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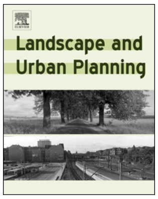

Research Paper

Avian anthrophobia? Behavioral and physiological responses of house finches (*Haemorhous mexicanus*) to human and predator threats across an urban gradient

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ABSTRACT

Urban environments present animals with many novel experiences, not the least of which is the physical presence of humans. However, most studies on urban predation do not take human presence into account. We examined behavioral and physiological responses of a songbird species (the house finch, *Haemorhous mexicanus*) that is abundant in both natural and urban areas to the presence of humans and to a native predator model to distinguish whether urban birds show consistently bolder behavior or if they differentially respond to a threatening native predator versus a potentially more benign human. During three field seasons (winter 2012, summer-fall 2012, and winter 2013), we captured birds at six sites (urban, suburban, and rural) and measured breath rate (an indicator of stress). We then tested behavioral reactions of caged finches to an approaching human and both a hawk (predator) and dove (control-bird) flyover. We found that rural birds had lower breath rates than urban birds, but that urban birds showed fewer activity behaviors (e.g., hops, flights) than rural birds in response to an approaching human. Urban and rural birds did not differ in their behavioral responses to either the hawk or dove mount, though there were seasonal differences. Because house finch behavioral responses varied as a function of type of stimulus presented, our results point to an example of plasticity rather than to a generalized bold urban phenotype and also implicate tolerance of human proximity as a key factor driving urban success in some avian species.

1. Introduction

The world's wildlife currently faces an unprecedented challenge. For the first time in human history, more people reside in cities than rural areas, and the growth of urban areas is projected to double by 2030, thus rapidly encroaching upon most natural ecosystems (U.N. DESA, 2003). Some species gain advantages by living in proximity to humans or cities (Marzluff, 2012), such as availability of anthropogenic food sources (Newsome, Garbe, Wilson, & Gehrt, 2015; Tryjanowski et al., 2015), urban-provided cover and nesting sites (Isaac, White, Erodiaconou, & Cooke, 2014; Møller, 2009), year-round water resources (Fokidis, Orchinik, & Deviche, 2009), and moderate weather (Shochat, Warren, Faeth, McIntyre, & Hope, 2006). In contrast, many animals suffer by living in proximity to humans or cities, due to habitat loss (Grimm et al., 2008) or exposure to nonnative competitors (Shochat et al., 2010) and predators (e.g., cats; Loss, Will, & Marra, 2013), pollution (Isaksson, 2015), and pathogens (Bradley & Altizer, 2007). These environmental changes have displaced many species, while others have adapted and persist in human-modified ecosystems. A large focus of urban ecology is identifying which factors are playing a role in these species shifts and how some species acclimate to these environments.

One way that animals seem to be adapting to urban areas is via modified behavioral responses (Marzluff, 2017). Features of urban environments cause many animals to modify their behavior and change, for example, their response to predators (Kitchen, Lill, & Price, 2010; Mccleery, 2009) or competitors (Hasegawa, Ligon, Giraudeau, Watanabe, and McGraw, 2010), habitat choices (Miller, Knight, & Miller, 1998; Yeh, Hauber, & Price, 2007), vocalizations (Brumm, 2004; Barber, Crooks, & Fristup, 2009), modify feeding tactics (Møller, 2008; Liker and Bokony, 2009), stress physiology (Fokidis & Deviche, 2011), and breeding behavior (Vaugoyeau et al., 2016). However, non-native predators, such as cats, are among the largest threats to urban-dwelling animals (Marzluff, 2017), thus leading to behavioral modifications in response to predators one of the most important drivers of behavioral differences among populations (Luttbeg & Sih, 2010; Stamps, 2007).

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Shochat et al. (2006) suggested that predation could be one of the primary forces shaping the composition of urban animal communities as well. Initially, the safe-habitat hypothesis (Tomialojc, 1982) proposed that animals experience reduced predation risk in urban areas due to lack of native predators. However, researchers have since come to realize that, while predation rates may be lower in cities, vertebrate predator densities can be higher (i.e. the "predation paradox"; Fischer, Cleeton, Lyons, & Miller, 2012). In addition, many studies of urban predation have failed to consider the role of humans, which, through actual or perceived predation, can negatively affect animal foraging behavior (Ward & Low, 1997), patch use (Fernandez-Juricic and Telleria, 2000), population density (Fernandez-Juricic, 2009), and fecundity (Zanette, White, Allen, & Clinchy, 2011).

As humans abound and expand their range worldwide, how a species responds to human presence – and the ability to differentiate humans from predators and identify their presence as less threatening – may be a key predictor of urban acclimation and adaptation. Studies that have evaluated how urban populations of animals respond to human physical presence have produced mixed results. Although several studies found that birds show a relaxed response to humans in urban environments, taking flight later in response to their presence (Arroyo, Mougeot, & Bretagnolle, 2017; Carrete & Tella, 2011; Carrete & Tella, 2017; Møller, 2008), Valcarcel and Fernandez-Juricic (2009) found that urban house finches (*Haemorhous mexicanus*) took flight sooner in the presence of humans than rural counterparts. In addition, recent studies have found that the amount of time to take flight in response to human/predator presence can be affected by the presence of bird feeders (Møller, Díaz, et al., 2015; Møller, Tryjanowski, et al., 2015), the direction of the approach (direct vs transiential; Møller & Tryjanowski, 2014), and vehicle speed (DeVault, Blackwell, Seamans, Lima, & Fernández-Juricic, 2014). Therefore, it appears that animals use many cues to assess humans as potential threats in their environments, and thus behavioral responses, and their underlying physiological causes, could be more complex and require a more detailed understanding of their nuances.

