Seasonal and predator-prey effects on circadian activity of free-ranging mammals revealed by camera traps

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Endogenous circadian and seasonal activity patterns are adapted to facilitate effective utilisation of environmental resources. Activity patterns are shaped by physiological constraints, evolutionary history, circadian and seasonal changes and may be influenced by other factors, including ecological competition and interspecific interactions. Remote sensing camera traps allow the collection of species presence data throughout the 24-hour period, and for almost indefinite periods. Here, we collate data from ten separate camera trap surveys in order to describe circadian and seasonal activity patterns of ten mammal species, and, in particular, to evaluate interspecific (dis)associations of five predator-prey pairs. We recorded 8,761 independent detections throughout Northern Ireland. Badgers, foxes, pine martens and wood mice were nocturnal; European and Irish hares and European rabbits were crepuscular; fallow deer and grey and red squirrels were diurnal. All species exhibited significant seasonal variation in activity relative to the timing of sunrise/sunset. Foxes in particular, were more crepuscular from spring to autumn and hares more diurnal. Lagged regression analyses of predator-prey activity patterns between foxes and prey (hares, rabbits and wood mice), and pine marten and prey (squirrel and wood mice) revealed significant annual and seasonal cross-correlations. We found synchronised activity patterns between foxes and hares, rabbits and wood mice and pine marten and wood mice, and asynchrony between squirrels and pine martens. Here, we provide fundamental ecological data on endemic, invasive, pest and commercially valuable species in Ireland, as well as those of conservation importance and those that could harbour diseases of economic and/or zoonotic relevance. Our data will be valuable in informing the development of appropriate species-specific methodologies and processes and associated policies.

1 Original Article

2 **Seasonal and predator-prey effects on circadian activity of free-ranging mammals revealed**

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23   **Abstract**

25   Endogenous circadian and seasonal activity patterns are adapted to facilitate effective utilisation

26   of environmental resources. Activity patterns are shaped by physiological constraints, evolutionary

27   history, circadian and seasonal changes and may be influenced by other factors, including

28   ecological competition and interspecific interactions. Remote sensing camera traps allow the

29   collection of species presence data throughout the 24-hour period, and for almost indefinite

30   periods. Here, we collate data from ten separate camera trap surveys in order to describe circadian

31   and seasonal activity patterns of ten mammal species, and, in particular, to evaluate interspecific

32   (dis)associations of five predator-prey pairs. We recorded 8,761 independent detections

33   throughout Northern Ireland. Badgers, foxes, pine martens and wood mice were nocturnal;

34   European and Irish hares and European rabbits were crepuscular; fallow deer and grey and red

35   squirrels were diurnal. All species exhibited significant seasonal variation in activity relative to

36   the timing of sunrise/sunset. Foxes in particular, were more crepuscular from spring to autumn and

37   hares more diurnal. Lagged regression analyses of predator-prey activity patterns between foxes

38   and prey (hares, rabbits and wood mice), and pine marten and prey (squirrel and wood mice)

39   revealed significant annual and seasonal cross-correlations. We found synchronised activity

40   patterns between foxes and hares, rabbits and wood mice and pine marten and wood mice, and

41   asynchrony between squirrels and pine martens. Here, we provide fundamental ecological data on

42   endemic, invasive, pest and commercially valuable species in Ireland, as well as those of

43   conservation importance and those that could harbour diseases of economic and/or zoonotic

44   relevance. Our data will be valuable in informing the development of appropriate species-specific

45   methodologies   and   processes   and   associated   policies.

46   **Introduction**

47   Animal activity patterns are influenced by a variety of environmental pressures, including food

48   availability (Larivière et al., 1994, Pereira, 2010), foraging efficiency (Lode, 1995; Prugh &

49   Golden, 2014), predator/prey activity (Fenn & McDonald, 1995; Middleton et al., 2013), human

50   disturbance (van Doormaal et al., 2015; Wang et al., 2015), mate availability and activity

51   (Thompson et al., 1989; Halle & Stenseth, 2000), and ecological competition (Rychlik, 2005;

52   Montorroso et al., 2014). Mammals exhibit a great diversity and flexibility in their activity

53   patterns. A recent study of 4,477 mammal species classified 69% as nocturnal (i.e. night-active),

54   20% diurnal (i.e. day-active), 8.5% cathemeral (i.e. active throughout the 24-hour cycle) and 2.5%

55   crepuscular (i.e. dawn- and/or dusk-active, e.g. lesser mouse deer; Bennie et al., 2014). Circadian

56   (i.e. recurring every 24 hours) and seasonal patterns of activity are adaptive behavioural traits

57   which allow species to effectively exploit their environment and the resources contained therein

58   (Phillips et al., 2013).

59   Activity patterns evolved in response to cyclical changes in the environment that

60   encouraged organisms to respond on a physiological and behavioural basis (Daan, 1981, Kronfeld-

61   Schor & Dayan, 2003; Roll et al. 2006; Bennie et al., 2014). Activity patterns are frequently related

62   to daily oscillation in illumination (e.g. changes in sunrise/sunset; Halle & Stenseth, 2000) and,

63   hence, the time(s) of the day during which species are active may vary according to season (i.e.

64   spring, summer, autumn, and winter). Indeed, it has been suggested that photic cues are the

65   dominant factor underlying behavioural rhythmicity and that a species' potential to adapt to non-

66   photic cues (e.g. ecological competitors, predators) may be constrained such that responses are

67   manifest within the normal active period rather than as a shift to a different rhythm (Kronfeld-

68   Schor & Dayan, 2003). The capacity for adaptive behavioural plasticity, while limited in some

69 species (Kronfeld-Schor & Dayan, 2003), is demonstrated in others by observations of

70 intraspecific variation of activity patterns (e.g. Ashby, 1972, Herte et al., 2017) that can result in

71 temporal niche switching (Fenn & McDonald, 1995; Ensing et al., 2014). For example, Ensing et

72 al. (2014) found that red deer (*Cervus elaphus*) were mostly diurnal in Canada, while conspecifics

73 in the Netherlands were mostly nocturnal. The difference in activity patterns was attributed to

74 higher levels of human disturbance and a lack of natural predators in the Netherlands.

75   The island of Ireland has a depauperate terrestrial mammalian community due to its

76 prolonged isolation since the last Glacial Maximum (Montgomery et al., 2014). The behavioural

77 ecologies of mammals in Ireland are almost entirely unknown and assumptions of behavioural

78 equivalence between Ireland and locations elsewhere in the species' range may not apply given

79 differences in land use, human activity and ecosystem composition. Quantifying fundamental

80 ecological parameters such as activity patterns has direct relevance to the management of endemic

81 (e.g. Irish hare, *Lepus timidus hibernicus*; Reid & Montgomery, 2007), invasive (e.g. European

82 hares, *Lepus europaeus*; Caravaggi et al., 2015), pest (e.g. foxes; Baker & Harris, 2006) and

83 commercially valuable (e.g. deer; Carden et al., 2011) species, as well as those that could harbour

84 diseases of economic (e.g. badgers, *Meles meles*; Griffin et al, 2005) and/or zoonotic relevance.

85 The relative dearth of mammalian herbivores and their predators in Ireland also makes the island

86 an ideal study system in which to investigate predator-prey relationships. However, recording and

87 quantifying daily activity patterns of wild, free-ranging mammals presents significant challenges,

88 including overcoming the observer effect whereby the presence of an observer influences the

89 behaviour of the subject (Stewart et al., 1997), and collecting sufficient data to address scientific

90 and conservation questions (*sensu* Cagnacci et al., 2010). A number of methodological techniques

91 have been used to overcome such challenges such as radio-tracking, GPS collars and live trapping,

92   each with varying degrees of success (Bridges & Noss, 2011). Radio-tracking has inherent

93   limitations, including periodic (i.e. non-constant) sampling (e.g. Lovari et al., 1994) and the

94   application of considerable survey effort (Palomares & Delibes, 1991; Reid, McDonald &

95   Montgomery, 2010). Furthermore, they may result in small sample sizes (Bridges & Noss, 2011),

96   capture a limited proportion of the population (Sadlier et al., 2004), and may be subject to signal-

97   based error and/or omission (Cagnacci et al., 2010) or alter the behaviour of tagged animals (e.g.

