Original Article

Urban and colorful male house finches are less aggressive

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Rapid human urbanization can have strong and varied impacts on the behavior and fitness of wild animals. The "credit-card hypothesis" predicts that low predation and high food predictability in cities lead to the presence of many weak competitors in urban populations. However, no experimental studies to date have found support for this hypothesis. Here, we studied the relationship between urbanization and aggressiveness in males of a widespread North American songbird (the house finch, *Haemorhous mexicanus*) while taking into account the degree of sexual signal elaboration (plumage coloration), which is known to impact competitive outcomes. In paired laboratory experiments, we found that colorful urban males were less aggressive than drab urban males, whereas there was no significant difference in aggressiveness between colorful and drab rural males. Moreover, we found that colorful urban males were less aggressive than colorful rural males, whereas there was no significant difference in aggressiveness between drab urban and drab rural males. In 4-bird trials (i.e., trials with colorful and drab males from both urban and rural environments), we found that colorful urban males were consistently less aggressive than all others. Taken together, these results support the credit-card hypothesis and the idea that plumage color is an important predictor of social status in urban environments. Finally, in a model-presentation study, we found that urban males with lower body condition avoided drab male models. Urban settings, along with the social and foraging conditions they create, may exert novel selection pressures that shape the competitiveness and status signaling systems of animals.

Key words: **aggression, competition, *Haemorhous mexicanus*, plumage coloration, sexual selection, urbanization.**

INTRODUCTION

Rapid worldwide urbanization is creating novel environments to which animals must adapt, a topic of growing interest for evolutionary biologists (Marzluff 2001; Shochat et al. 2006). Many studies have shown that urban animals differ in aspects of morphology (e.g., Liker et al. 2008), physiology (e.g., Bonier et al. 2007), and behavior (e.g., Yeh et al. 2007; reviewed in Shochat et al. 2006; Bókony et al. 2009; Lowry et al. 2013) relative to their rural counterparts. Urban areas typically contain fewer native predators (Marzluff 2001; Shochat 2004; Shochat et al. 2006) and provide a consistently high food base (e.g., garbage, bird feeders, artificial yard and park vegetation; Shochat et al. 2006). Under such conditions, selection for resource competitiveness may be relaxed, and urban populations are predicted to include a higher proportion of less-competitive individuals than rural populations living with unpredictable food sources (i.e., the credit-card hypothesis; Shochat 2004; Anderies et al. 2007). In other words, weak competitors can feed constantly and survive day-to-day without storing extra energy in urban areas, unlike in rural areas where they may face sudden food shortages.

Despite the potential applicability of the credit-card hypothesis to many organisms worldwide, as well as its potential explanatory power regarding population demographics and other key life-history features (e.g., large and skewed variance in life span and reproduction investment; Shochat 2004) of urban animals, we are aware of only 1 test of the credit-card hypothesis to date. Bókony et al. (2009) recently studied competitive behavior in house sparrows (*Passer domesticus*)—a cosmopolitan city species—as a function of urbanization. These authors failed to find any significant relationships between urbanization and several measures of competitiveness (e.g., fighting success; Bókony et al. 2009) and thus concluded that the effects of urbanization on population structure and competition (or aggression) could not be fully accounted for by the credit-card hypothesis (see also Liker et al. 2008; Bókony et al. 2012).

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One reason why Bókony et al. (2009) may have failed to uncover a general relationship between the degree of urbanization and competitiveness is because they did not account for the potentially confounding effect of sexual selection. Expression of sexually selected traits can be related to competitiveness, especially in males, if these traits are used to mediate intrasexual competitions (e.g., the black bib of the house sparrow; Nakagawa et al. 2008; reviewed in Senar 2006 and Santos et al. 2011). The effect of sexually selected traits may mask links between urbanization and competitiveness (i.e., the effect of urbanization on competitiveness is difficult to uncover under the confounding effect of sexually selected traits), and there have been no a priori predictions regarding how urbanization and sexually selected traits should interact to influence the competitiveness of individuals. Thus, to study the influence of urbanization on individual's competitiveness, expression and variance of sexually selected traits should be considered.

Here, we explored relationships between competitiveness, urbanization, and the expression of a sexually selected trait (carotenoid-based plumage coloration; see the next paragraph) in the house finch (*Haemorhous mexicanus*), a widespread North American passerine (Hill 1993). For 4 reasons, the house finch is an ideal species in which to test predictions of the credit-card hypothesis. First, they inhabit human-disturbed environments and have colonized most habitat types in the United States (e.g., Hill 2002; Shochat et al. 2004; Badyaev et al. 2008; Valcarcel and Fernández-Juricic 2009). Second, house finch population size or density is higher in urban areas compared with rural areas (e.g., Mills et al. 1989; Green and Baker 2003; Crooks et al. 2004), as predicted by the credit-card hypothesis (Shochat 2004). Third, house finches regularly consume food from urban and suburban bird feeders (Horn et al. 2013; rarely in rural areas, Lepczyk et al. 2004), and beak shape modifications have been reported in urban populations of this species, which may be due to consistent consumption of larger, harder-to-husk seeds at city feeders (Badyaev et al. 2008). Fourth, also as predicted by the credit-card hypothesis, urban populations of house finches have fewer native predators than rural ones (Valcarcel and Fernández-Juricic 2009; also see Fischer et al. 2012).

