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SHORT COMMUNICATION

# Circadian activity patterns of red foxes (*Vulpes vulpes*) in montane forests under different culling regimes

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**Abstract**

Mammals display a great variety of activity patterns. Although red foxes (*Vulpes vulpes*) are generally well studied, differences in their activity patterns related to seasonality and anthropogenic impacts remain not well known. Hunting is a major anthropogenic influence on fox populations across the globe. In this paper, we assess how circadian activity patterns of red foxes in a central European montane forest change throughout the year and test whether activity patterns differ between areas with different culling regimes. We found pronounced activity peaks around dawn and particularly dusk and high levels of activity throughout the night. Foxes generally avoided daylight hours, except in wintertime, potentially indicating an avoidance of human presence. The onset and cessation of activity tracked changes in day length. Circadian activity patterns were highly similar at sites with and without targeted culls during all seasons, not suggesting a direct reaction of red foxes to hunting. Red fox activity patterns in our study were thus overall comparable with those in other environmental contexts.

**Keywords** Disturbance · Hunting · *Vulpes vulpes* · Predator control · Seasonal behaviour · Wildlife camera trap

## Introduction

Animal activity patterns are influenced by a multitude of environmental constraints, such as resource availability, ambient conditions (e.g. daylight) and inter- and intra-specific interactions (Daan 1981; Halle 2000; Bennie et al. 2014). Differences in circadian activity patterns, i.e. the recurring variation in the relative degree of activity throughout a 24-h period, are a manifestation of adaptive behavioural traits optimized based on biological requirements (Halle 2000; Kronfeld-Schor and Dayan 2003). Mammals display a great variety of circadian activity patterns (Bennie et al. 2014), but often become increasingly nocturnal in response to human disturbance (Gaynor et al. 2018).

The red fox (*Vulpes vulpes*) is a common generalist mesopredator with circumglobal distribution (Hoffmann and Sillero-Zubiri 2016). Perhaps surprisingly, there are only few studies on how red fox activity patterns vary in relation to seasonality and anthropogenic impacts. In the past, some studies have employed VHF-telemetry to study movement activity of foxes (e.g. Blanco 1986; Servín et al. 1991; Cavallini and Lovari 1994; Weber et al. 1994; Reynolds and Tapper 1995), describing mostly nocturnal activity patterns (but see Servín et al. 1991, Cavallini and Lovari 1994). The increasing application of digital wildlife cameras has greatly simplified the quantification of circadian activity patterns (Rowcliffe et al. 2014; Lashley et al. 2018). This has recently led to studies on fox activity in several parts of Europe (Monterroso et al. 2014; Diaz-Ruiz et al. 2015; Oberosler et al. 2017; Caravaggi et al. 2018). Red foxes were predominantly nocturnal in all habitat situations, but there is behavioural plasticity with crepuscular activity peaks (e.g. Monterroso et al. 2014; Caravaggi et al. 2018) and diurnal activity (Monterroso et al. 2014; Diaz-Ruiz et al. 2015). In addition, most recent studies have focussed on

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spring and summer periods, leaving seasonal plasticity in activity largely in the dark.

Animals often exhibit behavioural responses to human disturbance akin to predation risk (Frid and Dill 2002; Ciuti et al. 2012; Gaynor et al. 2018) and nocturnality in red foxes has been associated with human influences, most commonly in the form of recreational outdoor activities (e.g. Diaz-Ruiz et al. 2015; Oberosler et al. 2017). Hunting represents another pervasive anthropogenic impact on fox populations across the globe, but our understanding of its behavioural effects is still limited. Direct or adaptive behavioural responses to differences in hunting have been shown for various ungulates (Benhaiem et al. 2008; Keuling et al. 2008; Crosmary et al. 2012; Lone et al. 2015), but to a much lesser extent for canids. Coyotes (*Canis latrans*) increased their diurnal activity following the cessation of long-term persecution (Kitchen et al. 2000) and dingoes (*Canis lupus dingo*) concentrated activity before dawn on properties with targeted removal (Brook et al. 2012). Despite the commonness of fox culls, it is unknown whether red foxes show similar reactions to avoid times of potentially high mortality risk.