98   Wilson et al., 2011). GPS collars have similar constraints to radio-tracking, particularly with

99   regards to sample sizes and potential signal issues. Moreover, inferences made from GPS collar

100   data can lead to misleading results and much depends on the frequency with which location fixes

101   are obtained (Merrill & Mech 2003). Live trapping has been used to investigate activity patterns

102   of small mammals, where each successful capture (i.e. the presence of an animal in a trap) is taken

103   as indicating activity (e.g. Elton et al., 1931; Bradley, 1967; Hoogenboom et al., 1984). However,

104   live trapping requires considerable time and effort, is relatively inefficient, may have implications

105   with regards to animal welfare (Torre et al., 2010), and is subject to species- and trap-specific

106   variations in capture probability (Leso & Kropil, 2010).

107   Remote-sensing camera traps (i.e. remotely activated cameras that are activated via motion

108   or infra-red sensors or light beams) are increasingly popular in conservation and ecological studies

109   as they are non-invasive and are subject to continuing technological improvements and decreasing

110   costs (Tobler et al., 2008a). They have been used in studies investigating population densities (e.g.

111   Trolle & Kéry, 2003, Karanth et al., 2006, Caravaggi et al., 2016), behaviour (e.g. Maffei et al.,

112   2005), ecosystem biodiversity (e.g. Silveira et al., 2003, Tobler et al., 2008b), and site occupancy

113   of rare or cryptic species (e.g. Linkie et al., 2007). Camera traps afford researchers the means to

114   conduct long-term surveys while minimising *in-situ* survey effort and disturbance of the focal

115   species (Kays & Slauson, 2008). As such, data derived from camera trap surveys of common

116   species and/or conducted at high camera densities are well suited to investigations of wildlife

117   activity patterns (e.g. Di Cerbo & Biancardi, 2013, Carbajal-Borges et al., 2014; Allen et al., 2018).

118   The size and scope of camera trap surveys are limited only by the cost of equipment and personnel

119   to conduct fieldwork and review and analyse data, while the length of time cameras can be left *in-*

120   *situ* is restricted by available memory, battery life and the possibility of mechanical failure. There

121   may be a trade-off between the proximity and angle of cameras with regards to targets, and the

122   likelihood of detecting and identifying species of varying size (Hofmeester et al., 2017).

123   Downward-facing cameras, for example, are more efficient at detecting small mammals, (De

124   Bondi et al., 2010). However, species identification is difficult where similar species occur in

125   sympatry (Claridge et al., 2010; Meek et al., 2013; Oliveira- Santos et al., 2010). This is often

126   particularly true of small mammals (e.g. Claridge et al., 2010; Meek & Vernes, 2016). However,

127   Ireland is home to six species of rodent and two species of shrew, few of which occur in sympatry

128   and all of which are uniquely identifiable.

129   Here, we describe the first study into temporal activity patterns of ten mammal species

130   found in Ireland, from 14g (wood mouse) to 60kg (fallow deer), captured via camera traps. In

131   addition, we investigate interspecific relationships, specifically whether predator-prey activity

132   patterns demonstrate (a)synchrony, demonstrating temporal (dis)association between ecologically-

133   linked species. We hypothesised that predator-prey pairs would exhibit non-random, interrelated

134   distribution of activity throughout the diel cycle. This distribution would either display a

135   considerable overlap between predators and prey (i.e. predators are attracted to prey), or

136   asynchrony between the species (i.e. temporal avoidance of predators by prey).

137   **Materials and methods**

138   We collated data from 10 camera trap studies conducted in Northern Ireland, where land use is

139   predominantly agricultural (75%) and forest cover, mixed and deciduous woodland and coniferous

140   forest plantations, is 8% of land area (Department of Agriculture, Environment and Rural Affairs,

141   2018; Forestry Comission, 2018). The focal species of the 10 studies were fallow deer (*Dama*

142   *dama*, Linnaeus 1758; n=6), Eurasian red squirrel (*Sciurus vulgaris*, Linnaeus 1758) and Eastern

143   North American grey squirrel (*S. carolinensis*, Gmelin 1788; n=2) and European brown hare

144   (*Lepus europeaus*, Pallas 1778) and Irish mountain hare (*L. timidus hibernicus*, Bell 1837; n=2).

145   However, as is common for camera trap studies, non-target species were also detected. Therefore,

146   in addition to the 5 focal species, we present additional information on a further 5 species: i)

147   European badger (*Meles meles*, Linnaeus 1758); ii) European rabbit (*Oryctolagus cuniculus*,

148   Linnaeus 1758); iii) wood mouse (*Apodemus sylvaticus*, Linnaeus 1758); iv) pine marten (*Martes*

149   *martes*, Linneus 1758); and v) red fox (*Vulpes vulpes*, Linnaeus 1758; hereafter 'fox'). The data

150   presented here resulted from a total of 1,164 camera deployments at 431 locations (defined herein

151   as broad study areas, rather than individual camera placements; Fig. 1). Deer surveys were

152   conducted from June 2013 to November 2016, squirrel surveys from January to March in 2014

153   and January to May in 2015 and hare surveys from April 2013 to August 2015, non-inclusive.

154   Constituent surveys were independent and, hence, methodologies were not standardised. There

155   was no evidence of intrageneric variation in the activity patterns of hare (Fig. S1) and squirrel (Fig.

156   S2) species, and, hence, both were grouped (i.e. 'hares' and 'squirrels') for the purposes of the

157   current study.

158

159   *Species surveys*

160   We included data from six independent deer studies (D1 – 6) in our analyses. D1 and 2 were

161   conducted over 15 1 km^2 squares with an average of 10 cameras per km^2 and 5 additional 1 km^2

162   squares set at a higher density of 20 camera traps per km^2. In total 38 camera trap units were

163   randomly deployed over 255 individual camera trap placements (Table 1) using a combination of

164   Bushnell Trophy Cam (119467), Bushnell Trophy Cam HD (119477), Reconyx (HC600) and

165   Scoutguard Camera (SG560P-8M) – the number of each model used differed between sites.

166   Camera traps were set at a height of 30cm, perpendicular to the ground. Cameras were set to

167   capture the maximum photographs per trigger (3-10 photographs depending on camera model) and

168   no delay between triggers. Cameras were left for 14 days before being collected and relocated.

169   D3 surveyed smaller areas of 0.05 km^2, 0.02 km^2 and 0.04 km^2 using ten Bushnell Trophy Cam

170   HD (119677) at each site. Each camera was set at a height of 40cm from the ground and set to

171   capture bursts of 3 still pictures and a 60-second video per trigger, with a delay of one second

172   between triggers. Cameras were left *in situ* for 7 days. D4 was focussed on areas of 0.05 km^{2}and

173   0.02 km^2 and used Bushnell Trophy Cam HDs (119477, 119577, 119676, 119677). Cameras were

174   set at a height of 40cm and set to capture either 3 still pictures or a 30s video, depending on the

175   camera model, with a one second delay between triggers. Cameras were deployed for 7 days.

176   Hare surveys were conducted over two independent studies (Table 1) across a total of

177   twenty-three 1km^2 squares. Each square contained twenty randomly placed Bushnell Trophy Cam

178   HD (119477) camera traps that were positioned on vertical aspects of linear features (i.e. trees in

179   hedgerows, fence posts), to a total of 460 camera locations (Table 1). Cameras were set at a height

180   of 30cm from the ground, at a 45º - 90 º angle away from the linear feature, with a 10-15º

181   downward tilt. Cameras were set to record video for a period of 60 seconds with a 60 second delay

182 between triggers. Cameras were deployed for 7 days. The use of video footage allowed the

183 detection of closely-associated conspecifics (see Caravaggi et al., 2016 for more on this study).

184   Data from two arboreal squirrel surveys are presented in this study. The first survey (S1)

185 was undertaken in 2014, within 63 forested areas > 5ha in size within Co. Fermanagh. A total of

186 16 Bushnell Trophy Cameras (119438) were deployed by 7 volunteers ('citizen scientists') and 1

187 scientist during a 3-month period (Table 1). Cameras were attached to trees at a height of 3-4m

188 and positioned up to 4m distant from and opposite a wooden squirrel feeder (Northumbrian

189 Wildlife Trust design) baited with peanuts and sunflower seeds. Cameras were left *in situ* for a

190 minimum of 7 and maximum of 24 days (median = 8). The second survey (S2) was conducted in

191 314 forested areas > 5ha in size across Northern Ireland by 70 citizen scientists and 1 scientist

192 during a 5-month period in 2015. A total of 65 Bushnell Trophy Cameras (16 x 119438; 12 x

193 119577; 37 x 119676) were deployed during this time for a minimum of 6 and maximum of 33

194 days (median = 7). Cameras were deployed at head height (1.5 -2m) on a tree opposite either a

195 wooden (as in 2014) or metal squirrel feeder (CJ Wildlife Product code 12335). In both years,

196 cameras were set to take 3 photos per burst with an interval of $1 - 20$ seconds between triggers. In

197 these surveys all citizen scientists were trained in the use of camera traps by the scientist (DT)

198 overseeing the research.

