

Antipredator strategies of house finches: are urban habitats safe spots from predators even when humans are around?

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Received: 7 May 2008 / Revised: 10 December 2008 / Accepted: 12 December 2008 / Published online: 17 January 2009
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Abstract Urbanization decreases species diversity, but it increases the abundance of certain species with high tolerance to human activities. The safe-habitat hypothesis explains this pattern through a decrease in the abundance of native predators, which reduces predation risk in urban habitats. However, this hypothesis does not consider the potential negative effects of human-associated disturbance (e.g., pedestrians, dogs, cats). Our goal was to assess the degree of perceived predation risk in house finches (*Carpodacus mexicanus*) through field studies and semi-natural experiments in areas with different levels of urbanization using multiple indicators of risk (flock size, flight initiation distance, vigilance, and foraging behavior). Field studies showed that house finches in more urbanized habitats had a greater tendency to flock with an increase in population density and flushed at larger distances than in less urbanized habitats. In the semi-natural experiment, we found that individuals spent a greater proportion of time in the refuge patch and increased the instantaneous pecking rate in the more urbanized habitat with pedestrians probably to compensate for the lower amount of foraging time. Vigilance parameters were influenced in different ways depending on habitat type and distance to flock mates. Our results suggest that house finches may perceive highly urbanized habitats as more dangerous, despite the lower number of native predators. This could be due to the presence of human activities, which could increase risk or

modify the ability to detect predators. House finches seem to adapt to the urban environment through different behavioral strategies that minimize risk.

Keywords Antipredator behavior · Birds · Flight initiation distance · Flock size · Foraging · Safe-habitat hypothesis · Vigilance

Introduction

Urban sprawl generates changes in the composition of bird communities, such as an increase in the density of certain species, generally accompanied with a decrease in species diversity (Marzluff 2001; McKinney 2006). Several mechanisms have been proposed to account for these population changes (Shochat et al. 2006), such as increases in the availability of food (e.g., human leftovers), changes in vegetation complexity, and reduction in extreme climatic conditions (e.g., higher temperatures). Another mechanism is the *safe-habitat hypothesis*, by which the abundance of natural predators decreases with the degree of urbanization, which generates lower nest predation rates, increasing breeding success, and eventually abundance (Tomialojc 1982). The decrease in predator abundance has also been associated with lower perceived predation risk in adult birds (e.g., Sorace 2002).

Empirical tests of the safe-habitat hypothesis have mainly focused on nest predation, yielding mixed results (Shochat et al. 2006). Shochat (2004) argued that the number of predators may not necessarily be associated with predation pressure and that *perceived predation risk* may be a better parameter to evaluate the safe-habitat hypothesis. The relatively scant empirical evidence on differences in predation risk between urban and non-urban habitats also

Communicated by P. Bednekoff

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shows mixed results. For instance, Roth et al. (2007) found that avian prey in rural, but not urban, habitats have a period prior to sunrise with lower *Accipiter* predator activity due to raptor intra-guild predation that would allow small passerines to increase foraging opportunities. Shochat et al. (2004) studied giving-up densities (the amount of food left in a patch) in Arizona and found habitat differences suggesting lower predation risk in urban areas than in desert areas. However, no study to date has characterized different types of antipredator behaviors in areas with different degrees of urbanization.

The prediction that urban habitats are safer for some species has overlooked the high levels of human activity in cities that can cause disturbance (Blair 1996; Fernández-Juricic 2000). Human activities can influence wildlife in different ways depending upon the degree of tolerance to humans. Wildlife can habituate to humans due to the higher frequency of interactions, particularly if there is no human persecution (e.g., Knight et al. 1987). However, several studies have shown that human disturbance in urbanized habitats can negatively affect foraging behavior (Ward and Low 1997), patch use (Fernández-Juricic and Telleria 2000), population density (Fernández-Juricic 2000), and species richness and composition (Blair 1996).

The goal of this study was to assess the degree of perceived predation risk in a social species, the house finch *Carpodacus mexicanus*, in areas with different levels of urbanization and human activity in Southern California during the non-breeding season. We chose house finches because they inhabit different habitat types, from rural to highly urbanized (Hill 1993). We focused on different indicators of antipredator behavior as they may suggest different levels of risk that may contribute to fitness unequally (Lind and Cresswell 2005). First, we assessed, through two different field studies, variations in flock size and flight initiation distance (FID) between more and less urbanized habitats. Second, in a semi-natural experiment, we studied changes in vigilance, foraging and patch use behaviors between different habitat types and under two levels of neighbor distances, which could affect safety perception.

Predictions

Predation risk can influence the decision to join flocks of different sizes, since larger groups can detect predators earlier (collective detection) and reduce the per capita risk of capture (dilution effect, reviewed in Krause and Ruxton 2002; Caro 2005). Under the safe-habitat hypothesis (Tomialojc 1982), we expected house finches to form larger flocks in the less than in the more urbanized habitats due to higher predation pressure.

Flight initiation distance depends on the ability of prey to detect and escape from a predator, the costs of

escaping, and the probability of being killed (Cooper and Frederick 2007). Flight initiation distance is a good indicator of fearfulness (Stankowich and Blumstein 2005), but it may also vary with the degree of habituation at the individual and population levels (e.g., Fernández-Juricic et al. 2001). Under the safe-habitat hypothesis, we expected lower flight initiation distances in the more urbanized in relation to the less urbanized habitats as a result of lower predation risk.

Instantaneous changes in predation risk are expected to modify the effort allocated to vigilance (Lima and Dill 1990; Lima 1998), which could influence foraging time due to time competition effects (Caraco 1979). In social species, these predation risk effects can be enhanced as the distance between group members increases (Fernández-Juricic and Kacelnik 2004; Fernández-Juricic et al. 2007). If predation risk costs increase (habitats associated with high abundance of predators or human disturbance), animals may increase scanning, leave foraging patches earlier, and increase their use of refuge patches (Brown 1988; Pickett et al. 2005). Under the safe-habitat hypothesis, we expected these changes in scanning and patch use to be more pronounced in the less urbanized habitat due to higher perceived predation risk. We also expected this habitat effect to be more marked when flock mates were located farther away since the domain of danger per individual would increase (Pöysä 1994; Fernández-Juricic et al. 2004), yielding an interaction effect between habitat and neighbor distance.

Materials and methods

General considerations

We chose study sites in Southern California with high and low degrees of urbanization (hereafter, more urbanized and less urbanized habitats). We selected 11 city parks located in Los Angeles and Orange counties as sampling areas for the more urbanized habitats and 11 regional parks, state parks, and reserves in Orange County for the less urbanized habitats (“Appendix 1”).

