1 **Mammals adjust diel activity across gradients of urbanization**
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36
43 **Abstract**
44 Time is a fundamental component of ecological processes. How animal behavior changes over
45 time has been explored through well-known ecological theories like niche partitioning and
46 predator-prey dynamics. Yet, changes in animal behavior within the shorter 24-hour light-dark
47 cycle have largely gone unstudied. Understanding if an animal can adjust their temporal activity

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48 to mitigate or adapt to environmental change has become a recent topic of discussion and is
49 important for effective wildlife management and conservation. While spatial habitat is a
50 fundamental consideration in wildlife management and conservation, temporal habitat is often
51 ignored. We formulated a temporal resource selection model to quantify the diel behavior of
52 eight mammal species across ten U.S. cities. We found high variability in diel activity patterns
53 within and among species and species-specific correlations between diel activity and human
54 population density, impervious land cover, available greenspace, vegetation cover, and mean
55 daily temperature. We also found that some species may modulate temporal behaviors to manage
56 both natural and anthropogenic risks. Our results highlight the complexity with which temporal
57 activity patterns interact with local environmental characteristics, and suggest that urban
58 mammals may use time along the 24-hour cycle to reduce risk, adapt, and therefore persist in
59 human-dominated ecosystems.

60
61 **Keywords:** behavior, human disturbance, nocturnality, temporal partitioning, urban wildlife

62
63 **Introduction**
64 Time is a fundamental axis that shapes ecological systems. Regarding animal behavior, time and
65 space are linked in that the spatial characteristics of an animal's local environment influences its
66 temporal behavior (Kronfeld-Schor and Dayan, 2003). For example, some species make seasonal
67 changes in diel (24-hour period) activity to be most active during optimal temperatures in their
68 local environment (Maloney et al., 2005), and other species temporally partition themselves from
69 heterospecific competition or aggression (Kronfeld-Schor and Dayan, 2003; van der Vinne et al.,
70 2019). While temporal behavior has yet to become a major focus in animal ecology (Gaston,
71 2019; Kronfeld-Schor and Dayan, 2003), how animals use time as an ecological resource has
72 inspired well-known ecological phenomenon like niche partitioning (Schoener, 1974) and
73 predator-prey dynamics (Tambling et al., 2015). From an applied perspective, understanding if
74 an animal can make temporal adjustments to mitigate or adapt to local environmental change
75 remains a topic of discussion (Wolkovich et al., 2014), and is important for effective wildlife
76 management and conservation (Levy et al., 2019).

77
78 Species that persist in human-dominated environments, like cities, require some degree of human
79 avoidance to safely navigate these complex landscapes (Gehrt et al., 2009; Murray and St. Clair,
80 2015; Riley et al., 2003). In urban ecosystems, few habitat patches remain for animals to seek
81 spatial refuge when confronted with human disturbance and/or negative interactions with other
82 species. In these cases, temporally partitioning from these potentially dangerous interactions
83 might be an alternative strategy. A recent global meta-analysis suggests that mammals become
84 more nocturnal in areas with greater human disturbance (Gaynor et al., 2018). However, only
85 7.8% (n = 11) of these studies assessed changes in nocturnal activity in urban areas, and all
86 explored these changes categorically between urban and non-urban areas. Binary urban and rural
87 categorizations generally fail to capture variation in urban development and cannot generate
88 generalizable results that correlate to other cities (McDonnell and Pickett, 1990). Additionally,
89 cities are unique and differ in size, land use, growth patterns, and human culture (Pacione, 2009).
90 Variation in both spatial and temporal characteristics within and among cities could have
91 differing effects on animal behavior. Thus, key questions remain regarding the way in which
92 animal diel activity varies across gradients of urbanization and among differing cities. For
93 example, the magnitude of change in diel activity patterns may be larger for more densely

94 urbanized cities or may depend on regional variation in day and night-time temperatures. Multi-
95 city investigations that include variation in urban intensity and regional climate can elucidate
96 such patterns.
97
98 Gaynor et al. (2018) found that most studies in urban environments also focused on carnivore
99 species, highlighting a gap in our understanding regarding changes in diel activity across taxa.
100 For example, carnivores likely avoid humans in both space and time because of inimical human
101 interactions (Clinchy et al., 2016; Kitchen et al., 2000). This may not be the case for mammals
102 that do not regularly come in conflict with humans or do not evoke such visceral reactions by
103 humans. Additionally, some species may be constrained by their morphology (e.g., number and
104 type of cones and rods in their eyes) or may otherwise lack the ability to be active in alternative
105 lighting. To fully understand the variability of activity patterns and assess temporal adjustments
106 in response to urban development, a comprehensive examination of the larger suite of urban
107 mammals and across multiple urban environments is required.
108
109 While spatial habitat is a fundamental consideration in wildlife management and conservation,
110 temporal habitat is often ignored (Gaston, 2019). Here, we link spatial landscape characteristics
111 with the diel activity patterns of eight terrestrial mammals using remote cameras deployed across
112 ten U.S. cities. Our objectives were to 1) determine which species change their diel activity
113 across gradients of urbanization and identify what characteristics of the urban environments have
114 the strongest association with changes in diel activity and 2) assess whether urbanization
115 influences nocturnal behavior and identify what characteristics of urban environments have the
116 strongest influence on changes in nocturnal behavior.
117
118 We found high variability in diel activity patterns within and among species and species-specific
119 correlations between diel activity and human population density, impervious land cover,
120 available greenspace, vegetation cover, and mean daily temperature. Our results indicate that in
121 high-risk environments, such as cities, animals may reduce risk by modulating their temporal
122 habitat use. Our study identifies a potential mechanism by which urban wildlife species may
123 adapt to human-dominated environments, and provides critical insight into activity patterns of
124 urban wildlife that will prove useful for managing these species in cities
125
126 **Results**
127 To quantify changes in mammal diel activity in response to urbanization, we used camera
128 detection data for eight common urban mammal species: bobcat (*Lynx rufus*), coyote (*Canis*
129 *latrans*), red fox (*Vulpus vulpus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*),
130 eastern cottontail (*Sylvilagus floridanus*), Virginia opossum (*Didelphis virginiana*), and white-
131 tailed deer (*Odocoileus virginianus*). Cameras were deployed in a systematic fashion across ten
132 U.S. metropolitan areas as part of the Urban Wildlife Information Network: Austin, TX,
133 Chicago, IL, Denver, CO, Fort Collins, CO, Indianapolis, IN, Iowa City, IA, Orange County,
134 CA, Madison, WI, Manhattan, KS, and Wilmington, DE (and Fidino et al., 2021 for details; see
135 Magle et al., 2019).
136
137 Across 41,594 trap nights (Table S1), we captured 79,659 total unique detection events. Total
138 detections per species ranged from 102-34,931, and each species was detected in 5-10 cities at an
139 average proportion of 0.16-0.77 sites per city (Table 1). Bobcat occurred at the lowest number of

