

**Fear of the dark? A mesopredator mitigates large carnivore risk through nocturnality, but humans moderate the interaction.**

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23 Fear of the dark? A mesopredator mitigates large carnivore risk through nocturnality, but humans
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37

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46 **Abstract**

47 While constrained by endogenous rhythms, morphology and ecology, animals may still exhibit
48 flexible activity patterns in response to risk. Temporal avoidance of interspecific aggression can
49 enable access to resources without spatial exclusion. Apex predators, including humans, can affect
50 mesopredator activity patterns. Human context might also modify temporal interactions between
51 predators. We explored activity patterns, nocturnality and the effects of human activity upon a guild
52 of carnivores (gray wolf, *Canis lupus*, Eurasian lynx, *Lynx lynx*, red fox, *Vulpes vulpes*) using travel
53 routes in Plitvice Lakes National Park, Croatia. Humans were diurnal, foxes nocturnal and large
54 carnivores active during the night, immediately after sunrise and before sunset. Carnivore activity
55 patterns overlapped greatly and to a similar extent for all pairings. Activity curves followed
56 expectations based on interspecific killing, with activity peaks coinciding where body size differences
57 were small (wolf and lynx) but not when they were intermediate (foxes to large carnivores). Carnivore
58 activity, particularly fox, overlapped much less with that of diurnal humans. Foxes responded to
59 higher large carnivore activity by being more nocturnal. Low light levels likely provide safer
60 conditions by reducing the visual detectability of mesopredators. The nocturnal effect of large
61 carnivores was however moderated and reduced by human activity. This could perhaps be due to
62 temporal shielding or interference with risk cues. Subtle temporal avoidance and nocturnality may
63 enable mesopredators to cope with interspecific aggression at shared spatial resources. Higher human
64 activity moderated the effects of top-down temporal suppression which could consequently affect the
65 trophic interactions of mesopredators.

66 **Significance statement**

67 Temporal partitioning can provide an important mechanism for spatial resource access and species
68 coexistence. Our findings show that carnivores partition the use of shared travel routes in time, using
69 the cover of darkness to travel safely where their suppressors (large carnivores) are more active. We
70 observed fox nocturnality to be flexible however; with responses depending on the activity levels but
71 also the composition of apex predators. High human activity modified the top-down temporal

72 suppression of mesopredators by large carnivores. The use of time by predators can have demographic
73 and trophic consequences. Prey accessibility and susceptibility can be temporally variable. As such,
74 the ecosystem services and the ecological roles of predators may be affected by human time use as
75 well as that of intraguild competitors. Temporal interactions should not be overlooked when
76 evaluating human use and conservation priorities in protected areas.

77 **Keywords**

78 Coexistence; Mesopredator suppression; Mesopredator release; Diel activity; Anthropogenic
79 disturbance; Red fox

80

81 **Introduction**

82 Top-down regulation and the suppression of mesopredators by large carnivores can be elicited via
83 direct killing, harassment and the risk associated with such encounters (Crooks and Soulé 1999;
84 Palomares and Caro 1999; Ritchie and Johnson 2009). Ecological differentiation along a niche axis is
85 deemed necessary for coexistence between competitors (Hardin 1960). Carnivores may spatially
86 avoid competitors or differentiate dietary niche (Azevedo et al. 2006; Bassi et al. 2012; Newsome and
87 Ripple 2014). Aggressive encounters between species are however not solely dependent upon niche
88 overlap but can also be affected by body size differences, resource availability, physical
89 characteristics, behavioural strategies and similarity in stimuli (appearance, behaviour, scent etc.) that
90 trigger agonistic behaviour due to common ancestry (Donadio and Buskirk 2006; Grether et al. 2013;
91 Haswell et al. 2018). Regardless of diet, intraguild aggression can still present risk for mesopredators
92 and some spatial resources such as linear travel routes may exacerbate this risk because of their
93 frequent use by apex predators (Shannon et al. 2014; Haswell et al. 2018). Accordingly, an animal's
94 circadian activity pattern may provide an important dimension for minimising the likelihood of
95 aggressive encounters.