Our study design made two main assumptions based on the literature: (1) the main difference in predation risk between habitat types is the result of the abundance of different types of predators (Tomialojc 1982) and (2) house finches react to humans in the same way as they do to other predators (Frid and Dill 2002), although the degree of such response could be lower due to their non-predatory nature (Stankowich and Coss 2006). We surveyed some of the native avian predators (e.g., raptors) in less and more urbanized parks to get relative indices of predation pressure that were likely to affect the perception of risk during the

non-breeding season. At the beginning of the results of each study, we present information on the factors that were expected to vary between habitats.

Flock size

Observational and experimental studies have found a positive relationship between population density and group size (Wirtz and Lörcher 1983; Ostro et al. 2001; Morgan and Fernández-Juricic 2007). From a theoretical perspective, group size is expected to increase with population density up to an optimal group size; above which the number of groups, rather than group size, is expected to increase with population density (Krause and Ruxton 2002). Because we compared flock size between different habitats types, we recorded flock size and also estimated the density of house finches during the non-breeding season (October 2006 to March 2007) in 11 more urbanized and 11 less urbanized parks (“Appendix 1”).

Data were collected in the mornings from sunrise until 10:00. We used 100×50-m (0.5 ha) line transects, which have been used to survey birds in different habitat types (Järvinen and Väisänen 1977). The number of transects, which were separated by 50–300 m, varied between one and ten per park, depending on their size. We surveyed each transect four times by recording within the transect limits the number of individuals and flocks. House finches were considered to be in a flock if they were within a maximum of 20 m of one another, foraged together, and flew away together (Whitfield 2003). Within these line transects, we also recorded the presence and number of potential avian predators. Although detectability could have biased our surveys due to the hunting behavior of different raptor species, we believe this effect was minimized because: (a) none of our study areas was densely forested; (b) we were able to spot different species while perched and flying in both habitat types; (c) surveys were conducted during the fall and winter when many trees did not have leaves; and (d) many raptors were spotted when passerines mobbed them.

The number of individuals and number of flocks were averaged for each transect (0.5 ha) across all visits. These means were then averaged across the park and the final values were expressed as means per 0.5 ha. For flock size, we used the median number of individuals per transect rather than the mean because it is a better indicator of the flock sizes experienced by the average individual (Giraldeau 1988). For raptors, we first estimated the density of the three species most likely to attack house finches: Cooper’s hawk (*Accipiter cooperii*), red-shouldered hawk (*Buteo lineatus*), and American kestrel (*Falco sparverius*). We also estimated

the density of all raptor species to assess overall predation pressure between habitats.

In each of the studied parks, we also measured park size, pedestrian rate, and vegetation structure (“Appendix 1”). We used general linear models to analyze differences in park size, human disturbance, and raptor density between less and more urbanized parks. We used a principal component analysis (PCA) to summarize the variability in vegetation structure. Our criterion to generate components was eigenvalues >1. The first principal component generated was used for the contrast between less and more urbanized habitats with a general linear model. Some variables were log-transformed (park area, number of pedestrians) to meet normality and homogeneity of variance assumptions.

We used general linear models to analyze differences in (a) house finch density between park types (less and more urbanized parks) and (b) mean number of flocks and median flock size, including park type as an independent factor. We ran models on number of flocks and flock size with and without house finch density as a covariate.

Results

Parks were larger in less urbanized habitats (log₁₀-transformed mean, 5.96±0.44 ha) than those in the more urbanized habitats (log₁₀-transformed mean, 2.07±0.45 ha, $F_{1, 20}=9.36$, $P=0.006$). The degree of urbanization, temperature, and wind speed did not vary between less and more urbanized parks (results available upon request).

We entered five variables in the PCA: grass cover, bush cover, total tree cover, number of stems >30-cm diameter at breast height (dbh), and mean bush height. The PCA generated a single component (PC1) with an eigenvalue=3.75, accounting for 62.56% of the variability in vegetation structure. All other components had eigenvalues <1 and were not extracted. Five of the six vegetation factors were highly correlated with PC1: grass cover (0.839), bush cover (−0.882), total tree cover (0.730), tree height (0.813), and number of stems >30 cm dbh (0.796). PC1 values varied significantly between habitats ($F_{1, 20}=132.52$, $P<0.001$, less urbanized=−0.90±0.08, more urbanized=0.91±0.14). More urbanized parks had greater grass and tree cover, less bush cover, taller trees, and more trees than less urbanized parks.

The number of pedestrians walking and sitting was significantly higher in more (log₁₀-transformed mean, 1.32±0.23 pedestrians per 0.5 ha) than in less (log₁₀-transformed mean, 0.66±0.20 pedestrians per 0.5 ha) urbanized parks ($F_{1, 20}=4.52$, $P=0.046$).

We found two species of predators during our surveys in the 11 more urbanized parks: Cooper’s hawk and red-tailed hawk (*Buteo jamaicensis*). The same two species plus the following five were found in the less urbanized parks: red-

shouldered hawk, osprey (*Pandion haliaetus*), American kestrel, northern harrier (*Circus cyaneus*), and white-tailed kite (*Elanus leucurus*). We assessed differences in the density of raptors in parks in which we recorded house finches. The combined density of Cooper's hawks, red-shouldered hawks, and American kestrels was higher in less urbanized (0.17 ± 0.04 individuals per 0.5 ha) than in more urbanized (0.01 ± 0.01 individuals per 0.5 ha) parks ($F_{1, 19} = 12.90$, $P = 0.002$). These species were found in two (out of ten) more urbanized parks and nine (out of 11) less urbanized parks. Considering all raptor species, we found that their density was significantly higher in less urbanized (0.37 ± 0.08 individuals per 0.5 ha) than in more urbanized (0.02 ± 0.01 individuals per 0.5 ha) parks ($F_{1, 19} = 16.99$, $P < 0.001$). These raptors were found in four (out of ten) more urbanized parks and 11 (out of 11) less urbanized parks.

We found house finches in all parks but one, Boughton Creek (more urbanized), which was not included in the analyses. House finch density did not differ between less urbanized (4.83 ± 1.23 individuals per 0.5 ha) and more urbanized (3.21 ± 0.48 individuals per 0.5 ha) parks ($F_{1, 19} = 1.38$, $P = 0.254$).

The number of flocks did not differ significantly between more and less urbanized parks ($F_{1, 19} = 1.12$, $P = 0.302$), without controlling for density effects. Similarly, we found no difference in number of flocks between more (0.64 ± 0.08 flocks per 0.5 ha) and less (0.75 ± 0.08 flocks per 0.5 ha) urbanized parks ($F_{1, 17} = 0.71$, $P = 0.411$), after controlling for house finch density ($F_{1, 17} = 2.37$, $P = 0.142$). The interaction between park type and house finch density was not significant ($F_{1, 17} = 0.38$, $P = 0.546$).

