamps et al. 2005) or agonistic encounters with competitors (e.g., Rohwer and Ewald 1981). Thus, when such behaviors are equally costly to all individuals, relatively unattractive males, which arguably stand to benefit the most in terms of mating success, should be more likely to invest into creating favorable social environments, compared to more attractive males.

Empirically testing the effects of social environment on mating success requires the ability to track the social behaviors, quantify sexual ornament elaboration, and evaluate pairing success of numerous simultaneously interacting individuals—thus presenting a particular challenge for studies in natural populations. As a result, a majority of previous work has focused on systems in which individuals have well-defined social hierarchies (e.g., cooperative display by dominant and subordinate males; McDonald and Potts 1994) or relatively stable territory neighborhoods (e.g., Sinervo and Clobert 2003), while species with more dynamic and reticulate social structures have proven less tractable.

The application of network theory, in which social behaviors can be represented as complex networks of interacting individuals (reviewed in Wey et al. 2008; Sih et al. 2009), provides a robust methodology for assessing not only overall population social structure (Clauset et al. 2004; Newman 2006) but also useful metrics from which patterns of individual behaviors can be inferred (Hanneman and Riddle 2005). The extent to which individuals actively sample among different social environments is reflected in their betweenness centrality (Freeman 1979), which relates to the frequency with which individuals interact with conspecifics in otherwise noninteracting social groups (McDonald 2007), a behavior that we will refer to here as social lability (Campbell 2008), which should reflect investment into sampling and searching for preferred social contexts.

In this study we use social network analysis to examine the relationship among male sexual ornament elaboration, social lability, and mating success in a wild population of house finches (*Carpodacus mexicanus*)—a highly gregarious species in which males display colorful plumage ornamentation that is important for mate choice (Hill 1991; Badyaev and Hill 2002). In the nonbreeding season, both sexes interact in flocks in which the majority of mate sampling and selection is thought to occur through comparative evaluation of potential partners (Oh and Badyaev 2006).

Here, we test the hypothesis that male social lability is related to individual ornament elaboration. First, we present networks describing overall social interactions during the nonbreeding season and provide evidence of pronounced population social structure: small groups of closely interacting individuals in which a significant proportion of pairing occurred. Second, we test the assumption that plumage ornamentation affects mating success (irrespective of male social behaviors) and document a general mating advantage of males with greater ornament elaboration. Third, we demonstrate a significant relationship between ornament elaboration and male sociality, such that less elaborate males exhibited greater social lability during the nonbreeding season, which effectively improved their relative attractiveness by the onset of mate choice. Finally, we assess the fitness consequences of both ornament elaboration and male social behavior and find that mating success increased with social lability but only in lesser ornamented males that presumably stand to benefit the most from adjustment of social context for mate choice, thus suggesting an important role of behavioral tactics in individuals' ability to shape their environment of sexual selection.

## Methods

### *Field Methods and Study Population*

We studied a resident population of wild house finches in southern Arizona from 2003 to 2006. Adults and juveniles within the study site were captured and assigned unique combinations of one aluminum and three plastic color bands to facilitate identification of individuals in the field. Adult house finches in this population exhibit strong site fidelity, with little dispersal occurring after the first year of life (Badyaev et al. 2006, 2008; Oh and Badyaev 2008). The population was systematically censused year-round at approximately 2-day intervals, rotating among seven permanent trapping locations distributed uniformly across the 42-ha study site. During the breeding season (late February to early August), pairs were identified by daily behavioral observations in the field or through attendance at nest sites.

House finches in this site are highly gregarious and typically forage and roost in mixed-sex flocks of 20–50 birds during the nonbreeding season (K. P. Oh, personal observation). Before the onset of the breeding season, flock sizes decrease until, at the time of nest initiation (late February), mated pairs are observed isolated from larger social groups, although the period of mate sampling and pair formation often extends into April (K. P. Oh, personal observation). Because shifts in behavioral patterns associated with nesting (e.g., mate guarding, incubation, pa-

rental care) are likely to influence the overall social structure during this time period, we restricted our analysis to a period preceding nest initiation in each year.