96 Circadian clocks help maintain optimal activity and likely provide restrictions to activity patterns
97 because divergence from endogenous rhythms can carry ecological and physiological costs (Kronfeld-
98 Schor and Dayan 2003; Relógio et al. 2011). Intrinsic characteristics, such as eye morphology and
99 visual acuity, may also restrict temporal niche (Veilleux and Kirk 2014; Banks et al. 2015). Animal
100 behaviour and decision making is however contextual (Haswell et al. 2017; Owen et al. 2017). Most
101 mammals (excepting anthropoid primates) retain a scotopic (low-light) eye design consistent with
102 nocturnal origins; yet mammals exhibit diurnal, cathemeral and nocturnal activity patterns (Heesy and
103 Hall 2010; Hall et al. 2012; Borges et al. 2018). Carnivore activity patterns may be particularly
104 affected by prey accessibility or susceptibility (Cozzi et al. 2012; Heurich et al. 2014). Time use can
105 be influenced by abiotic conditions, resource acquisition and foraging success, but may also be
106 affected by competition and risk (Reimchen 1998; Hayward and Slotow 2009; Theuerkauf 2009).

107 Temporal partitioning of activity may be a mechanism allowing mesopredators to avoid costly
108 interspecific interactions (Monterroso et al. 2014; Diaz-Ruiz et al. 2016). Complete spatial avoidance
109 of suitable habitat prevents access to resources, whereas temporal avoidance of competitors or
110 aggressors can enable coexistence (Holt and Polis 1997; Swanson et al. 2016). Recent methodological
111 advancements now permit the more detailed study of fine-scale activity patterns and temporal
112 interactions between species (Ridout and Linkie 2009; Frey et al. 2017; Gaynor et al. 2018).

113 Humans can act as super predators, exerting top-down pressure on carnivores (Darimont et al. 2015;
114 Smith et al. 2017). Human disturbance can make predators more nocturnal (Gaynor et al. 2018). The
115 presence of humans however, also makes a predator guild more complex. Human modification of risk
116 landscapes can consequently affect interactions between carnivores (Haswell et al. 2017). An
117 important question is how, or if, the human context modifies temporal interactions within predator
118 guilds. Humans may affect the activity patterns of mesopredators directly, but also in a cascading
119 manor, via temporal effects on large carnivores or interference with the mechanisms by which they
120 affect mesopredator behaviour.

121 The forest roads and trails of Plitvice Lakes National Park, Croatia, provided an ideal opportunity to
122 study temporal interactions. The park is home to large carnivores and mesopredators but is also used
123 by humans in non-consumptive capacities. We hypothesised that the activity patterns of a
124 mesopredator (red fox, *Vulpes vulpes*) would not coincide with that of sympatric apex carnivores
125 (wolves, *Canis lupus*, and lynx, *Lynx lynx*). We also hypothesised that foxes might show spatial
126 flexibility in their propensity for nocturnal activity depending upon the level of activity exhibited by
127 large carnivores or humans at a given locality. We hypothesised that human trail use would present
128 temporal restrictions to all carnivores and would interfere with intraguild interactions between large
129 carnivores and foxes.

130 **Methods**

131 *Study Site*

132 Plitvice Lakes National Park (Plitvice) is situated between 44° 44' 34" and 44° 57' 48" N and 15° 27'
133 32" and 15° 42' 23" E, in the Dinaric Mountains, Croatia (Šikić 2007). The mountainous karst
134 (limestone and dolomite) landscape ranges from 367 to 1279 m above sea level and, excepting the
135 iconic lakes and waterfalls, is characterised by scarce surface water (~1%), underground drainage
136 systems, sink holes and caves (Šikić 2007; Romanić et al. 2016). Annual precipitation is 1,550 mm
137 with temperatures fluctuating between winter lows of -3°C and summer highs of 36°C (Šikić 2007).
138 One camera station contained planted stands of Scots and black pine (*Pinus sylvestris* and *Pinus*
139 *nigra*), but elsewhere forest cover was predominantly Dinaric beech and fir trees (*Fagus sylvatica* and
140 *Abies alba*). Tourism and recreation are permissible within the 297 km² park where approximately
141 1770 people live within 19 settlements (Firšt et al. 2005; Romanić et al. 2016). The number of people
142 visiting Plitvice has grown from 928,000 visitors in 2007 to over 1.72 million in 2017 (Smith 2018).

