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

2   predators

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4   **Running title:** Fox squirrel behavior in urban areas

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6   **Authors:** Anna Kittendorf[1], Ben Dantzer[1,2]

7   [1]Department of Psychology, University of Michigan, Ann Arbor, MI, 48109, USA

8   [2]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI,

9   48109, USA

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11   **Correspondence:** Ben Dantzer (dantzer@umich.edu)

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21   **Conflict of Interests**

22   Both authors declare no conflict of interests.

23   **Abstract**

24   Animals in urban areas that experience frequent exposure to humans often behave differently

25   than those in less urban areas, such as exhibiting less vigilance or anti-predator behavior. These

26   behavioral shifts may be an adaptive response to urbanization, but it may be costly if animals in

27   urban areas also exhibit reduced anti-predator behavior in the presence of natural predators. In

28   trials with only a human observer as the stimulus, urban squirrels exhibited reduced vigilance

29   and anti-predator behavior compared to those in less urban areas. Next, we exposed squirrels in

30   multiple urban and less urban sites to acoustic playbacks of a control stimulus (non-predatory

31   bird calls), a natural predator (hawk), and dogs and recorded their vigilance and three different

32   anti-predator behaviors when a human approached them while either broadcasting one of these

33   three playbacks or no playbacks at all. Squirrels at urban sites also did not differ in their

34   behavioral responses to the playbacks from possible predators (hawks or dogs) when they were

35   compared to those at less urban sites exposed to these playbacks. Urban squirrels also exhibited

36   increased vigilance and anti-predator behavior when exposed to a human paired with hawk

37   playbacks compared to the control playbacks. Together, our results indicate that urban squirrels

38   did perceive and assess risk to the natural predator appropriately despite exhibiting increased

39   tolerance to humans. These results provide little support for the hypothesis that increased

40   tolerance to humans causes animals to lose their fear of natural predators.

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42   **Keywords**: Anti-predator behavior, cross-habituation, first alert distance, flight initiation

43   distance, stimulus generalization, urbanization

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Introduction

Behavior plays an important role in enabling animals to persist through environmental change (Baldwin, 1896; Bartholomew, 1964; West Eberhard, 1989; Price et al., 2003; Snell-Rood, 2013). Accordingly, it seems to play a major role in facilitating the ability of animals to cope with new challenges that they face in urban environments (Ditchkoff et al., 2006; Tuomainen and Candolin, 2011; Lowry et al., 2013; Ryan and Partan, 2014). One of the most common behavioral adjustments of animals in urban environments is reduced anti-predator behavior in the presence of humans. This is often reflected in measures of flight initiation distance (FID), which is the distance at which an animal flees from an approaching human and is thought to be an approximation of their sensitivity to risk of an approaching predator (Cooke, 1980; Ydenberg & Dill, 1986; Lima and Dill, 1990). Individuals with shorter FIDs are considered to be bolder than individuals with longer FIDs since they demonstrate reduced fear of the "predator".

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

Although reductions in the expression of anti-predator in urban environments is generally thought to be adaptive (Møller, 2008; Carrette et al., 2016), there may be potential costs for

69   urban animals if they reduce their overall expression of anti-predator behavior to not only

70   humans but also towards natural predators if those urban areas contain predators. This could be

71   due to the phenomenon of cross-habituation or stimulus-generalization. For example, birds that

72   are habituated to a threatening stimulus that are then presented with a second simulated predator

73   exhibit an attenuated response to this second stimulus compared to a group of naïve birds (Hinde,

74   1954; see also Curio, 1993). This type of stimulus generalization can occur where an animal

75   habituated to one stimulus exhibits an attenuated response to a second stimulus from the same *or*

76   different sensory modality (Guttman and Kalish, 1956; Thompson and Spencer, 1966; Rankin et

77   al., 2009). Related concepts occur in the context of "behavioral spillover" where individuals that

78   exhibit high levels of a behavior in one context also exhibit it in another context even though it

79   may not be adaptive, such as animals exhibiting higher levels of boldness in a courtship context

80   also exhibiting higher boldness in the presence of a predator (Arnqvist and Henriksson, 1997;

81   Sih et al., 2004).

82   If urban animals in areas containing predators exhibit reductions in vigilance and/or anti-

83   predator behavior not only toward humans but also to natural predators, it could conceivably

84   have important impacts on wildlife populations by increasing their vulnerability to predators

85   (Geffroy et al., 2015). To date, there is little consensus about whether animals in urban areas or

86   those exposed to increased human presence exhibit a reduced response to threats from natural

87   predators (Fitzgerald and Stronza, 2016). For example, some studies show that individuals in

88   areas with higher human activity exhibit less of a behavioral response when natural predators

89   were observed visiting the area (Olson and Acevedo-Gutiérrez, 2017) or due to acoustic

90   playbacks of a natural predator (McCleery, 2009). The latter suggests that animals experiencing

91   frequent exposure to human activity exhibit reduced responses to other stimuli from natural

92   predators. Other studies show that the response of animals in more urban areas to a stimulus

93   from a natural predator is not attenuated compared to those in more rural locations (Labra and

94   Leonard, 1999; Coleman et al., 2008; Seress et al., 2011; Bokony et al., 2012; Cavalli et al.,

95   2016; Weaver et al., 2018; Vincze et al., 2019).