While FID studies allow researchers to understand how animals respond to human presence in their environment, a more detailed understanding of behavioral responses, and the underlying physiological mechanisms, may identify additional behavioral differences that can better elucidate why some animals tolerate humans better than others. In addition, previous studies have not compared behavioral responses of animals to humans with those to native predators, to determine if urban and rural populations respond differently to different vertebrate threats, or perceive humans as threats at all (or as something novel). Here, we tested behavioral and physiological responses of house finches along an urbanization gradient to the presence of both an approaching human and a native (hawk) predator. By measuring finch responses to both a human, a hawk mount, and a control (dove mount) stimulus, we could (1) examine differences in behavioral and physiological stress responses to potential predators among rural, suburban, and urban populations, and (2) test whether urban birds show consistently bolder behavior toward potential vertebrate threats or differentially respond to a threatening native predator versus a potentially more benign human or dove. Because urban and suburban birds live in areas with higher human densities than rural birds but are not often directly or physically harmed by humans, we predicted that they would show lower levels of both behavioral and physiological stress when approached by a human, but that no such differences would be apparent when house finches were approached by a native predator (hawk), which can be found in both urban and rural environments. Though a previous study on house finches (Valcarcel & Fernandez-Juricic, 2009) found opposite results (i.e. that urban birds responded more strongly than did rural ones to the presence of humans), observations in our house finches, combined with several other published avian studies (Arroyo et al., 2017; Carrete & Tella, 2011; Carrete & Tella, 2017; Møller, 2008), led us to predict these results in our populations. We conducted our behavioral and physiological tests in two different seasons – winter and summer/fall – to examine if or how changes in climate or life-stage might influence responses of house finches to human and avian stimulus presentations.

2. Methods

2.1. Study system

To address our questions, we investigated house finches in the greater Phoenix, Arizona, USA area. House finches are native to the desert-southwestern USA and Mexico, but now also inhabit urban and suburban areas across most of the lower 48 United States (Badyaev, Belloni, & Hill, 2012). House finches also readily display behaviors like foraging and aggression in open environments (e.g., feeders, backyards), are abundant and easily captured, and are amenable to captive behavioral experimentation (Hill, 2002).

2.2. Field methods

Using basket traps baited with sunflower seeds, we trapped ca. 30 finches during each of three trapping seasons (see more below) at each of six sites (Supplementary Fig. 1): two urban (n = 185; 91 females, 94 males), two suburban (n = 183; 89 females, 94 males), and two rural (n = 184; 89 females, 95 males), based on urban land-use parameters measured by the Central Arizona Phoenix Long Term Ecological Research program (Giraudeau, Mousel, Earl, & McGraw, 2014). During the two winter seasons, we captured adult house finches, and during the summer season, we captured juveniles. We trapped finches during winter 2012 (January – March; human approach trials only: n = 153; 71 females, 82 males), summer-fall 2012 (July - September; both human approach and native predator trials: n = 206; 101 females, 105 males) and the subsequent winter (December 2012 – February 2013; native predator trials only: n = 192; 97 females, 95 males). We chose to study finches during winter and late summer/early fall since these should be contrasting times of environmental stress - summer molt (when it is extremely hot in the desert and birds are devoting energy to regrowing feathers; King, 1981) versus the winter non-breeding season (when the climate is mild and the only major resource investment is in self-maintenance; Bryant, 1997). In the first season, we focused on studying response to humans but decided in the second season that testing responses to both humans and a native predator would provide a more comprehensive test of behavioral variability. In our third season, we examined response to native predators only (since we already had two seasons of data on responsiveness to humans). At capture, we fitted each bird with a numbered United States Geological Survey metal identification band and measured breath rate, by counting number of breaths per minute for one minute just after capture as the bird was held in hand. This method of measuring stress is less invasive than taking a blood sample and previously was shown in great tits (*Parus major*) to increase following stressful situations and was correlated with anti-predator behavior, such that shyer birds had higher breath rates than those that were bolder (Carere & van Oers, 2004).

2.3. Human approach trials

After banding and measuring birds, we placed each individually in a large cage (0.77 m tall * 0.59 m long * 0.50 m wide; Fig. 1) in the field in similar light conditions (shaded in summer) to the trapping site between 0600 and 1100 h. The cage was equipped with a hide area and small dishes of sunflower seeds and water. Each bird had 20 min to acclimate to the cage while we recorded all behavior with a video camera (JVC Everio, Long Beach, CA, 24 Mbps recording) mounted on a tripod placed about three feet from the cage. After the acclimation period, one person (MW) walked toward the cage starting from a distance of 20 m at a pace of one step per second until reaching the cage and walked away at the same pace. We continued recording the

Fig. 1. Cage in which birds were housed during the human-approach trials, which included an escape route, food, water dish, and a cardboard box that served as a hide area.

Table 1
List of behaviors quantified for each trial and their definitions.