#### *Sexual Ornament Elaboration*

Ornamental plumage coloration in male house finches ranges from pale yellow to deep red/purple. To quantify elaboration of breast plumage ornaments, individuals were photographed along with red and yellow color standards against a neutral gray background (Kodak) using a 5-megapixel digital camera mounted on a tripod in a standard position (for details of protocol, see Badyaev et al. 2001). Ornament area (mm<sup>2</sup>), intensity (a relative measure of grayscale brightness, which ranges from black [0] to white [255]), and hue (measured as an angle around a 255° color continuum) were measured from resulting digital images using SigmaScan 5.0 software (SPSS). For all analyses presented here, values of hue and intensity were inverted, and hue was subsequently log transformed to achieve a normal distribution. Additionally, as all three measurements showed significant correlation with one another (area vs. hue:  $r = 0.44$ ,  $P < .0001$ ; area vs. intensity:  $r = -0.13$ ,  $P = .03$ ; hue vs. intensity:  $r = 0.26$ ,  $P = .001$ ), we used principal components analysis to describe overall ornament elaboration. The first two principal components (PC1 and PC2) described 83% of the total variance in coloration (47% and 36%, respectively). Large positive loading of ornament area and hue on the first principal component suggests that larger PC1 scores represent males with redder pigmentation and larger ornamented area. PC2 was primarily representative of ornament brightness, such that small scores corresponded with whiter plumage and larger scores with darker plumage.

#### *Social Network Analysis*

To assess patterns of social behavior and overall social structure, we assembled a network of interactions derived from pair-wise associations among individuals across the nonbreeding season (August–February) for each year. Social interactions were defined as occurring when two birds were captured in large walk-in traps in the same location within a 2-h trapping session. In testing the validity of this method, we found that social associations determined from captures were highly concordant with associations observed in the field ( $N = 51$  individuals; simple matching coefficient = 0.875,  $P < .05$ ), which is corroborated by observations of individuals within flocks commonly entering traps simultaneously. However, because a certain proportion of social associations inferred from such methods in natural populations are expected to result from chance co-occurrence as opposed to any active social af-

finity, all pair-wise associations were weighted using the half-weight index (HWI), which quantifies the strength of an association on the basis of the frequency of a dyadic interaction (Cairns and Schwager 1987). Association indexes were then compared to a null association rate (HWI<sub>null</sub>; Whitehead 1995), which estimates the expected value if individuals were interacting at random:

$$\text{HWI}_{\text{null}} = \frac{n_{\text{assoc}}}{N - 1},$$

where  $n_{\text{assoc}}$  is the average number of individuals captured together during a sampling interval and  $N$  is the population size (after Lusseau et al. 2005). Only associations with observed values greater than HWI<sub>null</sub> were included in the final network. Network assembly and calculation of association indexes were carried out using SOCPROG 2.3 (Whitehead 2009) and Ucinet 6 (Borgatti et al. 2002). Network graphs—in which social interactions are visualized as a series of nodes (individuals) interconnected by edges (social interactions)—were generated using a spring-embedding algorithm in NetDraw (Borgatti 2002).

The presence of structure within social networks was analyzed using an approach that iteratively divides individuals into groups in relation to the overall network modularity,  $Q$  (Newman 2003), a measure of the difference between the observed density of within-cluster associations and that expected if social interactions occurred randomly, with values of  $Q$  greater than 0.3 generally considered to reflect meaningful network structure (Clauset et al. 2004). Thus, this method not only infers the presence of social structure at the population level, but it also identifies membership of individuals into distinct groups on the basis of their patterns of social behavior. Within these groups, relative ornament elaboration of each was calculated as a  $z$  score for each individual by subtracting a male's trait value from the group mean and dividing by the within-group standard deviation.

#### *Male Social Behavior*

As a measure of individual movement among distinct social groups, betweenness centrality (BC; Freeman 1979) was calculated for all individuals within complete networks for each year. To control for differences in network size among years, values were standardized as a percentage of the maximum BC possible in each network (Hanneman and Riddle 2005). To assess the relationship between social lability and ornament elaboration, male BC scores were regressed over the first two principal components of ornament elaboration in general linear models with year and frequency of individual recaptures as covariates.

