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DR BEN DANTZER (Orcid ID : 0000-0002-3058-265X)

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Title: Urban fox squirrels exhibit tolerance to humans but respond to stimuli from natural predators

Running title: Fox squirrel behavior in urban areas

Authors: Anna Kittendorf¹, Ben Dantzer^{1,2}

¹Department of Psychology, University of Michigan, Ann Arbor, MI, 48109, USA

²Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, 48109, USA

Correspondence: Ben Dantzer (dantzer@umich.edu)

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Conflict of Interests

Both authors declare no conflict of interests.

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30 **Abstract**

31 Animals in urban areas that experience frequent exposure to humans often behave differently
32 than those in less urban areas, such as exhibiting less vigilance or anti-predator behavior. These
33 behavioral shifts may be an adaptive response to urbanization, but it may be costly if animals in
34 urban areas also exhibit reduced anti-predator behavior in the presence of natural predators. In
35 trials with only a human observer as the stimulus, urban squirrels exhibited reduced vigilance
36 and anti-predator behavior compared to those in less urban areas. Next, we exposed squirrels in
37 multiple urban and less urban sites to acoustic playbacks of a control stimulus (non-predatory
38 bird calls), a natural predator (hawk), and dogs and recorded their vigilance and three different
39 anti-predator behaviors when a human approached them while either broadcasting one of these
40 three playbacks or no playbacks at all. Squirrels at urban sites also did not differ in their
41 behavioral responses to the playbacks from possible predators (hawks or dogs) when they were
42 compared to those at less urban sites exposed to these playbacks. Urban squirrels also exhibited
43 increased vigilance and anti-predator behavior when exposed to a human paired with hawk
44 playbacks compared to the control playbacks. Together, our results indicate that urban squirrels
45 did perceive and assess risk to the natural predator appropriately despite exhibiting increased
46 tolerance to humans. These results provide little support for the hypothesis that increased
47 tolerance to humans causes animals to lose their fear of natural predators.

48

49 **Keywords:** Anti-predator behavior, cross-habituation, first alert distance, flight initiation
50 distance, stimulus generalization, urbanization

51

52

53 **Introduction**

54 Behavior plays an important role in enabling animals to persist through environmental
55 change (Baldwin, 1896; Bartholomew, 1964; West Eberhard, 1989; Price et al., 2003; Snell-
56 Rood, 2013). Accordingly, it seems to play a major role in facilitating the ability of animals to
57 cope with new challenges that they face in urban environments (Ditchkoff et al., 2006;
58 Tuomainen and Candolin, 2011; Lowry et al., 2013; Ryan and Partan, 2014). One of the most
59 common behavioral adjustments of animals in urban environments is reduced anti-predator
60 behavior in the presence of humans. This is often reflected in measures of flight initiation

61 distance (FID), which is the distance at which an animal flees from an approaching human and is
62 thought to be an approximation of their sensitivity to risk of an approaching predator (Cooke,
63 1980; Ydenberg & Dill, 1986; Lima and Dill, 1990). Individuals with shorter FIDs are
64 considered to be bolder than individuals with longer FIDs since they demonstrate reduced fear of
65 the “predator”.

66 Substantial evidence supports the hypothesis that animals in more urban environments
67 exhibit less anti-predator behavior, as reflected by a lower FID. For example, a meta-analysis of
68 180 bird species, 16 lizard species, and 16 mammal species, Samia et al. (2015) showed that
69 populations of these species that experienced elevated levels of human disturbance exhibited
70 lower FID. This could be because vigilance and anti-predator behaviors carry energetic or time
71 costs as they take time away for resource acquisition and animals in urban environments may
72 therefore optimize resource acquisition by exhibiting lower levels of anti-predator behavior
73 (Ydenberg and Dill, 1986; Cooper and Frederick, 2007; Møller, 2012).

74 Although reductions in the expression of anti-predator in urban environments is generally
75 thought to be adaptive (Møller, 2008; Carrette et al., 2016), there may be potential costs for
76 urban animals if they reduce their overall expression of anti-predator behavior to not only
77 humans but also towards natural predators if those urban areas contain predators. This could be
78 due to the phenomenon of cross-habituation or stimulus-generalization. For example, birds that
79 are habituated to a threatening stimulus that are then presented with a second simulated predator
80 exhibit an attenuated response to this second stimulus compared to a group of naïve birds (Hinde,
81 1954; see also Curio, 1993). This type of stimulus generalization can occur where an animal
82 habituated to one stimulus exhibits an attenuated response to a second stimulus from the same *or*
83 different sensory modality (Guttman and Kalish, 1956; Thompson and Spencer, 1966; Rankin et
84 al., 2009). Related concepts occur in the context of “behavioral spillover” where individuals that
85 exhibit high levels of a behavior in one context also exhibit it in another context even though it
86 may not be adaptive, such as animals exhibiting higher levels of boldness in a courtship context
87 also exhibiting higher boldness in the presence of a predator (Arnqvist and Henriksson, 1997;
88 Sih et al., 2004).

89 If urban animals in areas containing predators exhibit reductions in vigilance and/or anti-
90 predator behavior not only toward humans but also to natural predators, it could conceivably
91 have important impacts on wildlife populations by increasing their vulnerability to predators

92 (Geffroy et al., 2015). To date, there is little consensus about whether animals in urban areas or
93 those exposed to increased human presence exhibit a reduced response to threats from natural
94 predators (Fitzgerald and Stronza, 2016). For example, some studies show that individuals in
95 areas with higher human activity exhibit less of a behavioral response when natural predators
96 were observed visiting the area (Olson and Acevedo-Gutiérrez, 2017) or due to acoustic
97 playbacks of a natural predator (McCleery, 2009). The latter suggests that animals experiencing
98 frequent exposure to human activity exhibit reduced responses to other stimuli from natural
99 predators. Other studies show that the response of animals in more urban areas to a stimulus
100 from a natural predator is not attenuated compared to those in more rural locations (Labra and
101 Leonard, 1999; Coleman et al., 2008; Seress et al., 2011; Bokony et al., 2012; Cavalli et al.,
102 2016; Weaver et al., 2018; Vincze et al., 2019).