In house finches, the carotenoid-based plumage pigmentation of males is a sexually selected honest indicator of nutrition and health (e.g., Hill 1990, 1991; McGraw et al. 2001; Oh and Badyaev 2006). Additionally, previous experimental studies have shown that drab male house finches are more aggressive and dominant to colorful males (e.g., McGraw and Hill 2000a, 2000b; McGraw et al. 2007), but these studies have been conducted only on urban or suburban populations and thus no urban–rural context has been built into this line of work. Thus, we can investigate how coloration may factor into competitive interactions that occur in urban and rural areas.

We conducted a series of 4 laboratory experiments to investigate the competitiveness of urban and rural house finches. Because house finches compete over access to food at feeders and other concentrated food sources in the wild (e.g., Thompson 1960a, 1960b; Belthoff et al. 1994; McGraw and Hill 2000a, 2000b), we used direct aggression as a measure of food access and competitiveness here (sensu McGraw and Hill 2000a, 2000b; McGraw et al. 2007). In the first experiment, we compared aggression between colorful and drab males from the same habitat type ("within-site experiment"). Based on previous work (McGraw and Hill 2000a, 2000b; McGraw et al. 2007), we predicted that drab males would be more aggressive than colorful males. In our second experiment, we staged agonistic encounters between urban and rural males ("between-site

experiment") while matching for color type (i.e., colorful urban vs. colorful rural and drab urban vs. drab rural). According to the credit-card hypothesis, we expected urban birds to be less aggressive than rural birds. In our third experiment, we studied the relative aggressiveness of all 4 groups of birds (i.e., urban colorful, urban drab, rural colorful, and rural drab), by putting them into the same cage simultaneously ("group-competition experiment"), to study the interaction between urbanization, coloration, and aggressiveness. Last, we ran a "model-presentation experiment" (sensu Senar and Camerino 1998), in which we simultaneously presented each focal bird with a colorful and a drab house finch model and monitored its time spent perching near each model type. This approach removes the behavioral confound of live opponents and permitted us to assess how plumage coloration is used as a status signal per se, which may be a more effective approach than a direct plumage color manipulation of live birds (e.g., McGraw and Hill 2000b; because the behavior of manipulated birds may still affect the behavior of test birds). Based on previous work (McGraw and Hill 2000a, 2000b; McGraw et al. 2007), we predicted that drab models would be avoided due to the aggressiveness of drab birds.

MATERIALS AND METHODS
Capture and housing procedures

From 18 April–13 May 2011, 12 male house finches were captured using seed-baited basket traps (Hill 2002) at each of 2 urban sites and 2 rural sites in the greater Phoenix, Arizona metropolitan area, United States. Our 2 urban sites were the campus of Arizona State University (ASU) in Tempe (33′42″N, 111′93″W) and downtown Phoenix (33′46″N, 112′06″W). Our 2 rural sites—South Mountain Regional Park (33′35″N, 112′07″W) and the Estrella Mountain Regional Park (33′38″N, 112′37″W)—were located adjacent to the native desert habitats of house finches (see Giraudeau et al. 2014 for additional descriptions of the urban and rural characteristics of these sites). Though all 4 sites are relatively close to one another (within 10–40 km), we have never recaptured adults at sites different from the original site at which they were captured ($n > 1500$ birds), so we suspect that these are distinct adult populations; in fact, Badyaev et al. (2008) found that urban and rural populations of house finches in Arizona separated by only 6–10 km are genetically differentiated.

At capture, we weighed each bird (to the nearest 0.1 g), measured keel length (to the nearest 0.01 mm; Senar and Pascual 1997), and digitally photographed breast, head, and rump plumage to measure ornamental coloration (see Giraudeau et al. 2012, 2013 for detailed methods). To control for variation in lighting conditions, we calibrated plumage coloration by using a gray scale standard (Kodak gray scale; Tiffen Co., Hauppauge, NY) and a spectrophotometer (USB2000; Ocean Optics, Dunedin, FL; see Stevens et al. 2007). Because our experiments were conducted over a relatively short period outside the molting season (McGraw and Hill 2004; McGraw et al. 2007), relative colorfulness of birds (colorful and drab) remained unchanged during our experiment.

We sought to obtain males for our study that were at the ends of the color spectrum (referred to hereafter as colorful and drab), and we succeeded given that colorful and drab males differed significantly in breast hue and patch size (Table 1). However, 1 bird had to be removed from the Phoenix group (as we mistakenly captured 7 drab and 5 colorful males at this site), so our final sample size was 47 males.

Males were housed individually in indoor, animal-approved rooms in small wire cages (0.40 m × 0.29 m × 0.21 m; McGraw

Table 1

Comparison of measurements among the 4 categories of males

	Categories of males				P-values (from 2-way or repeated analysis of variance)			
	Urban colorful	Urban drab	Rural colorful	Rural drab	Time	Capture site (urban vs. rural)	Color type (urban vs. rural)	CS × CT
Plumage hue	13.07 ± 2.50	24.94 ± 3.37	10.25 ± 1.41	16.06 ± 3.82	—	<0.0001	<0.0001	<0.001
Color patch size	14.63 ± 4.35	12.51 ± 2.62	12.11 ± 2.48	9.85 ± 3.47	—	<0.01	0.03	NS
Keel length[a]	21.23 ± 0.52	21.26 ± 0.67	21.05 ± 0.55	21.28 ± 0.64	—	NS	NS	NS
Body mass at capture	18.80 ± 0.98	19.62 ± 1.24	18.79 ± 1.40	18.97 ± 0.72	—	NS	NS	NS
Body mass at experiment					0.02	NS	<0.001	NS
Of within site	17.64 ± 1.16	18.68 ± 1.74	17.78 ± 1.15	18.13 ± 0.67				
Of between site	17.60 ± 1.38	18.56 ± 1.63	17.58 ± 1.15	18.21 ± 0.66				
Of group competition	17.29 ± 1.24	17.64 ± 1.20	17.39 ± 1.21	17.77 ± 1.37				
Of model present	17.14 ± 0.93	18.18 ± 1.75	17.28 ± 1.32	17.74 ± 0.61				

