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

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24 <u>moderate the interaction</u>

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37

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.

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 km^2 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 km^2 with territory size of 1.43 km^2 (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   <u>Interspecific time use</u>

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 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 $\hat{\Delta}4$ 0.73 (95% CI, 0.65 to 0.82) and with lynx was $\hat{\Delta}4$ 0.75 (0.65 to

222   0.79). Wolf and lynx overlap was $\hat{\Delta}4$ 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, $\hat{\Delta}4$ 0.17

224   (0.14 to 0.17). Wolves and lynx had similar overlap with human activity curves. Wolf and human

225   overlap was $\hat{\Delta}4$ 0.28 (0.19 to 0.34). Lynx overlap with humans was also $\hat{\Delta}4$ 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 (Sarmento 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.

Compliance with ethical standards

Funding

Conflict of interest

The authors declare that they have no competing interests.

Ethical approval

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

Data availability

The datasets generated and/or analysed during the current study are available from the corresponding 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
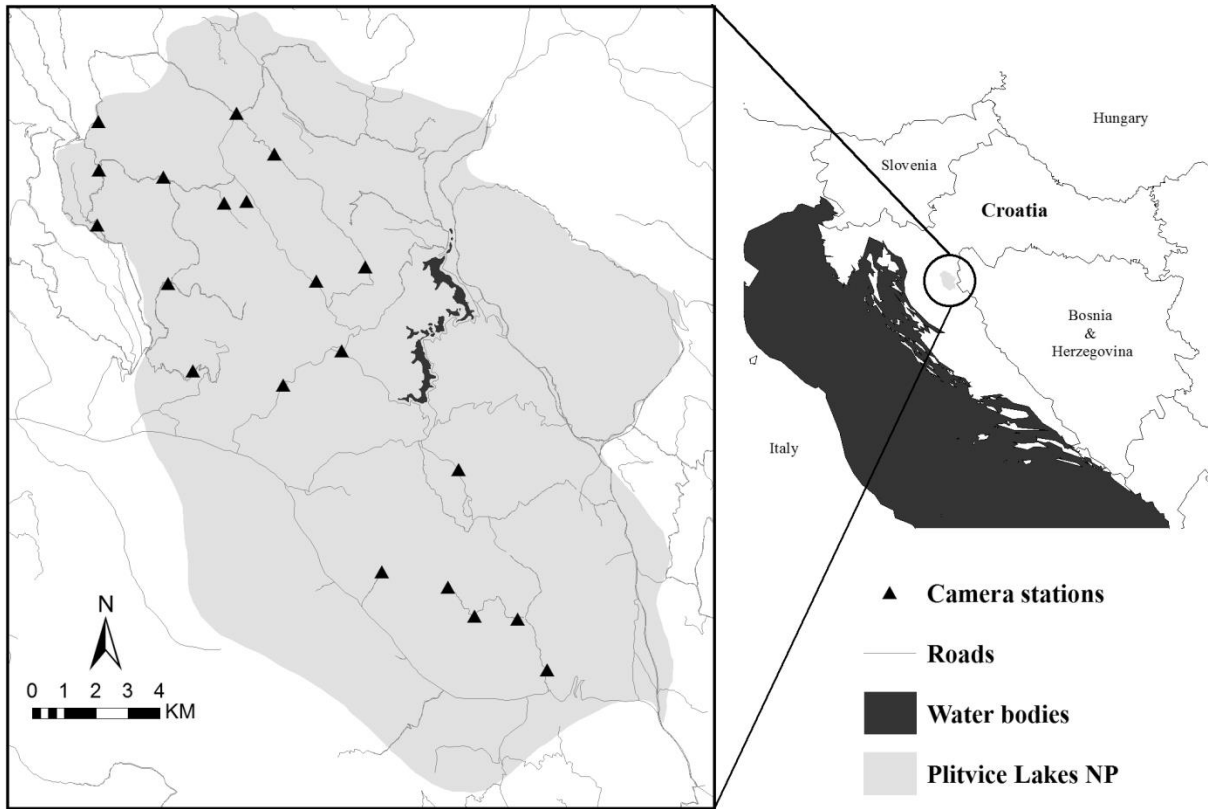
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587   **Fig 1.**