Behavior	Description
Hop	Bird relocates to a new place in the cage without using its wings
Fly	Bird relocates to a new place in the cage by flapping its wings
Ruffle	Bird puffs out feathers and shivers
Bill wipe	Bird wipes bill on cage/perch/feeder but not on self
Time on feeder	Time bird spends perched on or eating from feeder
Time in hide	Time bird spends in hide area
Latency approach feeder	How long it takes the bird to perch on feeder after the trial begins
Time to calm	Time bird first sits for five seconds without moving

behavior of the birds to measure direct response to the approaching/departing human and including the 10 min after the approach, to measure lasting effects of the human walk-by. We tested three birds at a time, each in its own cage at least 20 m from the nearest cage to prevent the birds from responding to an approach to a neighboring cage. We determined this distance by recording the distance at which the birds first reacted to human presence during a pilot study. Birds from winter 2012 were released immediately after the trial. Birds from summer-fall 2012 and winter 2013 were then placed in a paper bag and transported to campus for the native predator-presentation trials (see methods below). We tested a total of 12 birds per day and visited each site at least three times to obtain the required sample size of 28 birds per season, which we obtained from a power analysis with an effect size of 0.40. From each video, two independent observers scored several behaviors (see Table 1 for definitions of each behavior) using the software program Cowlog (Hänninen and Pastell, 2009): the number of hops and flights (used as measures of activity level), number of bill wipes and feather ruffles (proposed as indicators of stress; Clark, 1970; Tinbergen, 1940), and the amount of time spent on the feeders and in the hide area (Table 1). Data collected by each observer were tested for inter-person repeatability (Lessells & Boag, 1987), which measures the consistency between observers. Repeatability estimates for individual behaviors were > 0.75 (Supplementary Table 1), so the scores from the two observers were averaged for final analyses, except for two variables (Supplementary Table 1), where we had an impartial third party observe 20 videos and used the data of the person who was most closely repeatable to the third observer. Because videos were recorded in the field and sites were distinctive to those who had also participated in field work, observers are not blind to site when watching videos.

2.4. Native predator trials

Prior to participating in trials, we housed birds individually in small wire cages (60 cm * 40 cm * 30 cm) without visual access to one another within a climate-controlled vivarium and given an *ad libitum* diet of black sunflower seeds and tap water. The rooms were kept at a temperature of 25 °C on a natural outdoor light-dark cycle. The night before each trial, each bird's food was removed to ensure motivation to approach the feeder during the behavioral assays the following day. For the trial, we placed each bird individually in a large flight cage (2.75 m L * 1.5 m W * 2.75 m H) in a secluded courtyard on campus between 0600 and 1100 h, giving each bird 15 min to acclimate. Because there are four flight cages in the courtyard, we ran trials for four birds at a time, but birds did not have visual access to one another. After the acclimation period, either a stuffed sharp-shinned hawk (*Accipiter striatus*; treatment) or a stuffed mourning dove (*Zenaida macroura*; control) was flown over the aviary cages on a zipline with the appropriate species-specific bird vocalization being played via a portable speaker connected to an iPod. Each bird went through a hawk and a dove trial, thus testing each bird twice. Order of stimulus presentation was randomized to avoid order effects. The behavior of each finch was recorded following the flyover for 45 min; we chose this trial duration because pilot experiments showed that many birds did not approach the feeder for up to 30 min post-exposure. We conducted four sessions of trials/day (total of 16 trials/day) during the summer and five trial sessions/day (total of 20 trials/day) during the winter. We recorded trials on a video camera mounted to a tripod just outside of the aviary cages and scored the same behaviors listed above (see "Human Approach Trials") as well as latency to approach feeder (a common measure of boldness in predator studies (first defined by Greenberg & Mettke-Hofmann, 2001) and to 'calm' after stimulus presentation, which was the time it took for the bird to sit without moving for five seconds after the initial burst of flights that followed in every bird upon the model presentation (Table 1). As above, we tested data collected by each video observer for repeatability (Supplementary Table 2) and averaged the two values for use in statistical analyses. If a repeatability estimate fell below 0.75 (Supplementary Table 2), an impartial third party observed 20 videos, and we used the data of the person who was most closely repeatable to the third observer for averaging. To minimize observer bias, video watchers were blind to the origin site and bird identity.

2.5. Statistical methods

We ran all statistical analyses in the R computing environment (Ver. 2.15.1). To test for multicollinearity among finch behavioral variables, we ran initial correlations among the various finch behaviors and reduced number variables when two were significantly correlated (higher than 0.20 for Spearman's test). We found that the frequency of bill wiping and ruffling (displacement behaviors) were highly correlated (Supplementary Tables 3 and 4), so we randomly chose to analyze one

Table 2
Model-averaged estimates for life-history and ecological variables predicting behavioral responses of house finches during human-approach trials.