140   cities and proportion of sites, while raccoon occurred in all 10 cities and at the greatest
141   proportion of sites (Table 1, see Table S2 for the proportion of sites in each city). The number of
142   detections captured throughout the 24-hour diel period varied among species (Table 1).
143
144   *Modeling diel activity*
145   We formulated a hierarchical multinomial model to quantify the diel behavior of each species
146   and assess the effects that available greenspace, vegetation cover, impervious land cover, human
147   population density, and daily temperature had on diel behavior of each species. Our approach
148   operates similar to resource selection functions in which resources are selected in space.
149   However, substituting time for space allowed us to quantify changes in diel activity across
150   gradients of environmental change. This temporal resource selection model allowed us to
151   estimate temporal 'selection' and the probability of 'use' in each time category. Coefficient
152   estimates are estimates of selection for a particular time category relative to the available time in
153   the respective category and the difference from the reference time category ('day').
154   Exponentiated coefficient estimates greater than one indicates selection and less than one
155   indicates avoidance, relative to the day reference category. Using the softmax function
156   (Kruschke, 2011), we also estimated the influence that each predictor variable had on the
157   probability of activity in each time category, including the 'day' category.
158
159   *Among city variation in diel activity patterns*
160   We found that most species, on average, had a higher probability of being nocturnal (active at
161   night or during the darkest portions of night) with the exception of bobcat and white-tailed deer
162   (Fig. 1 and 2). Most species showed variation in diel activity among cities (e.g., bobcat; Fig. 1),
163   and some species (e.g., eastern cottontail, coyote, red fox, and bobcat) exhibited profound
164   variation in diel activity across individual sampling sites (Fig. 2). For example, the predicted
165   probability of nocturnal behavior for eastern cottontail at each sampled site ranged from 0.15 –
166   0.69 (see Table S3 for a full set of ranges for each species and each time category).
167
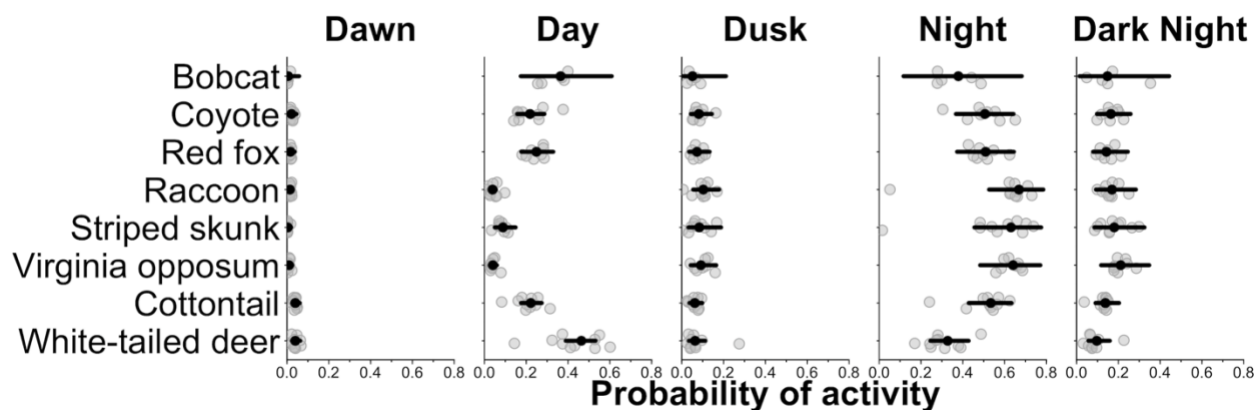
168
169   **Figure 1.** City-specific probability of activity for each species. Grey points are city specific
170   estimates of the average probability of activity in each time category. The black point indicates
171   the average probability of activity among cities and the horizontal lines are 95% credible interval
172   for the average probability estimates among cities. Wider credible intervals indicate more
173   variation among cities.

4

174   **Table 1.** The total number of detections for each species, number of cities each species was detected in, mean proportion of sites each
175   species was detected at per city, and total number of detections in each time category for eight urban mammal species across ten U.S.
176   metropolitan areas between January 2017 and December 2018.
177

Species	Total detections	No. of cities species detected	Mean proportion of sites species detected per city	No. of 'day' detections	No. of 'dawn' detections	No. of 'dusk' detections	No. of 'night' detections	No. of 'darkest night' detections
Bobcat	102	5	0.16	29	1	9	45	18
Coyote	2732	9	0.63	671	98	256	1318	389
Eastern cottontail	16102	10	0.61	3984	619	1097	8317	2085
Raccoon	34931	10	0.77	2638	642	3767	21723	6161
Red fox	1570	8	0.51	441	35	152	744	198
Striped skunk	990	10	0.24	89	24	98	584	195
Virginia opossum	8357	8	0.7	407	116	1027	5087	1720
White-tailed deer	14875	10	0.56	7965	658	816	4299	1137