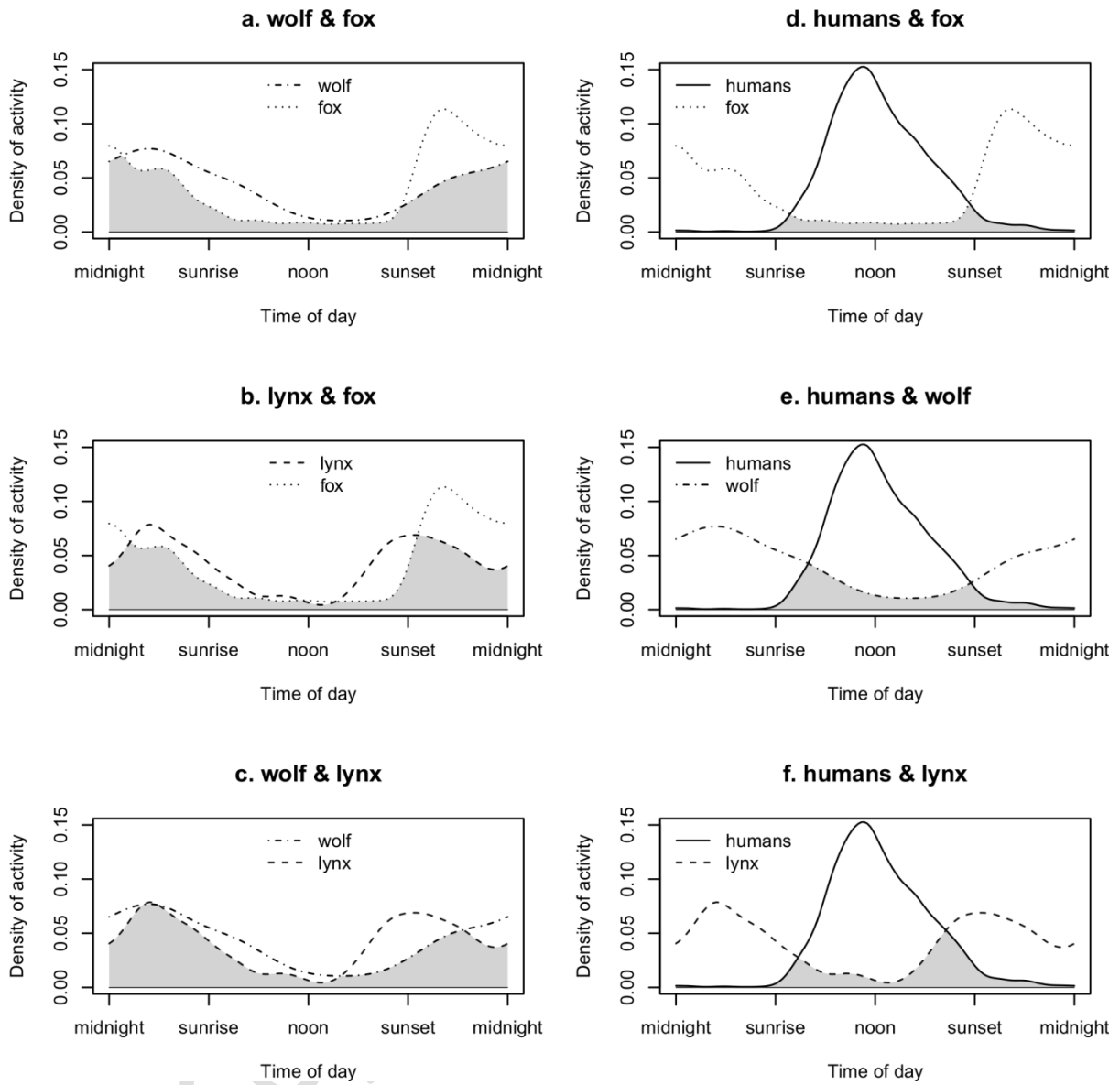599   **Fig 2.**

a. wolf & fox

d. humans & fox

b. lynx & fox

e. humans & wolf

c. wolf & lynx

f. humans & lynx

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