While male social lability across the nonbreeding season

may involve encounters with multiple social environments, the composition of a social group at the onset of pair formation should be most critical for mating success. Thus, to examine the mating consequences of male social behaviors, we extracted subnetworks for the period of mate sampling and pair formation (January–February). Individuals within these subnetworks were subsequently assigned into social modules from which male BC as well as relative ornament elaboration ( $z$  score) were calculated as above. Directional changes in relative attractiveness in relation to male social lability would suggest a role of such behaviors in determining social context of mate choice. Thus, we examined changes in male relative ornament elaboration across the nonbreeding season in relation to BC. Initial results suggested a significant effect of male ornament elaboration on the relationship between BC and changes in relative attractiveness ( $F_{\text{elaboration} \times \text{BC}} = 6.77$ ,  $df = 2, 52$ ,  $P < .02$ ); therefore, analysis was carried out separately on low (ornament elaboration PC1 < annual population mean) and high (PC1 > annual population mean) ornament elaboration groups.

#### *Sexual Selection Gradients*

Sexual selection on male ornaments was assessed by regressing pairing success on male plumage coloration ( $N = 307$  males). Once mated, individuals form strong pair bonds and frequently remate with the same partner over multiple seasons (K. P. Oh, unpublished data). Consequently, pairing success during the first breeding season is a critical component of fitness, as successful first-year males are significantly more likely to breed in subsequent years, compared to individuals that did not breed in their first year ( $\chi^2(1, N = 392) = 13.02$ ,  $P < .001$ ). Moreover, results from molecular paternity analysis suggest that extrapair fertilizations occur with relatively low frequency (Griffith et al. 2002) in this population, with only 15 of 206 (7.3%) genotyped offspring sired by males other than the social mate (K. P. Oh and A. V. Badyaev, unpublished manuscript). Thus, pairing success during the first breeding season is an overall important predictor of male reproductive performance and is unlikely to be biased by prior breeding experience with particular females. Fitness functions were first visualized by fitting male mating success to trait values using a cubic spline model with binomial error and a smoothing parameter selected via the method of cross-validation (Schluter 1988). Standard errors were obtained from bootstrapping (500 iterations). Linear selection gradients ( $\beta$ ) were calculated from least squares regression coefficients (Lande and Arnold 1983), and statistical significance was tested using logistic regression in a generalized linear model with binomial error and a logit link function (PROC GENMOD, SAS 9.1, SAS

Institute). Nonlinear selection gradients ( $\gamma$ ) were estimated as the doubled quadratic regression coefficients (Lande and Arnold 1983), where negative and positive values indicate patterns of stabilizing and disruptive selection, respectively.