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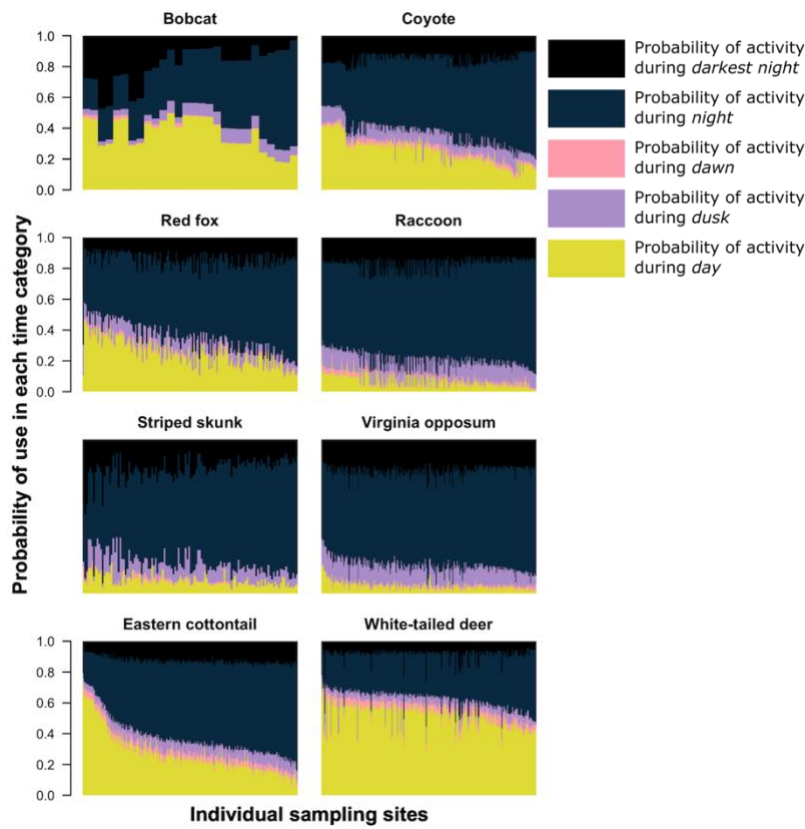
180
181 **Figure 2.** The predicted probability of activity in each time category at each sampling site (x-
182 axis) the species was detected. Each column on the x-axis is a stacked bar plot representing the
183 probability of activity in each time category at each sampling site. For each bar plot, all
184 categories sum to one. Sampling sites along the x-axis are ordered from the lowest probability of
185 nocturnal activity to the highest.

186
187 *Selection for particular time categories*
188 Of the three predator species that we analyzed (coyote, bobcat, and red fox), we found that
189 anthropogenic and natural features were associated with variation in diel activity for only coyote
190 and red fox (Fig. 3a,b,c). Coyote selected for both nocturnal and crepuscular hours in areas of
191 greater human population densities (Fig. 3b), and red fox avoided nocturnal hours in areas with
192 more available greenspace (Fig. 3c). Seasonality also had an effect on both coyote and fox diel
193 activity. Coyote selected for dawn hours (Fig. 3b) and red foxes selected for dusk hours during
194 periods of higher daily average temperatures (Fig. 3c). We found no evidence that bobcats varied
195 their diel activity across our environmental variables (Fig. 3a).

196
197 We found diel activity for all omnivore and herbivore species was affected by anthropogenic
198 features. Raccoon, eastern cottontail, and white-tailed deer avoided nighttime hours in areas of
199 greater human population density (Fig 3d,g,h), whereas Virginia opossum selected for nighttime
200 and dusk hours in areas with greater human densities (Fig. 3f). Raccoon, striped skunk, and
201 white-tailed deer all selected for nighttime hours in areas with greater impervious land cover
202 (Fig. 3d,e,h).

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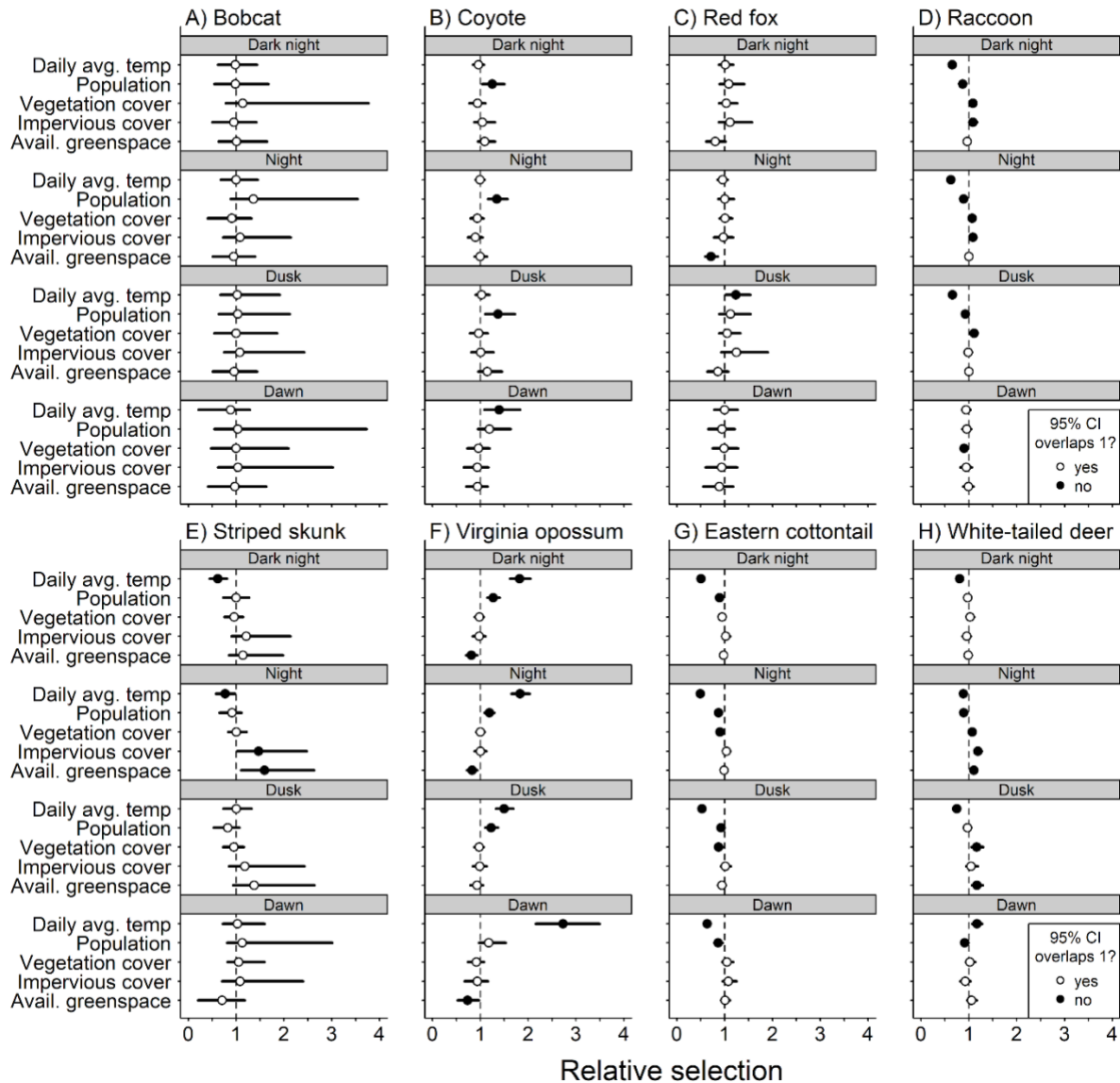
205
206 **Figure 3.** Mean (circle) and 95% credible intervals of estimated coefficients from natural and
207 anthropogenic features on temporal selection of dark night, night, dusk, and dawn relative to day.
208
209 Natural features were also associated with variation in diel activity for omnivore and herbivore
210 species. As vegetation cover increased, eastern cottontails were more likely to select daytime
211 hours (Fig. 3g), whereas raccoons and white-tailed deer were more likely to select for nighttime
212 hours and dusk (Fig. 3d,h). As available greenspace increased, striped skunk were more likely to
213 select nighttime hours (Fig. 3e), whereas Virginia opossum were less likely to select nighttime
214 and dawn hours (Fig. 3f). White-tailed deer were also more likely to select nighttime and dusk
215 hours as available greenspace increased (Fig. 3h).
216
217 We found seasonality effects on all omnivore and herbivore species. Virginia opossum were
218 more likely to avoid daytime hours as temperatures increased (Fig. 3f). Daily average