199   In deer and hare surveys, cameras were placed according to n_i randomly generated points

200 within each focal area and a clear field of view was ensured by clearing prominent vegetation

201 where appropriate. The density of deployed camera trap arrays means that it was possible that the

202 same individual would be captured more than once during the sampling period. Similarly, cameras

203 were pseudo-randomly placed during squirrel surveys according to suitably paired trees (one for

204 the camera, one for the feeder) of which there were an abundance in all locations. Recaptures were

205   highly likely given the use of baited stations. Surveys with >1 camera trap model did not

206   systematically deploy models predictably within and across arrays. In all surveys, cameras were

207   equipped with fitted with 8 GB HDSD cards, secured with Python security cables, motion detectors

208   were set to medium sensitivity and each capture was stamped with the date and time.

209

210   *Activity analysis*

211   We assumed that images were independent when separated by one hour (e.g. Cusack et al., 2015)

212   and that temporal detection frequency was a true reflection of circadian activity patterns of the

213   focal species. Animals can only be detected on camera traps only when active, specifically, when

214   in motion. The number of detections per hour therefore reflects the level of activity across the

215   circadian period. Prior to analysis, data for individual species were grouped into one-hour time

216   intervals, beginning at the hour mark (e.g. 11:00 – 11:59). . In cases where a group of individuals

217   of the same species (e.g. fallow deer) was detected in one image, a single event was recorded.

218   Detection frequencies were normalised to ease plot interpretation using the formula $z_i = \frac{x_i - x_{min}}{x_{max} - x_{min}}$

219   , where z_i = normalised detection frequency at the ith interval, and $x = (x_1 \ldots, x_n)$.

220   Variations in day length throughout the year has direct consequences for wildlife. For

221   example, an ostensibly nocturnal species may be more likely to remain active into daylight hours

222   during the summer months due to shortening nights to meet its energetic requirements (Schai-

223   Braun et al., 2012). To investigate intra-annual variation in activity relative to sunrise/sunset (i.e.

224   whether nocturnal/diurnal activity differed between seasons; solar cycle historical data obtained

225   from the HM Nautical Almanac Office, 2016), data were grouped according to season: spring

226   (March – May); summer (June – August); autumn (September – November); and winter

227 (December – February). Detections between 00:00 and 11:59 were offset relative to sunrise;

228 detections between 12:00 and 23:59 were offset relative to sunset. All daytime offsets were

229 converted to positive integers, night-time to negative. For example, a detection timed at 22:10,

230 with sunset at 20:00, would have an offset value of -2 hours and 10 minutes, indicating nocturnal

231 activity. We investigated intraspecific differences in seasonal offsets via one-way Analysis of

232 Variance (ANOVAs) with *post-hoc* Tukey tests where the dependent variable was the

233 sunrise/sunset offset, and season was the explanatory variable.

234   We defined the diurnal period as the time between one hour after sunrise and one hour

235 before sunset, and the nocturnal period as the time between one hour before sunrise and one hour

236 after sunset. We defined the crepuscular periods, dawn and dusk, as the hour before and the hour

237 after sunrise and sunset respectively (after Theuerkauf et al., 2003; Ross et al., 2013). Species

238 activity patterns were classified according to the diel period with the most activity.

239   We used overlap metrics and lagged regression cross-correlation functions (CCFs) to

240 examine annual and seasonal relationships between predator-prey pairs (i.e. autocorrelation),

241 specifically: fox and hare; fox and rabbit; fox and wood mouse; pine marten and squirrel; and pine

242 marten and wood mouse. These relationships were explored due to dietary studies indicating the

243 potential for predator-prey dynamics within the 24hr period. Lagomorphs are primary prey items

244 of the red fox in Ireland (e.g. Fairley, 1970). In Britain the field vole (*Microtus agrestis*) is a

245 secondary prey item for the red fox (Webbon et al., 2006) and primary item for the pine marten

246 (Caryl et al., 2012) but this species does not occur in NI where the wood mouse is the most

247 abundant small mammal species (Twinning et al., 2018). Data used to examine predator prey

248 relationships were restricted to locations where both species in each pair were detected. Sample

249 CCFs facilitate the identification of lags in the *x* variable which may be predictive of *y*. Positive

250 lag ($h+$) is the result of a correlation between x_{a+i} and y_a, where a = time. Conversely, negative lag

251 (h-) is the result of a correlation between x_{a-i} and y_a. Significant correlations describe a non-random

252 association between species detections at interval(s) h_i. Lagged regressions were calculated using

253 the ccf function in the core library of R (R Core Team 2016). The CCF function, however, does

254 not return quantified measures of significance. The significance of the correlation coefficient, r,

255 therefore, was established by calculating the t value, where $t = r\sqrt{\dfrac{n-2}{1-r^2}}$ and where the critical t

256 value (p = 0.05, 22 degrees of freedom, one-tailed) = 1.72. We calculated the degree of overlap

257 between each species pair on an annual basis and for each season using the *overlap* package

258 (Meredith & Ridout, 2017). Data were resampled 1,000 times per pair, per category, to generate

259 95% Confidence Intervals (CI). We defined overlap <0.5 as low overlap, 0.5-0.75 as moderate

260 overlap, and > 0.75 as high overlap (Monterroso et al., 2014). All statistical analyses were carried

261 out in R 3.4.3 (R Core Team, 2017; see Caravaggi et al., 2018, for data and code).

263   **Results**

264   A total of 8,761 independent detections of the ten species were recorded across 324 camera days.

265   Squirrel sightings ($n = 2{,}870$; Fig. 2g) comprised 33% of all records, rabbits 13% ($n = 1{,}175$; Fig.

266   2f), pine martens 11% ($n = 966$; Fig. 2e), badgers 11% ($n = 947$; Fig. 2a), wood mice 9% ($n = 816$;

267   Fig. 2h), hares 9% ($n = 751$; Fig. 2d), foxes 7% ($n = 645$; Fig. 2d), and fallow deer 7% ($n = 591$;

268   Fig. 2b; Table 2). Seasonal variations in the number of detections recorded reflected the time and

269   duration of the constituent studies: 47% in spring, 24% in summer, 18% in autumn, and 11% in

270   winter (Table 2).

271

272   *Species-specific activity patterns*

273   Foxes exhibited a nocturnal activity pattern, with some irregular diurnal activity. Nearly

274   three-quarters of all fox activity (73%) occurred between 21:00-07:00 (Fig. 3a). Pine marten

275   activity was nocturnal, with 70% of all detections occurring between 21:00 and 06:00 (Fig. 3b).

276   Badgers were nocturnal with a unimodal pattern of activity; the number of detections increased

277   rapidly after dusk and decreased rapidly around dawn. Fewer than 15% of all badger detections

278   were recorded between 06:00-19:00, indicating little diurnal activity (Fig. 3c). Hare activity

279   patterns were bimodal, demonstrating predominantly crepuscular behaviour with 71% of all

280   activity occurring between 04:00-08:00 (47%) and 20:00–23:00 (24%; Fig. 3a). Rabbits were also

281   crepuscular, with 35% and 32% of all detections occurring between 04:00-08:00 and 17:00-23:00,

282   respectively (Fig. 3a). Squirrels were diurnal, being active from dawn to dusk with fewer than 5%

283   of triggers occurred between 19:00 and 05:00 (Fig. 3b). Wood mice were nocturnal with 81% of

284   activity occurring between 21:00 and 06:00 (Fig. 3b). Overall, fallow deer were diurnal with 63%

285   of detections occurring between 06:00 and 18:00 (Fig. 3c)

286   There were significant differences in offsets across seasons in fox activity patterns ($F_{33,641}$

287    $= 23.36$, p < 0.0001); winter was significantly different from all other seasons due to decreased

288   activity during daylight and crepuscular periods (Fig. 4c). Significant differences were observed

289   across and between all seasons ($F_{3,962} = 86.28$, p < 0.0001), except spring-autumn in pine marten

290   activity patterns (Fig. 4b). Badger activity patterns exhibited significant differences in offsets

291   across seasons ($F_{3,943} = 32.54$, p < 0.0001; Fig. 4c) except for winter-autumn and summer-spring.