96   In this study, we characterized the vigilance and anti-predator behavior of fox squirrels

97   (*Sciurus niger*) in urban and less urban areas to achieve the following two objectives. First, we

98   conducted standard FID trials (with only stimuli from a human observer) to examine whether

99   squirrels in urban areas showed reduced vigilance and anti-predator behavior towards a human

100   observer compared to those in less urban areas. If squirrels in urban areas did exhibit reduced

101   vigilance and anti-predator behavior, this would support the hypothesis that squirrels in our

102   urban study populations were more tolerant of human presence, which would be consistent with

103   numerous other studies (Samia et al., 2015). Squirrels were located in their natural habitat and

104   we recorded the following four aspects of their vigilance and anti-predator behavior. First, we

105   recorded the distance to which the observer could get to before they exhibited vigilance behavior

106   towards the observer ("first alert distance" or FAD, similar to Fernández-Juricic and Schroeder,

107   2003; Blumstein et al., 2005). Second, we recorded how close the observer could get to them

108   before they ran away (FID). Third, was the probability that the squirrel escaped by running up a

109   tree. Fourth, the latency following the trial it took them to resume their typical behavior

110   (foraging or traveling off tree). We interpreted vigilance behavior was reflected in FAD and that

111   anti-predator behavior was composed of FID, probability of the squirrel escaping up a tree, and

112   the latency to resume typical behavior following the trial. However, we note that it is likely that

113   all four of these behaviors are quite similar in the sense that they measured anti-predator

114   behavior and that the latency to resume typical behavior following the trial may be affected by

115   motivational issues associated with nutritional state. Measuring all four of them can provide

116   additional insight, such as examining whether squirrels in less urban areas are more alert to

117   human presence than those in urban areas. Additionally, most studies on this topic are in birds

118   and only measure FID. Measuring whether the squirrel escaped by running up a tree and how

119   long the squirrel took to resume their typical behavior in addition to FID may provide greater

120   insight into the behavioral differences between animals in urban or less urban areas.

121   Our second objective was to examine whether urban animals exhibit reduced behavioral

122   responses to stimuli from natural predators when they are in the presence of humans. To do so,

123   we quantified the four behaviors described above when fox squirrels in urban or less urban areas

124   were presented with a human observer with a control acoustic playback (common non-

125   threatening bird), a human observer paired with the playback of a natural predator (hawk), or a

126   human observer paired with a playback of an invasive predator (dog). We predicted that squirrels

127   in the urban areas but not those in the less urban areas would exhibit no change in vigilance and

128   anti-predator behavior when they were exposed to the human+dog or human+hawk stimuli

129   compared to the human+control playback. We also predicted that squirrels in the urban sites

130   would exhibit less vigilance and anti-predator behavior when exposed to hawk or dog playbacks

131   compared to those at the less urban sites that were exposed to the hawk or dog playbacks. These

132   results would support the hypothesis that animals in urban environments exhibit less vigilance

133   and anti-predator not only to humans but also when faced with natural predators.

134

135   **Materials and Methods**

136   *Study species and sites*

137   Fox squirrels are ubiquitous in urban and suburban environments in the midwestern

138   United States (McCleery, 2008, 2009). Although arboreal tree squirrel species like fox squirrels

139   are common in urban areas worldwide, they continue to experience predation from natural

140   predators, although it may be rare compared to other sources of mortality (McCleery et al.,

141   2008). Urban squirrels also likely experience predation from domestic cats and dogs (Koprowski,

142   1994; Wauters et al., 1997; Tumlison, 2012; Loss et al., 2013; Jokimäki et al., 2017).

143   We studied natural populations of adult fox squirrels from six sites in and around Ann

144   Arbor, Michigan (Table S1 in Appendix). Sites were chosen based upon estimates of human

145   population density (Center for International Earth Science Information Network, 2018) with

146   urban sites having higher human density than less urban sites (see below and Table S1). Urban

147   sites included Prospect Park as well as two locations on the University of Michigan's (UM) main

148   campus (North and Central Campus) that are ~3-4 km away from one another. Prospect Park is

149   near downtown Ypsilanti, Michigan and about 13 km away from UM main campus. Less urban

150   sites included Nichols Arboretum, County Farm Park, and Saginaw Forest. Nichols Arboretum is

151   located ~1 km away UM main campus, County Farm Park is about ~4.5 km away, and Saginaw

152   Forest is ~7 km away. At all research sites, dogs are allowed but hunting is not. Squirrels may be

153   occasionally fed by humans at some of our study sites (e.g., Central Campus), but data were not

154   systematically collected to assess feeding rates. Approval to conduct this research at each site

155   was obtained from UM (Central Campus, Nichols Arboretum, North Campus, Saginaw Forest),

156   Washtenaw County Parks & Recreation (County Farm Park), and the City of Ypsilanti (Prospect

157   Park). All of our field procedures were non-invasive and involved behavioral observation or

158   short-term exposure to playbacks of acoustic stimuli. All experiments followed the guidelines set

159   by the Animal Behavior Society/Association for the Study of Animal Behaviour (Anonymous,

160   2012) and the US National Research Council and were approved by the UM Institutional Animal

161   Care and Use Committee (protocol # PRO00009076). We note that squirrels used in the study

162   may be STRANGE (*sensu* Webster and Rutz, 2020) in the sense that individual squirrels likely

163   have different rearing histories (though they are unknown and none should have been reared in

164   captivity) and that compliance to take part in the study was likely biased towards squirrels that

165   did not immediately run away when approached by the human observer.

166   Given that increased exposure to humans may cause animals in urban areas to exhibit less

167   anti-predator behavior towards them (McCleery, 2009; Rodriguez-Prieto et al., 2009; Vincze et

168   al., 2016; Uchida et al., 2019), we focused on human presence as the major factor difference

169   between our study sites (which should also reflect general urbanization). Sites were classified as

170   "urban" based upon having a human population density >1000 persons per km^2 whereas the less

171   urban sites had anywhere from 25-250 persons per km^2 (Saginaw) to 250-1000 persons per km^2

172   (County Farm Park, Nichols Arboretum). To support these classifications, we estimated human

173   and dog presence while we were visiting sites conducting our behavioral observations. We

174   counted the total number of dogs (on or off leash) but only counted the number of humans up to

175   50. If human presence exceeded 50 people, then a rough estimate of 50, 75, or 100 was recorded.