NS, not significant. Values are represented as mean ± SD. CS × CT denotes the interaction between Capture site and Color type.
Samples sizes were 11, 12, 12, and 12 for urban colorful, urban drab, rural colorful, and rural drab, respectively.
[a]Sample sizes were reduced into 11, 12, 12, and 11 for urban colorful, urban drab, rural colorful, and rural drab, respectively.

et al. 2007) on the campus of ASU. Birds had access to ad libitum wild-bird seed (Leach Grain and Milling Company, Downey, CA) and water, and they were visually isolated from one another using barriers between cages (to minimize familiarity with other birds that could affect our behavioral trials; see McGraw et al. 2007 for detailed information) and were kept at 25 °C and on the local/outdoor photoperiod.

General procedures for aggression trials

Aggression trials were conducted in a large wire cage (0.77 m × 0.59 m × 0.50 m) containing multiple perches and a single food dish of sunflower seeds that we positioned in the middle of the cage. The day before each trial (at 1700 h), food and water were removed from the cages of the focal birds in order to maximize motivation for resource acquisition during the trials the following day (e.g., McGraw et al. 2007). Individuals showed no apparent signs of behavioral stress during or after this brief deprivation period.

Trials were conducted for 30 min each and were completed between 0600 and 0900 h. Trial duration was determined based on previous work (McGraw and Hill 2000a, 2000b; McGraw et al. 2007) and was sufficient to observe several aggression events. On the day of the experiment, males were weighed (as previously described) and then placed into separate black boxes on the floor of the test cage. These boxes were attached to a long thread, which allowed us to start the trial by simultaneously lifting the boxes and releasing the males into the cage from a distance. From videotapes of each trial, we counted the number of aggressive encounters won by each bird (e.g., perch/feeder displacements; see McGraw et al. 2007) and deemed individuals as winners of a trial when they won at least 2 more aggressive encounters than their counterpart (cf., McGraw and Hill 2000a, 2000b; McGraw et al. 2007). No injuries were observed during aggression trials. Videos were watched by 2 observers, and we found high interobserver repeatabilities in the number of aggressive encounters won by each bird (>0.89, measured as original-scale repeatability assuming a Poisson distribution; sensu Nakagawa and Schielzeth 2010); thus, we used average values of their aggression scores in statistical analyses. To facilitate observer recognition of the similarly colored individual birds in each trial, males in a dyad randomly received either a green or blue plastic band on the right or left leg during the between-site and group-competition experiments. Birds were given food and water immediately after the trial when returned to their home cage.

Within-site experiment

We performed 23 trials (11 using urban birds and 12 using rural birds) from 24 to 29 May 2011. Phoenix (urban) males competed against Tempe (urban) males, whereas South Mountain (rural) males were paired with Estrella Mountain (rural) males, in order to avoid prior familiarity as a confounding factor. One trial with urban birds was excluded from the analyses because we were not able to determine a winner based on our behavioral criteria (only 1 aggressive/submissive interaction occurred; cf., McGraw et al. 2007). We observed a total of 355 aggressive/submissive interactions during the 22 successful trials (mean ± standard deviation [SD] interactions per trial = 16 ± 14).

Between-site experiment

Trials were conducted from 1 to 6 June 2011. The same males used in the within-site experiment were used in this experiment (n = 23 total trials). We tested statistically for potential winner/loser carryover effects in these trials (see Results), but we minimized such effects by conducting trials an average of 8 days (range = 6–10) after within-site experiment trials had ended (see Hsu et al. 2006).

In this experiment, urban (i.e., Phoenix or Tempe) males were pitted against rural (i.e., South Mountain or Estrella Mountain) males. The hierarchy of criteria used in pairing birds was to match them for similar rank of coloration (brighter vs. brighter and drabber vs. drabber in each color category) and body mass at capture. Again, there was 1 trial where birds interacted aggressively only once, so we omitted this trial from subsequent analyses. We observed a total of 298 aggressive interactions during the 22 successful trials (mean ± SD interactions per dyad = 14 ± 13).

Group-competition experiment

Trials were conducted from 8 to 10 June 2011, which for each bird was, on average, 5 days (range = 4–7) after trials from the prior experiment were completed. In each trial, 4 males were placed in cage, such that drab and colorful members of both the urban and rural populations were represented. In this experiment, male groupings were randomly assigned with respect to both coloration and body mass, except that no bird was ever grouped with another male with whom he had previously competed. We observed a total of 497 aggressive interactions during the 11 trials (mean ± SD interactions per quad = 44 ± 32). In addition to the number of aggressive encounters won, we also studied the number of

aggressive encounters lost in this experiment, as this provided additional information about the web of interactions that occurred in the 4-bird groups.