Flock size did not differ between more and less urbanized parks ($F_{1, 19} = 0.52$, $P = 0.478$), without controlling for density effects. Similarly, flock size did not differ between more (2.45 ± 0.45 individuals per flock per 0.5 ha) and less (2.02 ± 0.40 individuals per flock per 0.5 ha) urbanized parks ($F_{1, 17} = 0.38$, $P = 0.543$), after controlling for the significant effects of density ($F_{1, 17} = 33.68$, $P < 0.001$). However, we found a significant interaction effect between park type and density ($F_{1, 17} = 5.68$, $P = 0.029$), by which flock size increased more quickly with an increase in density in more urbanized than in less urbanized parks (Fig. 1). This suggests a greater tendency to flock when more individuals become available in more urbanized habitats.

Flight initiation distance

Flight initiation distance was recorded in more urbanized and less urbanized areas in Southern California during the non-breeding season (October 2006 through March 2007). We sampled between 06:00 and 10:00 in the 22 parks surveyed for flock size ("Appendix 1"), as well as the

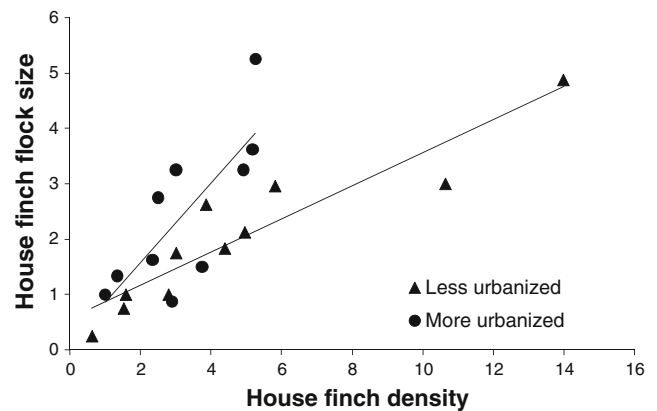


Fig. 1 Relationship between house finch density and flock size in two habitat types: more urbanized (circles) and less urbanized (triangles)

following areas: Peters Canyon Regional Park, Upper Newport Bay Ecological Reserve, Mayfair Park, Hudson Park, Cerritos College Campus, Whaley Park, and six streets with high tree cover in the city of Downey.

All approaches were conducted by a single observer (AV). Individuals on the ground or perched were approached at a steady pace (one step per second) in areas without visual obstruction between the observer and the bird. When approaching a group of birds, we chose one focal individual haphazardly prior to the approach and recorded its sex. Approaches began if the individual did not show any alert behavior to minimize the chances of using individuals that had been overtly aware of human presence. By dropping markers and later using a meter tape, we recorded (a) starting distance (the distance at which the approach started), (b) alert distance (the distance at the point where the bird began showing alert behavior), and (c) flight initiation distance (distance at which the bird flushed or moved away walking). Starting distances did not differ significantly between habitat types (less urbanized, 24.26 ± 1.78 ; more urbanized, 23.84 ± 1.14 ; $F_{1, 48} = 0.04$, $P = 0.839$). If the bird was perched, we measured the perching height and measured horizontal flight initiation distance and later calculated direct FID as follows: $FID_{direct} = \sqrt{[(FID_{horizontal}^2 + \text{perching height}^2)]}$. Birds were not marked, but we minimized the possibility of pseudoreplication by avoiding sampling in contiguous areas.

After the individual fled, the following secondary factors were measured in a 25-m² plot centered around the bird's original position: time of the day, temperature, distance to the nearest tree, and distance to the nearest shrub. We always wore neutral clothing and never performed measurements when there were other forms of disturbance such as pedestrian traffic or predators present or during rainy or windy days. We also measured rates of pedestrians and dogs around the spots in which we conducted the

approaches and analyzed the differences between less and more urbanized parks with general linear models.

We analyzed the effects of secondary factors (time of day, group size, distance to the nearest tree, distance to the nearest shrub, sex) on alert distance and flight initiation distance. Those factors that turned out to be significant were introduced in the final model in which we tested the effects of habitat type (more urbanized, less urbanized) with general linear models. Even though starting distance can affect flight initiation distance (Blumstein 2003), we included alert distance instead of starting distance in the final model since the former distance had a greater degree of association with flight initiation distance.

Results

The levels of human disturbance around the sampling plots where alert and flight initiation distances were recorded varied between habitats. The number of pedestrians was significantly higher in more urbanized (9.98 ± 1.58 pedestrians per 50 m^2 per 10 min) than in less urbanized (1.39 ± 1.71 pedestrians per 50 m^2 per 10 min) plots ($F_{1, 48} = 13.65$, $P < 0.001$). Similarly, the number of dogs was significantly higher in more urbanized (0.37 ± 0.09 dogs per 50 m^2 per 10 min) than in less urbanized (0.09 ± 0.09 dogs per 50 m^2 per 10 min) plots ($F_{1, 48} = 4.73$, $P = 0.034$).

We assessed the effects of several secondary factors on alert distance, and only time of day had a positive significant effect (e.g., alert distances were higher early in the day, coefficient = 56.04, $F_{1, 43} = 6.34$, $P = 0.016$). None of the other factors (group size, distance to the nearest tree, distance to the nearest shrub, sex) significantly influenced alert distances ($F_{1, 43} < 0.68$, $P > 0.413$). Alert distance did not differ between more urbanized (15.58 ± 0.87 m) and less urbanized (15.46 ± 0.95 m) plots ($F_{1, 47} = 0.01$, $P = 0.926$), controlling for the significant effects of time of day ($F_{1, 47} = 6.09$, $P = 0.017$).

None of the studied secondary factors (time of day, group size, distance to the nearest tree, distance to the nearest shrub, sex) significantly influenced flight initiation distance ($F_{1, 43} < 3.54$, $P > 0.067$); thus, they were not included in the final model. Alert distance significantly influenced flight initiation distance ($F_{1, 46} = 31.22$, $P < 0.001$), and so did habitat type ($F_{1, 46} = 30.88$, $P < 0.001$). However, the model yielded a significant interaction effect between alert distance and habitat type ($F_{1, 46} = 40.37$, $P < 0.001$), by which flight initiation distance did not vary substantially with alert distance in the less urbanized habitat, but it increased with alert distance in the more urbanized habitat (Fig. 2). Overall, flight initiation distances were higher (less tolerance) in more urbanized than in less urbanized habitats, controlling for alert distance (note differences in slope in Fig. 2).