103 In this study, we characterized the vigilance and anti-predator behavior of fox squirrels
104 (*Sciurus niger*) in urban and less urban areas to achieve the following two objectives. First, we
105 conducted standard FID trials (with only stimuli from a human observer) to examine whether
106 squirrels in urban areas showed reduced vigilance and anti-predator behavior towards a human
107 observer compared to those in less urban areas. If squirrels in urban areas did exhibit reduced
108 vigilance and anti-predator behavior, this would support the hypothesis that squirrels in our
109 urban study populations were more tolerant of human presence, which would be consistent with
110 numerous other studies (Samia et al., 2015). Squirrels were located in their natural habitat and
111 we recorded the following four aspects of their vigilance and anti-predator behavior. First, we
112 recorded the distance to which the observer could get to before they exhibited vigilance behavior
113 towards the observer (“first alert distance” or FAD, similar to Fernández-Juricic and Schroeder,
114 2003; Blumstein et al., 2005). Second, we recorded how close the observer could get to them
115 before they ran away (FID). Third, was the probability that the squirrel escaped by running up a
116 tree. Fourth, the latency following the trial it took them to resume their typical behavior
117 (foraging or traveling off tree). We interpreted vigilance behavior was reflected in FAD and that
118 anti-predator behavior was composed of FID, probability of the squirrel escaping up a tree, and
119 the latency to resume typical behavior following the trial. However, we note that it is likely that
120 all four of these behaviors are quite similar in the sense that they measured anti-predator
121 behavior and that the latency to resume typical behavior following the trial may be affected by
122 motivational issues associated with nutritional state. Measuring all four of them can provide

123 additional insight, such as examining whether squirrels in less urban areas are more alert to
124 human presence than those in urban areas. Additionally, most studies on this topic are in birds
125 and only measure FID. Measuring whether the squirrel escaped by running up a tree and how
126 long the squirrel took to resume their typical behavior in addition to FID may provide greater
127 insight into the behavioral differences between animals in urban or less urban areas.

128 Our second objective was to examine whether urban animals exhibit reduced behavioral
129 responses to stimuli from natural predators when they are in the presence of humans. To do so,
130 we quantified the four behaviors described above when fox squirrels in urban or less urban areas
131 were presented with a human observer with a control acoustic playback (common non-
132 threatening bird), a human observer paired with the playback of a natural predator (hawk), or a
133 human observer paired with a playback of an invasive predator (dog). We predicted that squirrels
134 in the urban areas but not those in the less urban areas would exhibit no change in vigilance and
135 anti-predator behavior when they were exposed to the human+dog or human+hawk stimuli
136 compared to the human+control playback. We also predicted that squirrels in the urban sites
137 would exhibit less vigilance and anti-predator behavior when exposed to hawk or dog playbacks
138 compared to those at the less urban sites that were exposed to the hawk or dog playbacks. These
139 results would support the hypothesis that animals in urban environments exhibit less vigilance
140 and anti-predator not only to humans but also when faced with natural predators.

141

142

Materials and Methods

Study species and sites

144 Fox squirrels are ubiquitous in urban and suburban environments in the midwestern
145 United States (McCleery, 2008, 2009). Although arboreal tree squirrel species like fox squirrels
146 are common in urban areas worldwide, they continue to experience predation from natural
147 predators, although it may be rare compared to other sources of mortality (McCleery et al.,
148 2008). Urban squirrels also likely experience predation from domestic cats and dogs (Koprowski,
149 1994; Wauters et al., 1997; Tumilson, 2012; Loss et al., 2013; Jokimäki et al., 2017).

150 We studied natural populations of adult fox squirrels from six sites in and around Ann
151 Arbor, Michigan (Table S1 in Appendix). Sites were chosen based upon estimates of human
152 population density (Center for International Earth Science Information Network, 2018) with
153 urban sites having higher human density than less urban sites (see below and Table S1). Urban

154 sites included Prospect Park as well as two locations on the University of Michigan's (UM) main
155 campus (North and Central Campus) that are ~3-4 km away from one another. Prospect Park is
156 near downtown Ypsilanti, Michigan and about 13 km away from UM main campus. Less urban
157 sites included Nichols Arboretum, County Farm Park, and Saginaw Forest. Nichols Arboretum is
158 located ~1 km away UM main campus, County Farm Park is about ~4.5 km away, and Saginaw
159 Forest is ~7 km away. At all research sites, dogs are allowed but hunting is not. Squirrels may be
160 occasionally fed by humans at some of our study sites (e.g., Central Campus), but data were not
161 systematically collected to assess feeding rates. Approval to conduct this research at each site
162 was obtained from UM (Central Campus, Nichols Arboretum, North Campus, Saginaw Forest),
163 Washtenaw County Parks & Recreation (County Farm Park), and the City of Ypsilanti (Prospect
164 Park). All of our field procedures were non-invasive and involved behavioral observation or
165 short-term exposure to playbacks of acoustic stimuli. All experiments followed the guidelines set
166 by the Animal Behavior Society/Association for the Study of Animal Behaviour (Anonymous,
167 2012) and the US National Research Council and were approved by the UM Institutional Animal
168 Care and Use Committee (protocol # PRO00009076). We note that squirrels used in the study
169 may be STRANGE (*sensu* Webster and Rutz, 2020) in the sense that individual squirrels likely
170 have different rearing histories (though they are unknown and none should have been reared in
171 captivity) and that compliance to take part in the study was likely biased towards squirrels that
172 did not immediately run away when approached by the human observer.

173 Given that increased exposure to humans may cause animals in urban areas to exhibit less
174 anti-predator behavior towards them (McCleery, 2009; Rodriguez-Prieto et al., 2009; Vincze et
175 al., 2016; Uchida et al., 2019), we focused on human presence as the major factor difference
176 between our study sites (which should also reflect general urbanization). Sites were classified as
177 "urban" based upon having a human population density >1000 persons per km² whereas the less
178 urban sites had anywhere from 25-250 persons per km² (Saginaw) to 250-1000 persons per km²
179 (County Farm Park, Nichols Arboretum). To support these classifications, we estimated human
180 and dog presence while we were visiting sites conducting our behavioral observations. We
181 counted the total number of dogs (on or off leash) but only counted the number of humans up to
182 50. If human presence exceeded 50 people, then a rough estimate of 50, 75, or 100 was recorded.
183 Human presence was recorded as 100 for all numbers estimated to be >100. We did not record
184 the distance from the observer to other humans but just whether the human was visible. Although

185 human and dog presence varied among the different sites (Table S1), the number of humans
186 observed per hour of observation averaged over all the urban sites (mean \pm SE = 7.23 ± 3.33
187 humans/hr) was higher than those observed averaged over all the less urban sites (0.51 ± 0.40 :
188 Mann-Whitney-Wilcoxon Test, $W = 1$, $p = 0.1$). We observed fewer dogs per hour at the urban
189 sites (0.065 ± 0.06 dogs/hr) compared to the less urban sites (0.33 ± 0.10 , Mann-Whitney-
190 Wilcoxon Test, $W = 9$, $p = 0.1$). These differences in humans or dogs observed per hour were not
191 significant but in general support our assumption that our urban sites likely experience greater
192 exposure to humans.