In this paper, we depict how circadian activity patterns of red foxes in a central European montane forest change throughout the year. We then assess whether foxes react to differences in hunting intensity by adapting their activity patterns. We expected a shift of red fox activity patterns deeper into the night (i.e. away from times of highest mortality risk at dawn and dusk and human presence during daylight hours) during and/or after the hunting season in areas with targeted fox culling.

## Material and methods

We used camera trap data obtained in the southern Black Forest, Germany, at elevations of 800–1.300 m. The area is characterized by mixed montane forests, fragmented by settlements and mountain pastures. The fox population was surveyed using motion-triggered infra-red automatic wildlife cameras (Bushnell Trophy Cam HD Aggressor Low Glow) across a network of plots with systematic spacing. Plots were placed within 20 rectangular study sites that differed in their red fox culling regime (i.e. 7 sites with targeted culls vs. 13 sites without targeted culls). The total area surveyed by camera trap plots during the study amounted to approximately 18.000 ha within a study area of approximately 30 × 40 km. The culling regime at the study sites and contained plots (targeted vs. no targeted culls) was determined in stakeholder meetings to ensure that study sites were selected based on culling effort rather than red fox density. Hunting of game in Germany is concession-based and the large majority of red fox culls in the study area took place annually during winter by shooting from hides (mainly in January and February and often at baited sites) and mainly during twilight or early darkness hours. We confirmed site classification after the surveys using interpolated hunting bag data at the plot locations (Wilcoxon-Mann-Whitney-test, bag size targeted vs. no targeted culls: $U = 6791$, $p < 0.001$; Fig. S1 in supplements). Maximum removal intensity was around five foxes per 100 ha at sites targeting foxes. For a more detailed description of the study area, the red fox culling regime and the research design please see the supplementary material and Kämmerle et al. (2019).

We surveyed red foxes at three sampling occasions during 1 year in 2017–2018, henceforth referred to as spring, autumn and winter: between March 15, 2017 and May 12, 2017 (i.e. to represent breeding populations after the hunting season); between September 13, 2017 and November 10, 2017 (i.e. post-breeding populations before the hunting season); and between January 29, 2018 and March 9, 2018 (i.e. during the hunting season when all study sites had snow cover). Cameras were deployed in two sessions of approximately equal effort per sampling occasion and placed as close as possible to the centre of a grid cell (i.e. the plot) along the next machine track or old logging track in spring ($N = 130$ cameras), autumn ($N = 134$) and winter ($N = 105$). In winter, snow limited camera placement to sites accessible on foot using snowshoes. Each trap remained operational for 14 days in winter and 21 days in each of the other seasons. Pictures were sorted to species level. We processed images and extracted the time of day for each event using the package camtrapR (Niedballa et al. 2017). Image sequences more than 5 min apart were considered independent events based on visual inspection of the data.

To characterize daily activity patterns and quantify differences in activity patterns between culling regimes, we used kernel density functions using time of day as a random circular variable (Oliveira-Santos et al. 2013; Cruz et al. 2018) using software R (R Core Team 2018) and packages circular (Agostinelli and Lund 2017) and overlap (Ridout and Linkie 2009). Kernel estimates are a non-parametric approach to obtain a continuous measure of density of the data, in this case, frequency distributions of camera trap events (Oliveira-Santos et al. 2013). This is a reliable standard approach to estimate animal activity curves given a sufficient sample size (Lashley et al. 2018). We estimated activity patterns from the pooled data of each respective season and separately for both culling regimes ('high' vs. 'low' culling) within each season. All times were set to UTC time. All activity patterns were estimated with identical settings (bandwidth = 2). We visually interpreted activity patterns in relation to sunrise and sunset times. Sunrise and sunset were the time when the centre of the sun was on the horizon at the location of the study sites. Variation in sunrise and sunset times during the study period was the time difference between the first and last day of the sampling interval. The uncertainty around the estimated activity patterns due to potential differences among trap sites and pooling of trap data was estimated by a non-parametric bootstrap for each season with 1.000 iterations each. Activity curves were then estimated from each boot sample. We quantified differences between circadian activity patterns between culling regimes in all seasons by calculating overlap coefficients (Δ, i.e. degree of overlap between the activity patterns; Ridout and Linkie 2009) and their bootstrap confidence intervals (10.000 bootstrap samples for overlap coefficients) as well as testing for differences between the respective two activity patterns using a non-parametric circular Watson's two-sample test. The level of significance was set at $\alpha = 0.05$.

