temporal

Circadian activity, seasonal changes in activity patterns, and predator-prey relationships of free-ranging mammals revealed by camera traps (#25740)

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temporal

Circadian activity, seasonal changes in activity patterns, and predator-prey relationships of free-ranging mammals revealed by camera traps

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Endogenous circadian and seasonal activity patterns facilitate the effective utilisation of the environment and resources by organisms. Activity patterns are shaped by several environmental factors including weather, ecological competition, human disturbance and predator-prey interactions. Remote sensing camera traps allow the collection of occurrence data throughout the 24-hour period, and for an almost indefinite period of time. Here we collate data from three camera trap surveys, of deer, hare, and squirrel, to describe activity patterns and seasonal occurrence of ten small-to-large mammal species, and predator-avoidance behaviour (via lagged regression) in three predator-prey pairs, in Northern Ireland. 8,761 detections were recorded. Badger (*n* = 947), fox (*n* = 645), pine marten (*n* = 966) and wood mice (*n* = 816) were largely nocturnal; hares (*n* = 751; two species) were crepuscular; fallow deer (*n* = 591) and rabbits were cathemeral; and squirrels were diurnal. All species exhibited significant seasonal variation in activity relative to sunrise/sunset. In particular, foxes became increasingly crepuscular from spring to autumn and hares increasingly diurnal. Lagged regression analyses of predator-prey activity patterns between foxes and hares, foxes and rabbits, and pine marten and squirrel revealed significant annual and seasonal cross-correlations. We found highly synchronised activity patterns between foxes and lagomorphs in spring and summer (to a lesser extent in hares than rabbits) and temporal predator avoidance behaviour by squirrels relative to pine marten in most seasons. These results demonstrate the capacity of camera trap surveys to provide fundamental ecological data for a wide range of species, which may improve our understanding of species' ecologies, inform subsequent research efforts and

facilitate effective management and/or conservation efforts.

Original Article

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Abstract

Endogenous circadian and seasonal activity patterns facilitate the effective utilisation of the environment and resources by organisms. Activity patterns are shaped by several environmental factors including weather, ecological competition, human disturbance and predator-prey interactions. Remote sensing camera traps allow the collection of presence ~~occurrence~~ data throughout the 24-hour period, and for an almost indefinite period of time. Here we collate data from three camera trap surveys, ~~of deer, hare, and squirrel,~~ to describe circadian and seasonal activity patterns ~~and seasonal~~ presence ~~occurrence~~ of ten small-to-large mammal species, and predator-avoidance behaviour (via lagged regression) in three predator-prey pairs, in Northern Ireland. 8,761 detections were recorded. Badger (*n* = 947), fox (*n* = 645), pine marten (*n* = 966) and wood mice (*n* = 816) were largely nocturnal; hares (*n* = 751; two species) were crepuscular; fallow deer (*n* = 591) and rabbits were cathemeral; and squirrels were diurnal. All species exhibited significant seasonal variation in activity relative to sunrise/sunset. In particular, foxes were more ~~became increasingly~~ crepuscular from spring to autumn and hares more ~~increasingly~~ diurnal. Lagged regression analyses of predator-prey activity patterns between foxes and hares, foxes and rabbits, and pine marten and squirrel revealed significant annual and seasonal cross-correlations. We found ~~highly~~ synchronised activity patterns between foxes and lagomorphs in spring and summer (to a lesser extent in hares than rabbits) and temporal predator avoidance behaviour by squirrels relative to pine marten in most seasons. These results demonstrate the capacity of camera trap surveys to provide fundamental ecological data for a wide range of species, ~~which may improve our understanding of species' ecologies,~~ inform subsequent research efforts and facilitate effective management and/or conservation efforts.

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Introduction

It is critical for the survival of individuals that their activities are temporally appropriate (Enright, 1970). Circadian (i.e. recurring every 24 hours) and seasonal patterns of activity are adaptive behavioural traits which allow species to effectively exploit their environment and the resources contained therein (Phillips et al., 2013). The activity patterns of species are shaped by a variety of environmental pressures, including food availability (Larivière et al., 1994), foraging efficiency (Lode, 1995), predator/prey activity (Middleton et al., 2013), human disturbance (van Doormaal et al., 2015; Wang et al., 2015), mate availability and activity (Halle & Stenseth, 2000), light/dark and temperature cycles (McElhinny et al., 1997), and ecological competition (Rychlik, 2005).

Mammals exhibit a great diversity and flexibility in their various activity patterns. A recent study of 4,477 mammal species classified 69% as nocturnal (i.e. night-active, e.g. European hedgehogs, *Erinaceus europaeus*; Rautio et al., 2016), 20% diurnal (i.e. day-active, e.g. eland, *Taurotragus oryx*; Shrestha et al., 2014; Jones et al., 2009), 8.5% cathemeral (i.e. active throughout the 24-hour cycle, e.g. cougar, *Puma concolor*; Gómez et al., 2005) and 2.5% crepuscular (i.e. dawn- and/or dusk-active, e.g. lesser mouse deer, *Tragulus kanchil*; Ross et al., 2013; Bennie et al., 2014). Furthermore, there is evidence for intraspecific variation of activity patterns (e.g. Ashby, 1972, McElhinny et al., 1997, Refinetti, 2004). For example, half of captive laboratory degus (*Octodon degus*), a nocturnal species in their native range, were found to become active during the light phase (lights-on), while the other half became active during the dark phase (lights-off) (Refinetti, 2006). Indeed, circadian activity patterns are frequently related to daily oscillation in illumination (i.e. changes in sunrise/sunset; Halle & Stenseth, 2000), and, hence, the time(s) of the day during which species are active may vary according to climatic ?? season.

Recording and quantifying daily activity patterns of wild, free-ranging mammals presents significant challenges, including overcoming the observer effect whereby the presence of an observer influences the behaviour of the subject (Stewart et al., 1997), and collecting sufficient data to address scientific and conservation questions (*sensu* Cagnacci et al., 2010). A number of methodological techniques have been used to overcome such challenges, with varying degrees of success (Bridges & Noss, 2011). Radio-tracking has been successfully employed in a number of activity-based studies of wild animals. However, such studies have inherent limitations, including periodic (i.e. non-constant) sampling (e.g. Lovari et al., 1994) and the application of considerable survey effort (Palomares & Delibes, 1991; Reid, McDonald & Montgomery, 2010). Furthermore, they may result in small sample sizes (Bridges & Noss, 2011), capture a limited proportion of the population (Sadlier et al., 2004), and may be subject to signal-based error and/or omission (Cagnacci et al., 2010) or alter the behaviour of tagged animals (e.g. Wilson et al., 2011). Live trapping has been used to investigate activity patterns of small mammals, where each successful capture (i.e. the presence of an animal in a trap) is taken as indicating activity. This has been successfully applied to a number of species, including common voles (*Microtus arvalis*; e.g. Hoogenboom et al., 1984), bank vole (*Myodes glareolus*) and wood mice (*Apodemus sylvaticus*; e.g. Elton et al., 1931), and the antelope ground squirrel (*Citellus leucurus*; e.g. Bradley, 1967). However, live trapping requires considerable time and effort, is relatively inefficient, may have implications with regards to animal welfare (Torre et al., 2010), and is subject to species- and trap-specific variations in capture probability (Leso & Kropil, 2010).

Remote-sensing camera traps are of increasing popularity in conservation and ecological studies due to their non-invasive nature, continuing technological improvements and decreasing costs (Tobler et al., 2008a). They have been used in studies investigating population parameters (e.g. Trolle & Kéry, 2003, Karanth et al., 2006, Caravaggi et al., 2016), behaviour (e.g. Maffei et al., 2005), ecosystem biodiversity (e.g. Silveira et al., 2003, Tobler et al., 2008b), and site occupancy of rare or cryptic species (e.g. Linkie et al., 2007). Camera traps afford researchers the means to conduct surveys while minimising ~~survey effort and~~ disturbance of the focal species, and over a longer period of time than may otherwise be feasible. As such, data derived from camera trap surveys of sufficiently common species and/or conducted at high camera densities are well suited to investigations of wildlife activity patterns (e.g. Di Cerbo & Biancardi, 2013, Carbajal-Borges et al., 2014). ~~The size of camera trap survey arrays are limited only by the cost of equipment, with time *in-situ* restricted by available memory, battery life and the possibility of mechanical failure.~~ Furthermore, remote camera surveys may be less biased than other methods due to their non-invasive nature (Kays & Slauson, 2008). However, camera trap surveys are not without their problems. These include equipment failure, false-triggers (i.e. detections triggered by non-target stimuli, such as vegetation; *sensu* Gregory et al., 2014), equipment theft, and poor performance due to, e.g. user skill, environmental conditions, and damage by animals (Swann et al., 2004, Kucera & Barrett, 2011). There is also a trade-off between the proximity and angle of cameras with regards to targets, and the likelihood of detecting and identifying species of varying size (Hofmeester et al., 2017). Downward-facing cameras, for example, are more efficient at detecting small mammals, while those in close proximity to bait stations are more likely to detect species which are drawn to the bait (De Bondi et al., 2010). These potential weaknesses can, however, be mitigated against by regular checks of equipment, field-tests (i.e. pilot studies), and the development of an appropriate species- or community-specific methodology (e.g. Gregory et al., 2014).