176   Human presence was recorded as 100 for all numbers estimated to be >100. We did not record

177   the distance from the observer to other humans but just whether the human was visible. Although

178   human and dog presence varied among the different sites (Table S1), the number of humans

179   observed per hour of observation averaged over all the urban sites (mean $\pm$ SE = 7.23 $\pm$ 3.33

180   humans/hr) was higher than those observed averaged over all the less urban sites (0.51 $\pm$ 0.40:

181   Mann-Whitney-Wilcoxon Test, $W = 1$, $p = 0.1$). We observed fewer dogs per hour at the urban

182   sites (0.065 $\pm$ 0.06 dogs/hr) compared to the less urban sites (0.33 $\pm$ 0.10, Mann-Whitney-

183   Wilcoxon Test, $W = 9$, $p = 0.1$). These differences in humans or dogs observer per hour were not

184   significant but in general support our assumption that our urban sites likely experience greater

185   exposure to humans.

186   We aged and sexed squirrels visually according to their size (small juvenile squirrels

187   were excluded) and anatomy (males were identified by presence of testes), respectively. Similar

188   to most studies that measure anti-predator using FID, trials were conducted on unmarked

189   squirrels at each site. We located squirrels by walking around each site and trials were started

190   when squirrels were observed. Focal individuals were selected randomly, however, only squirrels

191   that were feeding or foraging on the ground were included in this experiment. Because we did

192   not mark squirrels individually, it is possible that the same squirrel was observed on different

193   days, although we visited different areas of each study site to try and reduce this possibility. It is

194   unlikely that the same squirrel was observed multiple times on the same day, because after each

195   trial was completed, the observer walked approximately 20 meters away from the previous

196   location (in a continuous linear direction from where the first trial was conducted) and started a

197   trial with a different squirrel. Additionally, sites were only revisited after at least three days since

198   the previous visit to reduce the possibility of a squirrel becoming habituated to the trials should it

199   be sampled again. Although we cannot address habituation in this study, if squirrels at these sites

200   were habituating to our protocols, we would expect that their behavioral responses would decline

201   with trial number or date when the trial was conducted. The fact that none of our behavioral

202   variables were associated with date of when the trial was conducted (Tables 1-2) supports our

203   assumption that squirrels were not habituating to our protocols.

204   *Quantifying behavioral responses of squirrels*

205   In total, we observed fox squirrels for 52.36 hours over 30 different days. A single

206   observer (AK) conducted all trials. A total of 171 trials were conducted with 71 trials conducted

207   without any acoustic playback treatments and 94 trials conducted with an acoustic playback.

208   Sites were visited between 800 and 1900 h EST and data were collected from October 2019

209   through January 2020. Trials with no playbacks were conducted from 25 October 2019 to 16

210   November 2019 (from 812 to 1810 h) whereas trials using playbacks (playback trials) were

211   conducted from 18 November 2019 to 27 January 2020 (from 802 to 1609 h). We randomized

212   the order in which sites were visited and the version of playback treatments used (see below for

213   information on playback versions) at each site. No two sites were visited on the same day. All

214   trials with no playbacks were conducted prior to the playback trials in this study. This was due to

215   personnel limitations and prevents us from directly comparing trials with and without playbacks

216   given that squirrel behavior likely changes seasonally from October to January due to food

217   caching behavior in autumn but not winter. Trials were not conducted when it was raining or

218   snowing. Results from two one-way ANOVAs showed that the time of day for playback trials

219   did not vary among the three different treatment groups ($F_{2,91} = 0.44$, $p = 0.65$) and that the time

220   of day when trials were conducted did not vary among squirrels at the urban or less urban sites

221   (t-test: $t_{75.4} = 0.21$, $p = 0.83$). Air temperature varied during all the trials varied from -6.1° to

222   10.5°C (mean = 2.7° C).

223   We measured the behavioral responses of squirrels to humans or humans plus different

224   playbacks using protocols developed for tree squirrels (Dill and Houtman, 1989; Gustafson and

225   VanDruff, 1990; McCleery, 2009). At the beginning of each trial, a marker was placed at the

226   starting position of the observer and trial data were recorded (GPS location, time of day,

227   temperature, general weather conditions, and squirrel sex). The squirrel was approached by a

228   single observer (AK) at a slow and steady pace in a direct line to the squirrel (see Fig. S1 in

229   Appendix I). Additional markers were placed when a squirrel displayed the first alert and when

230   they fled. The FAD was defined as the distance between the observer and the squirrel when it

231   first stopped moving (froze) and looked at the observer with one or both eyes. FID was recorded

232   as the distance between the squirrel's initial position and the observer location when it actively

233   fled (stopped feeding and foraging and moved rapidly away from observer). A marker was also

234   placed at an estimate of the squirrel's initial position to the place where they fled to if refuge was

235   not taken in a tree, and the distance between this marker and the squirrel's initial position was

236   recorded as "flight distance". We recorded this because some studies have noted that FID is

237   variable depending on intruder starting distances and distance to a refuge (Dill & Houtman,

238   1989; Blumstein, 2003). Consequently, the distance between the observer and the focal squirrel

239   at the start of the trial (starting positions, hereafter referred to as "initial distance": mean ± SE

240   over all 171 trials = 21.2±0.61 m) and the distance between the focal squirrel's initial position

241   and the nearest tree were also measured ("distance to nearest tree": mean ± SE over all 171 trials

242   =3.2±0.11 m).

243   If the focal animal took refuge in a tree other than the one nearest, distance between the

244   squirrel's initial position and its refuge tree of choice ("distance to the chosen tree") was also

245   recorded. If an individual took refuge in a tree, a laser rangefinder was used to measure how high

246   they climbed, and this distance was recorded (same as vertical escape distance in Uchida et al.,

247   2017). Lastly, latency to resume behavior was recorded ("latency"). This was measured with a

248   stopwatch to determine how long it took for the animal to cease alert/vigilance behavior and

249   resume typical activity (foraging or traveling off tree). When the observer was recording latency,

250   they maintained as large a distance as possible (~15-20 m) from the tree to reduce the influence

251   on the squirrel's behavior. Out of all the trials, nearly all squirrels ceased alert behavior and

252   resumed typical behavior within a couple minutes (n = 171 trials, mean ± SE = 130.5 ± 10.3 s),

253   but there was one individual squirrel that remained alert for longer than ten minutes and we

254   recorded its latency as ten minutes. Distances were measured with a tape measure and presented

255   in meters.