Model-presentation experiment

Four stuffed house finch models were made from previously euthanized individuals that were captured from 2 sites (2 from the ASU campus and 2 from Chandler, AZ; 33′33″N, 111′91″W). We arbitrarily assigned these models to 2 treatments—colorful and drab—by coloring the ornamental feathers to be either red (for colorful models) or orange (for drab models) using Prismacolor™ nontoxic art markers (see McGraw and Hill 2000b; McGraw et al. 2007 for detailed methods and spectral measurements of colored feathers).

Trials were conducted from 13 to 16 June 2011 and lasted 10 min each (which is sufficient for studies of this kind; cf., Senar and Camerino 1998). In each trial, we randomly chose 1 colorful model and 1 drab model from the 4 models and positioned them on the outside of the cage (Figure 1). In front of each model, we placed 1 perch and 1 food tray containing sunflower seeds. We alternated the left/right positioning of the drab and colorful models among trials. Models that were originally captured from the ASU campus were not used in trials including focal birds from the ASU campus.

To exclude the possibility that some unmeasured characteristics of the models influenced behavioral decisions of focal males, we changed the coloration of the models after half of the trials; we did this by removing the previous marker color with 70% ethanol and then coloring previously orange models with red marker and previously red models with orange marker. We excluded 1 trial from the analysis due to an error in model arrangement. Also, because some focal males did not land on perches, these trials ($n = 9$; urban colorful $n = 1$; urban drab $n = 4$; rural colorful $n = 3$; rural drab $n = 1$) were excluded from analyses; thus, our final number of successful trials was 37. From the videotapes of each trial, we measured the time that each bird spent perched near each model (cf., Senar and Camerino 1998), which showed highly significant repeatabilities when assessed by our 2 observers (0.92 for colorful models and 0.93 for drab models; $F > 25.15$, $P < 0.0001$; Lessells and Boag 1987; Nakagawa and Schielzeth 2010).

Statistical analyses

A generalized linear mixed model (GLMM) with a Poisson error distribution was used to test the effect of predictor variables (see Tables 2–4) on the number of male aggressive interactions won per trial, using "lmer" in R package "lme4." The identity of focal birds was included as a random factor because the data were over-dispersed (Bates et al. 2011). Similar analyses assuming Poisson error distributions have been used in other aggression studies (e.g., Cronin and Field 2007; Santos et al. 2009). For the group-competition experiment, we used GLMMs to analyze both aggressive encounters won and lost. To avoid overfitting and the associated problem of detecting spurious effects with moderate sample size, we did not consider interactions between the predictors when studying the number of male aggressive interactions won and lost (Burnham and Anderson 2002). Continuous variables were standardized to 0 mean and unit variance before analysis, implying that coefficients denoted the effects of 1 SD of each variable in GLMMs (see Schielzeth 2010). A Wald test was used to test the statistical significance of each coefficient in the models. In the model-presentation experiment, we used nonparametric tests (e.g., Mann–Whitney). All data analyses were performed using the R (version 2.14.1) statistical package (R Development Core Team 2011).

RESULTS

Comparison of morphological traits

Keel length and body mass at capture were not significantly predicted by capture site, color category, or their interaction (Table 1). However, colorful males had lower body mass than drab males at the time experiments were run (Table 1), indicating that color grouping might be confounded by body mass in our trials. Thus, hereafter, we also statistically analyzed body mass taken at the time each experiment was run, and body mass change (i.e., body mass at experiment − body mass at capture), in relation to male aggressiveness.

Within-site experiment

In trials with urban males, drab males won more aggressive encounters than did colorful males (Table 2, Figure 2a). There were no significant effects of body mass, body mass change, capture date, or keel length on the number of aggressive interactions won (Table 2). In trials with rural males, the number of aggressive encounters won was not significantly predicted by plumage color, body mass, body mass change, capture date, or keel length (Table 2; Figure 2b).

Between-site experiment

In trials with colorful males, the number of aggressive encounters won was significantly predicted by capture site (Table 3); rural males won more aggressive encounters than urban males (Figure 3a). No other variables significantly predicted the number of aggressive encounters won (Table 3). For drab males, neither capture site, body mass, body mass change, capture date, nor keel length significantly predicted the number of aggressive encounters won (Table 3; Figure 3b).
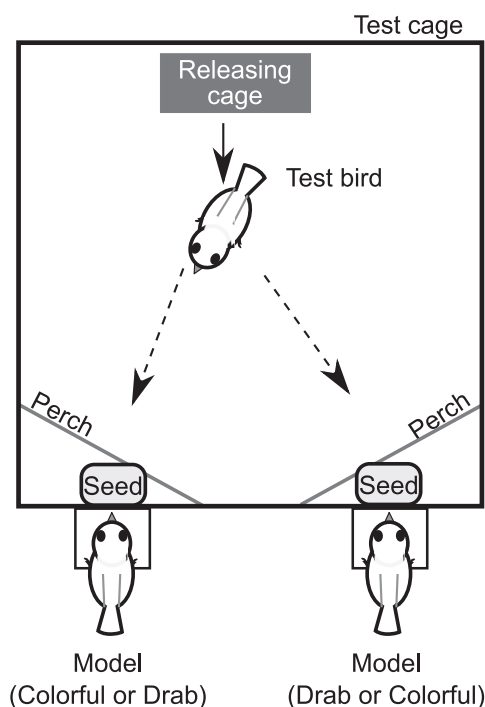

Figure 1
Design of the cage used in our model-presentation experiment.