292   Seasonal offsets differed significantly in hare activity patterns ($F_{3,747} = 19.33$, p < 0.0001),

293   specifically between spring and summer (p < 0.0001) and summer and autumn (p < 0.001; Fig.

294   4d); hares exhibited more diurnal activity both in spring and in autumn. There were significant

295   differences in offsets across and between seasons in rabbit ($F_{3,1171} = 12.93$, p < 0.0001; Fig. 4f) and

296   squirrel activity patterns ($F_{3,2866} = 76.52$, p < 0.0001; Fig. 4g). Fallow deer activity patterns

297   exhibited significant differences in offsets across seasons ($F_{3,587} = 16.7$, p < 0.0001), specifically

298   between spring and autumn (p < 0.0001) and summer and autumn (p > 0.0001; Fig.4b). Offsets

299   were significantly different across seasons in wood mouse activity patterns ($F_{3,81\ 2} = 39.31$, p $<$

300   0.0001), with diurnal activity increasing in summer (Fig. 4h).

301

Predator-prey relationships

303   There was evidence of correlative relationships between all predator-prey pairs both annually and

304   between seasons. Fox and hare annual activity patterns showed 73% overlap (CI 68% - 77%; Table

305   3) and were significantly positively correlated with a peak at -2hrs (peak lag $= pl$, hereafter;

306   r=0.663, t_{22}=4.15, p<0.0005, Table 4). The degree of overlap peaked in spring at 75% (CI 64% -

307   84, Table 3; pl = 1hr, r = -0.554, t_{22} = 3.12, p < 0.005, Table 4). There were significant correlations

308   in the summer (Table 4).Annual activity patterns of foxes and rabbits overlapped by 80% (CI 75%

309   - 83%, Table 3) and were significantly correlated, with a peak at -1hr (pl = -1hr, r = 0.661, t_{22} =

310   4.13, p < 0.0005, Table 4). Overlap was greatest during spring at 89% (CI 86% - 98%, Table 3;

311   pl = 1hr, r = 0.701, t_{22} = 4.61, p < 0.0005, Table 4) and lowest during winter (51%, CI 31% - 71%,

312   Table 3). Seasonal activity patterns between foxes and rabbits were positively correlated during

313   spring and summer (Table 4), but there were no significant correlations evident during the rest of

314   the year. Fox and wood mouse annual activity patterns overlapped by 81% (CI 75% - 87%; Table

315   3). Overlap was high in all seasons but was greatest in summer with at 85% (CI 81%-92%, Table

316   3). Annual activity was significantly correlated (pl =1hr, r = 0.754, t_{22}=5.39, p ≤ 0.0001, Table 4),

317   with similar peaks in cross-correlation coefficients in spring (Table 4) and autumn, with greatest

318   correlation occurring in summer (pl = 0hrs, r = 0.761, t_{22}=5.50, p ≤ 0.0001, Fig Table 4).

319   Pine marten and wood mouse annual activity patterns were correlated with a 71% (CI 64%-

320   74%) overlap (pl = 0hrs, r=0.536, t_{22}=2.98, p ≤ 0.05, Table 4). Overlap was greater than 50% for

321   all seasons with a peak of 77% (CI 66%-93%) occurring in winter months (Table 3). Activity

322   patterns were significantly correlated in spring (pl = 10 hrs, r=-0.44, t_{22}=2.29, p ≤ 0.05, Table 4)

323   and winter (pl = 3 hrs, r=-0.503, t_{22}=2.73, p ≤ 0.05). Pine marten and squirrel annual patterns

324   overlapped by 40% (CI 33% - 41%, Table 3) and their activity was significantly correlated (pl =

325   2hrs, r = -0.621, t_{22} = 3.72, p < 0.001; Table 4). Seasonal overlap peaked during summer at 54%

326   (CI 41% - 60%) but was almost entirely absent during winter (Table 3). Significant correlations

327   between seasonal activity patterns were observed in all seasons except during autumn: spring, pl

328   = 1hr, (r = -0.625, t_{22} = 3.76, p > 0.001); summer, pl = -2hrs (r = -0.512, t_{22} = 2.79, p < 0.001); and

329   winter, pl = -1hr (r = -0.665, t_{22} = 4.18, p < 0.0005, Table 4).

330

332   **Discussion**

333   This study describes the first investigation into the activity patterns of a range of mammal species

334   on the island of Ireland, adding to information gathered from across the species' ranges and to

335   those where little is recorded. The study also contributes to the growing body of literature that uses

336   remote camera traps to infer activity (e.g. Bridges & Noss, 2011; Monterroso et al., 2013; Ross et

337   al., 2013; Carbajal-Borges et al., 2014; Allen et al., 2018) and reveals that our focal species exhibit

338   differences in activity relative to sunrise/sunset and throughout the year. In some cases, activity

339   changed markedly. For example, pine martens and rabbits were more diurnal in the summer while

340   during the rest of the year they were nocturnal and cathemeral, respectively. Similarly, predator-

341   prey relationships were also found to vary throughout the year. The temporal overlap between the

342   activity patterns of foxes, lagomorphs (rabbits and hares) and wood mice, were high (>0.75) during

343   the spring and summer and declined during autumn and winter. It is important to acknowledge

344   that a wide variety of factors affect activity patterns and, while our data show positive correlations

345   in activity between some predator and prey species that could be indicative of a causal relationship,

346   we do not attempt to describe observed patterns as being driven by any specific stimulus.

347   Foxes were nocturnal with their activity increasing during dusk and decreasing at dawn,

348   although there was also some activity during daylight. The bimodal activity pattern suggested by

349   previous studies (e.g. Reynolds & Tapper, 1995) was not evident. Rural fox activity may be

350   influenced by anthropogenic disturbance; diurnal activity is more common where disturbance is

351   low (e.g. Díaz-Ruiz et al., 2016; Gorman, 2008). In the present study, however, diurnal activity

352   may have been facilitated, not by a lack of disturbance, but by the timing of the disturbance. Foxes

353   are subject to nocturnal lethal control (i.e. shooting, facilitated by high-powered spot-lamps, and

354   other methods) across Northern Ireland, such that nocturnal disturbance by hunting parties is likely

355   to be considerably greater than that which occurs during the day, albeit periodically. However,

356   nocturnal control, while frequent, is regionally variable and intermittent. Furthermore, the most

357   abundant and commonly taken prey animals are nocturnal (e.g. small rodents) or crepuscular (e.g.

358   lagomorphs). Irregularities in the activity patterns described herein may therefore be indicative of

359   the true activity signal along with occasional temporal displacement.

360   Hares were active throughout the night, with peaks of activity occurring between 20:00

361   and 23:00, and 04:00 and 08:00. Diurnal activity was most commonly recorded in the summer

362   months, when nights are shortest (*sensu* Flux & Angermann, 1990, Holley, 1992, Langbein et al.,

363   1999). This study is the first to quantify activity patterns of the Irish hare, which exhibited the

364   same bimodal crepuscular-nocturnal behaviour as the European hare. The Irish hare is a subspecies

365   of mountain hare that is endemic to Ireland while the European hare is almost exclusively found

366   in Mid-Ulster, likely having been introduced in the 1970s (Caravaggi et al., 2015). Previous studies

367   have demonstrated that the species are ecologically similar (Reid, 2011; Caravaggi et al., 2015),

368   occur in sympatry (Caravaggi et al., 2016) and exhibit a high degree of bidirectional hybridisation

369   (Prodohl et al., 2013). The similarity in activity patterns described herein adds additional support

370   to the suggestion that strong interspecific competition is likely where they occur in sympatry where

371   resources are limiting. The activity patterns of rabbits were similar to those in the Mediterranean

372   region where rabbits were active throughout the day, but most activity occurred in the early

373   morning and late afternoon (Monterroso et al., 2013). However, while our data suggest a similar

374   bimodal pattern, the second, evening peak was weak in our dataset.