Most studies of mammals tend to focus on distributions, current statuses and population estimates of a focal species, but few focus on quantifying activity patterns. Here, we demonstrate the utility of camera traps in elucidating mammalian temporal activity patterns (circadian and seasonal) ~~and seasonal variations in activity relative to sunrise/sunset~~. In addition, we use camera trap data to investigate interspecific relationships, specifically predation risk, between activity patterns of paired predators and prey. We hypothesise that prey species will exhibit temporal avoidance of predators.

Materials and methods

Data were collected from camera trapping studies of deer, squirrels, and hares in Northern Ireland. The climate was temperate with localised variation, most notably with regards to annual precipitation (Met Office, 2016). The landscape was largely comprised of agricultural fields (EEA, 2010), and human activity was variable depending on location. A total of 1,164 ~~individual~~ cameras ~~deployments~~ were deployed ~~used across the study periods~~, at 431 locations (defined herein as ~~broad~~ study areas, rather than individual camera placements) across Northern Ireland (Fig. 1). Deer surveys ran from June 2013 to November 2016, squirrel surveys from January to March in 2014 and January to May in 2015 and hare surveys from April 2013 to August 2015, non-inclusive. Ten commonly-detected target species were identified for the purposes of the ~~current~~ study, *a priori*: i) European badger (*Meles meles*, Linnaeus 1758); ii) fallow deer (*Dama dama*, Linnaeus 1758); iii) Red fox (*Vulpes vulpes*, Linnaeus 1758; hereafter 'fox'); iv) Irish hare (*Lepus timidus hibernicus*, Bell 1837); v) European brown hare (*L. europaeus*, Pallas 1778); vi) pine marten (*Martes martes*, Linneus 1758); vii) European rabbit (*Oryctolagus cuniculus*, Linnaeus 1758); viii) Eurasian red squirrel (*Sciurus vulgaris*, Linnaeus 1758); ix) North American grey squirrel (*S. carolinensis*, Gmelin 1788); x) wood mouse (*Apodemus sylvaticus*, Linnaeus 1758). There was no evidence of intrageneric variation in the activity patterns of hare (Fig. S1) and squirrel (Fig. S2) species, and, hence, both were grouped (i.e. 'hares' and 'squirrels') for the purposes of the current study.

Deer surveys

Data from four deer studies (DS1 – 4) were included in our analyses. DS1 – 2 were conducted over 15 1 km^2 ~~squares~~ grids with an average of 10 cameras per km and 5 additional 1 km^2 squares set at a higher density of 20 camera traps per km. In total 38 camera traps were deployed over 255 individual camera trap placements using a combination of Bushnell Trophy Cam (119467), Bushnell Trophy Cam HD (119477), Reconyx (HC600) and Scoutguard Camera (SG560P-8M). Camera traps were set at a height of 30cm, perpendicular to the ground. Cameras were set to capture the maximum photographs per trigger (3-10 photographs depending on camera model) and no delay between triggers. Cameras were left for at least 14 days before being collected and relocated. DS3 surveyed smaller areas of 0.05 km^2, 0.02 km^2 and 0.04 km^2 using 10 Bushnell Trophy Cam HD (119677) at each site. Each camera was set at a height of 40cm from the ground and set to capture bursts of 3 still pictures and a 60-second video per trigger, with a delay of one second between triggers. Cameras were left *in situ* for 7 days. DS4 was focussed on areas of 0.05 km^{2}and 0.02 km^2 and used Bushnell Trophy Cam HDs (119477, 119577, 119676, 119677). Cameras were set at a height of 40cm and set to capture either3 still pictures or a 30s video, depending on the camera model, with a one second delay between triggers. Cameras were left in situ for 7 days. In all deer surveys, cameras were equipped with fitted with 8 GB HDSD cards, secured with Python security cables, motion detectors were set to medium sensitivity, each capture was stamped with the date and time, and images were described as independent when separated by one hour.

Hare survey

Hare surveys were conducted over a total of ~~twenty-three~~ 23 1km^2 ~~squares.~~ grids Each ~~square~~ grid contained twenty randomly placed Bushnell Trophy Cam HD (119477) camera traps fitted with 8 GB HDSD cards, which were positioned on vertical aspects of linear features (i.e. trees in hedgerows, fence posts), to a total of 460 camera locations (Table 1). Cameras were attached using python cables at a height of 30cm from the ground, at a 45º - 90 º angle away from the linear feature, with a 10-15º downward tilt. Cameras were set to record date-and-time-stamped videos, with motion detectors set to medium sensitivity, for a period of 60 seconds with a 60 second delay between ~~triggers.~~ videos Cameras were left ~~*in-situ*~~ for 7 days. The use of video footage allowed the detection of closely-associated conspecifics, while the 60 second delay gave some measure of mitigation against re-detecting the same individual. For full details, see Caravaggi et al. (2016).

Squirrel and pine marten surveys

Data from two squirrel and pine marten surveys are used in this study. The first survey was undertaken in 2014, within 63 forested areas > 5ha in size within Co. Fermanagh. A total of 16 Bushnell Trophy Cameras (119438) were deployed by 7 citizen scientists and 1 scientist during a 3-month period. Cameras were attached to trees at a height of 3-4m, opposite a wooden squirrel feeder (Northumbrian Wildlife Trust design) baited with peanuts and sunflower seeds. Cameras were left ~~*in situ*~~ for a minimum of 7 and maximum of 24 days. The second survey was conducted in 314 forested areas > 5ha in size across Northern Ireland by 70 citizen scientists and 1 scientist during a 5-month period in 2015. A total of 65 Bushnell Trophy Cameras (119438; 119577; 119676) were deployed during this time for a minimum of 6 and maximum of 33 days. Cameras were deployed at head height (1.5 -2m) on a tree opposite either a wooden (as in 2014) or metal squirrel feeder (CJ Wildlife Product code 12335). Cameras were secured using python locks to trees. In both years, cameras were set to take photos with 3 photos per trigger and an interval of 1 – 20 seconds per trigger and images were recorded on 8GB HDSD cards.

Activity analysis

We assumed that temporal detection frequency was a true reflection of circadian activity patterns of the focal species. Prior to analysis, all species data were grouped according to one-hour time intervals, beginning at the hour mark (e.g. 11:00 – 11:59). Detections of animals which occurred at either side of the hour mark were both retained. In cases where a group of individuals of the same species (e.g. fallow deer) were detected in a single camera photo, a single event was recorded. Detection frequencies were normalised to ease plot interpretation using the formula $z_i = \frac{x_i - x_{min}}{x_{max} - x_{min}}$, where z_i = normalised detection frequency at the ith interval, and $x = (x_1 \ldots, x_n)$.

Due to the Earth's axial tilt, non-equatorial regions experience variations in day length throughout the year. This has direct consequences for wildlife. For example, a nocturnal species may be more likely to remain active well into twilight, or even daylight hours during the summer months due to shortening nights; unavoidable to meet its energetic requirements (Schai-Braun et al., 2012). To investigate intra-annual variation in activity relative to sunrise/sunset (i.e. whether nocturnal/diurnal activity differed between seasons; solar cycle historical data obtained from the HM Nautical Almanac Office, 2016), data were grouped according to season: spring (March – May); summer (June – August); autumn (September – November); and winter (December – February). Detections between 00:00 and 11:59 were offset relative to sunrise; detections between 12:00 and 23:59 were offset relative to sunset. All daytime offsets were converted to positive integers, night-time to negative. For example, a detection ~~timed~~ at 22:10, with sunset at 20:00, would have an offset value of -2 hours and 10 minutes, indicating nocturnal activity. Intraspecific differences in seasonal offsets were investigated via one-way Analysis of Variance (ANOVAs) with *post-hoc* Tukey tests.