Univariable GLMM analyses with Poisson distribution predicting variation in the number of aggressive encounters won in urban and rural males, respectively, during the "within-site" experiment

Variables	Urban			Rural		
	Coefficient ± SE	z	P	Coefficient ± SE	z	P
Color type	3.36 ± 0.98	3.43	**<0.001**	−0.48 ± 0.96	−0.50	0.61
Body mass at experiment	0.55 ± 0.56	0.99	0.32	−0.41 ± 0.48	−0.86	0.39
Body mass change	0.36 ± 0.55	0.65	0.51	0.44 ± 0.46	0.97	0.33
Capture date (1 April = 1)	1.07 ± 0.57	1.87	0.06	−0.45 ± 0.49	−0.92	0.36
Keel length[a]	0.77 ± 0.54	1.42	0.16	0.16 ± 0.52	0.31	0.76

Sample sizes were 20 and 24 for urban and rural males, respectively. Significant test result ($P < 0.05$) is indicated in bold.
Trial number and bird ID are included as random factors.
Body mass change was calculated by body mass at experiment – body mass at capture.
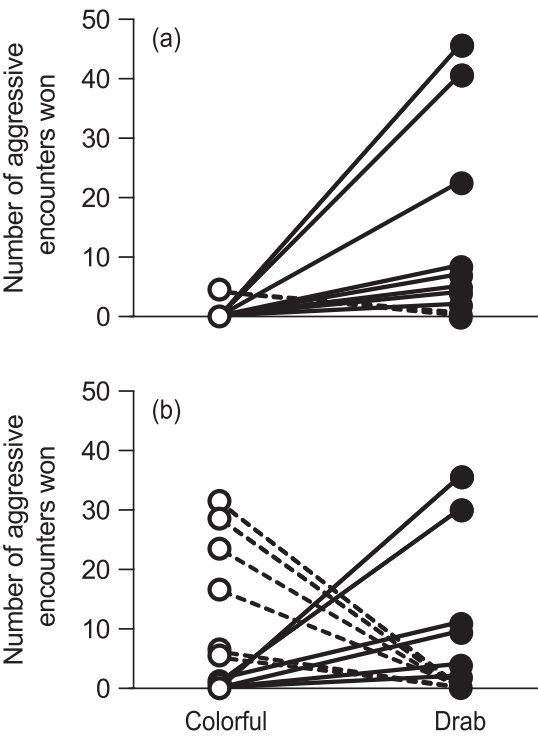[a]Sample size was reduced into 22 for rural males.

Figure 2
Point plots that compare aggressive encounters won by colorful males and drab males in (a) urban and (b) rural populations. Points show data for individual birds, and lines connect the points for birds that participated in the same trial. Dashed lines denote trials where colorful males had higher values than drab males, and solid lines denote trials where drab males had higher values than colorful males.

Figure 3
Point plots that compare aggressive encounters won by urban males and rural males in (a) colorful and (b) drab males. Points show data for individual birds, and lines connect the points for birds that participated in the same trial. Dashed lines denote trials where urban males had higher values than rural males, and solid lines denote trials where rural males had higher values than urban males.

These results remained unchanged qualitatively (i.e., capture site was significant [$P < 0.001$] in analyses of colorful male trials and not significant [$P > 0.8$] in analyses for drab male trials; data not shown) when we statistically controlled for the win/loss outcome of birds from the within-site trials. This indicates that colorful urban males lost more encounters independently of their experience in prior trials. Because win/loss outcome did not significantly predict the number of aggressive encounters won by drab males ($P = 0.12$, which contrasts with $P < 0.0001$ in colorful males; data not shown), previous experience does not appear to be a strong predicto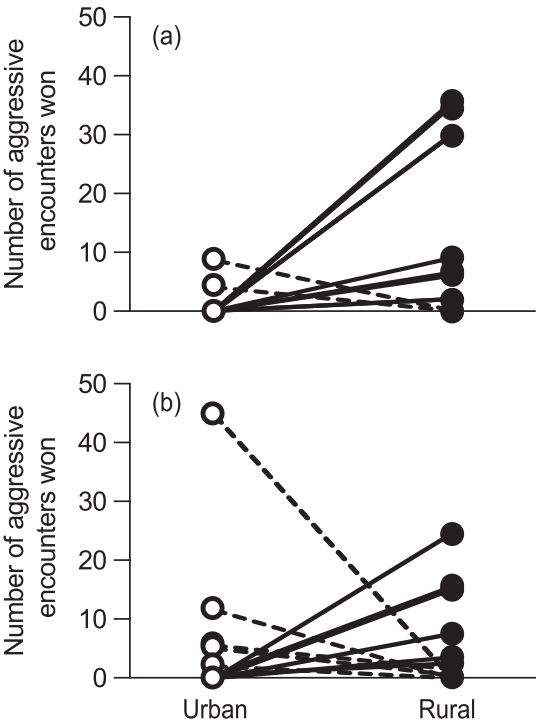r of aggression or dominance among individuals with similar competitiveness (see Tables 2 and 3; see also Group-competition experiment).