256   *Playback trials*

257   Playback trials (n = 94 total trials) were conducted using the same protocol shown above,

258   with the addition of an acoustic stimulus being broadcasted while the observer approached the

259   squirrels. The control stimulus consisted of recordings of black-capped chickadee calls (*Poecile*

260   *atricapillus*). Black-capped chickadees are not known to be predators of fox squirrels

261   (Korschgen, 1981; Koprowski, 1994) and a previous study in another tree squirrel species

262   showed that individuals exhibited a significantly reduced response to black-capped chickadee

263   playbacks compared to calls of other anthropogenic noises (car alarm, buzzer) and playbacks of

264   red-tailed hawks (Bohls and Koehnle, 2017). We therefore expected that black-capped chickadee

265   recordings would represent a neutral vocalization for fox squirrels and they can act as control to

266   ensure that any differences in squirrel behavior across playback treatments are attributable to the

267   vocalization information of the playback rather than an added exposure to noise. To simulate the

268   threat of a terrestrial predator, recordings of domestic dogs barking were broadcasted. Domestic

269   dogs are terrestrial predators of fox squirrels (Koprowski, 1994; Wauters et al., 1997) and other

270   species of tree squirrels that live in the same habitats as fox squirrels also adjust their risk-taking

271   behavior according to the abundance of domestic dogs (Bowers and Breland, 1996; Cooper et al.,

272   2008). For the avian predator, recordings of red-tailed hawk (*Buteo jamaicensis*) calls were

273   broadcasted to the focal individual. Red-tailed hawks were chosen since they are year-round

274   predators of fox squirrels in Michigan (Koprowski, 1994; personal observations) and other

275   studies illustrate that tree squirrels respond to hawk playbacks with increased anti-predator

276   behavior (McCleery, 2009; Lilly et al., 2019). No post-processing of sound files was performed.

277   Playbacks of the recordings were broadcasted to individuals at the start of the trial and

278   when the observer began the approach and suspended when the squirrel took flight.

279   Vocalizations were broadcasted through a JAMBOX speaker (Jawbone, San Francisco, CA)

280   connected to an Apple iPhone 6s (Mountain View, CA) with a constant volume set for the

281   speaker and phone. The speaker was carried by the observer during each trial. The amplitude of

282   the playbacks measured from 1 m away from the speaker was variable among the chickadee (67-

283   80 dB), dog (69-77 dB), and hawk (78-86 dB) playbacks (measured using a BAFX Sound Level

284   Meter, BAFX3370). We note that the initial starting distance of the playbacks was inherently

285   variable as we could not standardize the distance between the observer and squirrel when the

286   trials were started (mean ± SE over all 94 trials involving playbacks = 19.11±0.73 m).

287   Consequently, the actual realized sound level of the playbacks experienced by a squirrel varied.

288   Given how the trials were conducted in real time (not video recorded), the single observer (AK)

289   was not blind to the playback treatments or locations of where the experiments took place. All

290   vocalization recordings were found online (Control A: Place, 2015; Control B: Floyd, 2017a;

291   Control C: Floyd, 2017b; Dog A: Simion, 2016; Dog B: Simion, 2018; Dog C: Simion, 2017;

292   Hawk A: Chartier, 2008; Hawk B: Addison, 2017; Hawk C: Wilson, 2010). Each playback

293   treatment (control, dog, or hawk) had three separate recordings/exemplars (A, B, or C). We

294   tested whether there were any exemplar effects in separate ANOVAs that included playback

295   exemplar (A, B, C), playback treatment (chickadee, dog, hawk), and an interaction between the

296   two. We did this for each of our four behavioral response variables and did not find any

297   significant interactions between playback exemplar and treatment ($p = 0.12$-0.99), suggesting

298   that the version of the playback treatment did not influence the behavioral response.

299   *Statistical analyses*

300   We analyzed the data from trials with and without playbacks separately because the two

301   experiments were not conducted synchronously and seasonal changes from fall to winter in

302   Michigan may alter squirrel behavior. In trials without playbacks, we used three separate linear

303   mixed-effects models (LMMs) to examine the effects of urbanization on FAD, FID, and latency

304   to resume activity following the trial. Although the linear distance a squirrel climbed up a tree

305   (from base of tree to location of squirrel) has been used in other studies of tree squirrels (e.g.,

306   Uchida et al., 2017), the distance a squirrel climbed up a tree in our study exhibited a Poisson

307   distribution where many squirrels did not climb up a tree at all and a few climbed up very high

308   (squirrels did not climb a tree in 80 of 171 total trials; those that did climb a tree mean ± SE =

309   4.7 ± 0.34 m). This seemed to better approximate a behavioral decision made by a squirrel to

310   "climb or not climb" rather than "how high to climb". Consequently, a generalized linear mixed-

311   effect model (GLMM) with binomial errors was used to examine the effects of urbanization on

312   the probability that squirrels climbed a tree to escape during the trial. We note that the same

313   inferences for the linear distance a squirrel climbed a tree were gained if we instead ran a zero-

314   inflated Poisson mixed-effects model. Models included site category (urban, less urban), distance

315   to the nearest tree, sex, Julian date of the trial, and initial distance of the observer as fixed effects.

316   Distance to the nearest tree was included not only because previous studies show it can impact

317   anti-predator behavior (measured using FID: Dill & Houtman, 1989; Blumstein, 2003) but also

318   because it helps control for any differences in vegetation among the different study sites, which

319   could impact their behavior. Because we had repeated samples from the same site, we also

320   included a random intercept for site in all of our models. The same model structure was used in

321   separate LMMs or the GLMM for data from the playback trials to examine the effects of the

322   acoustic playback manipulations on the four squirrel behaviors described above but the models

323   included an interaction between playback treatment (control, dog, hawk) and site category

324   (urban, less urban). We then assessed the statistical significance of pairwise comparisons using

325   post-hoc Tukey's Honest Significant Differences that were corrected for multiple comparisons.