Overlap metrics and lagged regression cross-correlation functions (CCFs) were used to examine annual and seasonal relationships between predator-prey pairs (i.e. autocorrelation), specifically: fox and hare; fox and rabbit; and pine marten and squirrel. Data were restricted to locations where both species in each pair were detected~~, thus negating false inference.~~ The degree of overlap between each species pair on an annual basis and for each season was calculated using the *overlap* package (Meredith & Ridout, 2017). Data were resampled 1,000 times per pair, per category, to generate 95% Confidence Intervals (CI). Sample CCFs facilitate the identification of lags in the x variable which may be predictive of y. Positive lag (h+) is the result of a correlation between x_{a+i} and y_a, where a = time. Conversely, negative lag (h-) is the result of a correlation between x_{a-i} and y_a. Significant correlations describe a non-random association between species detections at interval(s) h_i. Lagged regressions were calculated using the ccf function in the core library of R (R Core Team 2016). The CCF function does not, however, return quantified measures of significance. The significance of the correlation coefficient, r, therefore, was established by calculating the t value, where $t = r\sqrt{\frac{n-2}{1-r^2}}$ and where the critical t value (p = 0.05, 22 degrees of freedom, one-tailed) = 1.72. All statistical analyses were carried out in R 3.4.3 (R Core Team, 2017).

Results

A total of 8,761 detections of the ten target species were recorded. Squirrel sightings ($n = 2,870$; Fig. 2g) comprised 33% of all records, rabbits 13% ($n = 1,175$; Fig. 2f), pine marten 11% ($n = 966$; Fig. 2e), badger 11% ($n = 947$; Fig. 2a), hares 9% ($n = 751$; Fig. 2d), woodmice 9% ($n = 816$; Fig. 2h), fox 7% ($n = 645$; Fig. 2d), and fallow deer 7% ($n = 591$; Fig. 2b; Table 2). Seasonal variations in the number of detections recorded reflected the time and duration of the constituent studies: 47% in spring, 24% in summer, 18% in autumn, and 11% in winter (Table 2).

Species-specific activity patterns

Foxes exhibited a largely nocturnal activity pattern, with some irregular diurnal activity. Nearly three-quarters of all fox activity (73%) occurred between 21:00-07:00 (Fig. 3a). There were significant differences in offsets across seasons ($F_{33,641} = 23.36$, $p < 0.0001$); winter was significantly different from all other seasons due to decreased activity during daylight and crepuscular periods (Fig. 4c). Start on next paragraph The activity pattern of hares was bimodal, demonstrating predominantly crepuscular behaviour. 71% of all activity occurred between the hours of 20:00-23:00 (24%) and 04:00-08:00 (47%). Diurnal detections (09:00-19:00) accounted for 18% of all activity (Fig. 3a). Seasonal offsets differed significantly ($F_{3,747} = 19.33$, $p < 0.0001$), specifically between spring and summer ($p < 0.0001$) and summer and autumn ($p < 0.001$; Fig. 4d); hares exhibited more diurnal activity both in spring and in autumn. Start on next paragraph Rabbits exhibited a cathemeral activity pattern with a peak around dawn and two smaller peaks in the evening. 35% of all detections occurred between 04:00-08:00; 32% between 17:00-23:00 (Fig. 3a). There were significant differences in offsets across and between seasons ($F_{3,1171} = 12.93$, $p < 0.0001$(Fig. 4f).

Pine marten activity was largely nocturnal, with 70% of all detections occurring between 21:00 and 06:00 (Fig. 3b). Significant differences were observed across and between all seasons ($F_{3,962} = 86.28$, $p < 0.0001$), except spring-autumn. Squirrels were diurnal, being active from dawn to dusk. Fewer than 5% of triggers occurred between 19:00 and 05:00 (Fig. 3b). There were significant differences across seasons ($F_{3,2866} = 76.52$, $p < 0.0001$; Fig. 4g). All between-season comparisons were significant at the $p > 0.0001$ level, except for winter-autumn and summer-spring.

Badgers were nocturnal with a unimodal pattern of activity; the number of detections increased rapidly after dusk and decreased rapidly around dawn. Fewer than 15% of all badger detections were recorded between 06:00-19:00 (Fig. 3c). There were significant differences in offsets across seasons ($F_{3,943} = 32.54$, $p < 0.0001$) and all between-season comparisons were significantly different ($p > 0.0001$) except for winter-autumn and summer-spring. Fallow deer exhibited a cathemeral activity pattern, with peaks of activity during early morning, late afternoon, and early evening with a lull around midday and after midnight (Fig. 3c). There were significant differences in offsets across seasons ($F_{3,587} = 16.7$, $p < 0.0001$), specifically between spring and autumn ($p > 0.0001$) and summer and autumn ($p > 0.0001$; Fig.4b). Wood mice were nocturnal (Fig. 3c; 4h); activity peaked between 01:00 and 04:00, during which time 41% of captures were recorded, and declined rapidly thereafter (Fig. 3h). Offsets were significantly different across seasons ($F_{3,81\ 2}= 39.31$, $p > 0.0001$), with diurnal activity increasing in summer (Fig. 4h).

Predator-prey relationships

There was evidence of correlative relationships between all predator-prey pairs both annually and between seasons. Fox and hare annual activity patterns showed 73% overlap (CI 68% - 77%; Fig. Table 3) and were significantly positively correlated with a peak at -2hrs (peak lag = *pl*, hereafter; $r=0.663$, $t_{22}=4.15$, $p<0.0005$, Fig. 5ai, Table 4). The degree of overlap peaked in spring at 75% (CI 64% - 84, Table 3; $pl = 1$hr, $r = -0.554$, $t_{22} = 3.12$, $p < 0.005$, Fig. 5aii, Table 4), with the degree of temporal separation suggesting increased predation risk. There were significant correlations in the summer (Fig. 5aiii, Table 4) but a lack of hare detections meant there were insufficient data available to conduct analyses for winter ($n = 9$, Fig. 5av). Annual activity patterns of foxes and rabbits overlapped by 80% (CI 75% - 83%, Table 3) and were significantly correlated, with a peak at -1hr ($pl = -1$hr, $r = 0.661$, $t_{22} = 4.13$, $p < 0.0005$, Fig. 5bi, Table 4). Overlap was greatest during spring at 89% (CI 86% - 98%, Table 3; $pl = 1$hr, $r = 0.701$, $t_{22} = 4.61$, $p < 0.0005$, Fig. 5bii, Table 4) and lowest during winter (51%, CI 31% - 71%, Table 3). Seasonal activity patterns between the species were positively correlated during spring and summer (Table 4), but there were no significant correlations evident during the rest of the year (Fig. 5biv - 5bv). Fox and wood mouse annual activity patterns overlapped by 81% (CI 75% - 87%; Table 3). Seasonal activity was high in all seasons but was greatest in summer with at 85% (CI 81%-92%, Table 3). Annual activity was significantly correlated ($pl = 1$hr, $r = 0.754$, $t_{22}=5.39$, $p \leq 0.0001$, Fig 5ci, Table 4), with similar peaks in cross-correlation coefficients in spring (Fig5 cii, Table 4) and autumn, with greatest correlation occurring in summer ($pl = 0$hrs, $r = 0.761$, $t_{22}=5.50$, $p \leq 0.0001$, Fig 5ciii, Table 4).

Pine marten and wood mouse annual activity patterns were correlated with a 71% (CI 64%- 74%) overlap ($pl = 0$hrs, $r=0.536$, $t_{22}=2.98$, $p \leq 0.05$, Fig. 6ai, Table 4). Overlap was greater than 50% for all seasons with a peak of 77% (CI 66%-93%) occurring in winter months (Table 3). Activity patterns were significantly correlated in spring ($pl = 10$ hrs, $r=-0.44$, $t_{22}=2.29$, $p \leq 0.05$,

Figure 6aii, Table 4) and winter (*pl* = 3 hrs, $r=-0.503$, $t_{22}=2.73$, $p \leq 0.05$, Figure 6aiv). No correlations were observed between pine marten or wood mouse activity patterns in autumn (Figure 6). Pine marten and squirrel annual patterns overlapped by 40% (CI 33% - 41%, Table 3) and their activity was significantly correlated (*pl* = 2hrs, $r = -0.621$, $t_{22} = 3.72$, $p < 0.001$; Fig. 6bi, Table 4). Seasonal overlap peaked during summer at 54% (CI 41% - 60%) but was almost entirely absent during winter (Table 3). Significant correlations between seasonal activity patterns were observed in all seasons except during autumn: spring, *pl* = 1hr, ($r = -0.625$, $t_{22} = 3.76$, $p > 0.001$, Fig. 6bii); summer, *pl* = -2hrs ($r = -0.512$, $t_{22} = 2.79$, $p < 0.001$, Fig. 6biii); and winter, *pl* = -1hr ($r = -0.665$, $t_{22} = 4.18$, $p < 0.0005$, Fig. 6bv, Table 4).