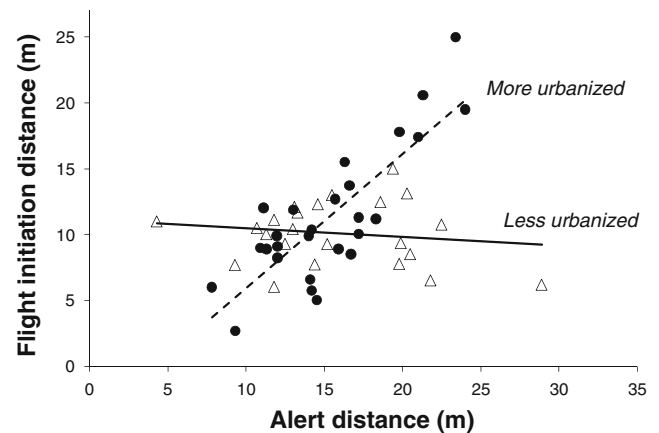


Fig. 2 Relationship between alert distance and flight initiation distance in two habitat types: more urbanized (circles) and less urbanized (triangles)

Scanning and foraging behavior

We decided to follow a repeated-measures design by exposing the same birds to exemplars of different habitat types and assessing their patch use, scanning, and foraging behaviors. We acknowledge that this approach constrained our ability to generalize and therefore our statistical inferences only apply to the sites used in this study. However, we believe we gained an understanding of within-individual responses to different habitats.

The experiment was conducted in a less urbanized area (Seal Beach, California) and a more urbanized area (California State University Long Beach campus, CSULB) during the non-breeding season (September–November 2005). Our experimental setup consisted of three sets of two enclosures, with a link connecting the enclosures of each set (“Appendix 2”). Within each set, one enclosure was considered the foraging patch (with seeds) and the other the refuge patch (with synthetic vegetation). One bird was placed in each set of enclosures, and we focused our analysis on the central set (focal bird). We manipulated two factors of interest: habitat type (less urbanized without pedestrians, more urbanized with pedestrians, and a control: more urbanized without pedestrians) and neighbor distance (close, 0 m separation between the sets of enclosures; far, 2 m separation between the sets of enclosures; “Appendix 2”). In the more urbanized without pedestrians treatment, we placed a black fence around the experimental area to screen out the view of pedestrians walking. In the more urbanized with pedestrians and less urbanized without pedestrians treatments, we did not use this fence. With video cameras, we recorded the scanning and foraging behaviors of the focal bird while on the ground (see details in “Appendix 2”).

We found that food deprivation time was significantly correlated with focal body condition ($r=0.31$, $P=0.004$) and temperature ($r=0.32$, $P=0.003$); thus, it was not included in the analyses. None of the other secondary factors (temperature vs. wind speed, $r=0.11$, $P=0.312$; temperature vs. body condition, $r=0.09$, $P=0.414$; wind speed vs. body condition, $r=-0.03$, $P=0.792$) was correlated among each other, and thus we included them in the models along with focal's sex. We analyzed the effects of habitat type, neighbor distance, and their interaction on the proportion of time spent in the refuge patch, head-up scan bout duration, head-up scan rate, and instantaneous pecking rate (number of pecking events per unit time head-down). Our general linear models included the subject identity as a repeated-measures factor. We used planned comparisons to test for differences between levels of a factor. We normalized the proportion of time in the refuge with an arcsine squared root transformation.

Results

We surveyed the two study areas for potential predators before, during, and after the completion of the semi-natural experiments. In Seal Beach (less urbanized), we found the following native predator species: Cooper's hawk, red-shouldered hawk, red-tailed hawk, American kestrel, and white-tailed kite. In CSULB campus (more urbanized), we found only the Cooper's hawk.

Focal house finches varied the amount of time spent in the refuge patch depending on the habitat type (Table 1, Fig. 3a), controlling for the marginally significant effects of sex (males, 0.49 ± 0.04 ; females, 0.39 ± 0.03 ; Table 1). They spent more time in the refuge in the more urbanized habitat with pedestrians in relation to the less urbanized habitat ($t_{26}=3.93$, $P<0.001$) and the more urbanized habitat without pedestrians ($t_{26}=-3.34$, $P=0.003$), without significant differences between the latter two ($t_{26}=0.91$, $P=0.371$, Fig. 3a). Neighbor distance and its interaction with habitat type did not influence the proportion of time in the refuge patch (Table 1).

Head-up scan bout duration was significantly affected by the independent effects of habitat type (e.g., higher in the less urbanized than in the more urbanized habitat with and without pedestrians) and neighbor distance (e.g., higher at close than at far distances) but also by their interaction (Table 1, Fig. 3b), after controlling for the confounding effects of temperature (parameter= -10.28) and body condition (parameter= 10.78). In the less urbanized habitat, house finches showed longer head-up scan bouts at close than at far neighbor distances ($t_{23}=-3.38$, $P=0.003$); this difference was smaller in the more urbanized habitat with pedestrians but still significant ($t_{23}=-2.16$, $P=0.041$), whereas a non-significant difference between neighbor

distances was found in the more urbanized habitat without pedestrians ($t_{23}=0.05$, $P=0.962$).

Head-up scan rate was only influenced by neighbor distance (Table 1), without significant effects of habitat type, its interaction with neighbor distance, or any of the secondary factors (Table 1). Head-up scan rate was higher at far (17.55 ± 0.82 events per minute) than at close (15.00 ± 0.82 events per minute) neighbor distances.

Instantaneous pecking rate was significantly affected by habitat type and neighbor distance, but not by their interaction (Table 1). None of the secondary factors exerted a significant effect (Table 1). Instantaneous pecking rate was higher in the more urbanized habitat with pedestrians (112.86 ± 7.10 pecks per minute) than in the less urbanized habitat (90.57 ± 7.48 pecks per minute; $t_{26}=2.49$, $P=0.020$) and than in the more urbanized habitat without pedestrians (80.53 ± 7.16 pecks pr minute; $t_{26}=-3.97$, $P<0.001$). No significant differences were found between the less urbanized habitat and the more urbanized habitat without pedestrians ($t_{26}=-1.10$, $P=0.279$). Instantaneous pecking rate was higher at far (100.46 ± 5.76 pecks per minute) than at close (88.84 ± 5.76 pecks per minute) neighbor distances.