193 We aged and sexed squirrels visually according to their size (small juvenile squirrels
194 were excluded) and anatomy (males were identified by presence of testes), respectively. Similar
195 to most studies that measure anti-predator using FID, trials were conducted on unmarked
196 squirrels at each site. We located squirrels by walking around each site and trials were started
197 when squirrels were observed. Focal individuals were selected randomly, however, only squirrels
198 that were feeding or foraging on the ground were included in this experiment. Because we did
199 not mark squirrels individually, it is possible that the same squirrel was observed on different
200 days, although we visited different areas of each study site to try and reduce this possibility. It is
201 unlikely that the same squirrel was observed multiple times on the same day, because after each
202 trial was completed, the observer walked approximately 20 meters away from the previous
203 location (in a continuous linear direction from where the first trial was conducted) and started a
204 trial with a different squirrel. Additionally, sites were only revisited after at least three days since
205 the previous visit to reduce the possibility of a squirrel becoming habituated to the trials should it
206 be sampled again. Although we cannot address habituation in this study, if squirrels at these sites
207 were habituating to our protocols, we would expect that their behavioral responses would decline
208 with trial number or date when the trial was conducted. The fact that none of our behavioral
209 variables were associated with date of when the trial was conducted (Tables 1-2) supports our
210 assumption that squirrels were not habituating to our protocols.

211 *Quantifying behavioral responses of squirrels*

212 In total, we observed fox squirrels for 52.36 hours over 30 different days. A single
213 observer (AK) conducted all trials. A total of 171 trials were conducted with 71 trials conducted
214 without any acoustic playback treatments and 94 trials conducted with an acoustic playback.
215 Sites were visited between 800 and 1900 h EST and data were collected from October 2019

216 through January 2020. Trials with no playbacks were conducted from 25 October 2019 to 16
217 November 2019 (from 812 to 1810 h) whereas trials using playbacks (playback trials) were
218 conducted from 18 November 2019 to 27 January 2020 (from 802 to 1609 h). We randomized
219 the order in which sites were visited and the version of playback treatments used (see below for
220 information on playback versions) at each site. No two sites were visited on the same day. All
221 trials with no playbacks were conducted prior to the playback trials in this study. This was due to
222 personnel limitations and prevents us from directly comparing trials with and without playbacks
223 given that squirrel behavior likely changes seasonally from October to January due to food
224 caching behavior in autumn but not winter. Trials were not conducted when it was raining or
225 snowing. Results from two one-way ANOVAs showed that the time of day for playback trials
226 did not vary among the three different treatment groups ($F_{2,91} = 0.44, p = 0.65$) and that the time
227 of day when trials were conducted did not vary among squirrels at the urban or less urban sites
228 (t-test: $t_{75.4} = 0.21, p = 0.83$). Air temperature varied during all the trials varied from -6.1° to
229 10.5°C (mean = 2.7°C).

230 We measured the behavioral responses of squirrels to humans or humans plus different
231 playbacks using protocols developed for tree squirrels (Dill and Houtman, 1989; Gustafson and
232 VanDruff, 1990; McCleery, 2009). At the beginning of each trial, a marker was placed at the
233 starting position of the observer and trial data were recorded (GPS location, time of day,
234 temperature, general weather conditions, and squirrel sex). The squirrel was approached by a
235 single observer (AK) at a slow and steady pace in a direct line to the squirrel (see Fig. S1 in
236 Appendix I). Additional markers were placed when a squirrel displayed the first alert and when
237 they fled. The FAD was defined as the distance between the observer and the squirrel when it
238 first stopped moving (froze) and looked at the observer with one or both eyes. FID was recorded
239 as the distance between the squirrel's initial position and the observer location when it actively
240 fled (stopped feeding and foraging and moved rapidly away from observer). A marker was also
241 placed at an estimate of the squirrel's initial position to the place where they fled to if refuge was
242 not taken in a tree, and the distance between this marker and the squirrel's initial position was
243 recorded as "flight distance". We recorded this because some studies have noted that FID is
244 variable depending on intruder starting distances and distance to a refuge (Dill & Houtman,
245 1989; Blumstein, 2003). Consequently, the distance between the observer and the focal squirrel
246 at the start of the trial (starting positions, hereafter referred to as "initial distance": mean \pm SE

247 over all 171 trials = 21.2 ± 0.61 m) and the distance between the focal squirrel's initial position
248 and the nearest tree were also measured ("distance to nearest tree": mean \pm SE over all 171 trials
249 = 3.2 ± 0.11 m).

250 If the focal animal took refuge in a tree other than the one nearest, distance between the
251 squirrel's initial position and its refuge tree of choice ("distance to the chosen tree") was also
252 recorded. If an individual took refuge in a tree, a laser rangefinder was used to measure how high
253 they climbed, and this distance was recorded (same as vertical escape distance in Uchida et al.,
254 2017). Lastly, latency to resume behavior was recorded ("latency"). This was measured with a
255 stopwatch to determine how long it took for the animal to cease alert/vigilance behavior and
256 resume typical activity (foraging or traveling off tree). When the observer was recording latency,
257 they maintained as large a distance as possible (~15-20 m) from the tree to reduce the influence
258 on the squirrel's behavior. Out of all the trials, nearly all squirrels ceased alert behavior and
259 resumed typical behavior within a couple minutes ($n = 171$ trials, mean \pm SE = 130.5 ± 10.3 s),
260 but there was one individual squirrel that remained alert for longer than ten minutes and we
261 recorded its latency as ten minutes. Distances were measured with a tape measure and presented
262 in meters.

263 *Playback trials*

264 Playback trials ($n = 94$ total trials) were conducted using the same protocol shown above,
265 with the addition of an acoustic stimulus being broadcasted while the observer approached the
266 squirrels. The control stimulus consisted of recordings of black-capped chickadee calls (*Poecile*
267 *atricapillus*). Black-capped chickadees are not known to be predators of fox squirrels
268 (Korschgen, 1981; Koprowski, 1994) and a previous study in another tree squirrel species
269 showed that individuals exhibited a significantly reduced response to black-capped chickadee
270 playbacks compared to calls of other anthropogenic noises (car alarm, buzzer) and playbacks of
271 red-tailed hawks (Bohls and Koehnle, 2017). We therefore expected that black-capped chickadee
272 recordings would represent a neutral vocalization for fox squirrels and they can act as control to
273 ensure that any differences in squirrel behavior across playback treatments are attributable to the
274 vocalization information of the playback rather than an added exposure to noise. To simulate the
275 threat of a terrestrial predator, recordings of domestic dogs barking were broadcasted. Domestic
276 dogs are terrestrial predators of fox squirrels (Koprowski, 1994; Wauters et al., 1997) and other
277 species of tree squirrels that live in the same habitats as fox squirrels also adjust their risk-taking

278 behavior according to the abundance of domestic dogs (Bowers and Breland, 1996; Cooper et al.,
279 2008). For the avian predator, recordings of red-tailed hawk (*Buteo jamaicensis*) calls were
280 broadcasted to the focal individual. Red-tailed hawks were chosen since they are year-round
281 predators of fox squirrels in Michigan (Koprowski, 1994; personal observations) and other
282 studies illustrate that tree squirrels respond to hawk playbacks with increased anti-predator
283 behavior (McCleery, 2009; Lilly et al., 2019). No post-processing of sound files was performed.