375   Overall, pine marten were nocturnal with activity becoming more diurnal between spring

376   and early autumn, similar to patterns reported elsewhere in the species' range (e.g. Monterroso et

377   al., 2013; Zalewski, 2007; Zielinksi et al., 1983). Previous studies have suggested that pine marten

378   activity patterns may be linked to those of prey species (Zielinski et al., 1983). The relationship

379   between predator and prey is highlighted by the suggestion that pine martens may play a role in

380   the control of the invasive grey squirrel, to the benefit of the native red (Sheehy & Lawton, 2014).

381   Although we have no direct evidence of this, pine marten activity in this study overlapped

382   considerably with that of the wood mouse in summer and winter. Studies indicate the importance

383   of wood mice to pine marten in Ireland in the absence of field voles (Lynch & McCann, 2007;

384   O'Meara et al., 2013; Twining et al., 2018) and seasonal comparisons, in particular, show that

385   wood mice are a major food source in all seasons but autumn (Twining et al., 2018) which is

386   reflected in the correlation of activity reported here.

387   Squirrel activity peaked several hours after dawn and ceased before sunset. The species

388   were almost exclusively diurnal between seasons, with detections occurring throughout the day

389   (Tonkin, 1983; Gurnell & Hare, 2008). There was some evidence of variation of circadian patterns

390   between seasons, with detections suggesting a bimodal pattern in the summer, and a unimodal

391   pattern in the winter. The bimodularity observed in summer was caused by low activity around

392   midday, possibly in response to increased temperatures (Tonkin, 1983; Zub et al., 2013). Similar

393   seasonal variation in activity has been observed in previous studies (e.g. Thompson, 1977; Tonkin,

394   1983; Gurnell & Hare; 2008). Sunrise/set offsets revealed some crepuscular/diurnal activity,

395   particularly during autumn and winter, behaviour that has not been reported in previous studies

396   (e.g. Tonkin 1983; Wauters & Dhondt 1987; Wauters et al., 1992). Foraging animals balance the

397   risk of predation against the benefits of energy gains (Dammhahn & Almeling, 2012) and the

398   acuity of squirrel eyesight is sub-optimal in low-light conditions (i.e. dawn/dusk; Jacobs, Birch &

399   Blackeslee, 1982). Crepuscular activity may, therefore, be a response to local predator activity,

400   thus rendering an apparently suboptimal strategy contextually advantageous (Dammhahn &

401   Almeling, 2012). The drivers of the observed crepuscular behaviour are unknown and are worthy

402   of further study.

403   Wood mice were nocturnal, although there was an increase in crepuscular and diurnal

404   activity recorded during summer when shorter nights may provide insufficient foraging time for

405   lactating female wood mice to meet their daily energetic requirements. Juveniles recently out of

406   the nest also may be active during daylight hours (Ian Montgomery, *pers. obs.*). The species has

407   previously been reported to exhibit temporal variability in activity patterns between seasons

408   (Miller & Elton, 1955, Wolton, 1983). Wood mouse detections were chance occurrences as none

409   of the camera trap projects that comprise this study specifically focussed on small mammals.

410   However, while small mammals may present identification challenges to camera trap studies (e.g.

411   Claridge et al., 2010; Meek & Vernes, 2016), wood mice were attracted to arboreal baiting stations,

412   often being the most recorded species. In contrast to other small mammals in Ireland, wood mice

413   are known to be arboreal, so the methodology used could be applied elsewhere in the world to

414   improve our knowledge of cryptic small mammals.

415   Anti-predator behaviours, which include avoidance (e.g. Curé et al., 2013), facilitate the

416   survival of the prey by mitigating predation (Sih & Christensen, 2001). In the current study, foxes

417   consistently occurred in sympatry with hares and rabbits, both of which are putative prey species

418   (Reynolds & Aebischer, 1991). Both predator-prey annual cross-correlations indicated that foxes

419   and lagomorphs are likely to be active simultaneously. In temperate zones, foxes typically mate in

420   late winter/early spring; litters may contain up to 12 cubs, with food availability being a significant

421   factor (Larivière & Pasitschniak-Arts, 1996). Here we describe foxes as becoming increasingly

422   crepuscular in late-spring and summer, thus increasing the potential for temporal overlap with both

423   species of lagomorph. This suggests that predation of these species may increase during the fox

424   breeding season. Indeed, lagomorphs may become an increasingly important food source as the

425   cubs grow, particularly if the vixen has many offspring, as both lagomorphs are amongst the most

426   substantial meals available to a medium-sized terrestrial predator in Northern Ireland. Given the

427   relative lack of carnivores in the country, we can be reasonably confident that the behavioural

428   repertoires of both hares and rabbits in Northern Ireland include fox-specific anti-predator

429   behaviours. Pine marten and squirrels showed a direct negative correlation in the annual

430   comparison, as well as during spring, summer, and winter. Thus, predator and prey activity are

431   simultaneously different (i.e. when pine martens are most active, squirrels are least active and vice-

432   versa). Squirrels are also subject to predation by diurnal birds of prey (e.g. Petty et al., 2003); by

433   avoiding nocturnal predators, the animals become diurnally vulnerable. However, while squirrels

434   have relatively poor nocturnal vision (Arden & Silver, 1962); their spatial acuity improves under

435   brighter conditions (Jacobs, Birch & Blackeslee, 1982). Foraging during the night thus greatly

436   increases the risk of predation.

437   It was not possible to optimise the present study *a priori*, comprising, as it does, several

438   individually-designed surveys. For example, there was considerable variation in the effective

439   densities of camera trapping arrays. Higher density arrays increase the chances of capturing an

440   animal in-transit, being placed near a resting site (i.e. sett, drey, form, etc.), and capturing the focal

441   species if it occurs at low densities. Camera trap surveys, therefore, would ideally consistently use

442   high-density arrays to return an abundance of data. This is rarely feasible, however, given time,

443   personnel, and financial constraints, all of which were limiting factors to the contributing surveys,

444   though, the involvement of trained citizen scientists spreads workload and increases the amount or

445   data available for analysis (e.g. Swanson et al., 2015). However, one of the key strengths of camera

446   trap research is the ability to collate data from disparate, methodologically unique studies to

447   describe fundamental ecological parameters. Moreover, the potential importance of bycatch data

448   from camera trap surveys cannot be over-stated and it is important that data can be aggregated

449   across independent surveys to answer relevant questions.

450   In contrast to terrestrial animals that move on a 2D plain, arboreal animals move within 3D

451   space, thus decreasing the likelihood of a random capture in transit. Squirrels were enticed to

452   specific locations for image capture by the use of baited stations. While baiting is certainly

453   effective, it is not without its problems. For example, animals may identify bait stations as a

454   reliable source of food, and thus frequently revisit them, thereby inflating counts (Rowcliffe &

455   Carbone, 2008). Moreover, feeding animals may spend a considerable amount of time in front of

456   the camera if undisturbed than those captured in transit, again affecting interpretations. The degree

457   of uncertainty increases considerably where the focal species does not exhibit individually-

458   identifiable colouration or markings. Captures from baited stations, therefore, may only represent

459   one, or a handful of individuals (Trolle & Kéry 2003, Weckel et al., 2006). However, the present

460   study is only concerned with activity, and, hence, the detection of any individual during a given

461   time period was assumed to be representative of the species as a whole. It should also be noted

462   that the data used in the present study are uncorrected for detection probability. Thus, observed

463   patterns could represent changes in animal activity, abundance or detectability over time. For

464   example, ambient noise can affect individual behaviour (Francis & Barber, 2013), subsequently

465   impacting the number of detections recorded during camera trap surveys along with associated

466   data and inferences. While we acknowledge that many factors will impact the detectability of a

467   species, including the height of emergent vegetation, camera placement, lighting condition (e.g.

468   daytime/night time), and the density and behaviour of the focal species (e.g. O'Brien et al. 2003;

469   Royle and Nichols 2003; Silveira et al., 2003; Larrucea et al., 2007; Harmsen et al., 2010;

470   O'Connell et al., 2010; Chandler et al., 2011; Meek et al., 2014; Cusack et al., 2015; Meek et al.,

471   2016), we are confident that, given our sample sizes, the data presented herein reflect actual

472   activity patterns of the reported species.

473   Understanding the activity patterns of wildlife, and seasonal variations thereof, is of

474   considerable benefit in furthering our understanding of species ecologies and informing future

475   research (e.g. the development and application of efficient ecological surveys), thus paving the

476   way for the development of appropriate management policies and/or conservation programmes.