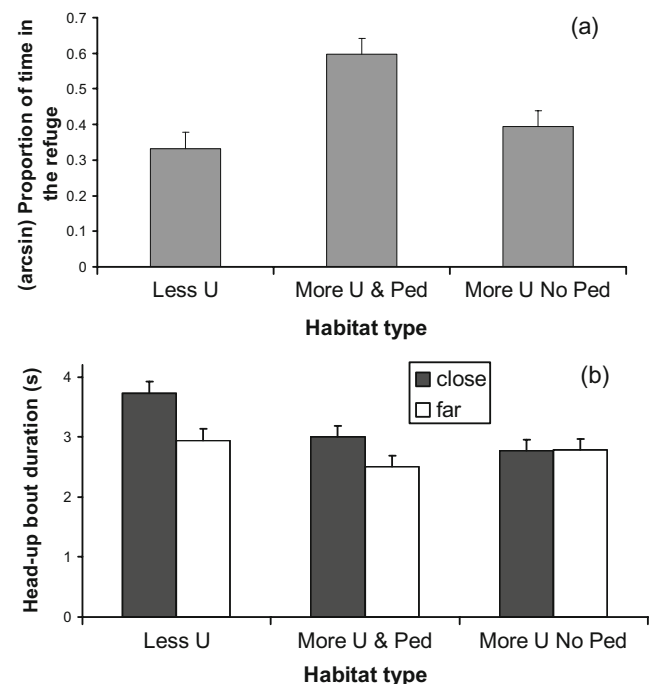


Fig. 3 Antipredator responses of House Finches under semi-natural conditions in different habitat types (*Less U*, less urbanized habitat; *More U & Ped*, more urbanized habitat with pedestrians; *More U No Ped*, more urbanized habitat without pedestrians) and different neighbor distances (close, far): **a** proportion of time in the refuge patch and **b** head-up scan bout duration

Table 1 Effects of habitat (more urbanized with and without pedestrians, less urbanized), neighbor distance (far, close), their interaction, and secondary factors (sex, temperature, body condition, wind speed) on the proportion of time spent in the refuge patch, head-up (food handling and scanning) bout duration and rate, and instantaneous pecking rate

	<i>F</i>	<i>df</i>	<i>P</i>
(arcsine) Proportion of time spent in the refuge patch			
Habitat	9.38	2, 26	0.001
Neighbor distance	0.34	1, 13	0.568
Sex	4.20	1, 23	0.052
Temperature	2.50	1, 23	0.127
Body condition	0.03	1, 23	0.860
Wind speed	1.59	1, 23	0.219
Habitat × neighbor distance	0.03	2, 23	0.969
Head-up (food handling and scanning) bout duration			
Habitat	6.80	2, 26	0.004
Neighbor distance	4.97	1, 13	0.044
Sex	0.79	1, 23	0.384
Temperature	4.56	1, 23	0.044
Body condition	4.79	1, 23	0.039
Wind speed	0.65	1, 23	0.428
Habitat × neighbor distance	6.40	2, 23	0.006
Head-up (food handling and scanning) rate			
Habitat	2.11	2, 26	0.141
Neighbor distance	13.30	1, 13	0.003
Sex	0.11	1, 23	0.747
Temperature	0.71	1, 23	0.450
Body condition	1.21	1, 23	0.282
Wind speed	0.67	1, 23	0.422
Habitat × neighbor distance	2.55	2, 23	0.010
Instantaneous pecking rate			
Habitat	8.24	2, 26	0.002
Neighbor distance	5.52	1, 13	0.035
Sex	0.07	1, 23	0.801
Temperature	3.60	1, 23	0.071
Body condition	1.28	1, 23	0.270
Wind speed	2.03	1, 23	0.168
Habitat × neighbor distance	2.74	2, 23	0.086

Significant results ($P < 0.05$) are marked in bold

Discussion

In the field component of our study, we found that house finches in more urbanized habitats had a greater tendency to flock with an increase in density and flushed at relatively larger distances than in less urbanized habitats. In the semi-natural component of our study, we found that individuals in the more urbanized habitat with pedestrians spent a greater proportion of time in the refuge patch and increased the instantaneous pecking rate in the foraging patch, and in the less urbanized habitat showed greater scan bout duration differences between neighbor distances. Furthermore at far neighbor distances, individuals increased scan

rate (decreasing scan bout duration) and instantaneous pecking rate.

The safe-habitat hypothesis assumes that native predator abundance is higher in less urbanized habitats; however, it does not consider the complex patterns that result from variations in the abundance of native and non-native predators. We indeed found that in the non-breeding season the overall abundance and number of avian native predators (e.g., raptors) was higher in less urbanized habitats and so was the abundance of the house finch predators (Cooper's hawks, red-shouldered hawks, and American kestrels). Native mammalian predators (e.g., bobcats, coyotes) are more abundant in less urbanized areas in Southern California as well (Crooks and Soule 1999; Crooks 2002) but probably pose greater risk during the breeding season (e.g., nest predation). Besides native avian predators, domestic cats have been shown to prey on birds (Crooks and Soule 1999) including house finches (Hill 1993) and happen to be at a higher abundance in more urbanized areas in Southern California (Crooks 2002). Furthermore, we found that humans, along with dogs, were more abundant in our more urbanized study areas. The direct and indirect risk of cat predation (Woods et al. 2003; Beckerman et al. 2007) and dog chases (Yalden and Yalden 1990; Lafferty 2001) can both have negative impacts on bird populations (e.g., Crooks and Soule 1999).

Birds are known to respond to an increase in predation risk by grouping (Whitfield 2003; Beauchamp 2004). Contrary to the predictions of the safe-habitat hypothesis, house finches showed a greater tendency to aggregate with an increase in density in more urbanized habitats. This finding could have different interpretations. First, food availability could be higher in more urbanized habitats (e.g., bird feeders), thereby attracting more house finches per patch (Barnard 1980; Walther and Gosler 2001), assuming population density remained similar, as found in this system. Second, greater flocking tendency can be influenced by vegetation structure (Lima et al. 1987). We found that larger trees were present in the more urbanized habitat, which could have actually lowered the need for joining larger groups if house finches perceived vegetation as a protective cover (Lima 1990; Lazarus and Symonds 1992; Whittingham and Evans 2004). Greater flocking tendency in more urbanized habitats would be expected if house finches perceived vegetation and/or buildings as obstructive cover, which may decrease the chances of detecting an attack by raptors that ambush prey (Roth and Lima 2003). Third, if house finches perceived humans, dogs, and cats as risky (Frid and Dill 2002), then greater flocking tendency can be related to the higher levels of disturbance in more urbanized habitats.