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219 temperature had a positive relationship with diurnal selection for raccoons, striped skunk, and
220 white-tailed deer (Fig. 3,d,e,h). Eastern cottontails, however, were more likely to select
221 crepuscular hours and nighttime hours as daily average temperatures increased (Fig. 3g).
222
223 *Probability of nocturnal activity*
224 Across all species, the probability of dawn and dusk activity was low (Figure 2 and 3).
225 Therefore, we report the probability of nocturnal activity for each species by combining the
226 probability of activity during night and darkest night. Coyote had a lower probability of being
227 nocturnal in areas with lower human densities, but that probability increased significantly as
228 human population increased (Fig. 4). With a one standard deviation (hereafter sd) increase from
229 the mean human population density (from 1,512 – 3,095 people/km^2), coyotes are 19% more
230 likely to use nighttime hours and 38% more likely with a two sd increase from 1,512 to 4,678
231 people/km^2 (Table 2). Red fox was the only species that had a significant change in the
232 probability of nocturnal use across the available greenspace gradient (Fig. 4). Red fox were 23%
233 less likely to use nighttime hours with a one sd increase in available greenspace from 0.41 to
234 0.57, and 41% less likely with a sd increase from 0.41 to 0.73 (Table 2). Note that predictor
235 values vary because they were collected at species-specific scales and not all species were
236 detected at the same sites.
237
238 White-tailed deer, eastern cottontail, and raccoon had a greater probability of being active at
239 night where human densities were low; this probability decreased as human population increased
240 (Fig. 4). White-tailed deer were 8% less likely to use nighttime hours with a one sd increase in
241 population density from 1,515 to 3,003 people/km^2, eastern cottontail were 9% less likely (from
242 2,226 to 4,633 people/km^2), and raccoon were 16% less likely (from 1,763 to 3,789 people/km^2;
243 Table 2). With a two sd increase in impervious cover (1,515 to 4,491 people/km^2 for white-tailed
244 deer, 2,226 to 7,040 for eastern cottontail, and 1,763 to 5,815 for raccoon), white-tailed deer
245 were 16% less likely to be nocturnal, eastern cottontail 18% less likely, and raccoon 12% less
246 likely to be nocturnal (Table 2). Conversely, white-tailed deer and raccoon showed a positive
247 relationship with increased impervious cover and nocturnality (Fig. 4). White-tailed deer were
248 13% more likely to be active at night with a one sd increase in impervious cover from 0.16 to
249 0.31 and 29% more likely with a two sd increase from 0.16 to 0.45 (Table 2). Raccoons were
250 10% more likely to be active at night with a one sd increase in impervious cover and 21% more
251 likely with an a two sd increase (Table 2).
252
253 Vegetation cover had a negative effect on the probability of nocturnal behavior of eastern
254 cottontail (Fig. 4). Cottontail were 7% less likely to be nocturnal when the proportion of
255 vegetation cover increased one sd above the mean from 0.67 to 0.92, and 14% less likely to be
256 nocturnal when vegetation cover increased two sd above the mean from 0.67 to 1 (Table 2). We
257 also found that white-tailed deer were 5% more likely to use nighttime hours when the
258 proportion of available greenspace increased one sd above the mean from 0.52 to 0.75)and 11%
259 more likely with an increase of two sd from the mean from 0.52 to 0.98 (Table 2). However,
260 Virginia opossum were 12% less likely to be nocturnal with a one sd increase in available
261 greenspace from 0.34 to 0.57 and 23% less likely with an increase of two sd from 0.34 to 0.78
262 (Table 2).
263
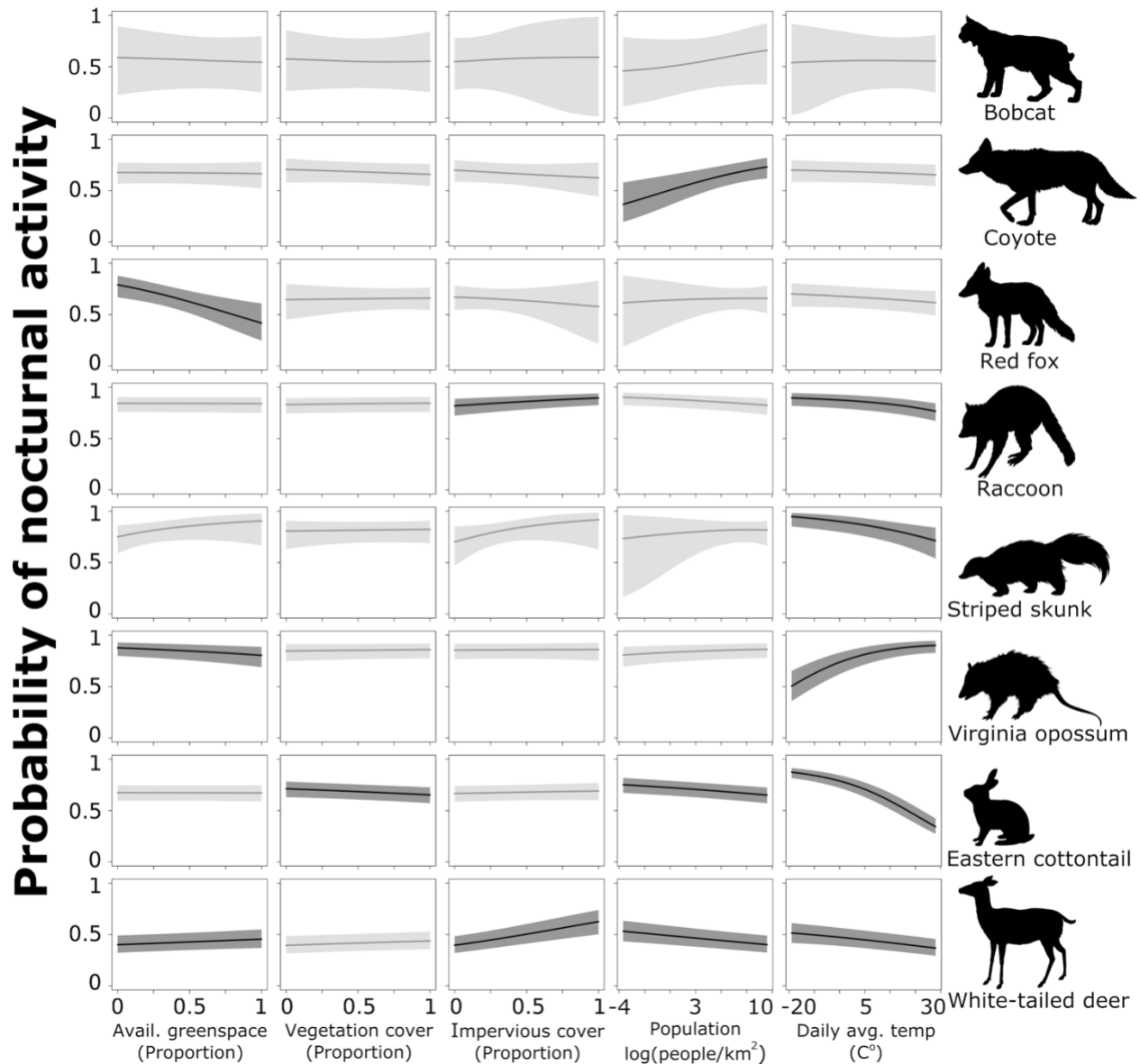
Figure 4. Probability of nocturnal activity (night and dark-night combined) across each of our natural and anthropogenic characteristics of the urban environment. Solid line indicates the median predicted line and shaded areas are 95% credible interval. Darker shading represent the relationships whose odds ratios did not overlap 1.