143 *Data collection*

144 We utilised records from 20 passive infrared motion sensor cameras placed on unpaved forest roads
145 and trails in Plitvice between October 2015 and October 2016. Behavioural data collection was blind
146 as activity record times were labelled by camera traps. Similarly to Santulli et al. (2014), we utilised

147 data that was initially collected for other purposes. Camera station placement was *ad hoc*, with
148 locations targeted according to large carnivore field signs (scats, tracks and markings). The national
149 parks desire to capture images of large carnivores may mean areas of lower large carnivore use are
150 underrepresented in the dataset but we do not believe this to be problematic for the questions being
151 posed. Camera locations and periods included in the analysis were selected *a priori* to data
152 examination. Fox density in Croatia is estimated at 0.7 per km² with territory size of 1.43 km² (Slavica
153 et al. 2010; Galov et al. 2014). Like Robinson et al. (2014), we assumed a circular territory size and
154 utilised the radius (675 m) as the minimum acceptable distance between camera stations.
155 Occasionally, an extra camera was deployed to capture both sides of a lynx spot pattern at promising
156 stations. When two cameras were present at the same time (N = 3), we only used data from a single
157 camera selected at random. Camera stations received almost year round coverage (range; 320-366
158 days). Considering the year as three 122 day periods based on fox reproductive behaviour (dispersal,
159 October – January 30th, denning, January 31st – May and weaning, June – September; see Haswell
160 (2019)), each station received at least 89 observation days during any seasonal period.
161 Cameras were placed between 1 and 1.5m high on trees or rocks adjacent to unbaited trails. A mixture
162 of Acorn 5210A covert infrared, Uovision UV565HD, Uovision UM565, Reconyx HC500 Hyperfire
163 and Bolyguard MG882K-8M cameras were utilised as logistics permitted. Cameras were checked
164 monthly in summer but only at the start and end of winter due to accessibility restrictions. Data were
165 collated in Camera Base 1.7 (www.atrium-biodiversity.org/tools/camerabase).

166 *Data analysis*

167 Like Rowcliffe et al. (2014), we defined activity records as the times of day that cameras were
168 triggered by a given species. Only independent triggers (>30 minutes apart) were utilised (Ridout and
169 Linkie 2009; Linkie and Ridout 2011; Torretta et al. 2016). Individual animals could not be
170 recognised, leading to some pseudoreplication.

171 Interspecific time use

172 In longer term studies of behavioural timings, it is important to ensure that actual timings, as given by
173 the position of the sun, are used instead of clock time to prevent the generation of false activity
174 patterns (Nouvellet et al. 2012). Clock time does not have any biological or environmental meaning,
175 whereas the sun's position in the sky does (Nouvellet et al. 2012). We adjusted the clock time of
176 activity records to sun time using the “overlap” package in R version 3.5.1 (Meredith and Ridout
177 2018b). Activity patterns were then estimated as probability density functions using kernel density
178 estimation (Ridout and Linkie 2009; Linkie and Ridout 2011; Meredith and Ridout 2018a).

179 We explored overlap in species activity patterns non-parametrically. Under the presumption that
180 animals were equally likely to be photographed at any time they were active on trails, we fitted kernel
181 density curves and estimated the coefficient of overlapping, Δ , which is the area lying under both
182 curves (Ridout and Linkie 2009; Linkie and Ridout 2011; Meredith and Ridout 2018a). The
183 coefficient of overlapping ranges from 0, indicating no overlap, to 1, indicating complete overlap
184 (Ridout and Linkie 2009; Linkie and Ridout 2011). Sample sizes for each species were >75 so, as
185 recommended when estimating overlap, we used the non-parametric estimator $\hat{\Delta}_4$ (Meredith and
186 Ridout 2018a). We note that human data reflects pooled observations of motorised and non-motorised
187 activity.

188 Within the “overlap” package in R, we generated 10,000 smoothed bootstrap samples to estimate a
189 mean coefficient of overlap and 95% confidence intervals for each species pairing (Meredith and
190 Ridout 2018a, b). The 2.5% and 97.5% percentiles of the bootstrap samples were adjusted to account
191 for bootstrap bias (approach “basic0”) (Meredith and Ridout 2018a). We performed interval
192 corrections on a logistic scale and back-transformed them to correct for any confidence interval
193 estimates falling outside the possible range of 0–1 (Meredith and Ridout 2018a).