We also found evidence that house finches have less tolerance to humans in more urbanized habitats, contrary to

the predictions of the safe-habitat hypothesis and the findings of previous studies showing that several European birds were more tolerant of human approaches in rural/suburban than in rural areas (Cooke 1980; Møller 2008). House finches in less urbanized habitats fled at similar distances irrespective of variations in alert distance, probably trying to avoid humans once they approached a threshold distance. Yet, in more urbanized habitats, house finches assessed the potential risk of the approach, fleeing at close or larger distances depending on the distance at which they became alert.

Why do house finches in more urbanized habitats seem to assess the risk of an approach? First, if food availability was higher in the urban habitat and if this influenced body condition, then individuals could allocate more time to the assessment of an approaching risk because their energetic demands are already met (Beale and Monaghan 2004). However, Shochat (2004) proposed that the body condition of birds inhabiting highly urbanized habitats should be lower due to higher competition and the lower energetic quality of food. Second, tree cover was higher in the more urbanized habitat, which may have given house finches the opportunity to assess the risk of the approach because they had enough cover to flee to the tree tops if disturbed. Distance to cover was found to affect flight initiation distances in previous studies (Dill and Houtman 1989; Martin et al. 2005). Third, house finches in the more urbanized habitats could have become sensitized rather than habituated as a result of the greater diversity of sources of predatory (some raptors, cats) and non-predatory (humans, dogs) disturbance. Finally, it is also possible that the observed changes are the result of variations in detection probabilities or perception of humans. If human activity reduces predator detection due to visual obstruction effects, house finches would be more responsive to direct human approaches in more urbanized habitats to avoid missing a potential threat. Similarly, if humans are perceived as less predictable in more urbanized habitats (e.g., some people may walk by, others may approach aggressively, others may try to provide food), then house finches would be more responsive to minimize the uncertainty of a potential threat.

Individuals can balance the time allocated to patches with food and cover depending on the imminent risk of predation (Brown 1988; Kotler 1997). We found that house finches spent more time in the refuge patch in the more urbanized habitat with pedestrians, probably to reduce the risk imposed by humans walking nearby. A previous study also found that blackbirds *Turdus merula* spent more time in less risky areas (perching in trees) with a temporal increase in pedestrian rates (Fernández-Juricic and Telleria 2000). Allocating more time to the refuge patch could have been costly because it reduced foraging time. However, house finches compensated through changes in their

foraging strategy by increasing the speed with which they pecked while head-down when exposed to pedestrians, probably to maintain a certain rate of food intake. This higher foraging speed could also reduce the probability of missing a quickly approaching threat. Higher instantaneous foraging rates were also reported in a captive study with oystercatchers *Haematopus ostralegus* in response to limitations in the time available for foraging due to tidal variations (Swennen et al. 1989). Newman et al. (1988) also showed in gray squirrels (*Sciurus carolinensis*) a similar trend towards increasing intake rate in risky situations (farther from cover) to achieve a minimum consumption rate. An alternative interpretation is that the higher number of pedestrians makes the visual background against which house finches would monitor for predators more complicated, which may trigger more scanning effort to compensate for a noisier visual environment.

While exploiting the foraging patch, longer scan bouts suggest higher perceived predation risk (Hart and Lendrem 1984), as individuals delay resuming foraging head-down to obtain more information from the environment (e.g., potential predators). In the less urbanized habitat, the differences in scan bout duration were the greatest, with longer bouts when conspecifics were closer than farther apart. This result is counterintuitive as flock mates located closer are supposed to benefit from information about potential predators being detected sooner (Hilton et al. 1999) and predators having more difficulty singling out targets (Bednekoff and Lima 1998), thereby reducing the need for vigilance. However, at very close neighbor distances, individuals may pay more attention to conspecifics and copy their vigilance behavior (Fernández-Juricic and Kacelnik 2004; Fernández-Juricic et al. 2004) or may use foraging information from companions to make decisions about patch quality (Krause and Ruxton 2002). A similar difference between neighbor distance, but less marked, was found in the more urbanized habitat with pedestrians but not in the more urbanized habitat without pedestrians. This suggests that the latter habitat was perceived as the least risky, likely because it screened out the visual presence of humans and potential predators. This conclusion is supported by an increase in food-searching behavior (e.g., proportion of time head-down) that we found in the same habitat (Valcarcel and Fernández-Juricic, unpublished data). The more urbanized habitat without pedestrians may have represented an artificial scenario because we eliminated most of the salient visual habitat cues by fencing; however, it allowed us to characterize baseline behavioral levels for comparisons with the other treatments.

The distance separating foragers also influenced the perceived predation risk independently of habitat type.

House finches increased scanning rate (and as a result shortened scan bouts) and instantaneous pecking rate at far neighbor distances. Increasing neighbor distance could make it harder for birds to get information from their flock mates (Fernández-Juricic et al. 2004); and consequently individuals may need to rely on personal information by performing short scans more often during foraging bouts (Templeton and Giraldeau 1995). This time budgeting competes with the time allocated to foraging, which may explain the faster pecking rate of house finches at far neighbor distances as a compensatory mechanism. Alternatively, this distance effect could be the result of the cages creating some kind of visual obstruction when farther apart.

Taken together, most of our parameters (e.g., flock size, flight initiation distance, patch use, and instantaneous pecking rate) varied in a way that suggests higher perceived risk in more urbanized habitats. Although house finches may experience predation from native and non-native species in both habitat types, perceived predation risk may be higher in more urban areas due to the combined effects of predatory and non-predatory sources of disturbance. The other option is that our results stem from differences in the probabilities of visually detecting predators rather than the risk imposed by human activities per se. In less urbanized habitats, with less visual distraction, predators could be detected with higher probability, which could reduce perceived risk, decrease the use of the refuge, and decrease flocking tendency. In more urbanized habitats, with more visual distraction due to human activity, predator detection may be more difficult, leading to an increase in vigilance, greater flocking tendency, and general wariness, which may cause a positive relationship between flight initiation distance and alert distance.

Why does a species known to exploit suburban and urban habitats show stronger antipredator responses in more urbanized habitats? One explanation is that the tolerance levels of this species may not be linear, which could generate the highest level of habitat suitability at intermediate levels of urbanization, as has been found in a study along a rural–urban gradient in California (Blair 1996). Another explanation is that house finches do not habituate to high levels of human disturbance because they have plenty of *alternative* foraging and suitable breeding habitats throughout the urban–suburban gradient, reducing the costs of interactions with humans. Overall, house finches seem to adapt to urban environments, though with certain limitations, using various behavioral mechanisms to reduce risk.

The implications of our results for the safe-habitat hypothesis is that, at least from the perspective of perceived predation risk by house finches, highly urbanized habitats may not be as safe even when the native predator

abundance is lower, due to the presence of human-related disturbance (e.g., pedestrians, dogs, cats). Future studies should address whether this pattern is caused by the non-predatory risk posed by humans or differences in predator detection due to higher visual noise in more urbanized areas.