Table 2. Odds ratios for each predictor variable and a one and two standard deviation increase across their values. Bolded text indicates scenarios where the 95% credible intervals do not overlap 1.

	Available greenspace		Impervious cover		Vegetation Cover		Human pop. density		Daily avg. temp.	
	1-unit increase	2-unit increase	1-unit increase	2-unit increase	1-unit increase	2-unit increase	1-unit increase	2-unit increase	1-unit increase	2-unit increase
Bobcat	0.97 (0.62-1.38)	0.95 (0.40-1.95)	1.03 (0.70-1.76)	1.06 (0.46-3.16)	0.98 (0.55-1.56)	0.99 (0.36-3.00)	1.22 (0.85-2.81)	1.51 (0.72-8.28)	0.99 (0.71-1.37)	0.99 (0.49-1.89)
Coyote	0.99 (0.88-1.11)	0.97 (0.76-1.23)	0.94 (0.80-1.08)	0.88 (0.64-1.18)	0.95 (0.82-1.06)	0.90 (0.68-1.13)	**1.19 (1.04-1.36)**	**1.38 (1.05-1.81)**	0.95 (0.87-1.03)	0.89 (0.75-1.05)
Red fox	**0.77 (0.65-0.90)**	**0.59 (0.41-0.81)**	0.95 (0.77-1.15)	0.90 (0.58-1.33)	1.01 (0.90-1.13)	1.01 (0.80-1.28)	1.00 (0.87-1.17)	1.00 (0.74-1.36)	0.92 (0.83-1.02)	0.85 (0.68-1.03)
Raccoon	1.00 (0.96-1.03)	0.99 (0.92-1.07)	**1.10 (1.05-1.16)**	**1.21 (1.1-1.34)**	1.01 (0.97-1.05)	1.02 (0.94-1.10)	**0.94 (0.90-0.97)**	**0.88 (0.81-0.95)**	**0.82 (0.77-0.87)**	**0.65 (0.57-0.73)**
Striped skunk	1.26 (0.93-1.76)	1.55 (0.82-3.00)	1.26 (0.92-1.83)	1.56 (0.80-3.31)	1.02 (0.86-1.21)	1.03 (0.74-1.46)	1.01 (0.79-1.22)	0.99 (0.57-1.46)	**0.73 (0.58-0.90)**	**0.54 (0.34-0.81)**
Virginia opossum	**0.88 (0.81-0.96)**	**0.77 (0.65-0.92)**	1.01 (0.91-1.12)	1.02 (0.83-1.25)	1.02 (0.95-1.09)	1.04 (0.91-1.18)	1.04 (0.97-1.12)	1.08 (0.93-1.24)	**1.27 (1.15-1.38)**	**1.49 (1.16-1.77)**
Eastern cottontail	1.00 (0.95-1.04)	1.00 (0.91-1.08)	1.02 (0.97-1.09)	1.05 (0.94-1.18)	**0.93 (0.88-0.98)**	**0.86 (0.78-0.95)**	**0.91 (0.87-0.95)**	**0.82 (0.75-0.89)**	**0.57 (0.54-0.61)**	**0.31 (0.28-0.35)**
White-tailed deer	**1.05 (1.00-1.10)**	**1.11 (1.00-1.22)**	**1.14 (1.07-1.21)**	**1.3 (1.15-1.46)**	1.04 (0.99-1.09)	1.08 (0.98-1.18)	**0.92 (0.88-0.96)**	**0.85 (0.78-0.92)**	**0.88 (0.84-0.92)**	**0.77 (0.71-0.84)**