326   In these pairwise comparisons, we were specifically interested in identifying 1) whether squirrels

327   in urban and less urban sites differed in their behavior in response to the playback treatments

328   (e.g., urban squirrels exposed to hawk playbacks differed in FID compared to less urban squirrels

329   exposed to hawk playbacks) and 2) whether squirrels within each type of site differed in their

330   response to the playbacks (e.g., whether squirrels in urban areas exhibited a higher FID in

331   response to hawk playbacks compared to those in urban areas exposed to control playbacks).

332   Continuous predictor variables were standardized to a mean of 0 and SD of 1. We

333   confirmed model diagnostics visually and all models met the appropriate assumptions (normality

334   of residuals, constant variance, no high leverage observations). Latency to resume behavior was

335   log+1 transformed (base e) to improve homoscedasticity and normality. There were also no

336   predictor variables that were found to be colinear as all variance inflation factors (VIFs) were

337   less than 3.68 (Zuur et al., 2010), though the higher VIF were due to interaction terms and VIF of

338   variables not in interactions were <1.5. All analyses were conducted in R version 4.02 (R Core

339   Team, 2020) with lme4 (version 1.1.23, Bates et al., 2015) and p-values estimated using

340   lmerTest (version 3.1.2, Kuznetsova et al., 2017). Tukey's post-hoc tests were used to evaluate if

341   the responses to the playback treatments differed between squirrels in urban and less urban areas

342   using emmeans (1.5.2-1: Lenth, 2020) and *p* values from these analyses were adjusted for

343   multiple comparisons. Mean and SE are presented below.

344

345   **Results**

346   *Behavioral responses to human-stimuli only*

347   Overall, urban squirrels (n = 38, 20 females and 18 males) exhibited greater tolerance to

348   humans as they allowed a human observer to get closer to them before they exhibited vigilance

349   (FAD) or fled (FID) and tended to be less likely to climb a tree during the trial and more quickly

350   return to typical behavior following the trial compared to those in less urban sites (n = 39, 19

351   females and 20 males; Table 1, Fig. 1). FID in the squirrels at the urban site (6.36 ± 0.52 m) was

352   97.2% shorter compared to those at the less urban sites (12.54 ± 0.62 m, *p* = 0.043, Table 1, Fig.

353   1B). Although the average FAD for squirrels observed at the urban site (10.09 ± 0.74 m) was

354   43.8% shorter than for those at the less urban sites (14.51 ± 0.69 m), this difference was not

355   significant (*p* = 0.10, Table 1, Fig. 1A). Squirrels at the urban sites were less likely to climb a

356   tree while the observer approached (34.2% of trials) compared to those at the less urban sites

357   (64.1%), although this difference was not significant (*p* = 0.093, Table 1, Fig. 1C). Latency to

358   resume behavior following the trial was shorter for urban squirrels (43.9 ± 14.4 s) compared to

359   those at the less urban sites (157.51 ± 25.35 s), but this difference was not significant (*p* = 0.11,

360   Table 1, Fig. 1D). Trials where the observer started the trial at a longer initial distance to the

361   squirrel had significantly longer FAD and FID but not probability of climbing a tree or latency to

362   resume behavior following the trial (Table 1). There were no significant effects of sex, Julian

363   date, or distance to the nearest tree on FAD, FID, probability of climbing a tree, or latency

364   (Table 1).

365   *Behavioral responses to stimuli from natural predators*

366   The effects of the playbacks on FAD depended upon whether the squirrels were located

367   at the urban or less urban sites (Table 2, Fig. 2A). Average FAD for urban squirrels exposed to

368   the hawk vocalizations (n = 12 trials, 17.17 ± 1.33 m) was 37% longer than urban squirrels who

369   were exposed to the control playback (n = 11, 12.56 ± 0.94 m, Tukey's p = 0.004) and 20%

370   longer than those exposed to the dog playbacks (n = 20, 14.30 ± 0.83 m, Tukey's p = 0.006, Fig.

371   2A). By contrast, the FAD of squirrels at the less urban sites were just longer overall (Fig. 2A)

372   and the FAD of those less urban squirrels who were exposed to the hawk playbacks (n = 16,

373   14.62 ± 1.14 m) did not differ from those exposed to the control playback (n = 15, 14.46 ± 0.88

374   m, Tukey's p = 0.99) or dog playbacks (n = 20, 14.85 ± 1.05 m, Tukey's p = 0.94, Fig. 2A).

375   There were no significant differences in FAD for squirrels exposed to dog playbacks and those

376   exposed to the control playback for squirrels at urban sites (Tukey's p = 0.99) or those at less

377   urban sites (Tukey's p = 0.99). When comparing squirrels at urban or less urban sites to a

378   specific playback treatment, squirrels at the urban and less urban sites did not differ in their FAD

379   when exposed to hawk playbacks (urban vs. less urban: Tukey's p = 0.64), dog playbacks (urban

380   vs. less urban: Tukey's p = 0.39), or the control stimulus (urban vs. less urban: Tukey's p = 0.49,

381   Fig. 2A).

382   Similar to FAD, the effects of the playbacks on FID also depended upon whether the

383   squirrels were located at the urban or less urban sites (Table 2, Fig. 2B). Average FID for urban

384   squirrels exposed to the hawk vocalizations (n = 12 trials, 14.95 ± 0.98 m) was 44.3% longer

385   than squirrels who were exposed to the control playbacks (n = 11, 10.37 ± 3.13 m, Tukey's p =

386   0.001) and 29.9% longer than those exposed to the dog playbacks (n = 20, 11.86 ± 2.65 m,

387   Tukey's p = 0.001, Fig. 2A). In squirrels at urban sites, there was no difference in FID between

388   those exposed to the control playback and those exposed to the dog vocalizations (Tukey's p =

389   0.99). In squirrels at less urban sites, FID for those exposed to the dog playbacks (13.60 ± 0.98

390   m) was similar to those exposed to the control (12.12 ± 0.88 m, Tukey's p = 0.14) or hawk

391   playbacks (13.11 ± 0.96 m, Tukey's p = 0.95, Fig. 2B). Unlike urban squirrels, the FID of those

392   at the less urban sites who were exposed to hawk playbacks was similar compared to those

393   exposed to the control playback (Tukey's p = 0.69). When comparing squirrels at urban or less

394   urban sites to a specific playback treatment, squirrels at the urban and less urban sites did not

395   differ in their FID when exposed to hawk playbacks (urban vs. less urban: Tukey's p = 0.98),

396   dog playbacks (urban vs. less urban: Tukey's p = 0.13), or the control stimulus (urban vs. less

397   urban: Tukey's p = 0.83).