194 Nocturnality

195 We created a dichotomous dependent variable, labelling daytime activity records (between sunrise
196 and sunset) as zero and night time records (before sunrise and after sunset) as one, using sunrise and
197 sunset times from the United States Naval Observatory (<http://aa.usno.navy.mil/data/index.php>). We

198 calculated photo capture rate indices (PCRI) for humans at each station, with PCRI being the number
199 of independent (>30 minutes apart) photo captures per 100 days (Rayan and Linkie 2016).
200 Additionally, we calculated the PCRI for both large carnivores combined. Using generalized linear
201 models (binomial distribution and logit link function) we examined if human PCRI affected whether
202 each carnivore's activity records occurred at night. The events variable was the number of nocturnal
203 records and the trials variable was the total number of records for each camera station. In the fox
204 model we also examined the effect of large carnivore PCRI and the interaction between large
205 carnivore PCRI and human PCRI. Null (intercept only) mixed models suggested no significant
206 random effect of camera station for any species so we did not develop multi-level models. Robust
207 standard error estimation was however used to provide more conservative tests of model parameter
208 significance; taking potential clustering effects into consideration.

209

210 Overlap between species activity patterns was conducted in R version 3.5.1 (R Core Development
211 Team 2008). Generalized linear models examining nocturnality were conducted in IBM SPSS
212 statistics 25 (IBM Corp 2017).

213 **Results**

214 During 6,833 camera trapping days, 1,197 activity records were obtained for fox, 80 for wolves, 156
215 for lynx and 3,715 for humans. Foxes had the highest proportion of records occurring at night (88%),
216 with wolves and lynx each having 71%. Humans were highly diurnal with only 4% of their records
217 occurring at night. Foxes and humans were observed at all camera stations, wolves at 15 (75% of
218 stations) and lynx at 16 (80%) stations.

219 *Interspecific time use*

220 Confidence intervals suggested all pairs of carnivores showed similar activity pattern overlap. Mean
221 overlap of foxes with wolves was $\hat{\Delta} 0.73$ (95% CI, 0.65 to 0.82) and with lynx was $\hat{\Delta} 0.75$ (0.65 to
222 0.79). Wolf and lynx overlap was $\hat{\Delta} 0.79$ (0.72 to 0.89). Carnivore activity overlap with humans was

223 lower than with other carnivores. Fox overlap with human activity curves was the lowest, $\hat{\Delta} 0.17$
224 (0.14 to 0.17). Wolves and lynx had similar overlap with human activity curves. Wolf and human
225 overlap was $\hat{\Delta} 0.28$ (0.19 to 0.34). Lynx overlap with humans was also $\hat{\Delta} 0.28$ (0.22 to 0.32).
226 Foxes were very inactive during daylight hours with activity peaking after sunset and declining across
227 the night, reaching low levels shortly after sunrise (Fig. 2a, b, d). The peak of fox activity did not
228 coincide with activity peaks of larger species, however all carnivores were highly active during the
229 night (Fig. 2a, b). Lynx activity peaked in the later part of the night between midnight and sunrise but
230 this period of higher activity was briefer than in wolves, with lynx utilising the early parts of the day
231 at levels intermediate between foxes (Fig. 2b) and wolves (Fig. 2c). Lynx had a second period of
232 higher activity around sunset - using the late afternoon more than foxes (Fig. 2b) and wolves (Fig. 2c).
233 Wolves were more active than foxes (Fig. 2a) and lynx (Fig. 2c) during the early hours of the day,
234 with activity lowest after noon, rising after sunset and peaking similar to lynx in the later part of the
235 night (Fig. 2c). Humans dominated the daylight hours with activity peaking just before noon, which
236 contrasted strongly to nocturnal carnivores (Fig. 2d, e, f).

237 *Nocturnality*

238 Generalized linear modelling revealed that large carnivore trail use (PCRI) had a significant effect on
239 whether fox activity records occurred at night (Wald $\chi^2 = 9.68$, $df = 1$, $P = 0.002$). Increases in large
240 carnivore PCRI increased the log odds that fox activity would be nocturnal ($\beta = 0.142$, 95% CI, 0.053
241 to 0.232). The effect of large carnivores was however moderated by this covariates' interaction with
242 human trail use (Wald $\chi^2 = 5.03$, $df = 1$, $P = 0.025$). Unit increases in human PCRI reduced the
243 nocturnal effect large carnivores had upon foxes ($\beta = -0.002$, -0.003 to -0.0002). Human PCRI had no
244 direct effect on fox nocturnality (Wald $\chi^2 = 2.19$, $df = 1$, $P = 0.139$). The fox model had utility in
245 predicting whether fox activity records occurred at night, providing a significant improvement in fit
246 over the null model (likelihood-ratio $\chi^2 = 15.09$, $df = 3$, $P = 0.002$). Human PCRI did not have a
247 significant effect on whether lynx (Wald $\chi^2 = 1.80$, $df = 1$, $P = 0.179$) or wolf records were nocturnal
248 (Wald $\chi^2 = 2.51$, $df = 1$, $P = 0.113$).