Group-competition experiment

Urban colorful males won fewer aggressive encounters than all other groups (Table 4; Figure 4a). The number of aggressive encounters won was not significantly predicted by body mass, body mass change, capture date, or keel length (Table 4). Additionally, urban colorful males tended to lose more aggressive encounters than other males (Table 4; Figure 4b). Neither body mass, body

Table 3

Univariable GLMM analyses with Poisson distribution predicting variation in the number of aggressive encounters won in colorful and drab males, respectively, during the "between-site" experiment

Variables	Colorful			Drab		
	Coefficient ± SE	z	P	Coefficient ± SE	z	P
Capture site (urban vs. rural)	3.38 ± 1.19	2.83	**<0.01**	0.11 ± 0.81	0.14	0.89
Body mass at experiment	0.02 ± 0.66	0.03	0.98	−0.18 ± 0.39	−0.45	0.65
Body mass change	0.79 ± 0.57	1.37	0.17	0.08 ± 0.40	0.21	0.84
Capture date (1 April = 1)	1.24 ± 0.68	1.82	0.07	−0.29 ± 0.40	−0.73	0.47
Keel length[a]	0.36 ± 0.66	0.55	0.58	0.19 ± 0.47	0.39	0.69

Sample sizes were 20 and 24 for colorful males and drab males, respectively. Significant test result (P < 0.05) is indicated in bold.
Trial number and bird ID are included as random factors.
Body mass change was calculated by body mass at experiment – body mass at capture.
[a]Sample size was reduced into 22 for drab males.

Table 4

Univariable GLMM analyses with Poisson distribution predicting variation in the number of aggressive encounters won and lost, respectively, during the "group-competition" experiment

Variables	Number of aggressive encounters won			Number of aggressive encounters lost		
	Coefficient ± SE	z	P	Coefficient ± SE	z	P
Male categories						
Intercept (urban colorful)	0.35 ± 0.49	0.7	0.48	2.46 ± 0.33	7.49	**<0.0001**
Urban drab	1.24 ± 0.67	1.86	0.06	−0.95 ± 0.44	−2.13	**0.03**
Rural colorful	1.51 ± 0.66	2.27	**0.02**	−0.79 ± 0.44	−1.79	0.07
Rural drab	1.38 ± 0.67	2.08	**0.04**	−0.54 ± 0.44	−1.24	0.22
Body mass at experiment	0.07 ± 0.24	0.3	0.76	0.01 ± 0.18	0.05	0.96
Body mass change	0.34 ± 0.23	1.47	0.14	−0.08 ± 0.18	−0.41	0.68
Capture date (1 April = 1)	0.14 ± 0.24	0.57	0.57	−0.19 ± 0.17	−1.12	0.26
Keel length	0.30 ± 0.27	1.12	0.26	0.14 ± 0.18	0.77	0.44

Sample size was 44 for each analysis, except for keel length (n = 40). Significant test results (P < 0.05) are indicated in bold.
Trial number and bird ID are included as random factors.
Body mass change was calculated by body mass at experiment – body mass at capture.

mass change, capture date, nor keel length significantly predicted the number of aggressive encounters lost (Table 4). When calculating the number of aggressive encounters won minus lost, the value for urban colorful males was significantly less than 0 (mean ± standard error [SE], −13.6 ± 5.7; 1-sample Wilcoxon signed-rank test: V = 9, P = 0.037). The values for the other 3 male categories were not significantly different from 0 (urban drab: 5.4 ± 8.5; rural colorful: 8.6 ± 9.0; rural drab: −0.2 ± 4.4; 1-sample Wilcoxon signed-rank test: all: 31 ≤ V ≤ 37, P > 0.50).

Model-presentation experiment

There was no significant difference in the amount of time that urban males spent at the perch near colorful versus drab models (Figure 5a). Of the 18 urban males, 10 spent more time near the colorful model (1-sample sign test, P = 0.81). Neither plumage color category, body mass, capture date, nor keel length differed significantly between males that spent more time near the colorful model and those that spent more time near the drab model (color type: Fisher's Exact test, P = 1.0; body mass, capture date, keel length: Mann–Whitney U test, all $|z|$ < 1.73, all P > 0.08). However, when comparing body mass change, males that spent more time with the colorful model lost more body mass in captivity than males that spent more time with the drab model (Mann–Whitney U test, z = 3.51, P < 0.0001; Figure 6).

Rural males spent significantly more time near the colorful model than near the drab model (Figure 5b). Of the 19 rural birds tested, 15

spent more time with the colorful model (1-sample sign test, P = 0.02). Neither color type, body mass, capture date, nor keel length differed significantly between males that spent more time with the colorful model and males that spent more time with the drab model (color type: Fisher's Exact test, P = 1.0: body mass, capture date, keel length: Mann–Whitney U test, all $|z|$ < 1.35, all P > 0.18). In addition, there was no significant difference in body mass change between males that spent more time with the colorful model (mean ± SE, −1.09 ± 0.27) and those that spent more time with the drab model (mean ± SE, −2.24 ± 0.47; Mann–Whitney U test, z = −1.75, P = 0.08).

DISCUSSION

Several studies in urban/suburban house finches have shown that colorful males are less aggressive and competitive than drab males in foraging contexts (McGraw and Hill 2000a, 2000b; Hill 2002; Duckworth et al. 2004; McGraw et al. 2007). Here, we tested resource competitiveness of colorful and drab males within an urban–rural context and found that colorful urban males were less competitive than all other males. To our knowledge, this is the first experimental study to demonstrate a link between urbanization and competitiveness in any animal species. The fact that urban populations contained less-competitive birds than rural populations is consistent with the credit-card hypothesis, which predicts the persistence of weak competitors in urban environments (Shochat 2004). To formally test the mechanisms underlying this pattern, future studies

should also assess food abundance and predation pressures in urban and rural populations and how these link to bird competitiveness.