## Results

Our camera traps obtained a total of $N = 2205$ red fox events during the study period. The majority of events were obtained in spring (i.e. March–May; $N = 1135$), followed by autumn (September–November; $N = 652$) and winter (January–February; $N = 418$; shorter sampling period). Bootstrap estimates indicated stable estimation of activity patterns for all seasons. Overlap coefficients of activity patterns at sites with and without targeted culls were highly similar in all seasons, being 0.93 (0.90–0.98) for spring, 0.94 (0.93–1.00) for

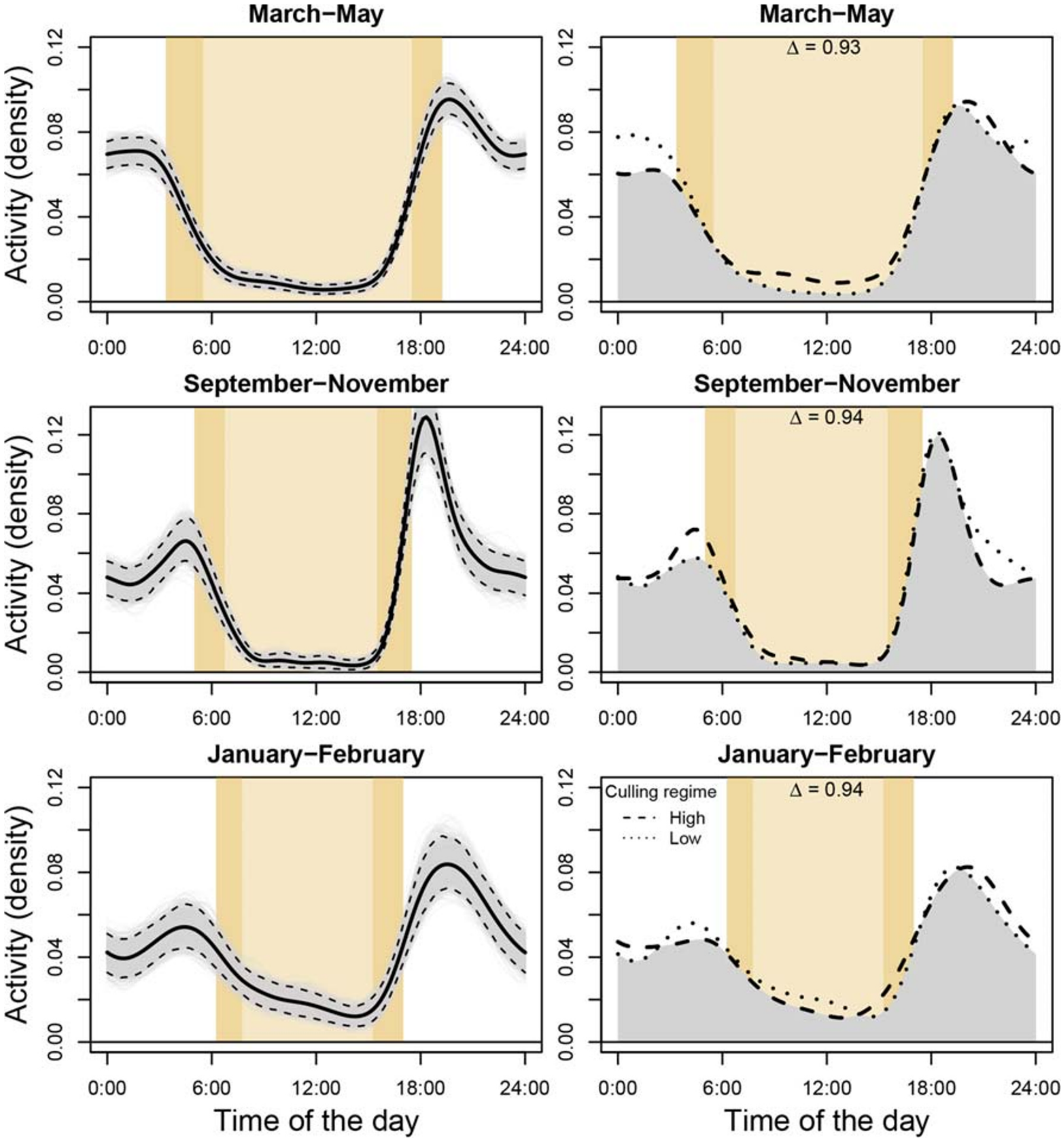

**Fig. 1** Circadian activity patterns of red foxes in montane forests estimated in three seasons (left column) and under two culling regimes (right column). Dashed lines (left column) represent 95% confidence intervals with bootstrap runs as grey lines. Grey areas (right column) depict the overlap between activity patterns and Δ values are the overlap coefficients of activity patterns between culling regimes. Shaded areas in the background indicate daylight periods with darker areas highlighting the change in sunrise and sunset times during each study period

autumn and 0.94 (0.93–1.00) for winter. The circadian distribution of fox events differed significantly between culling regimes in spring immediately after the hunting season ($U^2 = 0.195$, $p < 0.05$), but not in autumn or winter, although the overlap coefficient was only marginally smaller in spring. Circadian activity patterns of red foxes in the study area are displayed in Fig. 1.

## Discussion

With this study, we address an apparent gap in knowledge on the behaviour of a very common and generally well-studied mammal species. Red foxes displayed crepuscular activity peaks, but we also found high levels of activity during the night in all seasons. The evening peaks in activity were particularly pronounced and the timing of activity peaks tracked changes in day length throughout the year (Fig. 1). The relative magnitude of these peaks was largest in autumn, reduced in winter and smallest, although still apparent, during the denning season (i.e. spring; March–May) when we captured red fox events almost continuously throughout the night. This variation