249 **Discussion**

250 We observed temporal partitioning among carnivores and humans on trails within Plitvice. Fox
251 nocturnality was also contextual - dependant on the intensity of human and large carnivore activity.
252 Our findings support the notion of a level of flexibility in activity patterns, with animals avoiding
253 activity during high-risk periods (Lima and Bednekoff 1999; Kronfeld-Schor and Dayan 2003).
254 Higher large carnivore activity made foxes more nocturnal. The extent to which mesopredators utilise
255 nocturnal safety may however depend on the composition and activity level of local predator
256 communities. Humans reduced the nocturnal effect large carnivores had on foxes in Plitvice;
257 supporting the notion that humans can dampen the top-down ecological effects of large carnivores
258 (Hebblewhite et al. 2005).

259 Subordinate mesopredators may need to move their activity around the foraging bouts of larger
260 carnivores (Hayward and Slotow 2009). In response to their nocturnal intraguild competitors,
261 American mink, *Neovison vison*, have been observed to become diurnal; we did not however observe
262 this in foxes (Harrington et al. 2009). In Plitvice, fox activity was predominantly nocturnal and
263 overlapped highly, although not completely, with that of large carnivores. Activity curves show large
264 carnivores made more use of parts of the day when humans were less active, seemingly restricting
265 daylight activity by foxes. Activity peaks coincided in time where body size differences were small
266 (wolf and lynx) but not when they were intermediate (foxes to large carnivores). This follows the
267 patterns of interspecific killing associated with body size differences (Donadio and Buskirk 2006), but
268 not interspecific competition avoidance, which would be greater between similarly sized species
269 (Schoener 1974a, b). Confidence intervals however suggested no difference in activity overlap
270 between any carnivore pairing. Predators that evolved under similar ecological conditions and share
271 ecological traits may have similar activity patterns and co-occur often, limiting the potential for
272 substantial temporal avoidance (Kronfeld-Schor and Dayan 2003; Davis et al. 2018).

273 Foxes were more nocturnal where large carnivore activity was higher. Low light levels and visual
274 obstacles can increase spatial tolerance and reduce agonistic interactions between intraspecific

275 competitors (Reimchen 1998). Presumably the same might be true of interspecific competitors.
276 Animals may be less conspicuous in lower light levels; predation and harassment risk might therefore
277 be lower at night, providing a time period where habitat and resources can be accessed more safely
278 (Beauchamp 2007). Foxes avoided the risk of daytime trail encounters where large carnivores were
279 more active but made greater use of a broader temporal niche in less risky contexts. Mesopredators
280 can expand their niche axes in the absence of top-down pressure (Gese and Grothe 1995; Prugh et al.
281 2009; Kamler et al. 2013). Monterroso et al. (2013) observed foxes to be the dominant daytime user in
282 a Mediterranean national park devoid of larger carnivores (Cabañeros, Spain). Our findings suggest
283 that foxes can readily adjust their activity patterns as required in response to localised variation in top-
284 down pressure. Risk perception may play a pivotal role in informing such flexible behaviour (Leo et
285 al. 2015; Haswell et al. 2018; Kohl et al. 2018).

286 Behavioural responses to risk can result in significant demographic consequences (Preisser et al.
287 2005; Creel and Christianson 2008). Demographic consequences may however be negligible when
288 avoidance is on a very fine, moment-to-moment scale (Swanson et al. 2014, 2016). Avoiding
289 interspecific aggression along the temporal niche axis could however carry costs to individual body
290 condition (Harrington et al. 2009). Temporal obstruction by larger carnivores could also inhibit
291 mesopredator foraging, having indirect trophic consequences by offering respite to certain prey
292 species. For example, when diurnal prey (Orthoptera) provide an important dietary component for red
293 foxes, this can drive increased diurnal activity (Cavallini and Lovari 1991). Small mammal prey may
294 also be capable of altering their own activity patterns, becoming more diurnal to avoid encounters
295 with red foxes (Fenn and Macdonald 1995). Foxes, like other mesopredators, fulfil key trophic
296 functions (Smedshaug et al. 1999; Roemer et al. 2009). Whether temporal avoidance of large
297 carnivores occurs broadly across the landscape or at other microhabitat sites, resulting in demographic
298 and trophic consequences, requires further investigation. The scope of our study was also limited to
299 one year; temporal variation in factors such as mesopredator food availability might too result in
300 alternative dynamics and the consistency of interactions across years requires attention.