477   Knowing when a species is most or least likely to be active can lead to considerable methodological

478   improvements, including potentially reducing the probability of achieving false-negatives,

479   particularly for scarce or cryptic species. Camera trap surveys seeking to investigate circadian and

480   intra-annual species activity patterns should, ideally, be conducted over the course of an entire

481   year, focussing on areas which the focal species are known to frequent, and employing a large

482   number of traps. Furthermore, additional data such as climate, topography and habitat may further

483   inform interpretations and facilitate the application of statistical models. While the temporal

484   distribution of data herein are arguably suboptimal due to the application of varied (i.e. non-

485   standardised) methodologies, and environmental data are lacking, they are nevertheless of great

486   utility in describing fundamental aspects of species' ecologies.

487

488   **Conclusions**

489   Camera traps allow practitioners to concurrently survey across a wide range of species and

490   habitats, providing data that may be of great utility in informing subsequent investigations and/or

491   answering important ecological questions. In the present study, we draw together several disparate,

492   and very different camera trap surveys to describe fundamental behavioural parameters of ten

493   mammal species. We found that focal-species-specific and associated bycatch data derived from

494   camera traps are effective in providing insight into the daily lives of mammals. In particular, they

495   have provided an effective means of describing circadian activity patterns and seasonal variations

496   in temporal activity. In addition, they have utility in investigating temporal aspects of interspecific

497   interactions and directing further research into such relationships. Invasive alien species are an

498   ongoing issue and mitigating the threats posed to Irish hares and red squirrels by their respective

499   conspecifics and potential predators requires accurate ecological data to effectively guide

500   conservation efforts. Furthermore, prey switching is an issue with regards to carnivores of

501   conservation interest (e.g. pine martens) and shifts in the activity patterns of disease vectors (e.g.

502   deer, badgers) are relevant to their control. As many of the species described herein are of

503   economic, management and/or conservation interest, our data will help inform the development of

504   appropriate species-specific methodologies and processes and associated policies.

505

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Figure 1

Locations of sites used in camera trap wildlife studies in Northern Ireland from 2013 – 2016.

For species-specific maps, see Fig. S3.

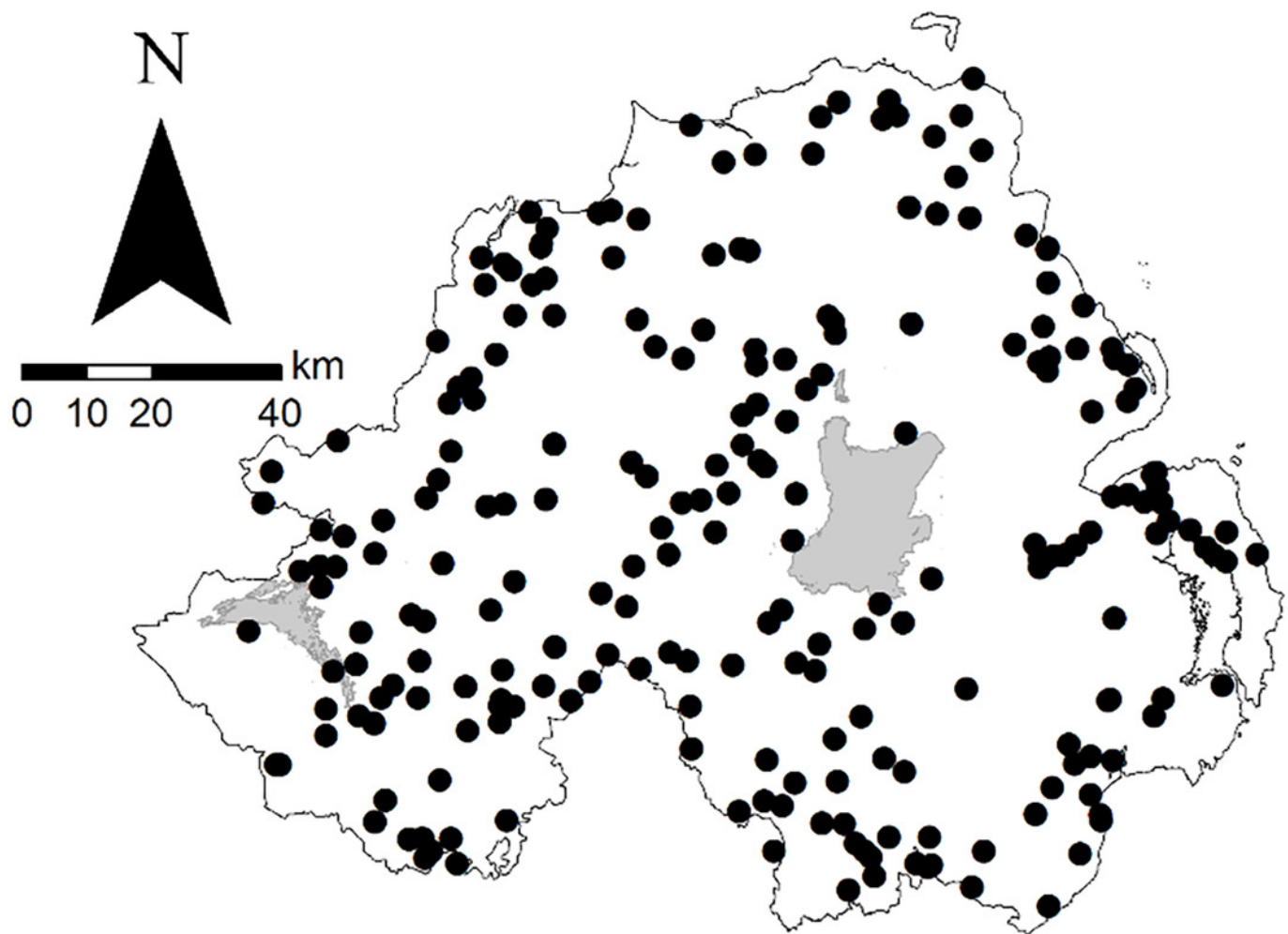



Figure 2

Camera trap images of ten mammal species detected in Northern Ireland between 2013-2016

(a) Badger, **(b)** fallow deer, **(c)** fox, **(d)** European hare, **(e)** Irish hare, **(f)** pine marten, **(g)** rabbit, **(h)** grey squirrel, **(i)** red squirrel, and **(j)** wood mouse (circled). Images provided by A. Caravaggi **(a, e, h, j)**, K. Hogg and M. Freeman **(b, c, g)** and D.G. Tosh **(f, i)**.

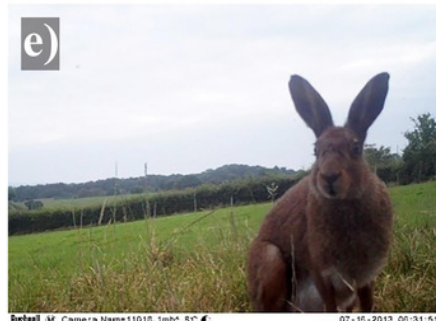



Figure 3

Circadian activity patterns of ten mammal species detected during camera trap surveys in Northern Ireland from 2013 – 2016.

(a) Fox (*Vulpes vulpes*) hare (Irish hare, *Lepus timidus hibernicus*, and European hare, *L. europaeus;* see Fig. S1) and rabbit (*Oryctolagus cuniculus*); **(b)** pine marten (*Martes martes*), wood mouse (*Apodemus sylvaticus*) and and squirrel (grey squirrel, *Sciurus californicus*, and red squirrel, *Sciurus vulgaris;* see Fig. S2); **(c)** badger (*Meles meles*) and fallow deer (*Dama dama*). Shaded areas represent night time.