Discussion

All ten species included in this study were found to change their activity patterns in relation to sunrise/sunset. Some species were found to markedly change their activity during a specific season. For example, foxes exhibited more nocturnal behaviour in winter and rabbits were more diurnal in the summer ~~months.~~ In contrast, the seasonal activity patterns of badgers, hares, pine marten, squirrels and wood mice were found to be distinct between ~~most~~ seasons. Fallow deer had the most consistent temporall~~y~~ ~~consistent~~ activity pattern, possibly due to the absence of predators, though they did exhibit some variability~~,~~ ~~particularly~~ during autumn. Similarly, predator-prey relationships were also found to vary throughout the year. The temporal activity overlap between ~~the activity patterns~~ ~~of~~ foxes and lagomorphs (rabbits and hares), were high during the spring and summer and declined later in the winter ~~year with an increase in hours of darkness~~. Pine marten and squirrels exhibited substantially low ~~less~~ overlap throughout most of the year with the ~~notable~~ exception of summer, during which ~~time~~ the ~~there was a considerable~~ ~~increase~~ ~~in~~ marten was significantly/ predominantly diurnal ~~activity,~~ an increase in crepuscular - and to a lesser extent, nocturnal - squirrel activity and interspecific overlap exceeded 50%.

Badgers were significantly/predominantly ~~almost exclusively~~ nocturnal, a finding in accordance with the literature (e.g. Neal & Cheeseman, 1986; Gorman, 2008; Fedriani et al., 1999). Nearly half (49%) of their total activity occurred in the hours between ~~around midnight (~~22:00-02:00~~)~~. Diurnal activity, while uncommon, is not unknown, reported ~~occurring~~ in rural areas with relatively limited ~~little~~ human presence ~~activity~~ (Harris, 1982; Neal & Cheeseman ,1996). In the present study, where data were collected from a sparsely populated agricultural landscape, diurnal activity accounted for less than 15% of all captures, ~~in accordance with the findings of~~ (Fedriani et al., (1999)). Fewer captures were recorded in autumn and winter (*n* = 68) than in spring and summer (*n* = 282). While badgers are less active ~~largely inactive~~ in winter, torpor

(Fowler & Racey, 1988) does not explain the low number of autumn captures which may instead be explained by spatial variation in badger density or occurrence, variations in the way the animals used the landscape and/or spatio-temporal variation in survey effort.

Maybe the animals were not just detected because some of the studies had cameras positioned way high above the ground???

Fallow deer were ~~found to be~~ active throughout the 24-hour period (*sensu* Chapman & Chapman, 1997). Activity was lowest during late morning through to early afternoon (~~13% of detections occurred between~~ 09:00-12:00), and in the hours around midnight (~~8% between~~ 23:00-01:00). Sunrise/sunset offsets described largely diurnal and cathemeral activity. It has been suggested that fallow deer are sensitive, and exhibit facultative behavioural responses to anthropogenic disturbance, such as an increase in nocturnal activity (Putman, 2008). Contributing factors such as disturbance, however, remain unquantified and data were not evenly spread such that inter-location pattern differences were sufficiently evident.

Foxes were ~~found to be~~ largely nocturnal; their activity ~~increased~~ during dusk and decreased at dawn, although some activity occurred during daytime. The bimodal activity pattern suggested by previous studies (e.g. Reynolds & Tapper, 1995) was not evident. As with fallow deer (although to a considerably lesser extent) ~~rural~~ fox activity may be influenced by anthropogenic disturbance; diurnal activity is more common where disturbance is low (e.g. Díaz-Ruiz et al., 2016; Gorman, 2008). In the present study, however, diurnal activity may have been facilitated, not by a lack of disturbance, but by the timing of the disturbance. Foxes are subject to nocturnal lethal control (i.e. shooting, facilitated by high-powered spot-lamps, and other methods) across Northern Ireland, such that nocturnal disturbance is likely to be considerably greater than that which occurs during the day, albeit periodically. However, the most abundant and commonly taken prey animals are nocturnal (e.g. small rodents) or crepuscular (e.g. lagomorphs). Thus, activity ~~periods~~ patterns of prey may dictate that of ~~rural~~ foxes in Northern Ireland.

Hares were active throughout the night, with peaks of activity occurring between 20:00 and 23:00 ~~(24%)~~, and 04:00 and 08:00 ~~(47%)~~. Diurnal activity was most commonly ~~recorded~~ in the summer ~~months, when nights are shortest.~~ These findings agree with previous observations of hare behaviour (e.g. Flux & Angermann, 1990, Holley, 1992, Langbein et al., 1999). Mean offset, however, was lower in summer ~~when compared to~~ than in autumn and winter. This may be explained in terms of decreased hare detectability due to vegetation growth. This study is the first to quantify activity patterns of the Irish hare, which exhibited the same bimodal crepuscular-nocturnal behaviour as the European hare. The Irish hare is a subspecies of mountain hare which is endemic to Ireland. The European hare was introduced to Ireland in the mid-to-late 1800s (Barrett-Hamilton, 1898); a remnant population exists in Mid-Ulster (Reid & Montgomery, 2007; Reid, 2011). Given that the species are ecologically equivalent (Caravaggi et al., 2015) and exhibit the same activity patterns, strong interspecific competition is likely where they occur in sympatry ~~where~~ and resources are limiting.

Rabbits ~~were found to be~~ cathemeral with crepuscular peaks of activity; activity ~~declined markedly~~ being low around midday and midnight. There was a suggestion of underlying bimodularity, though evening activity was somewhat irregular and inconsistent. Activity patterns of rabbits in Northern Ireland were similar to those in the Mediterranean region (Monterroso et al., 2013), though the second, evening peak was weak in our dataset. The irregularities observed may be the result of sampling artefacts; data were compiled from several (sub-)populations, each of which is undoubtedly subject to locally-distinct factors (e.g. human activity, predator density and/or activity, weather), and variations thereof. In this context, future studies focusing on rabbit activity patterns should investigate activity pattern differences between study sites.

Pine marten were predominantly nocturnal exhibiting sporadic periods of activity, behaviour which agreed with previous studies of the species in mainland Europe (e.g. Monterroso et al., 2013; Zalewski, 2007; Zielinksi et al., 1983). ~~Nocturnal detections accounted for 70% of all observations~~. Previous studies have suggested that pine marten activity patterns may be linked to those of prey species (Zielinski et al., 1983)~~, and that there may be intra-individual seasonal (Zielinski et al., 1983) and sexual (Zalewski, 2001) variation in behaviour~~. Although, individual identity and associated factors (e.g. sex, age) were unknown, our study supports pine marten activity in Ireland being ~~linked~~ associated with ~~to~~ its that of prey. Pine marten activity overlapped significantly with that of the wood mouse in spring, summer and winter. This reflects findings ~~of contemporary studies~~ from Ireland that indicate the importance of wood mice to pine marten diets (Lynch & McCann, 2007; O'Meara et al., 2013). Seasonal comparisons of diet, in particular, show that wood mice are the primary food source in all seasons ~~bar~~ but autumn which is reflected in the correlation of activity reported here (Twining et al., 2018). Seasonal offsets showed ~~an increase~~ higher ~~in~~ crepuscular and diurnal activity from late spring until early autumn. However, in contrast to of Zielinski et al. (1983), pine martens in this study did not become predominantly diurnal during warmer months, but rather demonstrated irregular activity throughout the 24-hour diel cycle.