301 Humans can provide additional predation risk and function as super predators (Walther 1969; Smith et
302 al. 2017). The general activity patterns we observed on trails in Plitvice suggest humans functioned as
303 dominant super predators with regard to the temporal niche. Humans were highly active during the
304 day, and carnivore activity, particularly that of foxes, overlapped much less with humans than other
305 carnivores. Nocturnality in carnivores could suggest avoidance, particularly when humans present
306 high risk (Kusak et al. 2005; Diaz-Ruiz et al. 2016). Limited temporal overlap might however be
307 expected given species adaptations and evolutionary history (Heesy and Hall 2010; Hall et al. 2012).
308 A lack of carnivore activity during the central parts of the day could reflect avoidance of heat, but
309 human activity during twilight can still affect carnivore hunting success (Hayward and Slotow 2009;
310 Theuerkauf 2009).

311 Unlike Gaynor et al. (2018), we did not find evidence to support increased mammal nocturnality in
312 response to higher human activity. Given that carnivores were already highly nocturnal in Plitvice, we
313 might not have detected variation in response to human activity, but it also might not have existed.
314 We did however find that human activity moderated top-down effects in Plitvice. The nocturnal effect
315 large carnivores had on foxes was dampened by human activity. Benitez-Lopez et al. (2018) suggest
316 that the human disturbance of apex predators from daylight activity might affect ecological
317 interactions. An undetected effect of humans on large carnivore daytime activity, with humans
318 shielding foxes from large carnivore daytime use, might explain our observations. That said, human
319 activity may have lessened the effect of large carnivores on foxes via an alternative mechanism. High
320 human activity might disrupt scent pictures and make the detection of risk cues from large carnivores
321 more difficult, resulting in foxes modifying their behaviour less even though large carnivores were
322 more active at a given station. The exact mechanism remains unknown but we can conclude that
323 humans disrupted ecological interactions in Plitvice.

324 Interference with predator to predator interactions and consequent changes to mesopredator foraging
325 activity could alter the pressure these efficient predators place upon prey communities (Vance-
326 Chalcraft et al. 2007; Ritchie and Johnson 2009). Such interactions are however unlikely to be solely
327 modern phenomena. Hominins have potentially been a part of European predator communities for 1.2

328 million years, with modern humans present at least 43,000 years (Carbonell et al. 2008; Benazzi et al.
329 2011). The spatial extent and numbers of humans in modern Europe is now, of course, dramatically
330 more substantial. A key issue for protected areas thus lies in understanding the tipping points at which
331 human activity becomes detrimental to biodiversity, ecosystem function and conservation efforts.

332 Observing changes in behaviour, such as activity patterns, can improve our understanding of
333 ecological processes but can also provide early warning signals, e.g. temporal avoidance of humans
334 might be a precursor to spatial exclusion, population decline or regional extinction following growing
335 anthropogenic pressure (Berger-Tal et al. 2011; Caravaggi et al. 2017). Intense human pressure is
336 prevalent in almost a third of global protected lands and undermines biodiversity preservation (Jones
337 et al. 2018). Furthermore, interference risks altering baselines, negating the function of reserves in
338 detecting ecological change, but also distorting public understanding of intact ecological processes
339 (Sarmiento and Berger 2017). Increasing intensity, temporal or spatial coverage of human activities
340 beyond species tolerance could also conflict with conservation goals (Firšt et al. 2005; Štrbenac et al.
341 2005). Human activities can negatively affect foraging success, territorial defence, mate acquisition
342 and reproductive output, as well as causing spatial displacement, stress and reduced energy intake,
343 which have the potential to ultimately affect body condition, survival, fitness and demography (Frid
344 and Dill 2002; Strasser and Heath 2013; Pauli et al. 2017). Given the lack of true wilderness areas in
345 Europe however, many believe the most probable scenario of saving wildlife will require the dynamic
346 interspersion of both wildlife and humans (Chapron et al. 2014).