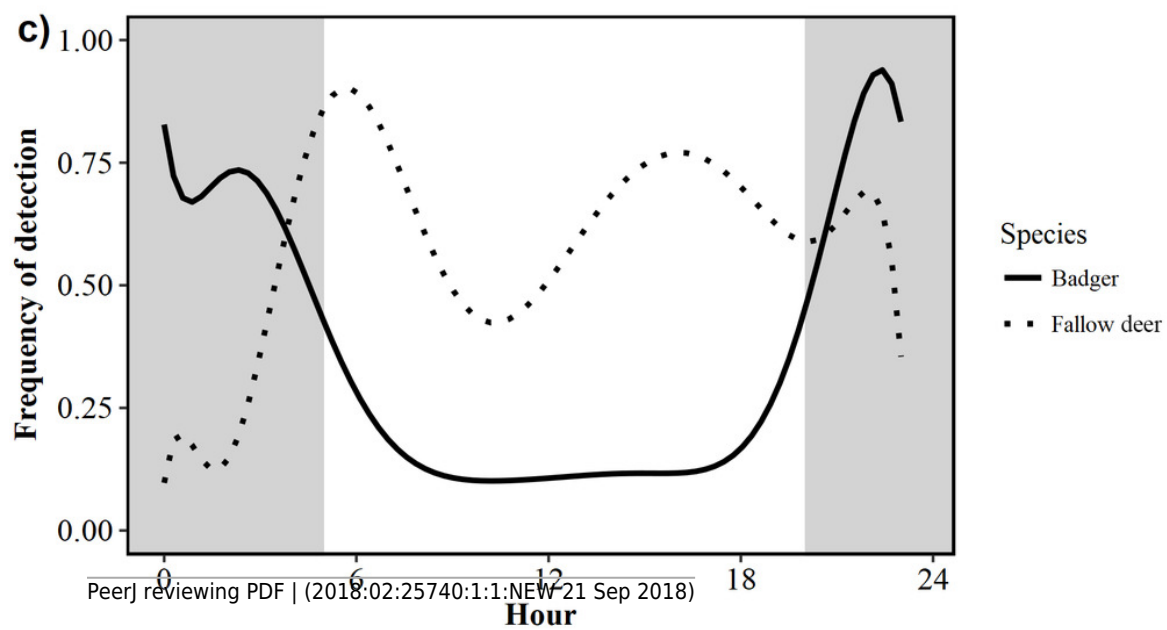
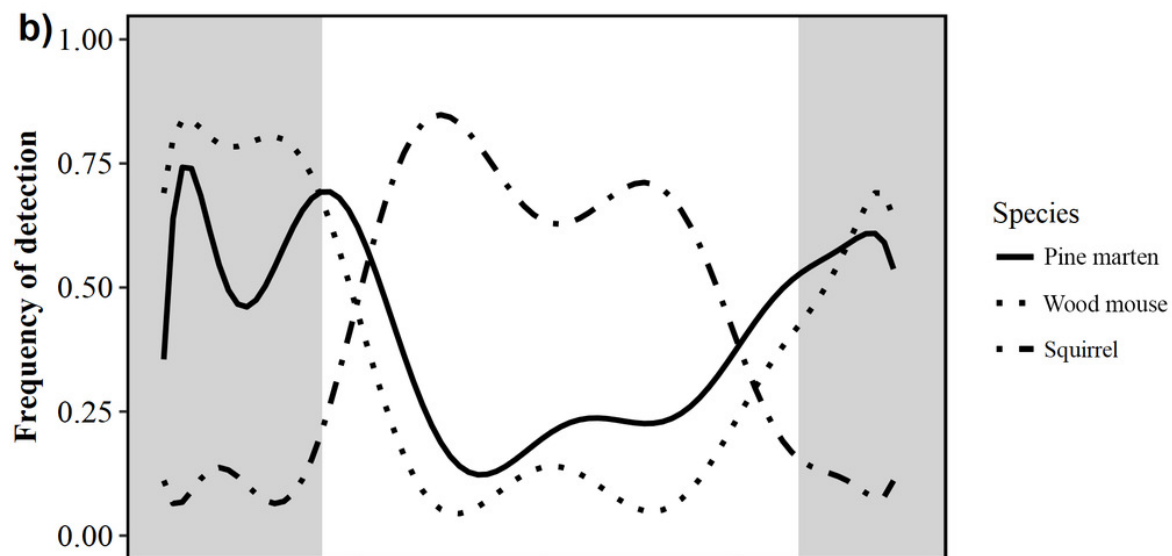
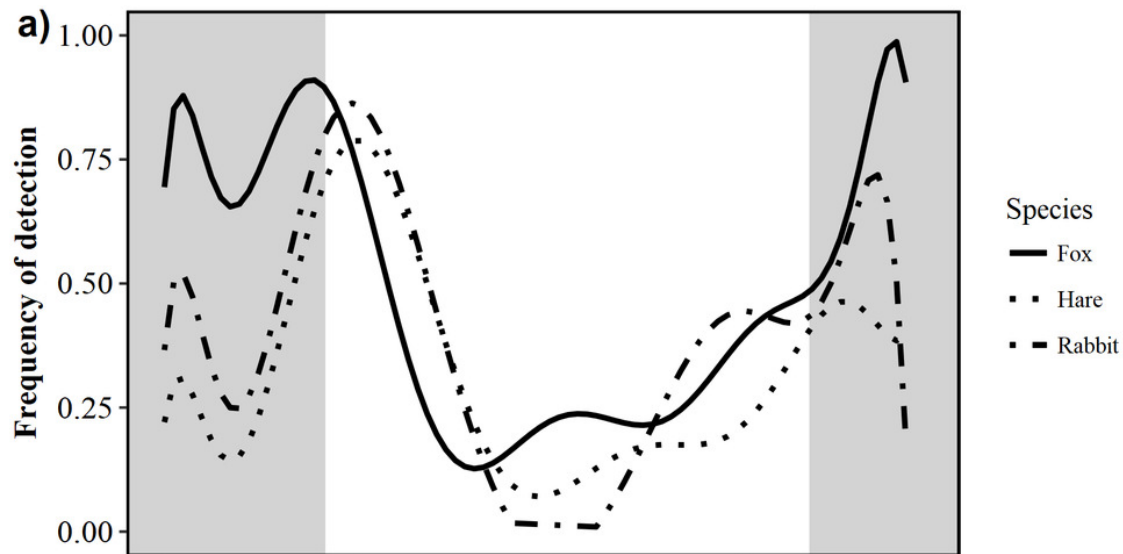
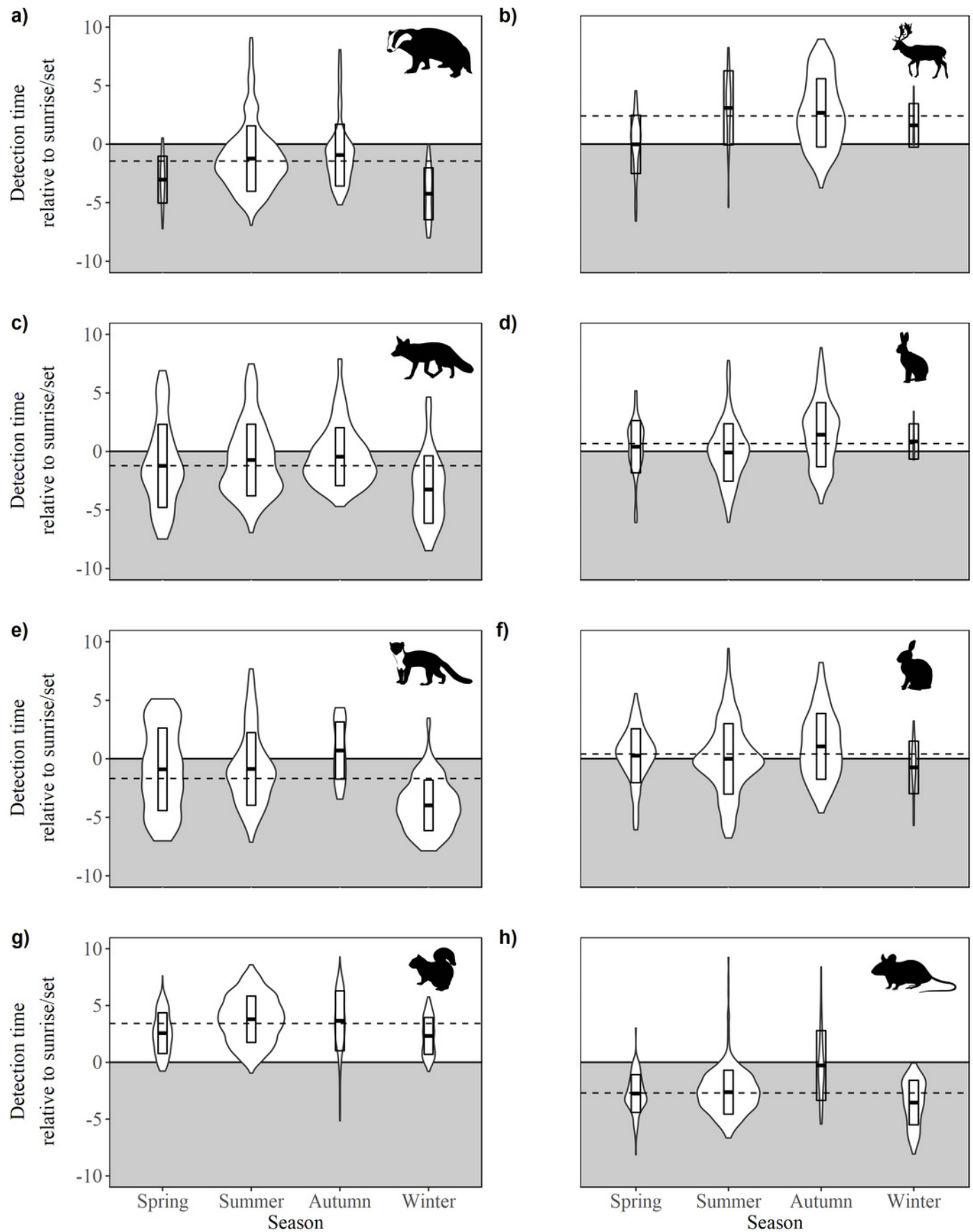