Acknowledgements We especially thank the following members of the Behavior and Conservation Laboratory (CSULB) who gladly helped in the different phases of this study: Laura Brandy Adams, Hans Chalco, Karin De Collibus, Tracy Dolan, Rachael Poston, Vanessa Tisdale, Mary Ellen Millard, Shane Oliver, Shelya Jones, Tim Morgan, Elizabeth Tran, Ronald Treminio, Jennie Wong, and Maura Palacios. Robert Cummings and Orange County Vector Control District facilitated access to the birds. Eyal Shochat, James Archie, Judith Brusslan, Dessie Underwood, and two anonymous referees provided valuable comments on earlier versions of the draft. This study was funded by the College of Natural Sciences and Mathematics (CSULB). Experimental protocols were approved by CSULB IACUC (protocol number 223).

Appendix 1. Study areas used and degree of urbanization

The table presents the list of parks in more and less urbanized habitats and their sizes used for this study.

Table 2 List of parks in more and less urbanized habitats and their sizes

Parks	Type	Hectares
Aliso Wood Wilderness	Less urbanized	1,618.76
Bolsa Chica Regional	Less urbanized	426.54
Crystal Cove	Less urbanized	1,214.07
San Joaquin Freshwater Marsh	Less urbanized	81.75
Laguna Coast Wilderness	Less urbanized	2,630.49
Newport Backbay	Less urbanized	404.69
Oneil Regional	Less urbanized	687.97
Peters Canyon	Less urbanized	143.26
Seal Beach	Less urbanized	36.42
Talbert Regional	Less urbanized	72.84
Whiting Ranch	Less urbanized	1,618.76
Admiral Kidd	More urbanized	3.76
Boughton Creek	More urbanized	0.32
Channel View	More urbanized	2.06
Cherry	More urbanized	3.40
College Estates	More urbanized	0.91
Deforest	More urbanized	10.52
El Dorado	More urbanized	122.62
Houghton	More urbanized	10.64
Los Cerritos	More urbanized	2.93
Siverado	More urbanized	4.56
CSULB campus	More urbanized	130.71

We quantified several aspects of these parks to confirm our classification. We obtained information on park area from the Long Beach Parks, Recreation and Marine website

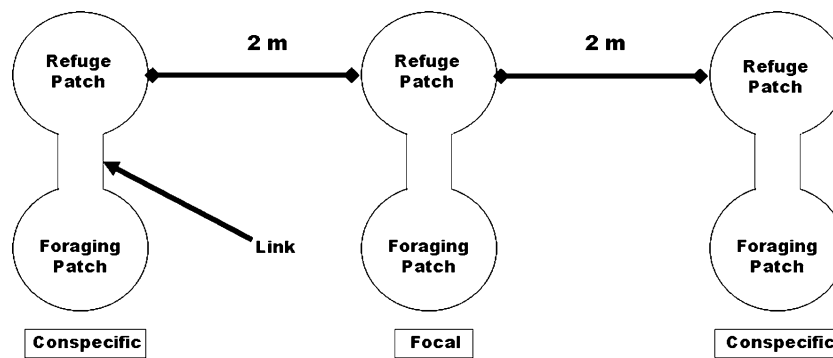


Fig. 4 Semi-natural experimental design testing habitat type and neighbor distance. Each enclosure consists of a foraging patch connected by a corridor to a refuge patch. This example shows the 2 m (far) neighbor distance treatment

(<http://www.longbeach.gov/park/facilities/parks>) for parks located within Long Beach and from the County of Orange, Harbors, Beaches, and Parks website (<http://www.ocparks.com/>) for those located in Orange County.

Human disturbance was characterized in the parks where flock surveys were conducted and where FID measurements were taken using different methodologies. We measured the number of pedestrians in the 22 parks listed above by counting the number of people walking and sitting detected within the transects during the flock surveys. In addition, we measured pedestrian rate on the spots in which flight initiation distance had been recorded using two 50-m² squared plots to better characterize human disturbance in the samples areas: one plot was centered where the focal bird was before flushing, and the other plot was in a random location 50–100 m away from the previous plot. Both pedestrian rate measurements were taken on the same day, but days after we recorded FID. At the center of the 50-m² plot, during a 10-min period, we counted the number of pedestrians walking and sitting, as well as the number of dogs (leashed and unleashed) that entered the plot and averaged the values from both plots.

We measured vegetation structure in 25-m² plots at the center of every transect used to survey flocks. We visually estimated (following Prodon and Lebreton 1981): grass cover, bush cover, and tree cover. We measured mean bush and tree height by using a tape meter when physically possible. For taller trees, we estimated height by visually rotating the location of the tip of the tree onto the ground and then measuring the ground distance with a meter tape (± 0.05 m; following Fernández-Juricic et al. 2005). We also recorded the number of tree trunks >30-cm dbh), as these represented potential perches for house finches (Fernández-Juricic et al. 2005).

Appendix 2. Description of the experimental procedures to assess scanning and foraging behavior

The semi-natural experiment was carried out from September to November 2005 in two locations separated by 3.87 km: Seal Beach (33° 45' N, 118° 05' W; less urbanized) and CSULB campus (33° 46' N, 118° 06' W; more urbanized).

Forty-two wild adult house finches were caught and color-banded from two Southern California populations: Seal Beach (33° 45' N, 118° 05' W) and Irvine (33° 39' N, 117° 51' W). We decided to capture birds from areas that had intermediate degrees of urbanization to avoid habituation effects towards humans. House finches were housed in 0.85×0.6×0.55-m cages under a 12:12-h light–dark cycle (lights went on 06:00) and were kept in visual and auditory contact with four birds per cage (male and female house finches were housed in the same cages). No breeding behavior was observed during the experimental period. Water and food (finch seed mix, Royal Feeds, Leach Grain and Milling, Co., Downey, CA, USA) were provided *ad libitum* except during experimental trials and the preceding periods of food deprivation. At the end of the experiments, birds were released at the same locations in which they were captured.

Our experimental setup consisted of three sets of two bottomless circular light wire mesh enclosures (0.5-m diameter, mesh opening 0.06 m, 85% open area) placed in a parallel arrangement. Each enclosure was placed on a round wooden tray and connected by a link (0.3×0.18×0.18 m) to the other enclosure of the same set (Fig. 4). One of the enclosures (hereafter, foraging patch) contained 3 cm of sawdust and 5.00±0.05 g of hidden sunflower seeds. The other enclosure (hereafter, refuge patch) had synthetic foliage placed around the top of the cage and one synthetic bush with the base in the center of the refuge. We placed

one bird in each set of enclosures during the experiment, totaling three birds per trial. We considered the individual in the central set as the focal animal to minimize edge effects.