1

274 Finally, we found an influence of daily average temperature (season) on eastern cottontail,
275 raccoon, striped skunk, white-tailed deer, and Virginia opossum (Fig. 4). Eastern cottontail were
276 43% less likely to use nighttime hours with a one sd increase in daily average temperature from
277 8.17 C to 18.76 C, and 69% less likely with a two sd increase from 8.17 C to 29.36 C (Table 2).
278 With a one sd increase in temperature from 12.00 C to 21.49 C, raccoon were 18% less likely to
279 use nighttime hours, and 35% less likely with a two sd increase from 12.00 C to 30.99 C (Table
280 2). Striped skunk were 27% less likely to exhibit nocturnal behavior with a one sd increase in
281 daily average temperature from 15.3 C to 24.62 C, and 46% less with a two sd increase from
282 15.3 C to 33.94 C (Table 2). White-tailed deer were 12% less likely with a one sd increase from
283 12.01C to 22.65 C and 23% less likely with a two sd increase from 12.01 C to 33.30 C (Table 2).
284 Virginia opossum, however, were 27% more likely to use nighttime hours with a one sd increase
285 in daily average temperature from 13.85 C to 22.28 C, and 49% more likely with a two sd
286 increase from 13.85 C to 30.71 C (Table 2). Again, temperature ranges vary because not all
287 species were detected at the same sites and same times.

288
289 **Discussion**
290 Ecological processes act across both space and time. We have, however, only just begun to study
291 how animals use diel-time as an ecological resource to avoid risk and adapt to environmental
292 change. We quantified the diel behavior of eight mammal species across urban gradients in ten
293 U.S. cities. Our findings indicated that mammals can modulate their use of time within the 24-
294 hour diel period as a resource to persist in urban ecosystems. We found that nocturnal activity
295 had the greatest response to urbanization and seasonality, and that changes in nocturnality in
296 response to urbanization were species-specific and varied among cities. Our results also
297 illustrated the complex trade-offs that urban wildlife species must make to contend with both
298 interspecific interactions (i.e., predation and competition) and human activity. These findings
299 offer insight into how mammals might use time as a resource to adapt and persist in urban
300 ecosystems.

301
302 We found that coyote had a greater probability of nocturnal behavior in areas with greater human
303 densities. These findings are in agreement with past studies from single cities that documented
304 increases in coyote nocturnal behavior in areas of higher human activity (Gallo et al., 2019; M. I.
305 Grinder and Krausman, 2001; Riley et al., 2003; Tigas et al., 2002). Notably, vehicular collisions
306 are a major mortality factor for coyotes (M. Grinder and Krausman, 2001) and coyotes have been
307 typically persecuted by humans when they come in close contact (Dunlap, 1988; Young et al.,
308 2019). Thus, a shift to nocturnal activity when traffic volumes are usually lower and humans are
309 less active outdoors may be particularly important to survival in urban landscapes (Murray and
310 St. Clair, 2015).

311
312 Red fox became less nocturnal as the proportion of local greenspace (i.e., available habitat)
313 increased, a finding which may be explained by competition with coyote. Coyote and red fox
314 exhibit a clear dominance hierarchy, whereby the dominant coyote negatively affects the
315 subordinate red fox via competition and predation (Gosselink et al., 2003). Research has shown
316 that urban coyotes occupy larger areas of greenspace (Gehrt et al., 2009). When more greenspace
317 is available around a site, and presumably a higher probability of coyote presence, red foxes may
318 become more diurnal to temporally avoid coyotes and reduce the risk of an interaction. Yet,

1

319   when greenspace is limited, and presumably there is a lower probability of coyote presence, red
320   foxes could be more active during nighttime hours with less risk of an interaction.
321
322   In most cases, the human aspects of urban environments captured by our predictor variables had
323   opposite effects on omnivores and herbivores. While human population densities increased
324   nocturnal activity for coyote, it decreased nocturnal activity for white-tailed deer, eastern
325   cottontail, and raccoon. Prey species are known to spatially distribute themselves near human
326   activity to act as a shield from predators (Berger, 2007; Shannon et al., 2014). In these cases,
327   prey species may also utilize time as a human-mediated shield, exhibiting more activity at times
328   of high human activity (daytime) in areas of high human densities. These results may seem
329   counterintuitive given that increasing impervious cover increased the probability of nocturnal
330   behavior exhibited by deer and raccoon (Fig. 4) and selection for nighttime hours by striped
331   skunk (Fig. 3). However, a majority of impervious surfaces in the U.S. are roads and parking lots
332   – places of high vehicular traffic (Frazer, 2005). Similar to coyote, vehicular collisions are a
333   major source of mortality for these species (Glista et al., 2009). Therefore, a shift to nocturnal
334   activity in areas with high impervious cover may be particularly important to their survival in
335   cities and a sign of fine-scale modulation of temporal selection based on local environments.
336
337   Similarly, raccoon and white-tailed deer selected more for nighttime hours (Fig. 3) in locations
338   with high levels of vegetation cover. More vegetation equates to more protective cover.
339   Therefore, we suggest that raccoons and white-tailed deer can use the same temporal habitat as
340   their predators (i.e., coyote) – but with less risk – when there is more physical cover. On the
341   other hand, eastern cottontail were more diurnal with increased vegetation (Fig. 3 and 4),
342   suggesting that more vegetation cover provides shelter from other perceived threats (i.e.,
343   humans; 22) and may allow eastern cottontail to select periods of high human activity (i.e. day).
344   Interactions between various urban characteristics, which we did not examine in this study,
345   should be further explored to fully understand how these characteristics jointly influence the
346   temporal patterns of urban wildlife species.
347
348   Our results highlight the complexity of trade-offs for urban wildlife. In most cases, we found
349   diverging activity patterns between coyote (a common urban apex predator) and subordinate or
350   prey species in response to physical characteristics of urban environments. To persist in urban
351   environments, it appears that urban species may have to modulate behaviors to contend with both
352   anthropogenic risks and risk from predation or competition. Our results add to a growing body of
353   literature that indicate species interactions in human-dominated landscapes may be better
354   understood by explicitly considering the role humans play in those interactions (Berger, 2007;
355   Blecha et al., 2018; Gallo et al., 2019; Magle et al., 2014).
356
357   We also found evidence that local climate, specifically temperature, regulated the diel behavior
358   of many species. For example, white-tailed deer, eastern cottontail, and striped skunk became
359   more diurnal as temperatures increased, presumably foraging more during the day in warmer
360   seasons when more vegetation biomass is available. Virginia opossum showed a decrease in
361   nocturnal behavior at lower temperatures. Given their poor thermoregulation abilities, poorly
362   insulated fur, and cold-sensitive hands, ears, and tails (Kanda, 2005), it seems likely that Virginia
363   opossum are morphologically constrained and thus unable to alter their diel activity patterns at
364   colder temperatures. These results call attention to the importance of considering the impacts of