## Results

### *Structure of Social Behaviors*

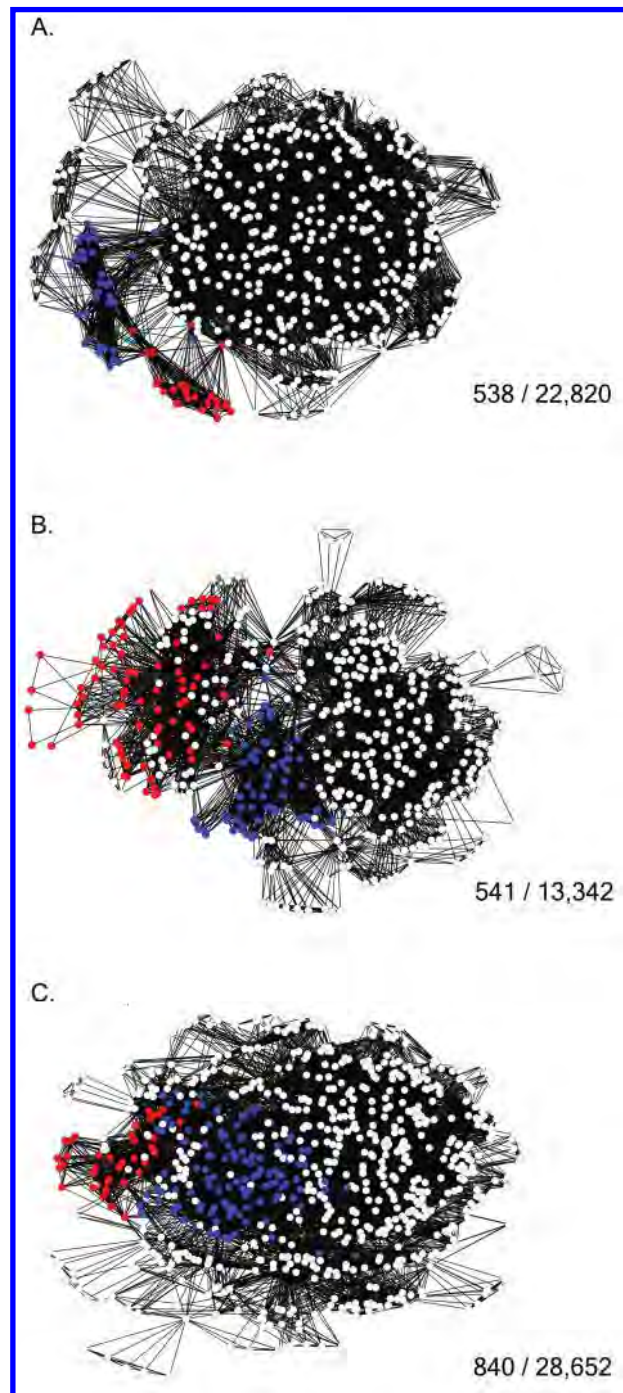
Social interactions across the nonbreeding season formed sparsely connected (mean density = 0.055; SD = 0.021) yet strongly clustered networks in all 3 years (fig. 1). The number of social clusters detected in each network was 20 (2004), 19 (2005), and 27 (2006), and overall network modularity ( $Q$ ; fig. 1) was 0.591, 0.687, and 0.599, respectively. The mean size of clusters was 28.18 individuals (SD = 18.26). Across all individuals included in the study, the sex ratio was significantly male-biased (proportion males = 0.53;  $N = 2,161$ ; two-tailed binomial test,  $z = 2.65$ ,  $P < .01$ ), and the proportion of first-breeding females that paired with males from within their clusters (0.34;  $N = 58$  pairings) was higher than expected under random mating (0.040; Fisher's exact test,  $P < .001$ ).

### *Male Pairing Success in Relation to Ornament Elaboration*

Among first-year breeding males ( $N = 262$ ), PC1 of ornament elaboration was a significant predictor of pairing success (fig. 2A; selection gradient  $\beta = 0.147$ ,  $P = .019$ ). PC2 of ornament elaboration had no significant effect on mating success (fig. 2B;  $\beta = 0.079$ ,  $P = .20$ ), and there was no significant stabilizing or disruptive selection on any component of ornament elaboration (fig. 2; PC1:  $\gamma = -0.020$ ,  $P = .48$ ; PC2:  $\gamma = -0.012$ ,  $P = .72$ ).

### *Male Social Lability in Relation to Ornament Elaboration*

Across years, first-breeding males on the whole had greater social lability (BC) than first-breeding females (asymptotic Mann-Whitney test,  $z = -2.08$ ;  $N = 1,094$ ; two-tailed,  $P < .04$ ). Among males, after controlling for effects of year ( $F_{\text{year}} = 4.41$ ,  $df = 2, 117$ ,  $P = .014$ ) and recapture frequency ( $F_{\text{recap}} = 39.6$ ,  $df = 1, 117$ ,  $P < .001$ ), males with greater ornamentation had fewer interactions with individuals in other social clusters (lower BC), compared to males with lesser ornamentation (fig. 3A;  $F_{\text{PC1}} = 4.49$ ,  $df = 1, 117$ ,  $P = .036$ ; standardized regression coefficient,  $b_{\text{ST}} = -0.18$ ). PC2 of ornament elaboration did not correlate with BC (fig. 3B;  $F_{\text{PC2}} = 0.12$ ,  $df = 1, 117$ ,  $P = .71$ ;  $b_{\text{ST}} = 0.03$ ), and thus only PC1 was retained in subsequent analyses. Change in relative attractiveness ( $z$  score of PC1) of individuals across the nonbreeding season co-