347 Our findings show that mesopredators apply temporal strategy to enable the use of shared travel
348 routes. How they use trails is affected by the level of use of other predators, as well as the interactions
349 between multiple trail users. The effect of large carnivore activity on mesopredator trail use and the
350 resultant trophic consequences may be dependent on the activity of humans. The significance and
351 costs of such interference to conservation goals requires further exploration. Given temporal
352 displacement may serve as an early warning sign to further ecological degradation, we urge parks to
353 carefully consider the spatial and temporal extent of recreation and to monitor its impacts.

354 **Compliance with ethical standards**

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359 *Conflict of interest*

360 The authors declare that they have no competing interests.

361 *Ethical approval*

362 All applicable institutional and/or national guidelines for the care and use of animals were followed.
363 The study was carried out with the permission of Bangor University and the University of Zagreb. In
364 Croatia, no permits were required for the use of motion activated cameras but field work was
365 conducted with the permission of Nacionalni park Plitvička Jezera.

366 **Data availability**

367 The datasets generated and/or analysed during the current study are available from the corresponding
368 author on reasonable request.

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566 **Figure Captions**

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568 **Fig. 1** Map of study location, Plitvice Lakes National Park, Croatia. Black triangles detail the camera
569 stations (Oct 2015 - Oct 2016). Solid pale grey areas detail the boundaries of the national park. Roads
570 are represented by solid grey lines, country boundaries by black lines and the lakes by dark grey areas

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572 **Fig. 2** Temporal niche overlap (grey area) between carnivores and humans in Plitvice Lakes National
573 Park, Oct 2015-Oct 2016. Dotted lines represent kernel density estimates for red foxes, *Vulpes vulpes*,
574 dot-dash lines for gray wolves, *Canis lupus*, dashed lines for Eurasian lynx, *Lynx lynx*, and solid lines
575 for humans, *Homo sapiens*. Kernel density estimates are plotted as a function of sunrise time

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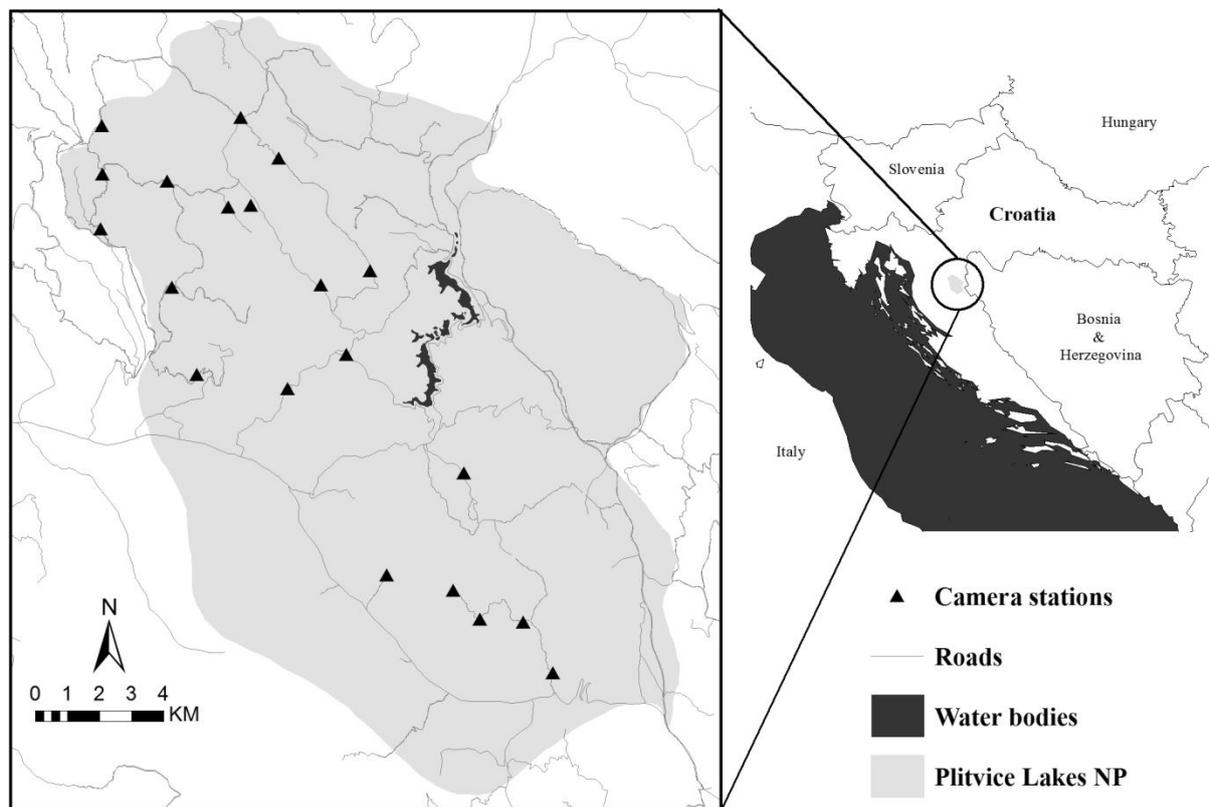
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587 **Fig 1.**