Squirrel activity peaked several hours after dawn and ceased before sunset. The species were ~~observed to be almost~~ exclusively diurnal, with detections occurring throughout the day, in accordance with previous studies (Tonkin, 1983, Gurnell & Hare, 2008). There was some evidence of temporal variation in circadian patterns between seasons, with detections suggesting a bimodal pattern in the summer, and a unimodal pattern in the winter. The bimodularity observed in summer was ~~caused by decrease in~~ due to low activity around midday, possibly in response to increased temperatures. Similar seasonal variation in activity has been observed in previous studies (e.g. Tonkin, 1983, Gurnell & Hare, 2008). Sunrise/set offsets revealed some crepuscular/nocturnal activity, behaviour which has not been reported in other populations. Foraging animals balance the risk of predation against the benefits of energy gains (Dammhahn & Almeling, 2012). The amount of risk an animal is willing to take is dependent on a number of factors including local predator density/impact, individual boldness, and its inherent ability to detect and respond to danger and environmental conditions. The acuity of squirrel eyesight is known to improve considerably in brighter conditions (Jacobs, Birch & Blackeslee, 1982). Thus, squirrels which are active in low or poor lighting conditions are seemingly at a distinct disadvantage. This may be a response to local predator activity, thus rendering an apparently suboptimal strategy contextually advantageous (Dammhahn & Almeling, 2012). However, the overlap between squirrels and pine martens was at its highest in summer ~~(>50%, though note that few martens were detected [n = 73])~~. The drivers of this behaviour are unknown and are worthy of further study.

Wood mice were exclusively and consistently nocturnal, although there was some diurnal activity recorded during summer when shorter nights may provide insufficient foraging time for wood mice to meet their daily energetic requirements. The species has previously been ~~described~~ reported to ~~as~~ exhibit~~ing~~ temporal variability in activity patterns between seasons (Miller & Elton, 1955, Wolton, 1983). This study also found high variability between seasons, with all seasonal comparisons but spring-autumn comparison significantly different from each other. It should be noted that the sample size in summer was small (n = 57), thus our summer data lack resolution. All wood mouse detections were opportunistic; none of the camera trap projects which comprise this study specifically focussed on small mammals. The presented pattern of activity, therefore, is highly unlikely to truly represent that of this species. Given an appropriate methodological approach (e.g. cameras placed in optimum locations and set at optimum angles; e.g. De Bondi et al., 2010), there is no doubt that camera trap surveys of small mammals would be extremely effective. It is no surprise, however, that studies of medium-to-large terrestrial mammals, the next-smallest of which is more than an order of magnitude larger than the wood mouse (rabbits, which can weight up to 2kg, compared to 27g for wood mice), should return poor (non-target) small mammal data.

Anti-predator behaviours, which include ~~direct~~ avoidance (e.g. Curé et al., 2013), facilitate the survival of the prey ~~population~~ by mitigating against ~~the impacts of~~ predat~~ors~~ion (Sih & Christensen, 2001). In the current study, foxes consistently occurred in sympatry with hares and rabbits, both of which are prey species (Reynolds & Aebischer, 1991). Both predator-prey annual cross-correlations showed a relationship which indicates that foxes and lagomorphs are likely to be active simultaneously. This correlation was maintained in spring and summer, but not for the rest of the year. While both lagomorphs exhibited similar behaviours, hare peak correlations (annual and summer) were typically found 2 hours before those found in rabbits, indicating perhaps a higher predator-avoidance behaviour in hares. Overlap estimates were smaller for hares than for rabbits, both annually and across seasons. In temperate zones, foxes typically mate in late winter/early spring; litters may contain up to 12 cubs, with food availability being a significant factor (Larivière & Pasitschniak-Arts, 1996). Here we describe foxes as becoming increasingly crepuscular in late-spring and summer, thus increasing the potential for spatiotemporal overlap with both species of lagomorph. This suggests that predation of these species may increase during the fox breeding season. Indeed, lagomorphs may become increasingly important as the cubs grow, particularly if the vixen has many offspring, as both lagomorphs are amongst the most substantial meals available to a medium-sized terrestrial predator in Northern Ireland. We can be reasonably confident, therefore, that the behavioural repertoires of both hares and rabbits in Northern Ireland include fox-specific anti-predator behaviours. Pine marten and squirrels showed a ~~direct~~ negative correlation in the annual comparison, as well as during spring, summer, and winter. Thus, predator and prey activity are simultaneously different (i.e. when pine martens are most active, squirrels are least active and vice-versa). Squirrels are also subject to predation by diurnal birds of prey (e.g. Petty et al., 2003); by avoiding nocturnal predators, the animals become diurnally vulnerable. However, while squirrels have relatively poor nocturnal vision (Arden & Silver, 1962); their spatial acuity improves under brighter conditions (Jacobs, Birch & Blackeslee, 1982). Foraging during the night thus greatly increases the risk of predation.

It was not possible to optimise the present study *a priori*, comprising, as it does, several individually-designed surveys. For example, there was considerable variation in the effective densities of camera trapping arrays. Detection probability and temporal resolution increase as a function of camera array and focal species densities. Higher array densities increase the chances of capturing an animal in-transit, being placed near a resting site (i.e. sett, drey, form, etc.), and capturing the focal species if it occurs at low densities. Camera trap surveys, therefore, would ideally consistently use high-density arrays to return an abundance of data. This is rarely feasible, however, given time, personnel, and financial constraints, all of which were limiting factors to the contributing surveys. Nevertheless, it is clear that even at relatively low densities, camera traps return important and useful ecological data. The utility and efficiency of camera trapping as an ecological survey tool is demonstrated by the fact that we were able to produce multiple analyses of temporal occurrence for a wide range of species, four of which were opportunistically captured, and which are largely in agreement with the published literature. It should be noted, however, that no cameras were set to effectively survey very small terrestrial mammals such as wood mice. Even though our data are limited, we have demonstrated that opportunistic 'bycatch' data captured by camera traps may broadly describe a species' temporal niche (e.g. nocturnal behaviour). However, it is certain that surveys utilising a more appropriate focal methodology would yield greater and more accurate small-mammal data.

In contrast to terrestrial animals which move on a 2D plain, arboreal animals move within 3D space, thus decreasing the likelihood of a random capture in transit. Squirrels were enticed to specific locations for image capture by the use of baited stations. While baiting is certainly effective, it is not without its problems. For example, animals may identify bait stations as a reliable source of food, and thus frequently revisit them, thereby inflating counts (Rowcliffe & Carbone, 2008). Moreover, feeding animals may spend a considerable amount of time in front of the camera if undisturbed than those captured in transit, again affecting interpretations. The degree of uncertainty increases considerably where the focal species does not exhibit individually-identifiable colouration or markings. Captures from baited stations, therefore, may only represent one, or a handful of individuals (Trolle & Kéry 2003, Weckel et al., 2006). However, the present study is only concerned with activity, and, hence, the detection of any individual during a given time period was assumed to be representative of the species as a whole.

Understanding the activity patterns of wildlife, and seasonal variations thereof, is of considerable benefit in furthering our understanding of species ecologies and informing future research (e.g. the development and application of efficient ecological surveys), thus paving the way for the development of appropriate management policies and/or conservation programmes. Knowing when a species is most or least likely to be active can lead to considerable methodological improvements, including potentially reducing the probability of achieving false-negatives, particularly for scarce or cryptic species. Camera trap surveys seeking to investigate circadian and intra-annual species activity patterns should, ideally, be conducted over the course of an entire year, focussing on areas which the focal species are known to frequent, and employing a large number of traps. Furthermore, climate and habitat data may further inform interpretations and facilitate the application of statistical models. While the temporal distribution of data herein are arguably suboptimal due to the application varied (i.e. non-standardised) methodologies, and environmental data are lacking, they are nevertheless of great utility in describing fundamental aspects of species' ecologies.

Conclusions

Certainly, camera traps have enormous potential for surveying a wide range of species and providing data which may be of great utility in informing subsequent investigations and/or answering important ecological questions. In the present study, we draw together several disparate, and very different camera trap surveys to describe fundamental behavioural parameters of ten mammalian species, only six of which were the focal subjects (fallow deer, hares, pine marten, and squirrels). We conclude that camera traps provide an effective means of describing circadian activity patterns of small–to–large mammals, seasonal variations in temporal activity, and have utility in investigating temporal aspects of interspecific interactions. These data serve as a proof-of-concept study; further studies are required to 'fill-in-the-blanks' and provide circa-annual data.

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AH undertook fieldwork, compiled data, carried out statistical analyses, and wrote the manuscript. MG contributed to statistical analyses and text. MCV compiled data, carried out preliminary analyses, and contributed to the manuscript. KH, MF, EF undertook fieldwork, provided substantial data and contributed to the manuscript. DT conceived the study, undertook fieldwork, provided substantial data and contributed to the manuscript. JTAD and NR were academic supervisors of much of original survey work, contributing to conceptual development of survey designs, managed resourcing with NR editing the final manuscript.

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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.