**Figure 1:** Empirically derived network of social interactions in a free-living population of house finches during the nonbreeding season, 2004–2006. Red and blue nodes represent two distinct clusters of highly interconnected individuals (other groups not colored for clarity) inferred using method of optimal modularity (see “Methods”). Numbers below graphs indicate total individuals and total associations. Graphs generated using spring-embedding algorithm. *A*, 2004, overall graph modularity index  $Q = 0.591$ ; *B*, 2005,  $Q = 0.687$ ; *C*, 2006,  $Q = 0.599$ .

varied positively with social liability for males with low ornament elaboration ( $F_{BC} = 5.15$ ,  $df = 1, 27$ ,  $P = .03$ ;  $b_{ST} = 0.40$ ) but not those with high ornament elaboration ( $F_{BC} = 2.93$ ,  $df = 1, 24$ ,  $P = .10$ ;  $b_{ST} = -0.33$ ).

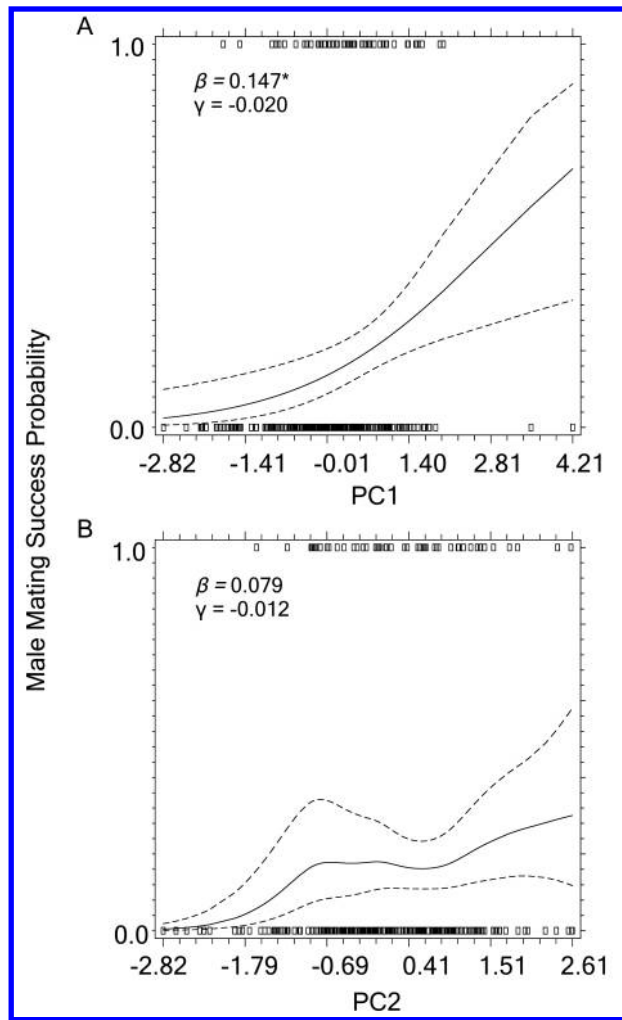
#### *Fitness Consequences of Male Social Liability*

Male mating success covaried positively with ornament elaboration (PC1:  $b = 0.15$ ,  $P = .002$ ) and BC ( $b = -1.09$ ,  $P = .019$ ), as well as the interaction of the two terms ( $b = 1.29$ ,  $P = .04$ ), indicating that the fitness consequences of ornament elaboration and male social liability were dependent on one another. The fitness landscape (fig. 4) revealed two peaks of high pairing success that represented elaborate males with low social liability (BC) and less elaborate males with high social liability.