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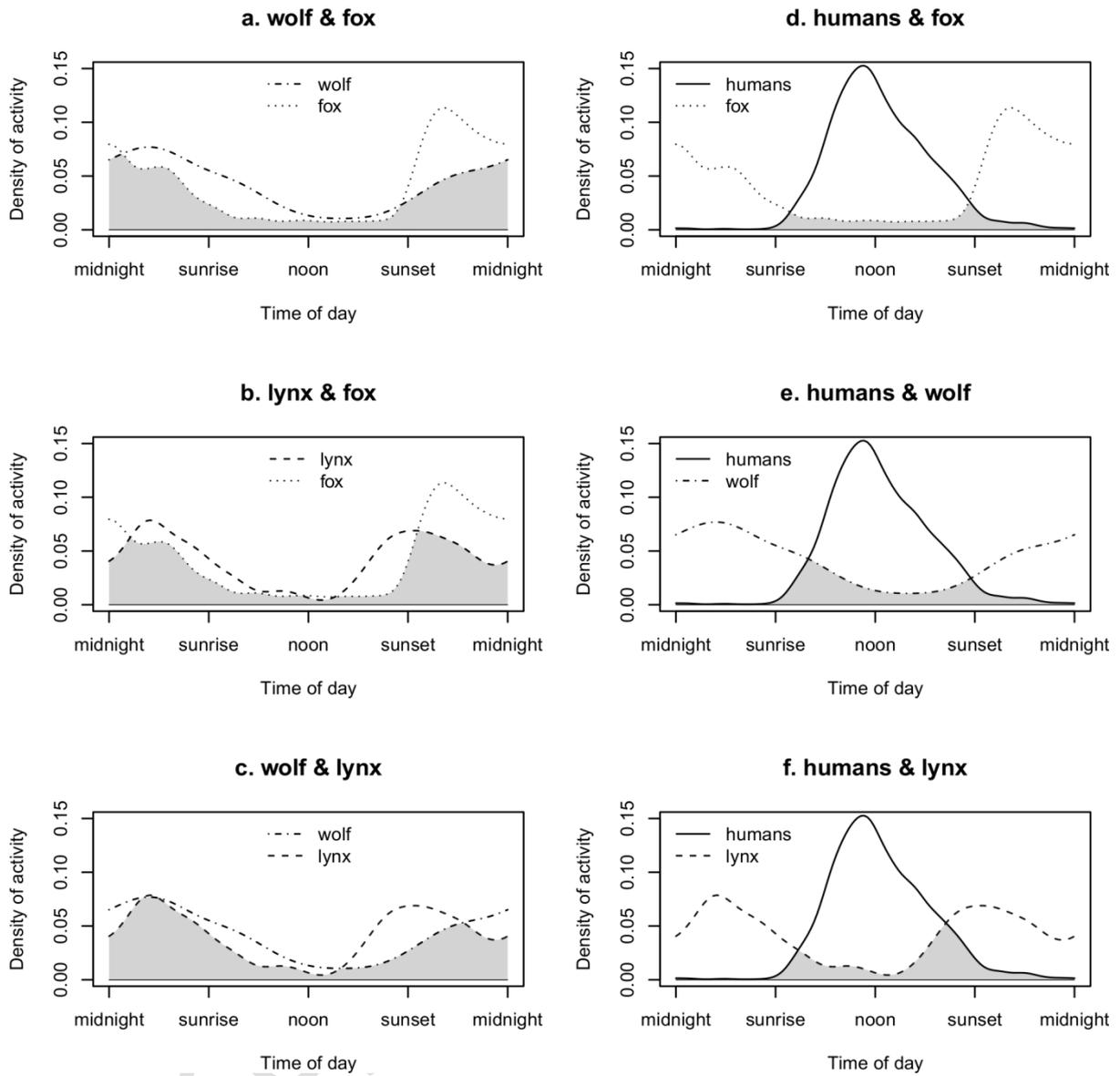
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