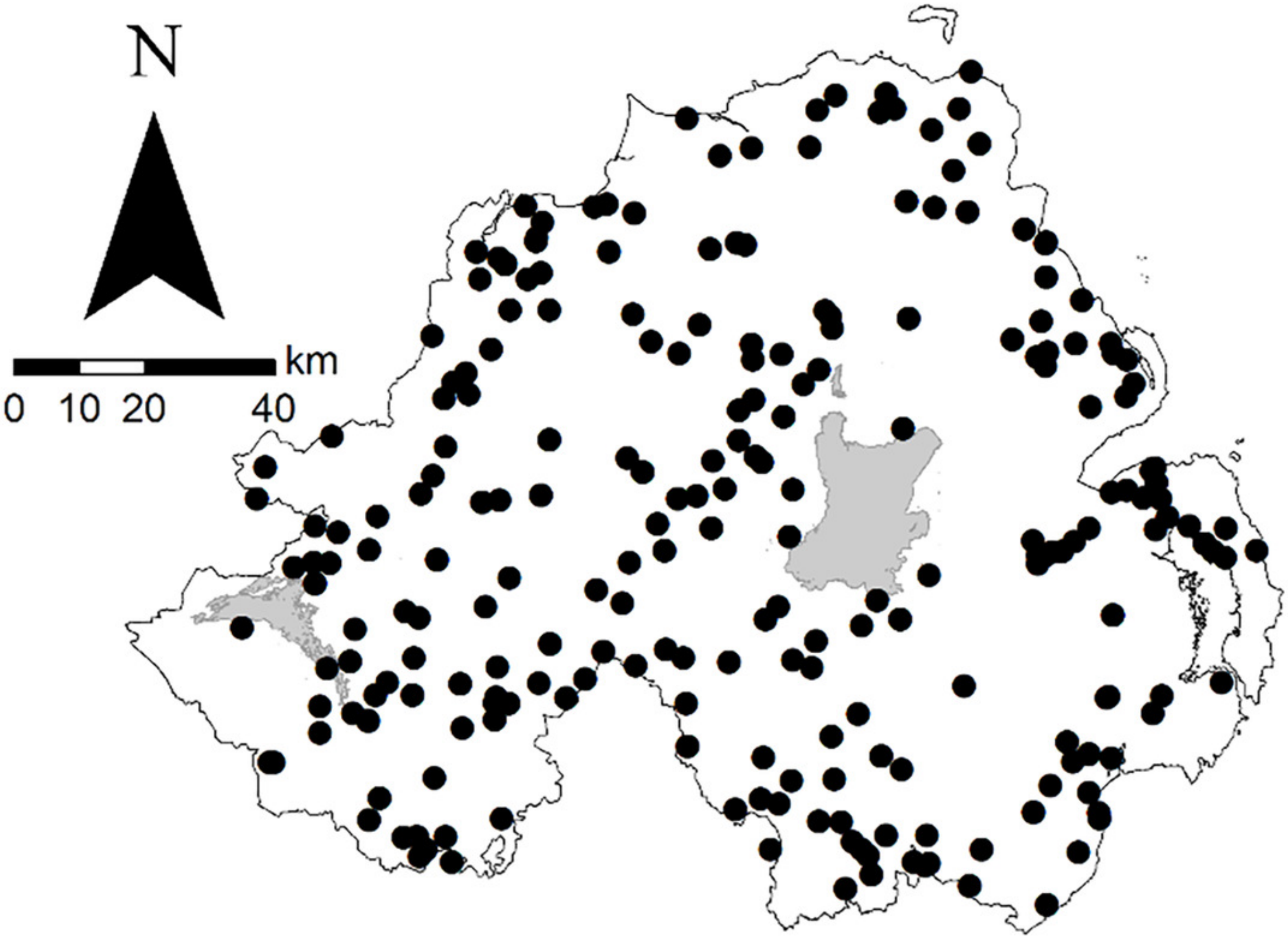

Figure 2

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

(a) badger, **(b)** fallow deer, **(c)** fox, **(d)** hare (here, an Irish hare), **(e)** pine marten, **(f)** rabbit, **(g)** squirrel (here, a red squirrel), and **(h)** wood mouse (circled).

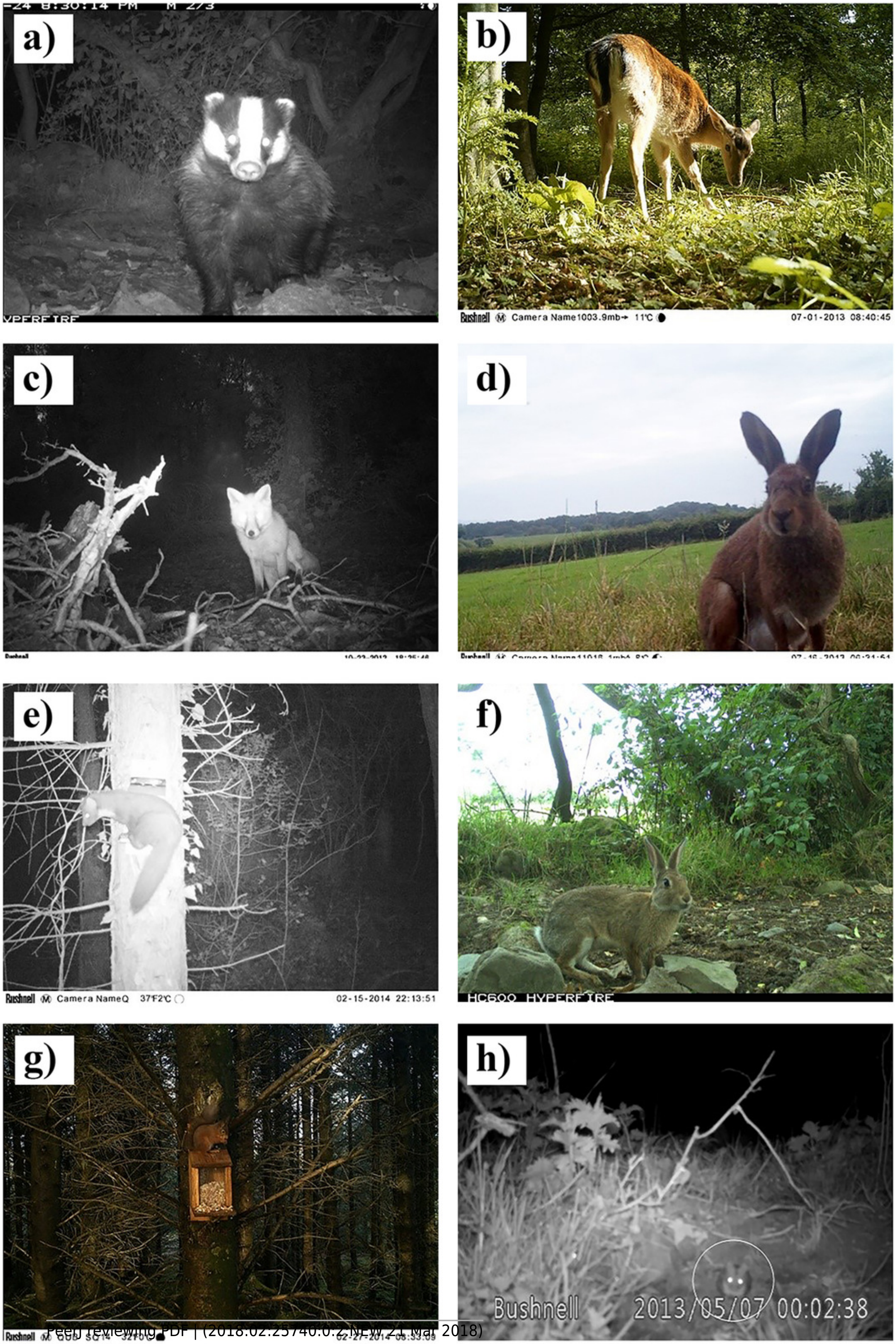
a)
-24 8:30:14 PM M 273
YPERFIRE
b)
Bushnell Camera Name1003.9mb 11°C
07-01-2013 08:40:45
c)
d)
e)
Bushnell Camera NameQ 37°F2°C
02-15-2014 22:13:51
f)
HC600 HYPERFIRE
g)
h)
Bushnell 2013/05/07 00:02:38

Figure 3

Circadian activity patterns of ten mammal species.

(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.