#### Discussion

Behaviors that enable organisms to choose their environment can have profound evolutionary consequences at the population level by modifying selection pressures on phenotypes (Bogert 1949; Plotkin 1988; Huey et al. 2003; Duckworth 2009). Across diverse animal taxa, there is considerable evidence that males actively seek or create environments with physical properties that enhance their attractiveness or conspicuousness to females through amplification or background contrast (e.g., Jones et al. 1994; Endler and Théry 1996; Laland et al. 1999) or preferentially associate with particular social partners (Sinervo et al. 2006; McDonald 2007; Ryder et al. 2009). Because searching and sampling are often costly (Rosenzweig 1981; Stamps et al. 2005), the expression of these behaviors should differ among individuals, such that, all else being equal, the greatest investment is expected in individuals that stand to benefit the most from a change in their environment of selection (e.g., Williams 1966; Stearns 1992; Reznick et al. 2000; Badyaev and Qvarnström 2002).

Here we found that in a free-living house finch population, a metric of social behavior (betweenness centrality) was associated with an individual’s environment of sexual selection. As with many other gregarious species (Newman 2006; Wey et al. 2008), social structure in this population was composed of dense clusters of closely interacting individuals (fig. 1) and few interactions between groups (i.e., small-world networks, sensu Watts and Strogatz 1998). The importance of these social groups as arenas for mate choice was evidenced by a significantly greater frequency of pairings between individuals within clusters than expected by chance, and an overall male-biased sex ratio implies competition among males for a limited number of females. Overall, ornament elaboration was an important predictor of mating success in this population (fig.

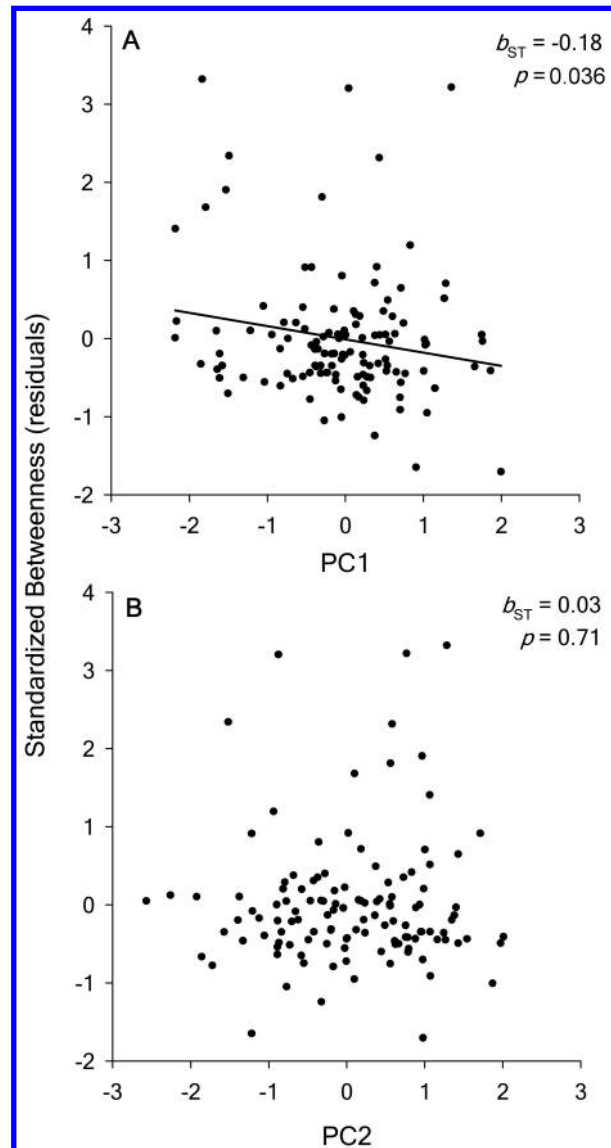


**Figure 2:** Mating success in relation to principal components of plumage ornamentation among first-year male recruits (2004–2006;  $N = 262$  males). Graphs are cubic splines of fitness functions, with dashed lines indicating bootstrapped standard errors. A, Principal component 1 (PC1); B, PC2;  $\beta$ , directional selection gradient;  $\gamma$ , stabilizing selection gradient; asterisk,  $P < .05$ .