284 Playbacks of the recordings were broadcasted to individuals at the start of the trial and
285 when the observer began the approach and suspended when the squirrel took flight.
286 Vocalizations were broadcasted through a JAMBOX speaker (Jawbone, San Francisco, CA)
287 connected to an Apple iPhone 6s (Mountain View, CA) with a constant volume set for the
288 speaker and phone. The speaker was carried by the observer during each trial. The amplitude of
289 the playbacks measured from 1 m away from the speaker was variable among the chickadee (67-
290 80 dB), dog (69-77 dB), and hawk (78-86 dB) playbacks (measured using a BAFX Sound Level
291 Meter, BAFX3370). We note that the initial starting distance of the playbacks was inherently
292 variable as we could not standardize the distance between the observer and squirrel when the
293 trials were started (mean \pm SE over all 94 trials involving playbacks = 19.11 \pm 0.73 m).
294 Consequently, the actual realized sound level of the playbacks experienced by a squirrel varied.
295 Given how the trials were conducted in real time (not video recorded), the single observer (AK)
296 was not blind to the playback treatments or locations of where the experiments took place. All
297 vocalization recordings were found online (Control A: Place, 2015; Control B: Floyd, 2017a;
298 Control C: Floyd, 2017b; Dog A: Simion, 2016; Dog B: Simion, 2018; Dog C: Simion, 2017;
299 Hawk A: Chartier, 2008; Hawk B: Addison, 2017; Hawk C: Wilson, 2010). Each playback
300 treatment (control, dog, or hawk) had three separate recordings/exemplars (A, B, or C). We
301 tested whether there was any exemplar effects in separate ANOVAs that included playback
302 exemplar (A, B, C), playback treatment (chickadee, dog, hawk), and an interaction between the
303 two. We did this for each of our four behavioral response variables and did not find any
304 significant interactions between playback exemplar and treatment ($p = 0.12-0.99$), suggesting
305 that the version of the playback treatment did not influence the behavioral response.

306 *Statistical analyses*

307 We analyzed the data from trials with and without playbacks separately because the two
308 experiments were not conducted synchronously and seasonal changes from fall to winter in

309 Michigan may alter squirrel behavior. In trials without playbacks, we used three separate linear
310 mixed-effects models (LMMs) to examine the effects of urbanization on FAD, FID, and latency
311 to resume activity following the trial. Although the linear distance a squirrel climbed up a tree
312 (from base of tree to location of squirrel) has been used in other studies of tree squirrels (e.g.,
313 Uchida et al., 2017), the distance a squirrel climbed up a tree in our study exhibited a Poisson
314 distribution where many squirrels did not climb up a tree at all and a few climbed up very high
315 (squirrels did not climb a tree in 80 of 171 total trials; those that did climb a tree mean \pm SE =
316 4.7 ± 0.34 m). This seemed to better approximate a behavioral decision made by a squirrel to
317 “climb or not climb” rather than “how high to climb”. Consequently, a generalized linear mixed-
318 effect model (GLMM) with binomial errors was used to examine the effects of urbanization on
319 the probability that squirrels climbed a tree to escape during the trial. We note that the same
320 inferences for the linear distance a squirrel climbed a tree were gained if we instead ran a zero-
321 inflated Poisson mixed-effects model. Models included site category (urban, less urban), distance
322 to the nearest tree, sex, Julian date of the trial, and initial distance of the observer as fixed effects.
323 Distance to the nearest tree was included not only because previous studies show it can impact
324 anti-predator behavior (measured using FID: Dill & Houtman, 1989; Blumstein, 2003) but also
325 because it helps control for any differences in vegetation among the different study sites, which
326 could impact their behavior. Because we had repeated samples from the same site, we also
327 included a random intercept for site in all of our models. The same model structure was used in
328 separate LMMs or the GLMM for data from the playback trials to examine the effects of the
329 acoustic playback manipulations on the four squirrel behaviors described above but the models
330 included an interaction between playback treatment (control, dog, hawk) and site category
331 (urban, less urban). We then assessed the statistical significance of pairwise comparisons using
332 post-hoc Tukey’s Honest Significant Differences that were corrected for multiple comparisons.
333 In these pairwise comparisons, we were specifically interested in identifying 1) whether squirrels
334 in urban and less urban sites differed in their behavior in response to the playback treatments
335 (e.g., urban squirrels exposed to hawk playbacks differed in FID compared to less urban squirrels
336 exposed to hawk playbacks) and 2) whether squirrels within each type of site differed in their
337 response to the playbacks (e.g., whether squirrels in urban areas exhibited a higher FID in
338 response to hawk playbacks compared to those in urban areas exposed to control playbacks).

339 Continuous predictor variables were standardized to a mean of 0 and SD of 1. We
340 confirmed model diagnostics visually and all models met the appropriate assumptions (normality
341 of residuals, constant variance, no high leverage observations). Latency to resume behavior was
342 log+1 transformed (base e) to improve homoscedasticity and normality. There were also no
343 predictor variables that were found to be colinear as all variance inflation factors (VIFs) were
344 less than 3.68 (Zuur et al., 2010), though the higher VIF were due to interaction terms and VIF of
345 variables not in interactions were <1.5. All analyses were conducted in R version 4.02 (R Core
346 Team, 2020) with lme4 (version 1.1.23, Bates et al., 2015) and p-values estimated using
347 lmerTest (version 3.1.2, Kuznetsova et al., 2017). Tukey's post-hoc tests were used to evaluate if
348 the responses to the playback treatments differed between squirrels in urban and less urban areas
349 using emmeans (1.5.2-1: Lenth, 2020) and *p* values from these analyses were adjusted for
350 multiple comparisons. Mean and SE are presented below.

351

352

Results

Behavioral responses to human-stimuli only

354 Overall, urban squirrels (*n* = 38, 20 females and 18 males) exhibited greater tolerance to
355 humans as they allowed a human observer to get closer to them before they exhibited vigilance
356 (FAD) or fled (FID) and tended to be less likely to climb a tree during the trial and more quickly
357 return to typical behavior following the trial compared to those in less urban sites (*n* = 39, 19
358 females and 20 males; Table 1, Fig. 1). FID in the squirrels at the urban site (6.36 ± 0.52 m) was
359 97.2% shorter compared to those at the less urban sites (12.54 ± 0.62 m, *p* = 0.043, Table 1, Fig.
360 1B). Although the average FAD for squirrels observed at the urban site (10.09 ± 0.74 m) was
361 43.8% shorter than for those at the less urban sites (14.51 ± 0.69 m), this difference was not
362 significant (*p* = 0.10, Table 1, Fig. 1A). Squirrels at the urban sites were less likely to climb a
363 tree while the observer approached (34.2% of trials) compared to those at the less urban sites
364 (64.1%), although this difference was not significant (*p* = 0.093, Table 1, Fig. 1C). Latency to
365 resume behavior following the trial was shorter for urban squirrels (43.9 ± 14.4 s) compared to
366 those at the less urban sites (157.51 ± 25.35 s), but this difference was not significant (*p* = 0.11,
367 Table 1, Fig. 1D). Trials where the observer started the trial at a longer initial distance to the
368 squirrel had significantly longer FAD and FID but not probability of climbing a tree or latency to
369 resume behavior following the trial (Table 1). There were no significant effects of sex, Julian

370 date, or distance to the nearest tree on FAD, FID, probability of climbing a tree, or latency
371 (Table 1).