2

365 morphology, physiology, and life history on a species' capacity to adapt to environmental
366 change. Given the interacting effects of climate change and urbanization (Stone, 2012), future
367 research should explore how life history traits mediate temporal distributions of species activity
368 – particularly as cities are rapidly warming (Oleson et al., 2015).
369
370 We did not find changes in diel activity for some species in response to our predictor variables.
371 These results could be due to a lack of data on a particular species (i.e., bobcat) or because we
372 did not sample across a large enough urban-rural gradient. Remote regions were not sampled in
373 our study design, and some species may change their behavior at a lower level of urban intensity
374 that we did not sample. Combining datasets from more rural and remote areas (e.g., Snapshot
375 Serengeti (Swanson et al., 2015), Snapshot USA (Cove et al., 2021)) could allow us to identify
376 the level of human development that elicits changes in diel activity for potentially sensitive
377 species. Finally, our analysis was limited to the physical characteristics of cities. Additional
378 characteristics like chronic noise, light pollution, resource supplementation, and species
379 interactions influence animal behaviors and should be explored in future research .
380
381 Resource selection functions have been a popular and valuable tool to measure the relationship
382 between available resources and animal populations, and have been used intensely in wildlife
383 management and conservation (Strickland and McDonald, 2006). However, very little work has
384 been done to quantify temporal habitat selection specifically (Cox et al., 2021; Gaston, 2019).
385 Here, we built upon Farris et al. (Farris et al., 2015) and developed an analytical approach to
386 quantify temporal resource selection across environmental gradients. While we have developed
387 an analytical tool to measure temporal selection, a theoretical context for temporal habitat
388 selection is needed and a further understanding of disproportional selection relative to the
389 number of hours available is a promising avenue for future animal biology research.
390
391 Temporal partitioning may facilitate human-wildlife coexistence and effectively increase
392 available habitats for species in cities. Temporal partitioning may also limit contact between
393 people and animals, potentially reducing negative encounters like disease transmission and
394 attacks on people (Gaynor et al., 2018). From a management perspective, ignoring diel behavior
395 can result in biased estimates of species abundance and patterns of habitat use and lead to
396 misinformed conservation measures (Gaston, 2019). Additionally, recognizing plasticity in
397 species behavior can lead to better predictions of vulnerability to anthropogenic disturbances
398 (Gaynor et al., 2018). Therefore, we recommend that diel activity and temporal partitioning be
399 considered in conservation and management approaches.
400
401 We have shown that mammals have significant variation in the use and selection of time
402 throughout the diel period. Additionally, our approach allowed us – for the first time – to
403 quantify changes in diel activity across gradients of environmental change and across multiple
404 urban areas, revealing that changes in diel patterns are influenced by natural and human
405 landscape characteristics. Our results highlight the need to understand how a larger proportion of
406 the animal community responds to urbanization, and provide evidence of behavioral plasticity
407 that allows some species to adapt to and persist in human-dominated systems.
408
409 **Materials and Methods**
410

3

411 *Study Design*
412 The number of sampling sites per city ranged from 24-113 ($\bar{x}$ = 45.30, sd = 28.65). In each city,
413 sampling sites were placed along a gradient of urbanization (high to low population density and
414 impervious cover). At each sampling site (n = 453) we placed one Bushnell motion-triggered
415 infrared Trophy Cam (Bushnell Corp., Overland Park, KS, USA). Sampling sites were located in
416 greenspaces, such as city parks, cemeteries, natural areas, utility easements, and golf courses. To
417 increase the detection probability of each species we placed one synthetic fatty acid scent lure in
418 the camera line of sight, and lures were replaced on two-week intervals if missing to remain
419 consistent throughout the study. However, Fidino et al. (2020) later found that this type of lure
420 has little to no effect on the detectability of most urban mammals. We used observation data
421 collected between January 2017 and December 2018. However, not all cities were sampled
422 continuously throughout the study period (Table S1).
423
424 *Data processing*
425 For each species, we defined a single detection event as all photos taken within a 15-minute
426 period at each camera station (Farris et al., 2015; Ridout and Linkie, 2009). We categorized each
427 detection event as either 'dawn', 'dusk', 'day', 'night', and 'darkest night' using the *suncalc*
428 package (Thieurmel and Elmarhraoui, 2019) in R ver 4.2.0 (R Core Team, 2019). The suncalc
429 package defines and calculates 'dawn' as starting when morning astronomical twilight begins
430 and ending when the bottom edge of the sun touches the horizon. 'Dusk' was defined as the
431 beginning of evening twilight to the point when it became dark enough for astronomical
432 observations. 'Day' was defined as the period between dawn and dusk. We considered the
433 nighttime as two distinct time periods (night and darkest night), because some species may be
434 nocturnal but use the darkest hours of the night to reduce the risk of human interactions (Gehrt et
435 al., 2009). We defined 'night' as the periods between the end of dusk and one hour before the
436 darkest moment of the night (when the sun is at the lowest point), and from one hour after the
437 darkest moment to dawn. The 'darkest hours' of the night were categorized as one hour before
438 and after the darkest moment in the night. We accounted for the date, geographical location, and
439 daylight savings time of each detection events. Therefore, the amount of time available in each
440 category could vary geographically and seasonally.
441
442 *Predictor Variables*
443 To assess how characteristics of urban environments influenced diel activity of urban wildlife
444 mammals, we calculated site-level predictor variables within a fixed-radius buffer around each
445 sampling site. Fixed-radius buffers varied in size among species and were based on the typical
446 home range of each species: 500 m fixed-radius buffer for eastern cottontail (Hunt et al., 2014),
447 Virginia opossum (Fidino et al., 2016; Wright et al., 2012), and white-tailed deer (Etter et al.,
448 2002); 1 km fixed-radius buffer for striped skunk (Weissinger et al., 2009) and raccoon (Rosatte,
449 2000), and 1.5 km fixed radius buffer for coyote (Gehrt et al., 2009; Riley et al., 2003), red fox
450 (Mueller et al., 2018), and bobcat (Riley et al., 2003). In our analysis, we included variables that
451 described two contrasting characteristics of urban ecosystems, the natural and the human-built
452 environment (Table S4). We also included average temperature to account for possible seasonal
453 changes in diel activity.
454
455 *Urban features* – To characterize urbanization around each sampling site, we calculated human
456 population density (individuals/km^2) and mean impervious cover (%). Population density was