An alternative explanation for our results could be that colorful urban males were less likely to be involved in aggressive interactions over food due to a better body condition at the start of experiment.
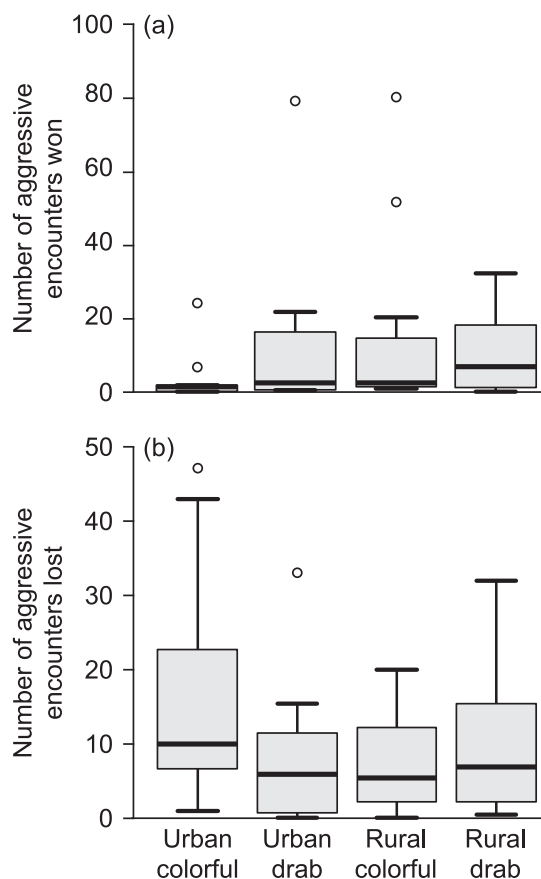

Figure 4
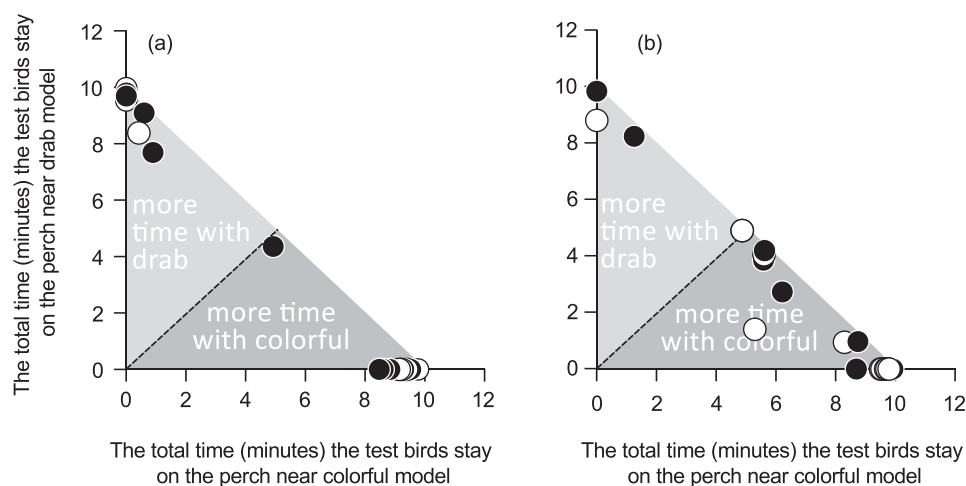Boxplots showing the number of aggressive encounters (a) won and (b) lost by each category of males.

However, this explanation seems unlikely because we kept the birds in captivity for 2 weeks with ad libitum food supply before the start of the experiments, which should reduce difference in body condition among individuals. Additionally, neither male body mass nor body mass change significantly predicted aggressive behavior in our trials. Finally, colorful males in our study had, on average, lower body condition at the start of experiments than drab males (Table 1), suggesting that colorful males should have been more aggressive if condition was a driver of aggression in this study.

One might predict, based on prior work (McGraw and Hill 2000a, 2000b; Hill 2002; Duckworth et al. 2004; McGraw et al. 2007), that drab males are more aggressive than colorful males within rural environments as well, but we did not find such a pattern. This suggests labile intraspecific relationships between coloration and aggression, at least for carotenoid-based ornaments in house finches. In fact, although there are clear mechanistic links between other forms of color (such as melanin-based) and aggressiveness in various bird species (i.e., pleiotropic gene effects; reviewed in Ducrest et al. 2008), exaggeration of carotenoid ornaments is not as consistently coupled with aggressive behavior (reviewed in Senar 2006). Perhaps mainly due to the extrinsic inputs (e.g., diet), links between carotenoid ornaments and aggressiveness may be shaped by each local environment (i.e., urbanization in the current case; see the next 2 paragraphs) rather than by pleiotropic genetic links.

In urban environments, females may have greater access to males due to higher population densities (Shochat 2004; Kokko and Rankin 2006); thus, regardless of geographic consistency of female mate preference, there should be more intense sexual selection for high-quality, colorful males as mates in urban sites (e.g., Hill 1991; Toomey and McGraw 2012). Given their mating advantage, more colorful urban males may have less incentive for aggressive competitions. The more consistent food (i.e., backyard-feeder) resources available in urban areas (see Introduction) may further reduce the need to be aggressive/competitive, except for drab urban males, whose mating disadvantages may drive them to pursue an alternative, "best-of-a-bad-job" aggressive strategy (sensu McGraw et al. 2007).