Figure 4

Time of detection relative to sunrise/sunset during spring, summer, autumn, and winter for ten mammal species observed during camera trap surveys in Northern Ireland between 2013 – 2016

(a) Badger, **(b)** fallow deer, **(c)** fox, **(d)** hare (Irish hare and European hare), **(e)** pine marten, **(f)** rabbit, **(g)** squirrel (grey squirrel and red squirrel), and **(h)** wood mouse. The upper, unshaded area denotes daytime, the lower, shaded area denotes night. Dashed lines indicate mean annual offset. Boxes represent the mean ± Standard Deviation. Violin plots represent the density and spread of all contributing data points.

Number of remote-sensing camera traps deployed (i.e. 'camera locations') by mammal studies carried out in Northern Ireland between 2013-2016.

Contributory studies were independent, thus methodologies were not standardised; study locations (size, shape) and camera array densities varied considerably. For more information, see the main Methods section. Squirrel surveys were focussed on presence and did not attempt to quantify the effective survey area of all camera placements.

Focal species	Year	Total survey area (km^2)	Active cameras	Deployments	Total camera locations
Deer (D1)	2013-14	20.00	38	23	255
Deer (D2)	2015	0.05	10	4	40
Deer (D3)	2015	0.02	10	2	20
Deer (D4)	2015	0.04	10	2	20
Deer (D5)	2015	0.05	17	1	17
Deer (D6)	2015	0.02	21	1	21
Hares	2013-14	17.00	20	17	340
Hares	2015	6.00	12	6	72
Squirrels (S1)	2014	n/a	16	63	63
Squirrels (S2)	2015	n/a	65	314	314

Total number of species detections during camera trap surveys in Northern Ireland from 2013 – 2016

Hare = Irish hare (*Lepus timidus hibernicus*) and European hare (*L. europaeus*); squirrel = grey squirrel (*Sciurus carolinensis*) and red squirrel (*S. vulgaris*). BM = body mass (Jones et al., 2009). Hare and squirrel body mass are given as a mean of the two detected species: European hare = 3.82 kg; Irish hare = 3.11 kg; grey squirrel = 0.55 kg; red squirrel = 0.33 kg. Species are ordered according to body mass.

Species			Season				
Common name	**Latin name**	**BM (kg)**	**Spring**	**Summer**	**Autumn**	**Winter**	$\sum$
Fallow deer	*Dama dama*	57.00	38	484	61	8	591
Badger	*Meles meles*	11.00	618	225	36	68	947
Fox	*Vulpes vulpes*	4.80	198	183	149	115	645
Hare	*Lepus sp.*	3.46	301	339	105	6	751
Rabbit	*Oryctolagus cuniculus*	1.59	492	417	238	28	1,175
Pine marten	*Martes martes*	1.30	251	73	356	286	966
Squirrel	*Sciurus sp.*	0.44	1,798	317	462	293	2,870
Wood mouse	*Apodemus sylvaticus*	0.02	449	57	119	191	816

Annual and seasonal overlap (%, with 95% Confidence Intervals [CIs]) in the activity patterns of five predator-prey pairs.

Animals were detected during camera trap surveys in Northern Ireland between 2013 – 2016. Hare = Irish hare (*Lepus timidus hibernicus*) and European hare (*L. europaeus*); squirrel = grey squirrel (*Sciurus carolinensis*) and red squirrel (*S. vulgaris*). Few hares were detected during winter. Activity data were resampled 1,000 times per pair, per category, to generate CIs.

Species			Season			
Predator	**Prey**	**Annual**	**Spring**	**Summer**	**Autumn**	**Winter**
Fox	Hare	73 (68-77)	75 (64-84)	67 (60-73)	48 (31-52)	-
Fox	Rabbit	80 (75-83)	89 (86-98)	78 (71-85)	52 (38-55)	51 (31-71)
Fox	Wood mouse	81 (75-87)	78 (67-89)	85 (81-92)	69 (57-74)	68 (65-98)
Marten	Squirrel	40 (33-41)	28 (16-30)	54 (41-60)	40 (32-41)	5 (0-5)
Marten	Wood mouse	71 (64-74)	69 (57-82)	71 (56-82)	63 (52-66)	77 (66-93)

Temporal (dis)associations between activity patterns of five predator-prey pairs.

Lag range and peak lag were calculated using cross-correlation functions (ccfs). t = t value, where the critical value (p = 0.05, df = 22) = 1.72. r = correlation coefficient. Positive values indicate that detections of predators preceded/succeeded those of prey species. Negative values indicate the opposite. Statistical significance is indicated by asterisks, where: * ≤ 0.05; ** ≤ 0.001; *** ≤ 0.0001.

Predator	Prey	Season	Lag (hrs)		Peak lag	t	r
			From	To			
Fox	Hare	Annual	-4	0	-2	4.15	0.663**
Fox	Hare	Spring	-2	3	1	3.12	-0.554*
Fox	Hare	Summer	-5	0	-3	3.54	0.602**
Fox	Hare	Autumn	-3	-1	-3	2.08	0.405*
Fox	Rabbit	Annual	-10	-8	-9	2.13	0.413*
Fox	Rabbit	Annual	-3	1	-1	4.13	0.661**
Fox	Rabbit	Annual	8	11	10	2.10	-0.409*
Fox	Rabbit	Spring	-1	2	1	4.61	0.701***
Fox	Rabbit	Spring	-	-	11	2.14	-0.415*
Fox	Rabbit	Summer	-12	-9	-4	2.52	-0.473*
Fox	Rabbit	Summer	-4	1	-1	4.06	0.654**
Fox	Mouse	Annual	-12	-10	-11	2.56	-0.480*
Fox	Wood mouse	Annual	-2	3	1	5.39	0.754***
Fox	Wood mouse	Spring	-2	3	1	3.26	0.570*
Fox	Wood mouse	Summer	-10	-9	-10	2.09	-0.407*
Fox	Wood mouse	Summer	-1	1	0	5.50	0.761***
Fox	Wood mouse	Autumn	0	2	2	3.04	0.544*
Pine marten	Squirrel	Annual	-12	-7	-9	2.15	0.416*
Pine marten	Squirrel	Annual	-1	4	1	3.72	-0.621**
Pine marten	Squirrel	Spring	-10	-4	-6	2.50	0.470*
Pine marten	Squirrel	Spring	0	5	1	3.76	-0.625**
Pine marten	Squirrel	Summer	-4	-1	-2	2.79	-0.512*

Pine marten	Squirrel	Summer	-	-	8	2.46	0.464*
Pine marten	Squirrel	Winter	-9	-7	-8	2.79	0.511*
Pine marten	Squirrel	Winter	-2	3	-1	4.18	-0.665**
Pine marten	Squirrel	Winter	9	11	10	3.11	0.553*
Pine marten	Wood mouse	Annual	-1	1	0	2.98	0.536*
Pine marten	Wood mouse	Spring	7	11	10	2.29	-0.440*
Pine marten	Wood mouse	Summer	3	-2	-2	2.24	0.431*
Pine marten	Wood mouse	Summer	-	-	8	2.46	0.464*
Pine marten	Wood mouse	Winter	2	4	3	2.73	-0.503*
Pine marten	Wood mouse	Winter	6	7	6	2.05	0.400*