4

457 extracted from Block Level Housing Density data (Radeloff et al., 2018) created from 2010 U.S.
458 Census data (U.S. Census Bureau, 2010). Mean impervious cover was calculated from the 2011
459 National Land Cover Database (NLCD) 30-m resolution Percent Developed Imperviousness data
460 (Homer et al., 2015).
461
462 *Natural features* – To characterize natural features, we calculated the proportion of vegetation
463 cover and the proportion of available greenspace (i.e., potential habitat) around each site. To
464 calculate the proportion of vegetation cover around each sampling site, we first calculated the
465 Normalized Difference Vegetation Index (NDVI) using U.S. Geological Survey 30-m resolution
466 LandSat 8 data that 1) covered the entire study area of each city, 2) was taken during a summer
467 month that coincided with the respective city's sampling period, and 3) contained less than 15%
468 cloud cover. LandSat 8 imagery was downloaded with R using the *getSpatialData* package
469 (Schwalb-Willmann, 2019). We then calculated vegetation cover as the proportion of cells within
470 each fixed-radius buffer that had an NDVI value representing substantial vegetation cover (> 0.2;
471 https://climatedataguide.ucar.edu/climate-data/ndvi-normalized-difference-vegetation-index-
472 noaa-avhrr). To calculate available greenspace, we extracted the proportion of 2011 NLCD Land
473 Cove 30-m resolution raster cells within each fixed-radius buffer that were classified as forest,
474 shrubland, herbaceous, wetland, and developed open space (which included urban green spaces).
475
476 *Seasonality* – Because weather that defines each calendar season varies across our sampled
477 longitudinal gradient, we used daily average temperature (i.e., mean temperature on the day of a
478 given detection event) as a continuous covariate to describe seasonality. For each day and
479 location of a detection event, we recorded the daily average temperature from the National
480 Climatic Data Center using the R package *rnoaa* (Chamberlain, 2020). We used data from the
481 nearest weather station to each city that recorded daily weather during our study period (Table
482 S5).
483
484 *Quantifying the influence of urban characteristics on diel patterns*
485 By splitting diel time into *k* in 1,…,K categories, we estimated the probability a detection event
486 occurs in each category for each species. To do so, we let y_i be the time category of the ith in
487 1,…,*I* detection events, and assume it is a Categorical random variable, where $\boldsymbol{\phi}$ is a probability
488 vector of the K categories $\boldsymbol{\phi} = [\phi_1 \phi_2 \phi_3 \phi_4 \phi_5], \phi_1 = 1 - \phi_2 - \phi_3 - \phi_4 - \phi_5$, and $\mathbf{1} \cdot \boldsymbol{\phi} = 1$
489 such that:
490

$$y_i \sim \text{Categorical}(\boldsymbol{\phi}). \tag{1}$$

491
492 To understand mechanistic changes in species-specific diel activity patterns and assess the
493 influence that each predictor variable had on the temporal activity of each species, we let $\boldsymbol{\phi_i}$ be a
494 function of covariates with the softmax function,
495

$$\phi_{i,k} = \frac{exp(\lambda_{i,k})}{\sum_{k=1}^{K} exp(\lambda_{i,k})} \tag{2}$$

496
497 where $\lambda_{i,k}$ is the log-linear predictor for detection event *i* and category *k*. We set our reference
498 category as 'day' (i.e., $k = 1$). In our model the log-linear predictor of each outcome is then

5

499

$$\lambda_{i,k} = \begin{cases} log(\alpha_{i,k}) & k = 1 \\ x_j^T \boldsymbol{\beta}_{j,k} + \beta_{c[i],k} + log(\alpha_{i,k}) & k > 1. \end{cases} \qquad (3)$$

500 In Eq. 3, $\boldsymbol{\beta}_{j,k}$ coefficients correspond to the effect of greenspace availability, impervious cover,
501 vegetation cover, human population density, and daily average temperature for k > 1. As
502 detection events within each city may not be wholly independent, we included a random
503 intercept for city, $\beta_{c[i],k}$, where $\mathbf{c}$ is a vector of length I that denotes which city detection event i
504 occurred (Gelman and Hill, 2006). Finally, to account for the different amount of time available
505 to animals among the K categories, we also included a log offset term, $log(\alpha_{k,i})$, where $\alpha_{k,i}$ is the
506 number of hours available in category k at the time of detection event i. This form of multinomial
507 regression is equivalent to a logistic regression model with a spatial categorical covariate with K
508 levels, where the offset accounts for varying availability. As such, our model approximates the
509 weighted distribution used in resource selection functions assuming an exponential link (Hooten
510 et al., 2017). Exponentiated coefficient estimates greater than one indicates 'selection' and less
511 than one indicates 'avoidance', relative to the day reference category.
512
513 Because we considered 'day' (k = 1) as our reference outcome, we set $\beta_{c[i],1} = 0$ and $\beta_{j,1} = 0$ (Eq.
514 3). The remaining $\boldsymbol{\beta}_{j,k}$ parameters were given Laplace(0,π) priors as a form of categorical
515 LASSO regularization (Tutz et al., 2015). We took a fully Bayesian approach to variable
516 selection by estimating the hyperparameter π (van Erp et al., 2019), which was given a
517 uniform(0.001,10) prior distribution. $\beta_{c[i],k}$ was given a Normal(μ_k,τ_k) prior for each city where μ_k
518 ~ Normal(0,10) and τ_k ~ Gamma(1,1).
519
520 Models were fit using an Markov Chain Monte Carlo (MCMC) algorithm implemented in JAGS
521 ver 4.2.0 (Plummer, 2003) using the *runjags* package (Denwood, 2016) in R. Fourteen parallel
522 chains were each run from random starting values. The first 20,000 iterations from each chain
523 were discarded and every 7th iteration was kept to reduce autocorrelation among the samples. A
524 total of 75,000 iterations were obtained for each model. Model convergence was assessed by
525 checking that the Gelman-Rubin diagnostic statistic for each parameter was <1.1 (Gelman and
526 Rubin, 1992) and by visually inspecting the trace plots of MCMC sample
527

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536

537 **Competing Interest Statement:** No Competing Interests
538

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