in activity peaks agrees with previous studies covering more than one season (Iberian Peninsula: Monterroso et al. 2014; Ireland: Caravaggi et al. 2018). Fox activity patterns were thus overall similar to those in other environmental contexts (Monterroso et al. 2014; Diaz-Ruiz et al. 2015; Oberosler et al. 2017; Caravaggi et al. 2018). Foxes almost completely avoided daylight hours in spring and autumn. However, we recorded higher levels of daytime activity in winter (especially during the morning hours; Fig. 1), coinciding with the mating season. In addition, during the winter sessions, all sites experienced prolonged cold temperatures and snow cover, but also a marked reduction of human presence owing to the temporary inaccessibility of many sites. This may support the assumption that nocturnal activity patterns of foxes are in parts related to human presence during daylight hours (e.g. Diaz-Ruiz et al. 2015; Oberosler et al. 2017), which may have been relaxed once disturbance decreased. In contrast to our expectation, there was no evidence for behavioural differences between areas of different culling regimes. The marginal size of the difference in overlap coefficients between spring and the other two seasons ($\Delta = 0.01$) may indicate that the statistical significance of the difference for this season was mainly due to a large sample size, as spring was the study period with the largest dataset. The similarity of activity patterns at sites with and without targeted culls (reflected by large overlap coefficients irrespective of significance) does not suggest the presence of a direct reaction of red foxes to hunting. This may be due to the lack of opportunity for adaptation under a high-intensity culling regime (i.e. high risk of mortality of the affected individuals prevents a behavioural response) or because hunting events remain rare compared with other human encounters (e.g. recreation), even under an intensive culling scenario (i.e. occurring every couple of days). A potentially directional selection effect of hunting on fox activity is difficult to disentangle from other potential drivers of fox activity and this goes beyond our data.

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