Behavioral response	Predictor	Estimate	SE	SE (adjusted)	z	p
Flight rate						
	(Intercept)	5.82	0.25	0.25	23.42	< **0.0001**
	Pre-approach flight rate	0.00	0.00	0.00	5.49	< **0.0001**
	Habitat (suburban)	−0.45	0.27	0.27	1.66	0.097
	Habitat (urban)	−0.42	0.26	0.26	1.62	0.106
	Season (winter)	−0.69	0.17	0.17	3.96	< **0.0001**
	Sex (male)	0.65	0.07	0.07	8.96	< **0.0001**
Wipe rate						
	(Intercept)	0.10	0.42	0.43	0.24	0.812
	Pre-approach wipe rate	0.03	0.00	0.00	6.85	< **0.0001**
	Habitat (suburban)	−1.01	0.46	0.46	2.19	**0.029**
	Habitat (urban)	−1.55	0.49	0.49	3.17	**0.002**
	Season (winter)	1.10	0.42	0.42	2.64	**0.008**
	Sex (male)	−0.09	0.24	0.24	0.36	0.716
Feed rate						
	(Intercept)	−2.49	1.46	1.46	1.71	0.088
	Pre-approach feeding rate	0.00	0.00	0.00	7.10	< **0.0001**
	Habitat (suburban)	−2.23	1.20	1.21	1.85	0.065
	Habitat (urban)	−2.23	1.21	1.21	1.84	0.066
	Season (winter)	0.68	0.79	0.79	0.86	0.390
	Sex (male)	−0.83	0.68	0.68	1.22	0.222
Hide rate	(Intercept)	1.54	0.50	0.50	3.08	**0.002**
	Pre-approach hiding rate	0.00	0.00	0.00	9.15	< **0.0001**
	Habitat (suburban)	−0.18	0.45	0.45	0.40	0.686
	Habitat (urban)	0.07	0.35	0.35	0.21	0.838
	Season (winter)	−0.85	0.66	0.67	1.27	0.204
	Sex (male)	−0.04	0.27	0.27	**0.14**	0.886
Breathing rate	(Intercept)	3.91	0.03	0.03	122.33	< **0.0001**
	Pre-approach breath rate	0.01	0.00	0.00	31.75	< **0.0001**
	Habitat (suburban)	0.00	0.00	0.00	0.03	0.977
	Habitat (urban)	0.00	0.00	0.00	0.06	0.949
	Season (winter)	0.00	0.01	0.01	0.05	0.959
	Sex (male)	0.00	0.00	0.00	0.02	0.987

The values are bolded if they have a significant p value.

of those behaviors (bill wipes) to reduce the number of behaviors examined. Interestingly, frequency of hopping and flying (activity behaviors) were also highly correlated in the human-approach trials, but in predator trials hopping frequency was correlated with frequency of bill wiping and ruffling (instead of with flying), so we analyzed flight frequency as the activity behavior for both experiments (Tables 2, 3). Since none of the remaining behaviors were highly correlated with one another, we analyzed each behavior rather than combining them using principal components analysis. We also calculated the repeatability (Lessells & Boag, 1987) of an individual's behavioral responses to hawk and dove since each bird participated in both trials (Table 4) and repeatability of behavioral responses to the birds who participated in both predator trials and the human approach trials in summer 2012 ($n = 124$; Table 4). Values higher than 0.20 were considered repeatable as $p < 0.01$ for those values.

We used generalized linear mixed models (with the *glmer* function in lme4 package; Bates, Mächler, Bolker, & Walker 2015) to evaluate the influence of several predictor variables on house finch behavior, including individual finch identity as a random effect in our models. Specifically, we evaluated the effects of habitat type (three categories: rural, suburban, urban), season (molt, winter), pre-stimulus behavior on finch response to the different stimuli. For example, when analyzing flights, we included an individual's pre-stimulus (either human approach or model flyover) flights, as well as the other predictor variables to control for any trial-specific behavioral tendencies unrelated to the specific stimulus (model or human). Additionally, we employed an information-theoretic model-averaging approach to incorporate parameter estimates from multiple models, in accordance with the relative strength of each model (Burnham & Anderson 2002; Burnham, Anderson, & Huyvaert 2010). Specifically, we limited our model-averaging to the 95% Confidence Set (the set of models that, collectively, have a summed Akaike weight of 0.95; Burnham & Anderson 2002). Within this framework, variables that only appear in poorly-supported models exhibit negligible parameter estimates, and variables that appear repeatedly in well-supported models will have larger parameter estimates (Supplementary Tables 5, 6). We used Cohen's d to calculate effect sizes, which were all ≥ 0.54.

3. Results

3.1. Behavioral responses to an approaching human

We observed higher rates of flying and bill-wiping after the human approached the cage than before the approach, indicating that birds were responding to the stimulus (Table 2). Capture site significantly predicted bird activity in the minute just after the human approached the cage (Table 2), such that rural birds flew more than both urban and suburban birds (Fig. 2). We found that urban and suburban birds had lower bill-wiping rates than rural birds during the trials, and overall birds flew and bill-wiped more in the 10 min after the human approached than during the 20-min acclimation period (Table 2, Fig. 2). We also found significant season and sex effects, such that birds had a higher flight rate during the molt season but higher bill-wiping rate during the winter season, and males had a higher flight rate overall than females (Table 2, Fig. 2). We found no significantly effects of site, season, sex, or their interactions on breath rate (Table 2).

3.2. Behavioral responses to aerial avian presentations

Though capture site did not predict any of the behavioral measures

Table 3
Model-averaged estimates for life-history and ecological variables predicting behavioral responses of house finches during avian model presentations. Habitat estimates are made relative to rural populations, model presentation estimates are made relative to dove models, season estimates are made relative to molt season, and sex estimates are made relative to female finches.