In contrast, both colorful and drab males may benefit from being aggressive in harsher, rural areas, where they may have to compete more for scarce, unpredictable food resources (see Introduction)
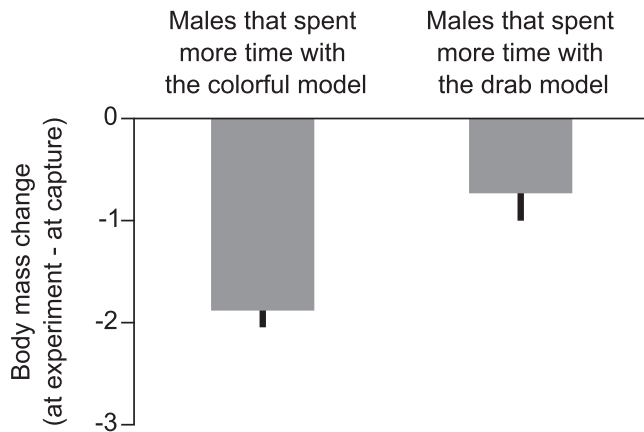

Figure 5
Male attendance time (minutes). Points above the dashed line indicate males that spent more time with the drab model; points below dashed line indicate males that spent more time with the colorful model. (a) Urban male and (b) rural male. Filled circles indicate colorful focal males, and hatched circles indicate drab focal males.

Figure 6

Difference in the body mass change (i.e., body mass at experiment – body mass at capture) between males that spent more time with the colorful model and males that spent more time with the drab model in urban males. Bars depict mean ± SE.

and for females who are less likely to encounter with (due to low population densities). It should also be noted that aggression often carries significant costs (in terms of associated behaviors, Schuett et al. 2010), including risks of predation, physiological stress, and injury (reviewed in Senar 2006). These costs suggest that submissive behavior among colorful city finches may not arise simply as the result of relaxed selection, as proposed by the original credit-card hypothesis (Shochat 2004), but as an adaptive response to a consistently high food base in urban contexts. The relative importance of nonadaptive and adaptive responses to urban environment remains to be explored in future studies.

This hypothesized scenario predicts that sexual selection pressures and expression of ornamentation should be elevated in urban sites, which at first seems to contrast with observed population differences in plumage coloration (i.e., finches are generally more colorful in rural compared with urban sites; Table 1). Unfortunately, selection cannot be inferred from the observed population differences in plumage coloration, as plumage coloration depends on carotenoid availability in each habitat (Hill 1993; Hill et al. 2002; see also Isaksson and Andersson 2008) as well as the actual sexual selection pressure itself. Consistent with this possibility, levels of some circulating and plumage carotenoids (e.g., 3-hydroxy-echinenone) are lower in urban environments (Giraudeau M and McGraw KJ, in preparation). Scarcity of carotenoid pigments would decrease mean male plumage coloration and increase variance of plumage coloration in urban populations (Table 1), which may in turn reinforce motivational asymmetries for resources and, as a result, differential male aggressiveness.

Given that differences in male coloration are associated with differences in aggressiveness within urban populations, males should pay attention to plumage coloration of potential opponents in these habitats. Although urban males did not exhibit consistent avoidance of drab mounts in our model-presentation experiment, urban males with lower body condition avoided perching near drab male models. One explanation for this condition-dependent behavior is that the need for immediate food intake increased with decreasing body condition. Thus, males with lower body condition may cautiously avoid energy-demanding, time-consuming competitive interactions with drab birds. Consistent with this explanation, male body mass change tended to be negatively correlated with the latency to perch beside models in this experiment ($n = 18$, Kendall's

rank correlation coefficient, $\tau = -0.34$, $P = 0.052$), indicating that male cautiousness increased with decreasing body condition. The observed pattern is consistent with the idea that carotenoid-based plumage coloration of house finches is used for assessing the aggressiveness of the opponent.

On the other hand, it was intriguing that rural males consistently avoided drab models in our model-presentation experiment. This could be due to a rare-male effect (i.e., frequency-dependence; Gray and McKinnon 2007), given that we infrequently encounter non-red males at our rural sites. Because colorfulness of plumage indicates nutritional and health status in this species, such rare-male avoidance could allow rural males to avoid potentially problematic individuals, especially in populations with abundant carotenoids (e.g., infected males may have fewer available carotenoids for feather ornamentation due to the allocation of carotenoids to immune activity; e.g., Brawner et al. 2000; Hill 2002). Thus, the observed male responses toward opponents are regarded to be adaptive in each environment.

In summary, we documented a link between urbanization and aggressiveness after accounting for plumage coloration, a sexually selected ornament. Thus, we suggest that sexual selection should be carefully considered when studying the impacts of urbanization on animal behavior. Additionally, the results of our model-presentation study, where we found that urban and rural males discriminated colorful and drab models differently, suggest that urbanization may serve as a novel selection pressure shaping visual signaling systems. Future studies should assess costs and benefits during food contest (or interference) competitions, in both cities and rural areas, and especially compared with other forms of competition (e.g., scramble competition for food, direct competition for mates).

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