372 *Behavioral responses to stimuli from natural predators*

373 The effects of the playbacks on FAD depended upon whether the squirrels were located
374 at the urban or less urban sites (Table 2, Fig. 2A). Average FAD for urban squirrels exposed to
375 the hawk vocalizations ($n = 12$ trials, 17.17 ± 1.33 m) was 37% longer than urban squirrels who
376 were exposed to the control playback ($n = 11$, 12.56 ± 0.94 m, Tukey's $p = 0.004$) and 20%
377 longer than those exposed to the dog playbacks ($n = 20$, 14.30 ± 0.83 m, Tukey's $p = 0.006$, Fig.
378 2A). By contrast, the FAD of squirrels at the less urban sites were just longer overall (Fig. 2A)
379 and the FAD of those less urban squirrels who were exposed to the hawk playbacks ($n = 16$,
380 14.62 ± 1.14 m) did not differ from those exposed to the control playback ($n = 15$, 14.46 ± 0.88
381 m, Tukey's $p = 0.99$) or dog playbacks ($n = 20$, 14.85 ± 1.05 m, Tukey's $p = 0.94$, Fig. 2A).
382 There were no significant differences in FAD for squirrels exposed to dog playbacks and those
383 exposed to the control playback for squirrels at urban sites (Tukey's $p = 0.99$) or those at less
384 urban sites (Tukey's $p = 0.99$). When comparing squirrels at urban or less urban sites to a
385 specific playback treatment, squirrels at the urban and less urban sites did not differ in their FAD
386 when exposed to hawk playbacks (urban vs. less urban: Tukey's $p = 0.64$), dog playbacks (urban
387 vs. less urban: Tukey's $p = 0.39$), or the control stimulus (urban vs. less urban: Tukey's $p = 0.49$,
388 Fig. 2A).

389 Similar to FAD, the effects of the playbacks on FID also depended upon whether the
390 squirrels were located at the urban or less urban sites (Table 2, Fig. 2B). Average FID for urban
391 squirrels exposed to the hawk vocalizations ($n = 12$ trials, 14.95 ± 0.98 m) was 44.3% longer
392 than squirrels who were exposed to the control playbacks ($n = 11$, 10.37 ± 3.13 m, Tukey's $p =$
393 0.001) and 29.9% longer than those exposed to the dog playbacks ($n = 20$, 11.86 ± 2.65 m,
394 Tukey's $p = 0.001$, Fig. 2A). In squirrels at urban sites, there was no difference in FID between
395 those exposed to the control playback and those exposed to the dog vocalizations (Tukey's $p =$
396 0.99). In squirrels at less urban sites, FID for those exposed to the dog playbacks (13.60 ± 0.98
397 m) was similar to those exposed to the control (12.12 ± 0.88 m, Tukey's $p = 0.14$) or hawk
398 playbacks (13.11 ± 0.96 m, Tukey's $p = 0.95$, Fig. 2B). Unlike urban squirrels, the FID of those
399 at the less urban sites who were exposed to hawk playbacks was similar compared to those
400 exposed to the control playback (Tukey's $p = 0.69$). When comparing squirrels at urban or less

401 urban sites to a specific playback treatment, squirrels at the urban and less urban sites did not
402 differ in their FID when exposed to hawk playbacks (urban vs. less urban: Tukey's $p = 0.98$),
403 dog playbacks (urban vs. less urban: Tukey's $p = 0.13$), or the control stimulus (urban vs. less
404 urban: Tukey's $p = 0.83$).

405 There were no significant effects of the playback treatments or site differences on the
406 likelihood squirrels climbed a tree. Squirrels at urban sites were not more likely to climb a tree
407 when exposed to a hawk playback compared to a dog (Tukey's $p = 0.30$) or control (Tukey's $p =$
408 0.67) playback and were not more likely to climb a tree when exposed to a dog playback versus a
409 control playback (Tukey's $p = 0.99$). Squirrels at less urban sites exhibited a similar probability
410 of climbing a tree when they were exposed to hawk playbacks compared to dog (Tukey's $p =$
411 1.0) or control (Tukey's $p = 0.73$) playbacks or when exposed to dog playbacks compared to a
412 control playback (Tukey's $p = 0.73$). Squirrels at the urban and less urban sites did not differ in
413 their probability of climbing a tree when exposed to hawk playbacks (urban vs. less urban:
414 Tukey's $p = 0.99$), dog playbacks (urban vs. less urban: Tukey's $p = 0.12$), or the control
415 stimulus (urban vs. less urban: Tukey's $p = 0.99$).

416 Squirrels at the urban and less urban sites did not differ in their latency to resume typical
417 behavior following exposure to hawk playbacks (urban vs. less urban: Tukey's $p = 0.98$), dog
418 playbacks (urban vs. less urban: Tukey's $p = 0.89$), or the control stimulus (urban vs. less urban:
419 Tukey's $p = 0.88$, Table 2, Fig. 2D). However, there were differences in how squirrels responded
420 to the playback treatments within each of the two types of study sites. Squirrels at urban sites that
421 were exposed to the hawk playbacks took 436% longer to resume their pre-trial behavior (213.33
422 ± 28.9 s) compared to those who were exposed to the control playback (39.82 ± 7.70 s, Tukey's
423 $p < 0.001$) and 147% longer than those exposed to dog playbacks (86.25 ± 13.30 s, Tukey's $p =$
424 0.027). Squirrels at the urban sites also took 114% longer to resume typical behavior if they were
425 exposed to dog playbacks compared to those exposed to the control playback (Tukey's $p <$
426 0.001). Similarly, squirrels at the less urban sites that were exposed to the hawk playbacks took
427 218% longer to resume their pre-trial behavior (291.25 ± 35.45 s) compared to those who were
428 exposed to the control playback (91.47 ± 25.45 s, Tukey's $p < 0.001$) and 55.7% longer than
429 those exposed to dog playbacks (187.05 ± 21.38 s, Tukey's $p = 0.12$, Fig. 2D). Squirrels at the
430 less urban sites also took 95.6% longer to resume typical behavior if they were exposed to dog
431 playbacks compared to those exposed to the control playback (Tukey's $p < 0.001$).

432 There was no effect of sex or Julian date of trial, on any of the behaviors (Table 2). There
433 was no effect of the initial distance that a squirrel was from a tree when the trial started on FAD,
434 FID, or probability to climb a tree, but squirrels were less likely to climb a tree if they were
435 closer to one when the trial started (Table 2). Trials that started with the human observer a
436 greater distance away from the squirrel had longer FAD, FID, and latency to resume typical
437 behavior, but not the probability to climb a tree (Table 2).