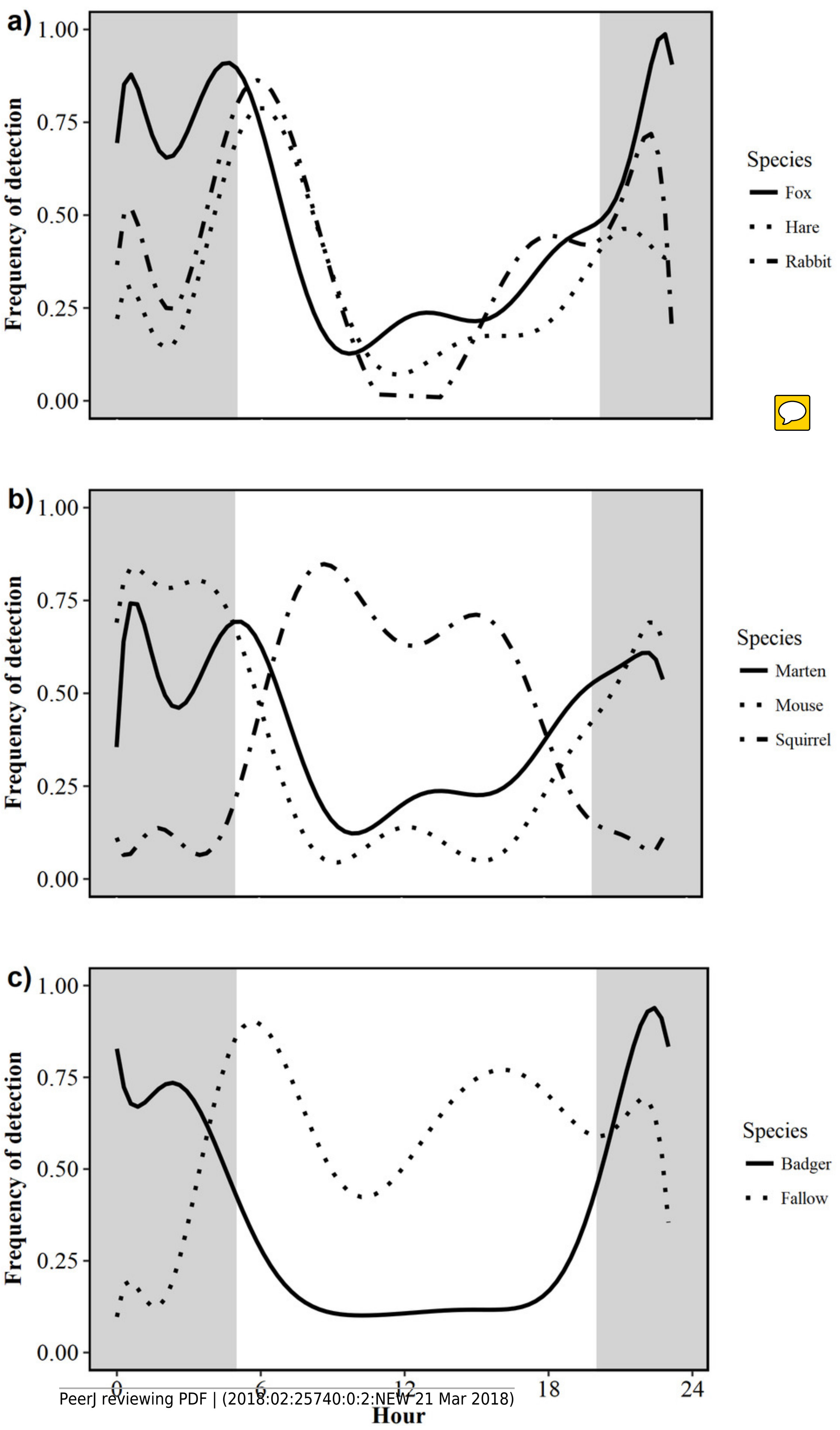
a)
b)
c)
Frequency of detection
1.00
0.75
0.50
0.25
0.00
Hour
0
6
12
18
24
Species
Fox
Hare
Rabbit
Marten
Mouse
Squirrel
Badger
Fallow

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.

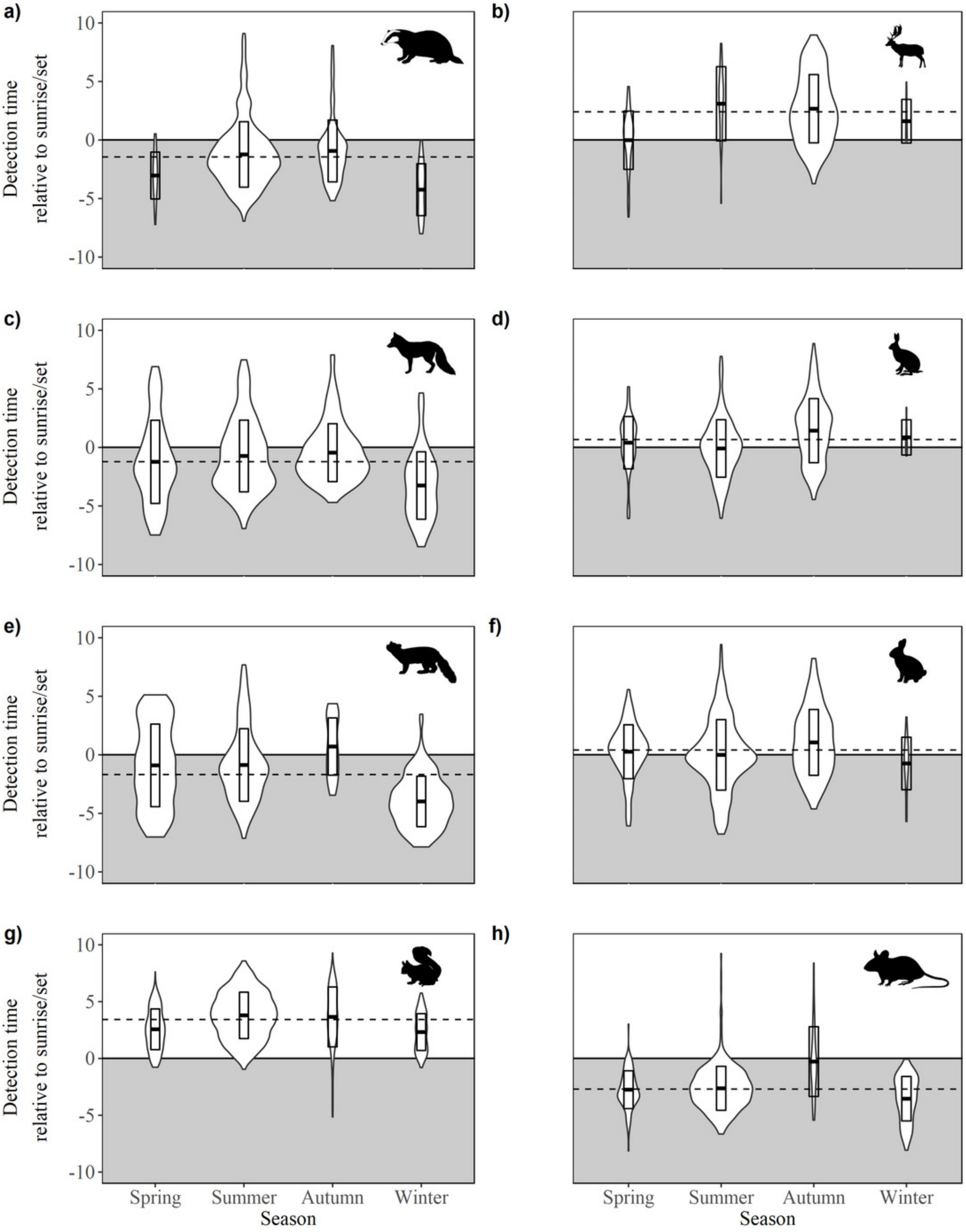
a)
b)
c)
d)
e)
f)
g)
h)
Detection time relative to sunrise/set
10
5
0
-5
-10
Spring
Summer
Autumn
Winter
Season

Figure 5

Cross-correlated paired circadian activity patterns of predator (fox) and prey (hare, rabbit, mouse) species.

Data were derived from camera trap surveys in Northern Ireland from 2013 – 2016**. (a)** Foxes and hares, **(b)** foxes and rabbits, and **(c)** foxes and wood mice. Plots describe **(i)** annual, and **(ii – v)** seasonal data: **ii)** spring; **iii)** summer; **iv)** autumn; and **v)** winter. Lag is the result of a correlation between $x_{a\pm i}$ and y_a, where a = time. Correlations which extend beyond the dotted lines (highlighted) are significant at the p ≤ 0.05 level.