398   There were no significant effects of the playback treatments or site differences on the

399   likelihood squirrels climbed a tree. Squirrels at urban sites were not more likely to climb a tree

400   when exposed to a hawk playback compared to a dog (Tukey's p = 0.30) or control (Tukey's p =

401   0.67) playback and were not more likely to climb a tree when exposed to a dog playback versus a

402   control playback (Tukey's p = 0.99). Squirrels at less urban sites exhibited a similar probability

403   of climbing a tree when they were exposed to hawk playbacks compared to dog (Tukey's p =

404   1.0) or control (Tukey's p = 0.73) playbacks or when exposed to dog playbacks compared to a

405   control playback (Tukey's p = 0.73). Squirrels at the urban and less urban sites did not differ in

406   their probability of climbing a tree when exposed to hawk playbacks (urban vs. less urban:

407   Tukey's p = 0.99), dog playbacks (urban vs. less urban: Tukey's p = 0.12), or the control

408   stimulus (urban vs. less urban: Tukey's p = 0.99).

409   Squirrels at the urban and less urban sites did not differ in their latency to resume typical

410   behavior following exposure to hawk playbacks (urban vs. less urban: Tukey's p = 0.98), dog

411   playbacks (urban vs. less urban: Tukey's $p = 0.89$), or the control stimulus (urban vs. less urban:

412   Tukey's $p = 0.88$, Table 2, Fig. 2D). However, there were differences in how squirrels responded

413   to the playback treatments within each of the two types of study sites. Squirrels at urban sites that

414   were exposed to the hawk playbacks took 436% longer to resume their pre-trial behavior (213.33

415   ± 28.9 s) compared to those who were exposed to the control playback (39.82 ± 7.70 s, Tukey's

416   $p < 0.001$) and 147% longer than those exposed to dog playbacks (86.25 ± 13.30 s, Tukey's p =

417   0.027). Squirrels at the urban sites also took 114% longer to resume typical behavior if they were

418   exposed to dog playbacks compared to those exposed to the control playback (Tukey's $p <$

419   0.001). Similarly, squirrels at the less urban sites that were exposed to the hawk playbacks took

420   218% longer to resume their pre-trial behavior (291.25 ± 35.45 s) compared to those who were

421   exposed to the control playback (91.47 ± 25.45 s, Tukey's $p < 0.001$) and 55.7% longer than

422   those exposed to dog playbacks (187.05 ± 21.38 s, Tukey's p = 0.12, Fig. 2D). Squirrels at the

423   less urban sites also took 95.6% longer to resume typical behavior if they were exposed to dog

424   playbacks compared to those exposed to the control playback (Tukey's $p < 0.001$).

425   There was no effect of sex or Julian date of trial, on any of the behaviors (Table 2). There

426   was no effect of the initial distance that a squirrel was from a tree when the trial started on FAD,

427   FID, or probability to climb a tree, but squirrels were less likely to climb a tree if they were

428   closer to one when the trial started (Table 2). Trials that started with the human observer a

429   greater distance away from the squirrel had longer FAD, FID, and latency to resume typical

430   behavior, but not the probability to climb a tree (Table 2).

431

432   **Discussion**

433   Squirrels at urban sites in the no playback trials exhibited a significantly shorter FID

434   compared to those at the less urban sites and also exhibited a lower FAD and likelihood to climb

435   a tree during the trial, and shorter latency to resume typical behavior following the trial, though

436   only the difference in FID was statistically significant. In the trials where squirrels were exposed

437   to playbacks from possible predators (hawks or dogs), squirrels at the urban sites did not differ in

438   their vigilance (FAD) or anti-predator behavior response (FID, likelihood to climb a tree, latency

439   to resume typical behavior following the trial) compared to those at the less urban sites. When

440   we compared the behavior responses of squirrels within each site type (urban or less urban),

441   squirrels at the urban sites exhibited longer FAD (hawk > dog = control) and FID (hawk > dog =

442   control) when exposed to hawk playbacks compared to control or dog playbacks, suggesting

443   increased vigilance (FAD) anti-predator behavior (FID) when exposed to vocalizations from

444   potential predators. By contrast, squirrels at the less urban sites had longer overall FAD and FID

445   than those at urban sites regardless of playback treatment and there was no effect of hawk or dog

446   playbacks on FAD (hawk = control = dog) or FID (hawk = control = dog), suggesting no

447   increase in vigilance or anti-predator behavior when exposed to vocalizations from potential

448   predators. Squirrels at both urban and less urban sites were not more likely to climb a tree

449   following playbacks from possible predators (hawk = dog = control) but both urban and less

450   urban squirrels exhibited a longer latency to resume typical behavior following the hawk or dog

451   playbacks compared to the control (hawk > dog > control), suggesting increased anti-predator

452   behavior when exposed to vocalizations from potential predators. Overall, our results indicate

453   that squirrels in urban areas are more tolerant to humans but still exhibit a high level of vigilance

454   and anti-predator behavior when exposed to predator stimuli. In terms of the STRANGEness of

455   our results (Webster and Rutz, 2020), our results may be generalizable to other squirrel

456   populations or different species but we note that our results are biased towards squirrels that

457   voluntarily participated in the trials (i.e., did not run away when approached). We also note that

458   the significance of our results may be limited to urban populations where predators are present in

459   those areas.