438

439 Discussion

440 Squirrels at urban sites in the no playback trials exhibited a significantly shorter FID
441 compared to those at the less urban sites and also exhibited a lower FAD and likelihood to climb
442 a tree during the trial, and shorter latency to resume typical behavior following the trial, though
443 only the difference in FID was statistically significant. In the trials where squirrels were exposed
444 to playbacks from possible predators (hawks or dogs), squirrels at the urban sites did not differ in
445 their vigilance (FAD) or anti-predator behavior response (FID, likelihood to climb a tree, latency
446 to resume typical behavior following the trial) compared to those at the less urban sites. When
447 we compared the behavior responses of squirrels within each site type (urban or less urban),
448 squirrels at the urban sites exhibited longer FAD (hawk > dog = control) and FID (hawk > dog =
449 control) when exposed to hawk playbacks compared to control or dog playbacks, suggesting
450 increased vigilance (FAD) anti-predator behavior (FID) when exposed to vocalizations from
451 potential predators. By contrast, squirrels at the less urban sites had longer overall FAD and FID
452 than those at urban sites regardless of playback treatment and there was no effect of hawk or dog
453 playbacks on FAD (hawk = control = dog) or FID (hawk = control = dog), suggesting no
454 increase in vigilance or anti-predator behavior when exposed to vocalizations from potential
455 predators. Squirrels at both urban and less urban sites were not more likely to climb a tree
456 following playbacks from possible predators (hawk = dog = control) but both urban and less
457 urban squirrels exhibited a longer latency to resume typical behavior following the hawk or dog
458 playbacks compared to the control (hawk > dog > control), suggesting increased anti-predator
459 behavior when exposed to vocalizations from potential predators. Overall, our results indicate
460 that squirrels in urban areas are more tolerant to humans but still exhibit a high level of vigilance
461 and anti-predator behavior when exposed to predator stimuli. In terms of the STRANGEness of
462 our results (Webster and Rutz, 2020), our results may be generalizable to other squirrel

463 populations or different species but we note that our results are biased towards squirrels that
464 voluntarily participated in the trials (i.e., did not run away when approached). We also note that
465 the significance of our results may be limited to urban populations where predators are present in
466 those areas.

467 Similar to most other studies in terrestrial animals (Samia et al., 2015) and in studies in
468 tree squirrels (McCleery, 2009; Engelhardt and Weladji, 2011; Sarno et al., 2015; Uchida et al.,
469 2020), our results from trials with no playbacks suggest that squirrels in urban sites were more
470 tolerant of humans. Specifically, squirrels in urban areas exhibited a shorter FAD and FID, lower
471 probability to climb a tree to escape the human observer, and a shorter latency to resume typical
472 behavior following the trial, although only FID was significantly different between habitat types.
473 The congruency of our results with previous studies strongly supports this assumption that
474 squirrels at our urban sites were more tolerant of humans. These are presumably sympatric
475 populations with a large amount of gene flow among them as the linear distance between some
476 urban and less urban sites is ~1 km. Unless selection favoring reductions in anti-predator
477 behavior is extremely strong in urban areas or features of urban landscapes strongly impede gene
478 flow (Johnson and Munshi-South, 2017), it seems likely that these behavioral differences are
479 driven by plasticity given that the likely exchange of individuals between suburban and urban
480 sites prevents local genetic adaptation to these different sites (see discussion in Sol et al., 2013).
481 It is also possible that these behavioral differences are due to personality-dependent colonization
482 of urban habitats (Carrete and Tella, 2010; Sprau and Dingemanse, 2017), but we cannot
483 distinguish among these possibilities at this time.

484 Although squirrels at our urban sites were more tolerant of humans, they still exhibited a
485 strong behavioral response to acoustic stimuli from natural predators. Specifically, they exhibited
486 increased vigilance (FAD) and anti-predator behavior (FID, latency to resume typical behavior
487 after the trial) when exposed to the playbacks of a natural predator (hawk) compared to the
488 control playback or the dog playbacks. The behavioral responsiveness to hawk vocalization is
489 somewhat surprising because hawks do not vocalize while hunting, but squirrels still responded
490 to their presence suggested through acoustic cues. These results indicate that urban squirrels do
491 still pay attention to predation risk and can discriminate and respond accordingly by becoming
492 vigilant and fleeing when the human is at a greater distance if the human is also paired with
493 hawk playbacks. By contrast, squirrels at less urban sites did not exhibit differences in FAD

494 when exposed to the different playbacks, perhaps due to some ceiling effect given that FAD of
495 squirrels at less urban sites was much longer than FAD of squirrels at urban sites. Furthermore,
496 when we compared the effects of hawk or dog playbacks on FAD or FID, there were no
497 differences between squirrels at the urban and less urban sites. Our results therefore reject the
498 hypothesis that urban squirrels are less responsive to natural predators due to increased tolerance
499 to humans. Previous studies (see also Labra and Leonard, 1999; Seress et al., 2011; Cooper et al.,
500 2008; Bokony et al., 2012; Cavalli et al., 2016; Weaver et al., 2018; Vincze et al. 2019) together
501 with our results support that animals in urban habitats or those frequently exposed to humans,
502 even if more tolerant of human presence, still exhibit increases in anti-predator behavior in
503 response to a non-human predator. However, future studies that test this hypothesis need to have
504 increased sample sizes and should also include a playback treatment that uses both visual and
505 acoustic cues of humans as a control stimulus.

506 There are two other interesting results from our trials with playbacks. First is the finding
507 that squirrels that were closer to a tree at the start of the trial were less likely to climb a tree. This
508 is opposite of what we would expect and future studies need to better assess if this is caused by
509 some larger habitat difference between urban and less urban areas and/or reflect differential
510 escape strategies. For example, squirrels at urban sites may be more distant to a tree at the start
511 of the trials and escape from humans by running away rather than going up a tree. However, in a
512 post-hoc analysis using our entire dataset of trials conducted with or without playbacks ($n = 171$
513 trials), squirrels in urban areas ($n = 81$ trials, 3.30 ± 0.16 m) and those in less urban areas ($n = 90$
514 trials, 3.05 ± 0.15 m) did not differ in their distance to a tree at the start of the trials (general
515 linear model: $t_{169} = 1.13$, $p = 0.26$). Second, we expected that squirrels would respond to the dog
516 playbacks in similar way to how they responded to the hawk playbacks as both are stimuli from
517 potential predators. Previous studies in tree squirrels also show that they exhibit increased
518 vigilance or FID to the physical presence of a dog with a human handler (Gustafson and
519 VanDruff, 1990; Cooper et al., 2008) or behave in such a way in areas with high levels of dogs
520 and cats that suggests that they perceive a higher predation risk in such areas (i.e., giving up
521 density was higher in study areas where cats and dogs are present: Bowers and Breland, 1996).
522 Instead, we found that squirrels at both sites did not differ in their vigilance (FAD) when
523 exposed to dog playbacks compared to the control playbacks. Additionally, only squirrels in less
524 urban sites had a slightly (non-significantly) longer FID when exposed to dog playbacks

525 compared to the control playback. Although we did find that squirrels exposed to dog
526 vocalizations took longer to resume typical behavior following the trials, our results generally
527 differ from previous studies in tree squirrels and owls showing that FAD and/or FID were
528 increased in squirrels or owls in urban areas when they were presented with a human plus dog
529 compared to just a human (Gustafson and VanDruff, 1990; Cooper et al., 2008; Cavalli et al.,
530 2016). This suggests that squirrels, especially those in urban sites, were more tolerant to dog
531 vocalizations when paired with a human observer, whereas squirrels in less urban areas may
532 have viewed the sounds of dogs paired with humans as threatening. We predict that squirrels in
533 urban environments exhibit selective tolerance where the response to humans or stimuli from
534 their commensals (dogs) is attenuated but the increased response to natural predators is
535 maintained despite this tolerance to humans and their dogs.