Behavioral response	Predictor	Estimate	SE	SE (adjusted)	z	*p*
Flight rate						
	(Intercept)	5.923	0.10	0.10	61.43	< **0.0001**
	Pre-flyover flight rate	0.000	0.00	0.00	54.54	< **0.0001**
	Habitat (suburban)	0.006	0.10	0.10	0.06	0.952
	Habitat (urban)	0.153	0.15	0.15	1.00	0.317
	Model (hawk)	0.018	0.00	0.00	4.80	< **0.0001**
	Season (winter)	−0.031	0.08	0.08	0.41	0.680
	Sex (male)	−0.021	0.07	0.07	0.33	0.744
Wipe rate						
	(Intercept)	1.130	0.16	0.16	7.06	< **0.0001**
	Pre-flyover wipe rate	0.003	0.00	0.00	6.28	< **0.0001**
	Habitat (suburban)	0.274	0.21	0.22	1.27	0.203
	Habitat (urban)	−0.056	0.15	0.15	0.38	0.704
	Model (hawk)	−0.005	0.01	0.01	0.31	0.758
	Season (winter)	1.344	0.14	0.15	9.26	< **0.0001**
	Sex (male)	0.304	0.17	0.17	1.77	0.076
Feed rate						
	(Intercept)	6.119	0.14	0.14	43.96	< **0.0001**
	Pre-flyover feeding rate	0.000	0.00	0.00	33.15	< **0.0001**
	Habitat (suburban)	−0.051	0.13	0.13	0.41	0.682
	Habitat (urban)	−0.044	0.11	0.11	0.39	0.697
	Model (hawk)	−0.012	0.00	0.00	3.52	< **0.001**
	Season (winter)	0.144	0.16	0.16	0.90	0.368
	Sex (male)	0.058	0.11	0.11	0.51	0.610
Latency to return to feeder						
	(Intercept)	4.880	0.09	0.09	53.65	< **0.0001**
	Pre-flyover feeder latency	0.000	0.00	0.00	41.11	< **0.0001**
	Habitat (suburban)	−0.004	0.05	0.06	0.07	0.943
	Habitat (urban)	0.012	0.06	0.06	0.20	0.843
	Model (hawk)	0.054	0.00	0.00	12.16	< **0.0001**
	Season (winter)	1.037	0.11	0.11	9.13	< **0.0001**
	Sex (male)	−0.003	0.06	0.06	0.05	0.961
Latency to calm						
	(Intercept)	4.573	0.14	0.14	33.62	< **0.0001**
	Pre-flyover feeder latency	−0.001	0.00	0.00	6.67	< **0.0001**
	Habitat (suburban)	−0.013	0.09	0.09	0.15	0.884
	Habitat (urban)	0.021	0.09	0.09	0.23	0.822
	Model (hawk)	−0.253	0.01	0.01	29.00	< **0.0001**
	Season (winter)	−1.059	0.17	0.17	6.25	< **0.0001**
	Sex (male)	0.010	0.09	0.09	0.12	0.909

The values are bolded if they have a significant p value.

during the avian-presentation trials, we did find significant effects of season and model presentation on finch behavior (Table 3). Birds had higher flight and bill-wiping rates, ate less, took longer to approach the feeder, and took longer to calm during the hawk flyover versus the dove flyover (Fig. 3, Table 3). We saw higher rates of flying and bill-wiping after the flyovers, regardless of model type, indicating that birds were responding to the stimulus (Table 3). Finches also had a higher bill-wiping rate and took longer to calm during the winter season than the summer-fall (Fig. 3, Table 3) Fig. 4.

3.3. Repeatability of behavior across trials

Flight rate was the most repeatable behavior between the two aerial avian trials (Table 4), and time spent on feeder was the least repeatable. Suburban birds showed the most consistency between trials (Table 4), whereas rural birds were consistent in flight rate and bill-wiping rate but not time spent on feeder or time to approach the feeder (Table 4). Urban birds were consistent in flight rate, latency to approach feeder, and in time spent on feeder, but not in latency to calm or bill-wiping rate (Table 4). We also tested repeatability of behaviors in birds who went through both the avian-flyover and human-approach trials (n = 124; Table 4). Birds from all three sites were repeatable in flight rate and time on feeder, as urban birds had the greatest repeatability in flight rate and suburban birds had the greatest repeatability in time spent on feeder (Table 4). None of the sites were repeatable on bill wiping rate, however (Table 4).

4. Discussion

In this study, we tested behavioral and physiological responses of house finches from urban, suburban, and rural sites to the approach of humans and native birds. As predicted, we observed greater behavioral differences across sites in the human-approach trials than the avian-flyover trials. We also found that rural birds were more active (i.e. flew around more in the cage) than both suburban and urban finches in the minute just after the human approach, and that this response was consistent among seasons. Many studies that evaluate the response of urban animals to humans utilize flight initiation distances (FID) to determine fear levels toward humans (Arroyo et al., 2017; Carrete & Tella, 2011; Carrete & Tella, 2017; Møller, 2008; Valcarcel & Fernandez-Juricic, 2009), predicting that animals that allow an approaching human to get close to them are less affected by human presence. While most of these studies have found that, in more than 25 species ranging from songbirds to raptors, urban birds had shorter FIDs than those from rural areas (Arroyo et al., 2017; Carrete & Tella, 2011; Carrete & Tella, 2017; Møller, 2008), which is consistent with our

Table 4
Repeatability between finch behavior in the aerial-flyover trials hawk vs dove and hawk vs dove vs human.