2), suggesting that less elaborate males should benefit the most from selecting social environments that increased their relative attractiveness (e.g., Møller 2002; Bateson and Healy 2005). Consistent with this prediction, we found that social lability was greater in less elaborated males, whereas more elaborated males interacted mostly with individuals within their clusters (fig. 3). Moreover, by the onset of pair formation, males that exhibited greater social lability effectively increased their attractiveness relative to local conspecifics. Thus, these results demonstrate that the interaction between structured social networks, highly localized mate choice, and distinct patterns of social behavior among males in relation to ornament elaboration produces

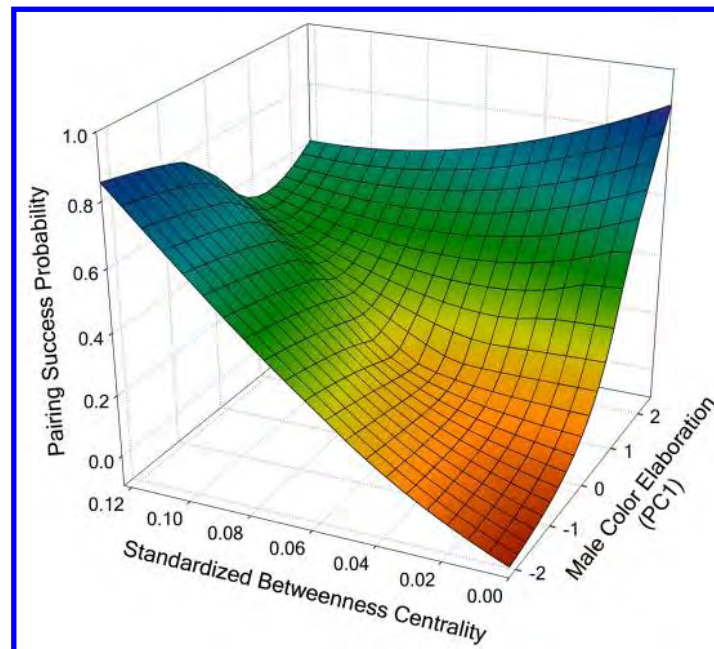
a fitness landscape (fig. 4) in which the relationship between sexual trait elaboration and male mating success was influenced by individuals' social behaviors.

Preferential association with particular social contexts requires a behavioral mechanism that enables individuals to reliably identify and discriminate among different groups (Endler 1993; Dall et al. 2005). Our results imply nonrandom grouping of individuals in relation to the sexual ornament elaboration of conspecifics, suggesting that



**Figure 3:** Social lability (betweenness centrality) in relation to principal component 1 (PC1; A) and PC2 (B) of ornament elaboration in first-year breeding males ( $N = 122$ ), 2004–2006. Values on ordinate are residual scores controlling for variation between years and frequency of recapture. Solid line represents least squares regression.





**Figure 4:** Pairing success probability (contour lines) in relation to social liability (betweenness centrality) and plumage color elaboration (PC1) among first-year breeding male house finches ( $N = 44$ ) during period of pair formation (January–February). Contour surface estimated using local bisquare smoothing algorithm with polynomial regression.

decisions regarding social affiliation may be based on an assessment of other males' ornament elaboration within current and prospective groups encountered. Recent work in other vertebrate systems suggests that individuals may use such types of social information in decisions regarding dispersal (Cote and Clobert 2007) or territory establishment (Sinervo et al. 2006). In contrast to active sampling and decision making, the observed patterns might alternatively be explained by a more passive process if less elaborated males are competitively subordinate to more elaborated males, and thus the apparent high betweenness centrality in the former reflects their frequent displacement from social groups. However, this explanation is unlikely in house finches as less elaborate males tend to be dominant over more elaborate males in agonistic interactions (Belthoff and Gauthreaux 1991; Belthoff and Gowaty 1996; Duckworth et al. 2004). Indeed, this observation suggests that, if resident individuals within a flock tend to show increased aggression toward newcomers (e.g., Balph 1979), less elaborate (and thus socially dominant) males may in fact be better able than more elaborate males to successfully join new social groups. Overall, the degree to which such dominance interactions might determine the size and composition of social groups in this species remains to be studied.