460   Similar to most other studies in terrestrial animals (Samia et al., 2015) and in studies in

461   tree squirrels (McCleery, 2009; Engelhardt and Weladji, 2011; Sarno et al., 2015; Uchida et al.,

462   2020), our results from trials with no playbacks suggest that squirrels in urban sites were more

463   tolerant of humans. Specifically, squirrels in urban areas exhibited a shorter FAD and FID, lower

464   probability to climb a tree to escape the human observer, and a shorter latency to resume typical

465   behavior following the trial, although only FID was significantly different between habitat types.

466   The congruency of our results with previous studies strongly supports this assumption that

467   squirrels at our urban sites were more tolerant of humans. These are presumably sympatric

468   populations with a large amount of gene flow among them as the linear distance between some

469   urban and less urban sites is ~1 km. Unless selection favoring reductions in anti-predator

470   behavior is extremely strong in urban areas or features of urban landscapes strongly impede gene

471   flow (Johnson and Munshi-South, 2017), it seems likely that these behavioral differences are

472   driven by plasticity given that the likely exchange of individuals between suburban and urban

473   sites prevents local genetic adaptation to these different sites (see discussion in Sol et al., 2013).

474   It is also possible that these behavioral differences are due to personality-dependent colonization

475   of urban habitats (Carrete and Tella, 2010; Sprau and Dingemanse, 2017), but we cannot

476   distinguish among these possibilities at this time.

477   Although squirrels at our urban sites were more tolerant of humans, they still exhibited a

478   strong behavioral response to acoustic stimuli from natural predators. Specifically, they exhibited

479   increased vigilance (FAD) and anti-predator behavior (FID, latency to resume typical behavior

480   after the trial) when exposed to the playbacks of a natural predator (hawk) compared to the

481   control playback or the dog playbacks. The behavioral responsiveness to hawk vocalization is

482   somewhat surprising because hawks do not vocalize while hunting, but squirrels still responded

483   to their presence suggested through acoustic cues. These results indicate that urban squirrels do

484   still pay attention to predation risk and can discriminate and respond accordingly by becoming

485   vigilant and fleeing when the human is at a greater distance if the human is also paired with

486   hawk playbacks. By contrast, squirrels at less urban sites did not exhibit differences in FAD

487   when exposed to the different playbacks, perhaps due to some ceiling effect given that FAD of

488   squirrels at less urban sites was much longer than FAD of squirrels at urban sites. Furthermore,

489   when we compared the effects of hawk or dog playbacks on FAD or FID, there were no

490   differences between squirrels at the urban and less urban sites. Our results therefore reject the

491   hypothesis that urban squirrels are less responsive to natural predators due to increased tolerance

492   to humans. Previous studies (see also Labra and Leonard, 1999; Seress et al., 2011; Cooper et al.,

493   2008; Bokony et al., 2012; Cavalli et al., 2016; Weaver et al., 2018; Vincze et al. 2019) together

494   with our results support that animals in urban habitats or those frequently exposed to humans,

495   even if more tolerant of human presence, still exhibit increases in anti-predator behavior in

496   response to a non-human predator. However, future studies that test this hypothesis need to have

497   increased sample sizes and should also include a playback treatment that uses both visual and

498   acoustic cues of humans as a control stimulus.

499   There are two other interesting results from our trials with playbacks. First is the finding

500   that squirrels that were closer to a tree at the start of the trial were less likely to climb a tree. This

501   is opposite of what we would expect and future studies need to better assess if this is caused by

502   some larger habitat difference between urban and less urban areas and/or reflect differential

503   escape strategies. For example, squirrels at urban sites may be more distant to a tree at the start

504   of the trials and escape from humans by running away rather than going up a tree. However, in a

505   post-hoc analysis using our entire dataset of trials conducted with or without playbacks (n = 171

506   trials), squirrels in urban areas (n = 81 trials, 3.30 ± 0.16 m) and those in less urban areas (n = 90

507   trials, 3.05 ± 0.15 m) did not differ in their distance to a tree at the start of the trials (general

508   linear model: t_{169} = 1.13, p = 0.26). Second, we expected that squirrels would respond to the dog

509   playbacks in similar way to how they responded to the hawk playbacks as both are stimuli from

510   potential predators. Previous studies in tree squirrels also show that they exhibit increased

511   vigilance or FID to the physical presence of a dog with a human handler (Gustafson and

512   VanDruff, 1990; Cooper et al., 2008) or behave in such a way in areas with high levels of dogs

513   and cats that suggests that they perceive a higher predation risk in such areas (i.e., giving up

514   density was higher in study areas where cats and dogs are present: Bowers and Breland, 1996).

515   Instead, we found that squirrels at both sites did not differ in their vigilance (FAD) when

516   exposed to dog playbacks compared to the control playbacks. Additionally, only squirrels in less

517   urban sites had a slightly (non-significantly) longer FID when exposed to dog playbacks

518   compared to the control playback. Although we did find that squirrels exposed to dog

519   vocalizations took longer to resume typical behavior following the trials, our results generally

520   differ from previous studies in tree squirrels and owls showing that FAD and/or FID were

521   increased in squirrels or owls in urban areas when they were presented with a human plus dog

522   compared to just a human (Gustafson and VanDruff, 1990; Cooper et al., 2008; Cavalli et al.,

523   2016). This suggests that squirrels, especially those in urban sites, were more tolerant to dog

524   vocalizations when paired with a human observer, whereas squirrels in less urban areas may

525   have viewed the sounds of dogs paired with humans as threatening. We predict that squirrels in

526   urban environments exhibit selective tolerance where the response to humans or stimuli from

527   their commensals (dogs) is attenuated but the increased response to natural predators is

528   maintained despite this tolerance to humans and their dogs.