Trial	Behavior	Habitat Type	Repeatability
Hawk vs dove	Flight	Rural	0.57
		Suburban	0.64
		Urban	0.51
	Bill wipe	Rural	0.53
		Suburban	0.68
		Urban	0.19
	Time to calm	Rural	0.23
		Suburban	0.30
		Urban	0.09
	Time on feeder	Rural	0.09
		Suburban	0.23
		Urban	0.30
	Latency to feeder	Rural	0.09
		Suburban	0.25
		Urban	0.33
Hawk vs dove vs human	Flight	Rural	0.35
		Suburban	0.34
		Urban	0.58
	Bill wipe	Rural	0.03
		Suburban	0.14
		Urban	0.15
	Time on feeder	Rural	0.39
		Suburban	0.47
		Urban	0.28

findings, Valcarcel and Fernandez-Juricic (2009) found that house finches in urban areas actually took flight *earlier* than rural populations. Unfortunately, we could not calculate FID *per se* in our study because of the generally high levels of finch activity during confinement and acclimation, which makes it difficult to accurately compare our results to those of Valcarcel and Fernandez-Juricic (2009). However, we also found that rural house finches more frequently bill-wiped in response to the approaching human than urban and suburban birds, which is another indicator that rural birds were experiencing greater levels of stress in the presence of a human.

While we recognize that having only one mount of each stimulus type may be a limitation to our study, we still found that finches took longer to calm after the hawk flyover versus the dove, suggesting that the predator presentation may have served as a greater threat or stressor than the more benign dove. We found this same result in the human approach trials, as birds across sites showed differences in behavior before and after approach. We, of course, cannot ignore that these studies were conducted in captivity, which might have resulted in artificial differences across populations. To mitigate this, we conducted human approach trials in the field within five minutes of capture to get the most ecologically relevant results. Another limitation of this study is that we used different populations of birds across different seasons, which we discuss in more detail below.

In contrast to the results from the human-approach trials, we found no effect of capture site (i.e. urbanization) on any of the behaviors in response to an avian flyover (whether hawk or dove). This finding suggests that finches from urban, suburban, and rural sites show a consistent response to the threat of an aerial (*accipiter*) predator. Though a handful of studies have demonstrated that urban animals tend to be bolder in the presence of a predator than rural ones (Evans, Boudreau, & Hyman, 2010; Mccleery, 2009; Myers and Hyman, 2016; Seress, Bokony, Heszberger, & Liker, 2011), Cote, Fogarty, Tymen, Sih, and Brodin (2013) showed that behavioral differences in populations of mosquitofish (*Gambusia affinis*) vanished in the face of predation, when all individuals tended to behave similarly when faced with a known threat. Since finches at all of our sites are exposed to aerial predators (pers. obs.), we would predict that birds from all sites would respond similarly to these predators. In addition, birds of all populations demonstrated a high level of repeatability in activity behavior between

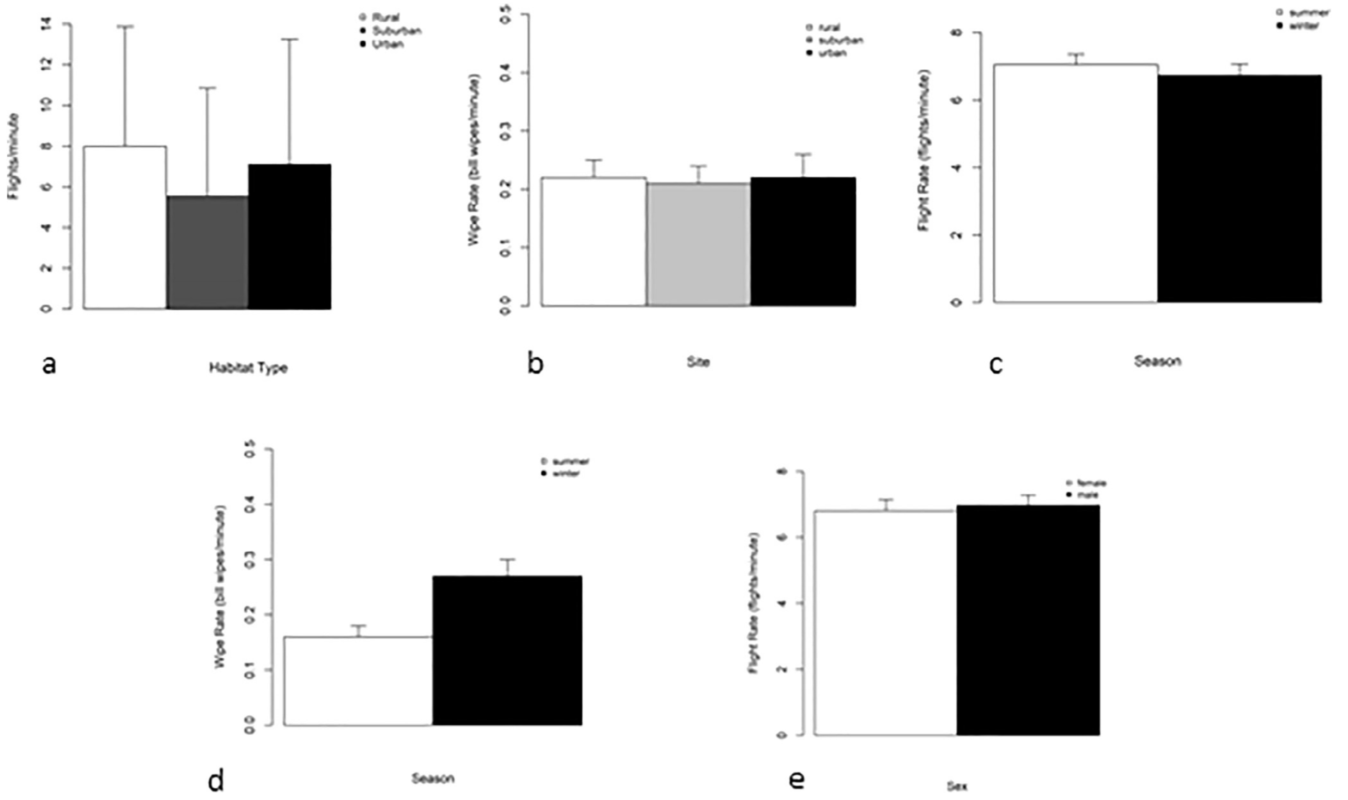

Fig. 2. During the human-approach trials, rural birds flew more than both urban and suburban birds in the minute just after approach (a), rural birds had a higher bill-wiping rate than both urban and suburban birds (b), birds had a higher flight rate in the summer than during winter (c), birds had a higher bill-wiping rate in the winter than during summer (d), and males had a higher flight rate than females (e). Mean + standard error shown in all panels.