536 Together, our results provide insight into how urbanization may shape the behavioral
537 characteristics animals in two main ways. First, as most studies on this topic are in birds (Samia
538 et al., 2015), which can escape from humans using flight, it is important to consider if the same
539 patterns are found in terrestrial animals. Our results show that non-volant animals in urban
540 environments exhibit less vigilance and anti-predator behavior. Second, we show that squirrels in
541 urban environments were more tolerant to humans but still exhibited a strong response reflecting
542 increased vigilance and anti-predator behavior to acoustic stimuli from a natural predator
543 (hawks) and that squirrels in urban areas did not differ in their behavioral response when
544 exposed to stimuli from two types of possible predators compared to those exposed to those
545 stimuli in less urban areas. Although we do not wish to imply that tolerance or habituation to
546 humans is cost-free, most studies fail to find evidence that populations where individuals are
547 more tolerant of humans (or in some cases habituated to their presence) also exhibit reduced
548 vigilance and/or anti-predator behavior to stimuli from natural predators. Given that urbanization
549 is unlikely to slow, increased effort is needed to determine if increased tolerance and/or
550 habituation to humans carries costs (Geffroy et al., 2015). Some studies suggest the costs of
551 human tolerance may be more nuanced, such as tolerance to humans reducing the latency to
552 return to the nest following a disturbance in nesting shorebirds, but potentially causing increased
553 chick mortality due to the presence of dogs that often are paired with human stimuli (Baudains
554 and Lloyd, 2007). Other studies that increased tolerance of humans could even be beneficial for
555 populations that cannot avoid anthropogenic stimuli due to seasonal food pulses coinciding with

556 a large influx of tourists (Wheat and Wilmers, 2016). Clearly more work is needed on this
557 subject, especially on a greater number of species including species that are not “urban
558 exploiters” like tree squirrels, but the existing evidence rejects the hypothesis that there is a cost
559 to human tolerance in terms of lowering the vigilance and/or anti-predator behavior of animals to
560 other natural predators. If predatory species re-colonize urban areas, our results suggest that they
561 should respond appropriately to stimuli indicating their presence.

562

563 **Data Availability Statement**

564 All data are available through the FigShare account associated with the senior author (Dantzer,
565 2021).

566

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Table 1. Differences between fox squirrels at urban and less urban sites that were not exposed to any playbacks for first alert distance (FAD), flight initiation distance (FID), probability of escaping the observer by climbing a tree during the trial, and latency to resume behavior following the trial. A random effect for site identity was included in the model for FAD ($\sigma^2 = 6.9$), FID ($\sigma^2 = 6.24$), probability of climbing a tree ($\sigma^2 = 1.23$), and latency ($\sigma^2 = 1.22$). Latency was $\ln+1$ transformed. Results are from 77 trials from six sites.

Response Variable	Variable	<i>b</i>	SE	<i>t</i> or <i>z</i>	<i>P</i>
First alert distance (FAD)	Intercept (Less urban, Female)	14.11	1.63	8.67	0.0007
	Site (Urban)	-4.79	2.26	-2.11	0.10
	Distance to tree	-0.37	0.38	-0.98	0.33
	Sex (Male)	1.17	0.66	1.77	0.08
	Julian Date	0.15	0.40	0.39	0.70
	Initial Distance	2.63	0.35	7.51	<0.0001
Flight initiation distance (FID)	Intercept (Less urban, Female)	12.16	1.54	7.89	0.0009
	Site (Urban)	-6.22	2.14	-2.90	0.043
	Distance to tree	-0.56	0.35	-1.59	0.12
	Sex (Male)	0.85	0.61	1.38	0.17
	Julian Date	0.01	0.37	0.03	0.97
	Initial Distance	1.38	0.32	4.24	<0.0001
Probability of climbing a tree	Intercept (Less urban, Female)	0.71	0.79	0.89	0.37

	Site (Urban)	-1.89	1.12	-1.68	0.09
	Distance to tree	-0.09	0.32	-0.27	0.78
	Sex (Male)	0.17	0.55	0.31	0.76
	Julian Date	0.47	0.35	1.34	0.18
	Initial Distance	0.23	0.30	0.76	0.45
Latency to resume behavior	Intercept (Less urban, Female)	4.48	0.67	6.70	0.002
	Site (Urban)	-1.87	0.93	1.99	0.11
	Distance to tree	-0.07	0.13	-0.57	0.57
	Sex (Male)	0.06	0.23	0.25	0.80
	Julian Date	0.07	0.14	0.52	0.61
	Initial Distance	0.002	0.12	0.02	0.98

Table 2. Effects of acoustic playbacks (control, hawk, dog) on first alert distance (FAD), flight initiation distance (FID), probability of escaping human observer by climbing a tree, and latency to resume behavior following the trial for fox squirrels observed at urban or less urban sites. Reference (intercept) was “less urban” for site, “control playback” for treatment, and “female” for sex. A random effect for site identity was included in the model or FAD ($\sigma^2 = 6.5$), FID ($\sigma^2 = 4.9$), probability of climbing a tree ($\sigma^2 = 0.07$), and latency ($\sigma^2 = 0.37$). Latency was $\ln+1$ transformed. Results are from 94 trials from six study sites.

Response Variable	Variable	<i>b</i>	SE	<i>t</i> or <i>z</i>	<i>P</i>
First alert distance (FAD)	Intercept (Less urban, Female, Control)	14.94	0.89	16.71	<0.0001

	Site (Urban)	-2.32	1.33	-1.74	0.11
	Dog playbacks	0.51	0.90	0.57	0.57
	Hawk playbacks	-0.29	0.98	-0.30	0.76
	Distance to tree	0.36	0.29	1.23	0.22
	Sex (Male)	0.29	0.58	0.51	0.61
	Julian Date	-0.10	0.28	-0.34	0.73
	Initial Distance	3.20	0.29	10.84	<0.0001
	Site (Urban) x Dog playbacks	0.07	1.35	0.05	0.96
	Site (Urban) x Hawk playbacks	4.29	1.49	2.86	0.005
Flight initiation distance (FID)	Intercept (Less urban, Female, Control)	12.3	0.95	7.31	<0.0001
	Site (Urban)	-1.64	1.39	-1.18	0.27
	Dog playbacks	1.89	0.79	2.40	0.018
	Hawk playbacks	1.21	0.85	1.42	0.16
	Distance to tree	0.08	0.26	0.30	0.76
	Sex (Male)	0.01	0.50	0.01	0.99
	Julian Date	-0.39	0.25	-1.59	0.11
	Initial Distance	2.99	0.26	11.51	<0.0001
	Site (Urban) x Dog playbacks	-1.52	1.18	-1.29	0.20
	Site (Urban) x Hawk playbacks	2.53	1.30	1.94	0.056
Probability of climbing a tree	Intercept (Less urban, Female,	-0.20	0.62	-0.33	0.74