529   Together, our results provide insight into how urbanization may shape the behavioral

530   characteristics animals in two main ways. First, as most studies on this topic are in birds (Samia

531   et al., 2015), which can escape from humans using flight, it is important to consider if the same

532   patterns are found in terrestrial animals. Our results show that non-volant animals in urban

533   environments exhibit less vigilance and anti-predator behavior. Second, we show that squirrels in

534   urban environments were more tolerant to humans but still exhibited a strong response reflecting

535   increased vigilance and anti-predator behavior to acoustic stimuli from a natural predator

536   (hawks) and that squirrels in urban areas did not differ in their behavioral response when

537   exposed to stimuli from two types of possible predators compared to those exposed to those

538   stimuli in less urban areas. Although we do not wish to imply that tolerance or habituation to

539   humans is cost-free, most studies fail to find evidence that populations where individuals are

540   more tolerant of humans (or in some cases habituated to their presence) also exhibit reduced

541   vigilance and/or anti-predator behavior to stimuli from natural predators. Given that urbanization

542   is unlikely to slow, increased effort is needed to determine if increased tolerance and/or

543   habituation to humans carries costs (Geffroy et al., 2015). Some studies suggest the costs of

544   human tolerance may be more nuanced, such as tolerance to humans reducing the latency to

545   return to the nest following a disturbance in nesting shorebirds, but potentially causing increased

546   chick mortality due to the presence of dogs that often are paired with human stimuli (Baudains

547   and Lloyd, 2007). Other studies that increased tolerance of humans could even be beneficial for

548   populations that cannot avoid anthropogenic stimuli due to seasonal food pulses coinciding with

549   a large influx of tourists (Wheat and Wilmers, 2016). Clearly more work is needed on this

550   subject, especially on a greater number of species including species that are not "urban

551   exploiters" like tree squirrels, but the existing evidence rejects the hypothesis that there is a cost

552   to human tolerance in terms of lowering the vigilance and/or anti-predator behavior of animals to

553   other natural predators. If predatory species re-colonize urban areas, our results suggest that they

554   should respond appropriately to stimuli indicating their presence.

555

556   **Data Availability Statement**

557   All data are available through the FigShare account associated with the senior author (Dantzer,

558   2021).

559

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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 or 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	*b*	SE	*t* or *z*	*P*
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	*b*	SE	*t* or *z*	*P*
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, Control)	-0.20	0.62	-0.33	0.74
	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.
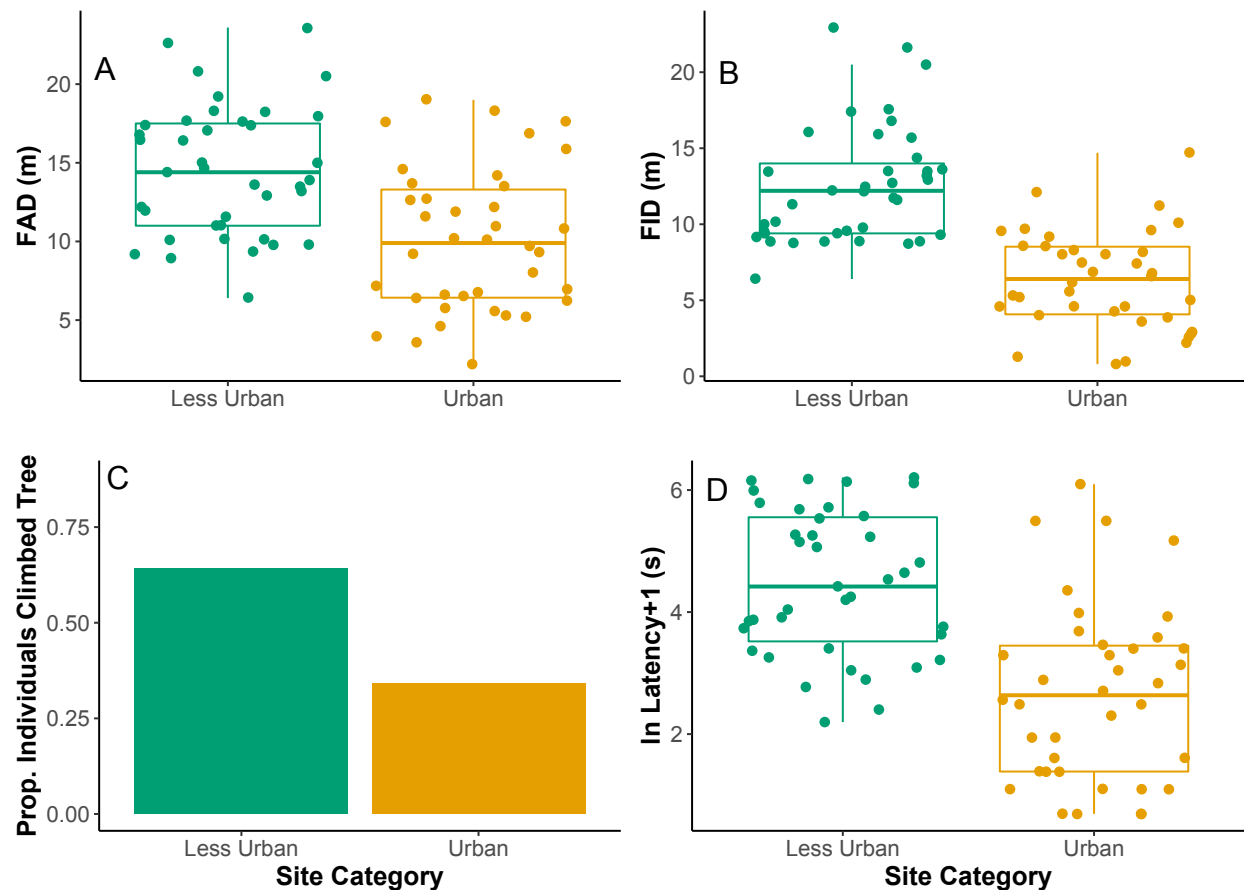
Figure 2. Effects of human observer approaching a squirrel while broadcasting one of three playback treatments (control playback, hawk or dog vocalizations) on A) first alert distance (FAD), B) flight initiation distance (FID), C) proportion of individuals escaping up a tree during the trial, and D) 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.