We manipulated two different treatments: habitat type (three levels: less urbanized without pedestrians, more urbanized with pedestrians, and more urbanized without pedestrians) and neighbor distance (two levels: close, 0-m separation between the sets of enclosures, and far, 2-m separation between the sets of enclosures, Fig. 4). Thus, each focal bird was exposed to six different treatments (one per day) in a random order. Trials were performed in the mornings from 07:00 to 12:00 but not during high winds or rain.

The treatments in the more urbanized habitat were conducted at CSULB campus on a grassy area 20 m from a pathway frequented by pedestrians and 15 m from a large old pine tree and a four-story campus building. For the more urbanized habitat without pedestrian treatment, we surrounded the experimental area with a 2.0-m-high fence and black tarp to screen out visual stimuli (e.g., pedestrians), but the building was still in the visual field of animals. The purpose of this treatment was to obtain the baseline behavior of birds without the influence of pedestrians or habitat openness that would trigger changes in vigilance to monitor for a potential predator. The downside is that it created a visual obstruction effect that may have blocked the need for vigilance.

For the more urbanized habitat with pedestrians treatment, we used the same location without the fence so that birds were exposed to pedestrians as well as an assistant walking in a parallel path 9 m away from the enclosures to simulate the presence of humans. The less urbanized habitat treatment was performed at Seal Beach in an area without a fence. This experimental site was not near any human structures or trees and did not have any pedestrian traffic. The vegetation consisted of native bushy plants and bare ground. The differences in habitat structure between these sites mirrored the ones found between more and less urbanized parks.

Out of the 42 birds, 14 served as focals (seven males and seven females) and were used in a total of 84 trials. The remaining 28 non-focal birds (conspecifics) were assigned to a focal bird and went through all trials with the same focal individuals but were randomly assigned to the right and left sets of enclosures. All birds were food-deprived for 2 h prior to the experiments and transported to the CSULB experimental site by walking and to the Seal Beach location by car. Animals were then placed in the shade until their trial time. During transport, and, while awaiting their trial, they were provided water *ad libitum*.

The use of a car as a means of transporting the animals to the less urbanized habitat to run the semi-natural

experiment could have produced changes in their behavior. To test this possibility, we ran another experiment at only the CSULB campus site, in which house finches experienced two treatments. In the first treatment (driving), birds were driven for 10 min and then placed back in their aviary cages for 30 min before they were used in the experiments. This treatment was conducted with the same car used during the experiments and replicated the less urbanized treatment procedures in the main experiment. In the second treatment (non-driving), birds were not driven at all but were walked to the experimental site replicating the more urbanized treatment procedures in the main experiment. The same three sets of enclosures were placed 0.5 m apart (Fig. 4), with one bird in each under similar conditions as described in the “Materials and methods.” We screened out visual stimuli by fencing around the cages in all treatments. We recorded the foraging and scanning behavior of eight focal birds during 10 min, with each focal being exposed to each treatment. The birds used in this experiment were different from those used in the one presented in the main text.

None of the secondary factors (temperature vs. food deprivation time, $r=0.24$, $P=0.255$; temperature vs. body condition, $r=0.30$, $P=0.150$; food deprivation time vs. body condition, $r=0.04$, $P=0.840$) was correlated among each other. Using general linear models (repeated-measures design), we found that the proportion of time spent in the refuge did not vary between treatments (driving, 0.03 ± 0.01 ; non-driving, 0.02 ± 0.01 ; $F_{1, 4}=1.39$, $P=0.303$), controlling for temperature ($F_{1, 4}=0.00$, $P=0.968$), food deprivation time ($F_{1, 4}=0.07$, $P=0.811$), and body condition ($F_{1, 4}=2.82$, $P=0.168$). Scan rate (driving, 18.19 ± 2.25 events per minute; non-driving, 16.83 ± 2.25 events per minute; $F_{1, 4}=0.38$, $P=0.572$) and scan bout duration (driving, 2.25 ± 0.29 s; non-driving, 2.83 ± 0.29 s; $F_{1, 4}=2.12$, $P=0.219$) did not differ between treatments, controlling for the three secondary factors (scan rate: temperature, $F_{1, 4}=1.51$, $P=0.287$; food deprivation time, $F_{1, 4}=1.26$, $P=0.324$; body condition, $F_{1, 4}=0.11$, $P=0.754$; scan bout duration: temperature, $F_{1, 4}=5.60$, $P=0.077$; food deprivation time, $F_{1, 4}=3.15$, $P=0.151$; body condition, $F_{1, 4}=1.14$, $P=0.346$). Finally, there was no difference in pecking rates between treatments (driving, 21.75 ± 2.86 events per minute; non-driving, 18.28 ± 2.86 events per minute; $F_{1, 4}=1.29$, $P=0.321$), controlling for the secondary factors (temperature, $F_{1, 4}=6.28$, $P=0.066$; food deprivation time, $F_{1, 4}=5.16$, $P=0.086$; body condition, $F_{1, 4}=0.09$, $P=0.776$). Therefore, we conclude that driving the birds to conduct the less urbanized treatment would not substantially affect their behavior.

During the main experiment, the focal individual was recorded for 20 min using a Sony DCR-TRV38 digital video camera starting from the time it began pecking in the

foraging patch. The camera was placed on a tripod 3 m from the focal's set of enclosures, which allowed us to record its scanning and foraging behavior while in the foraging patch and its use of the refuge patch. We recorded behavior using an event-recording program (JWatcher 1.0; Blumstein et al. 2006). When birds were in the foraging patch, they could be on the ground or hanging on the cage wall. We only focused on their behavior on the ground as a proxy of normal foraging behavior. House finches alternated bouts of food-seeking behavior with their heads down and bouts of scanning behavior with their heads up. We recorded the number of head-up scanning events and their duration, including head-up food-handling behavior as they use it for vigilance (Fernández-Juricic and Tran 2007). While house finches were head-down, we recorded the number and duration of pecking events. We calculated the following dependent variables: head-up scan bout duration, head-up scan rate, and instantaneous pecking rate (number of pecking events per unit time head-down). We also recorded and calculated the proportion of time the focal bird spent in the refuge patch. Video analysis was performed by AV after extensive self-training. At the time of recording, there was less than a 5% difference between two scorings of the same tape. For every trial, we recorded several potential confounding factors: food deprivation time, ambient temperature, wind speed, and focal body condition (body mass/wing length).

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