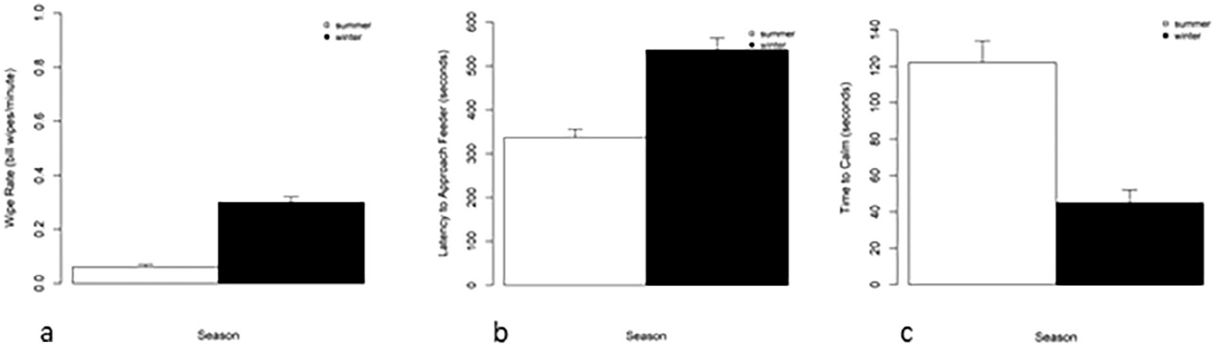

Fig. 3. During the bird-mount flyover trials, birds had a higher bill-wiping rate during the winter than during summer (a), took longer to approach the feeder after flyover in the winter than in summer (b), and took longer to calm during the winter than summer (c). Mean + standard error shown in all panels.