	Control)				
	Site (Urban)	-0.61	0.92	-0.66	0.51
	Dog playbacks	1.14	0.82	1.39	0.16
	Hawk playbacks	1.26	0.90	1.40	0.16
	Distance to tree	-0.64	0.27	-2.34	0.02
	Sex (Male)	0.61	0.55	1.10	0.27
	Julian Date	-0.26	0.27	-0.97	0.33
	Initial Distance	0.01	0.27	0.04	0.96
	Site (Urban) x Dog playbacks	-1.52	1.20	-1.27	0.20
	Site (Urban) x Hawk playbacks	0.18	1.34	0.14	0.89
Latency to resume behavior	Intercept (Less urban, Female, Control)	3.83	0.39	9.69	0.0001
	Site (Urban)	-0.60	0.57	-1.05	0.33
	Dog playbacks	1.14	0.23	4.91	<0.0001
	Hawk playbacks	1.71	0.25	6.76	<0.0001
	Distance to tree	0.03	0.07	0.39	0.70
	Sex (Male)	0.24	0.15	1.61	0.11
	Julian Date	0.07	0.07	-0.91	0.36
	Initial Distance	0.06	0.08	0.82	0.41
	Site (Urban) x Dog playbacks	0.03	0.35	0.10	0.92
	Site (Urban) x Hawk playbacks	0.22	0.39	0.57	0.57

Figures and Figure Legends

Figure 1. Variation in A) vigilance (first alert distance: FAD), B) anti-predator behavior (flight initiation distance: FID), C) proportion of individuals that escaped up a tree during the trial, and D) latency to resume behavior following the trial among fox squirrels at urban (n = 38 trials) and less urban (n = 39) sites in trials where squirrels were not exposed to any playbacks. Squirrels in urban areas had significantly shorter FID compared to those in the less urban sites, but there were no other significant differences (Table 1). Each symbol corresponds to a different trial. Upper and lower hinges correspond to first and third quartile, respectively. Upper/lower whiskers extend from the hinge to the highest/lowest value that is within 1.5x the interquartile range. Solid horizontal line shows median.

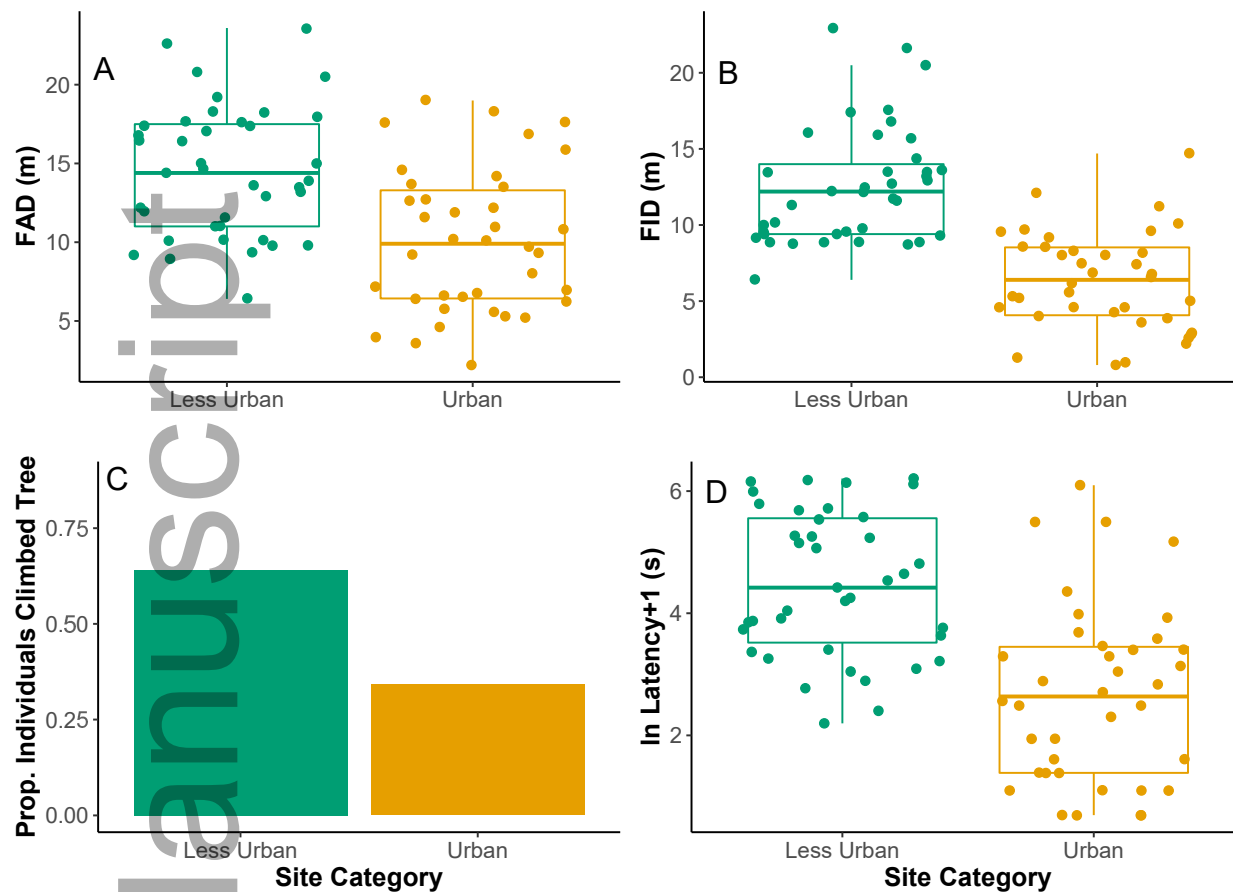


Figure 2. Effects of human observer approaching a squirrel while broadcasting one of three playback treatments (control playback, hawk or dog vocalizations) on A) first alert distance (FAD), B) flight initiation distance (FID), C) proportion of individuals escaping up a tree during the trial, and D) latency to resume typical behavior following the trial. Trials were conducted at less urban (n = 15 control, 20 dog, 16 hawk) and urban (n = 11 control, 20 dog, 12 hawk) sites. Results shown in Table 2. Upper and lower hinges correspond to first and third quartile, respectively. Each symbol corresponds to a different trial. Upper/lower whiskers extend from the hinge to the highest/lowest value that is within 1.5x the interquartile range. Solid horizontal line shows median.