Given the apparent benefit to mating success, the ob-

served variation in social liability among male house finches suggests that such behaviors are costly in terms of time and energy spent sampling (Brown et al. 1990) or increased exposure to transmissible pathogens or parasites (e.g., Côté and Poulin 1995). In addition, costs of social liability may arise if individuals entering new social groups are subject to increased dominance conflicts with resident males, especially if a newcomer is perceived to be a competitive threat (Rohwer and Ewald 1981). Finally, the degree to which investment in searching for preferred social environments might trade off with components of male reproductive output other than pairing success could have significant fitness consequences. Such deferred search costs (Stamps et al. 2005) in this system might arise, for example, when investment into searching for preferred social contexts reduces males' allocation to mate guarding or paternal care. Indeed, while pairing success among first-year males is a robust predictor of paternity and remating success in this population (K. P. Oh and A. V. Badyaev, unpublished manuscript), more precise estimates of individual lifetime reproductive success would ultimately involve additional components (e.g., offspring quality, male longevity) not measured here. Nevertheless, this study provides several important insights with regard to the behavioral and social processes that contribute to variation in

male fitness and thus patterns of sexual selection in natural populations.

First, our results demonstrate a process by which male social behaviors and sexual trait elaboration interact to influence mating success. This not only emphasizes the importance of considering whole-organism performance in studies of sexually selected traits (Badyaev and Qvarnström 2002) but also suggests an interesting link between population social structure and male mating strategies. For example, house finch populations across North America have effective population sizes that differ by several orders of magnitude (Veit and Lewis 1996; Hawley et al. 2006), which should have important consequences for the types of social interactions during mate choice. In large populations (this study) in which females' ability to sample the complete range of male phenotypes is likely constrained, social groups represent important arenas for mate choice, whereas females in smaller populations (Oh and Badyaev 2006) may be able to effectively sample the entire range of available males at any given moment, in which case male social lability is expected to provide little mating benefit. Thus, sexual selection may favor distinct suites of male social behaviors in different populations or in response to changes in social structure within populations.

Second, while overall patterns suggest that a general mating advantage for greater ornament elaboration persists within this population (fig. 2A), the effects of male social lability contribute to the ruggedness of the fitness landscape (fig. 4), thereby potentially slowing the rate of evolutionary change. As a corollary, such interactions may also contribute to the maintenance of genetic variation in sexual plumage traits in this population (Reinhold 2000; Gorelick and Bertram 2003) if lesser ornamented variants that might have otherwise been eliminated by persistent directional sexual selection are buffered. Indeed, a number of recent empirical studies of local variation in demography (Kasumovic et al. 2008), female preferences (Chaine and Lyon 2008), or environmental conditions (Cockburn et al. 2008) have similarly highlighted the role of localized social interactions in generating mosaic patterns of sexual selection (e.g., Gosden and Svensson 2008).

Third, our results show that two distinct combinations of ornament elaboration and male social lability have roughly equivalent mating success (fig. 4), a pattern often considered to favor the evolution of alternative mating strategies (Gross 1996). This outcome is unlikely in house finches because male plumage ornamentation is determined, in part, by physiological condition at molt and by the availability of diet-derived carotenoids (Brush and Power 1976; Hill 1992) such that individuals often differ in elaboration of ornamentation from one molt year to the next (Badyaev and Duckworth 2003). Thus, a more probable outcome is the evolution of a conditional mating

strategy in which, depending on their physiological status at molt, males invest resources into distinct suites of behaviors that maximize fitness given their condition and residual reproductive value. Indeed, such plasticity in male reproductive tactics is evident in populations in which distinct combinations of male plumage color and parental care have equal fitness and in which integration of ornamental elaboration and behaviors is mediated by a shared hormonal mechanism (Duckworth et al. 2003; Badyaev and Vleck 2007).

In conclusion, here we have shown that, by preferentially associating with certain conspecifics, individuals are capable of influencing the sexual selection they experience. In addition to providing insight regarding the social and behavioral processes by which variation in mating success arises, these results suggest that studies of sexual selection in gregarious species should consider the effects of social structure on estimates of sexual selection and predicted evolutionary change.

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