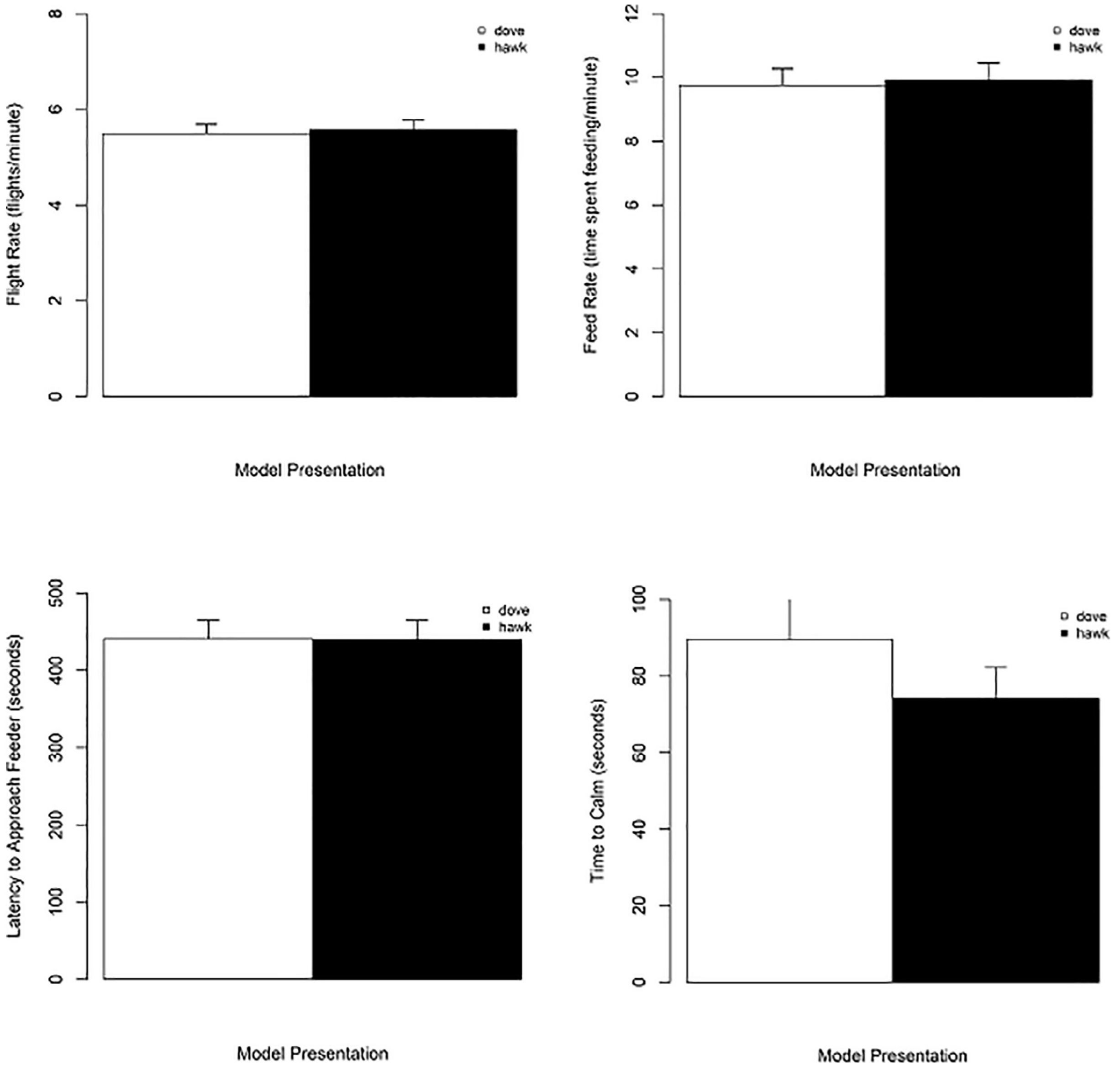

Fig. 4. Birds had a higher flight rate (a), ate less frequently (b), took longer to approach the feeder (c), and took longer to calm (d) after the hawk flyover compared to the dove flyover. Mean + standard error shown in all panels.

the three trials. However, while bill wiping was repeatable between hawk and dove trials, it was not repeatable between aerial trials and human trials, demonstrating that all populations are showing a great deal of plasticity in their response to larger vertebrates in their environments.

We did find several seasonal differences in both studies, as birds had a higher bill-wiping rate and took longer to approach the feeder during the winter avian-flyover trials than during the summer-fall. Also, in the human-approach trials, birds again bill-wiped more frequently in the winter than in summer but had a higher flight rate in summer compared to winter. However, it is also noteworthy that the majority of birds captured during the summer season were juveniles, whereas the majority captured during the winter were adults. Age can affect boldness, as juvenile perch (*Perca fluviatilis*) are less bold than adults when exposed to predators (Magnhagen & Borcherding, 2008), but boldness was found to decrease with age in domestic dogs (Starling, Branson, Thomson, & McGreevy, 2013). In addition, Frost, Winrow-Giffen, Ashley, and Sneddon (2007) found that previous experience altered boldness in rainbow trout (*Oncorhynchus mykiss*), such that individuals with previous experience with predators were less bold and exploratory. However, the majority of studies on juvenile behavioral traits have found that juvenile behavior, particularly boldness, does not predict adult behavior (Bell & Stamps, 2004; Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013; Sinn, Gosling, and Moltschaniwskyj, 2008). Thus, difference in age (and experience with predators) may have contributed to our seasonal patterns. Future behavioral studies with juvenile finches have been planned to investigate this possibility.

In addition to measuring finch behavioral responses to humans and hawk/dove mounts, we also measured breath rate as an indicator of physiological stress (as in great tits; Carere & van Oers, 2004). Contrary to our prediction, we found no differences in breath rate among urban, suburban, and rural birds. This appears to conflict with our behavioral results, in which rural birds had higher activity levels and displayed more stress behaviors than urban and suburban birds in the human-approach tests. However, these tests were conducted at different time scales (immediately upon capture for breath rate versus monitoring behavior during a 30- or 60-min trial), which could capture different components of stress responsiveness, just as measuring corticosterone levels immediately after a stressor versus 3–5 min afterwards captures different stress measurements because corticosterone takes 3–5 min to increase in the blood post-stressor (Wingfield, Vleck, & Moore, 1992). Studies that have attempted to identify differences in breath rate across an urban gradient have been mixed as some studies have shown that urban great tits have higher breath rates (Charmantier, Demeyrier, Lambrechts, Perret, & Grégoire, 2017; Torné-Noguera, Pagani-Nú-ez, & Senar, 2014), while urban dark-eyed juncos had lower breath rates (Abolins-Abols, Hope, & Ketterson, 2016). However, another study in great tits found no difference in birds captured at urban and rural sites as breath rate can be affected by numerous seasonal and ecological variables (Senar et al., 2017). Future studies measuring breath rate in a variety of contexts, and pairing this information with both behavioral data and blood corticosterone levels, could lead to a better understanding of why rural birds in our study exhibited behavioral differences but no difference breath rate in response to humans.

5. Conclusions

Urban areas continue to grow at rapid rates. While cities are thought to be a safe haven from predators, studies have produced conflicting results about how animals perceive humans as threats. Although some studies have shown urban-rural differences in avian behavioral responses to humans, to our knowledge few studies have considered if such responses should be similar to or different from those when exposed to native predators or to benign heterospecific bird species. Here we showed that house finches display behavioral plasticity in response to presence of different vertebrates, such that differences in urban-rural responses to an approaching human did not also occur during native predator flyovers. Thus, when designing studies to test wildlife behavioral response to humans, it is important to also understand species responses to stimuli from both human-impacted and natural environments. Moreover, the fact that a bird species responded differently to humans versus aerial vertebrates as a function of urbanization indicates that human presence could indeed be an important reason behind why certain species avoid and are excluded from urban environments.

Ethics statement

This work was approved by the Arizona State University Institutional Animal Care and Use Committee (protocol 12-1234R), the Arizona Game and Fish Department (collecting permit # SP654951), U.S. Fish and Wildlife Service (collecting permit MB088806), and the Federal Bird Banding Lab (permit 23362). This work was funded by Arizona State University, Animal Behavior Society, Sigma Xi, and the Central Arizona Phoenix Long Term Ecological Research Project.

Conflict of interest

There were no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.landurbplan.2018.07.001.

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