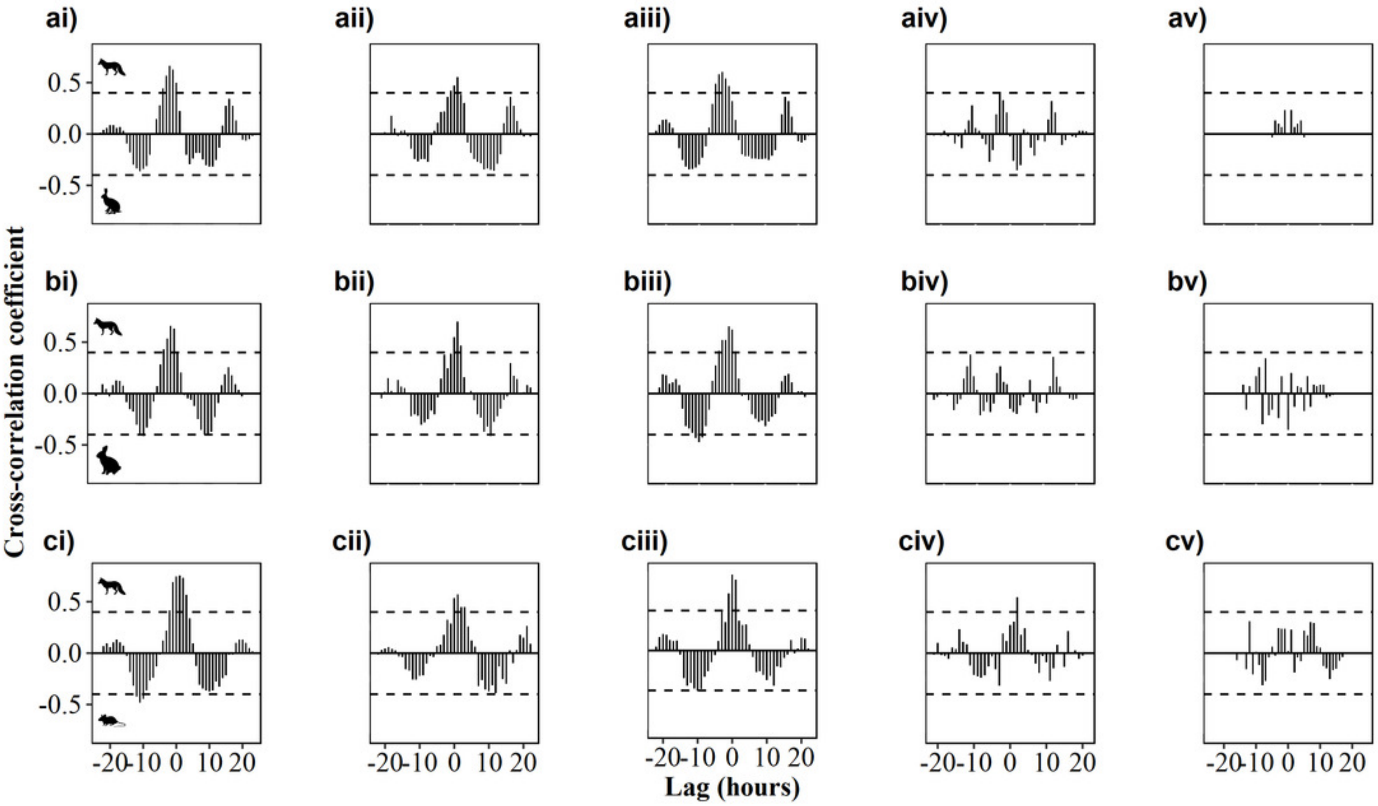

Figure 6

Cross-correlated paired circadian activity patterns of predator (pine marten) and prey (wood mouse, squirrel) species.

Data were derived from camera trap surveys in Northern Ireland from 2013 – 2016**. (a)** pine marten and wood mice, **(b)** pine marten and squirrels. Plots describe **(i)** annual, and **(ii – v)** seasonal data: **ii)** spring; **iii)** summer; **iv)** autumn; and **v)** winter. Lag is the result of a correlation between $x_{a\pm i}$ and y_a, where a = time. Correlations which extend beyond the dotted lines (highlighted) are significant at the p ≤ 0.05 level.

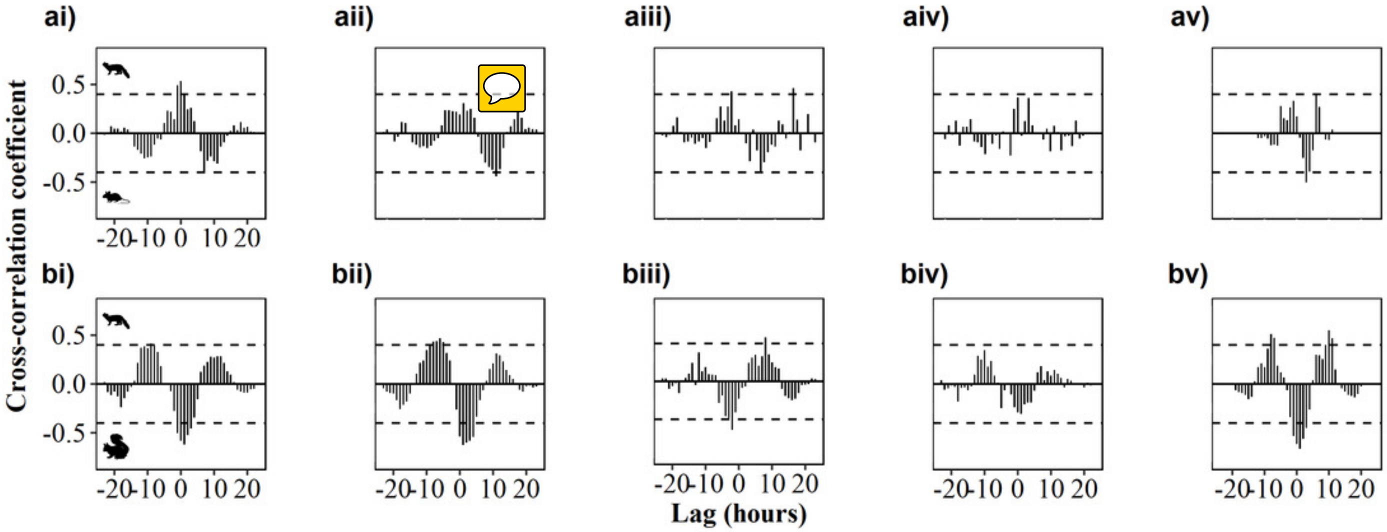

Table 1(on next page)

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. * = not all cameras were deployed at each location. 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*	2013-14	20.00	38	23	255
Deer	2015	0.05	10	4	40
Deer	2015	0.02	10	2	20
Deer	2015	0.04	10	2	20
Deer	2015	0.05	17	1	17
Deer	2015	0.02	21	1	21
Hares	2013-14	17.00	20	17	340
Hares	2015	6.00	12	6	72
Squirrels	2014	n/a	16	63	63
Squirrels	2015	n/a	65	314	314

Table 2(on next page)

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*).

Species		**Season**				Total detections
Common name	**Latin name**	**Spring**	**Summer**	**Autumn**	**Winter**	~~Σ~~
Badger	*Meles meles*	618	225	36	68	947
Fallow deer	*Dama dama*	38	484	61	8	591
Fox	*Vulpes vulpes*	198	183	149	115	645
Hare	*Lepus sp.*	301	339	105	6	751
Pine marten	*Martes martes*	251	73	356	286	966
Rabbit	*Oryctolagus cuniculus*	492	417	238	28	1175
Squirrel	*Sciurus sp.*	1798	317	462	293	2870
Wood mouse	*Apodemus sylvaticus*	449	57	119	191	816

Table 3(on next page)

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)

Table 4(on next page)

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

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Data were derived from camera trap studies conducted in Northern Ireland between 2013-2016. 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. See Figs 5 & 6 for ccf results along all paired time series.

			Lag (hrs)				
Predator	**Prey**	**Season**	**From**	**To**	**Peak lag**	***t***	***r***
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	-0.48*
Fox	Wood mouse	Annual	-2	3	1	5.39	0.754***
Fox	Wood mouse	Spring	-2	3	1	3.26	0.57*
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	0.47*
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	-0.44*
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	0.4*