



Seasonal variation in the activity pattern of red squirrels and their mammalian predators

Nadine Kalb¹ · Xenia Schlindwein¹ · Thomas K. Gottschalk³ · Jan Dvorak² · Christoph Randler¹

Received: 16 October 2023 / Accepted: 1 May 2024 / Published online: 14 May 2024
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Abstract

Camera traps are a powerful tool to monitor the activity pattern of species over long time periods. Camera data can be used to analyze activity patterns of or temporal niche partitioning among species. Temporal niche partitioning plays an important role for species coexistence and is under constant evolutionary pressure from predator-prey relationships. Our study aimed to investigate temporal shifts in activity patterns of red squirrels and two mammalian predators, red fox and marten (*Martes spec.*). Previous studies yielded different activity patterns for these species depending on location, season, predator-prey interactions, and food-availability. We used camera traps to monitor the activity of squirrels, red fox and martens throughout a whole year in a mountainous forest in southwestern Germany. We also investigated a possible difference in activity among different color morphs as coloration in mammals is often associated with concealment, for squirrels, however, such an effect could not be demonstrated so far. We found a diurnal activity for squirrels in all seasons with a bimodal activity pattern during spring, trimodal in summer and unimodal in fall and winter. Activity patterns did not differ between black and red color morphs. The activity of the squirrels showed only low to moderate overlaps with fox and marten, but there was still slight variation among seasons. Activity overlaps were higher in spring and summer, which coincides with breeding season. Our results suggest that predators might adjust their activity during squirrel breeding season to increase the chance of preying on their offspring. Squirrels in turn could benefit by minimizing the activity overlap during wintertime when they are highly visible to predators as trees are leaf-free or even snow might enhance the contrast between them and their background. Lastly, our results indicate that temporal niche partitioning among red squirrel, red fox and martens might be rather fine scaled.

Keywords Camera trapping · Circadian rhythm · Diurnal activity · *Sciurus vulgaris* · *Vulpes vulpes* · *Martes*, predator-prey · Mammals · Seasonal variation, niche partitioning

Nadine Kalb and Xenia Schlindwein have contributed equally to this work.

✉ Nadine Kalb
nadine.kalb@uni-tuebingen.de

¹ Department of Biology, Eberhard Karls Universität Tübingen, Auf der Morgenstelle 24, D-72076 Tübingen, Germany

² Department of Food Informatics / Computational Science Hub (CSH), University of Hohenheim, D-70599 Stuttgart, Germany

³ Department of Regional Management, University of Applied Forest Sciences Rottenburg, Schadenweilerhof, D-72108 Rottenburg am Neckar, Germany

Introduction

Mammals show a range of activity patterns, with some having distinct activity peaks during the day (diurnal), at night (nocturnal) or during twilight (crepuscular) and others that lack distinct activity peaks throughout a 24-hour cycle (cathebral) (Refinetti 2008). Activity pattern of a species is known to be affected by abiotic components such as ambient light (Halle 2000) and temperature (Maloney et al. 2005; Shuai et al. 2014) as well as biotic components such as inter-/intraspecific competition over resources (Cunningham et al. 2019; Monterroso et al. 2020; Mori et al. 2020; Lear et al. 2021; Tsunoda et al. 2022; Watabe et al. 2022). Spatial or temporal niche partitioning are common strategies to minimize competition among coexisting species. There is a growing body of research investigating the

circadian activity pattern of animals using camera trapping (Di Cerbo and Biancardi 2013; Blount et al. 2021; Delisle et al. 2021; Cordier et al. 2022). Camera trapping can be used to automatically collect data over long time periods making it possible to analyze temporal and seasonal variation in the activity of target species (Bridges and Noss 2011; Rowcliffe et al. 2014; Frey et al. 2020).

The Eurasian red squirrel (*Sciurus vulgaris*) is an abundant species distributed across Eurasia. It is a small (180–240 mm head and body length; weight approx. 200–400 g) and mainly diurnal rodent (Ikeda et al. 2016). Despite its name, the squirrels' fur may occur in numerous shades between solid red and black, with or without white bellies. In most populations two distinct color types are present whereby the relative proportion of fur color (brown/red brown or bright chestnut to gray brown or black) varies geographically (Lurz et al. 2005). Colouration is of adaptive significance for many mammalian species (Caro 2005). Hence, it is also frequently discussed if and how the morphotypes in squirrels might affect survival rate by better adaptation to temperature, elevation or predation even though such effects have not been demonstrated so far (Wauters et al. 2004 and references therein). Ancillotto and Mori (2017) showed that coat colouration in Sciuromorpha is mostly related to concealment. As there are two color morphs present in our study area, we were interested in studying differences in their circadian activity. The circadian or diurnal activity of red squirrels varies annually due to environmental factors such as day length, temperature, weather, and food availability (Tonkin 1983; Wauters et al. 1992; Steen and Barmoen 2017). Generally, squirrel activity patterns have been found to change over the course of the year, from unimodal in the winter months to a bimodal activity pattern in the summer (Tonkin 1983; Wauters et al. 1992; Steen and Barmoen 2017). However, Di Cerbo and Biancardi (2013) challenged this assumption and reported a trimodal pattern in summer, indicating that seasonal activity may be more complex than previously thought. To our knowledge, there is only one study yet that addresses the full annual cycle in northern Italy (Wauters et al. 2002). Because the habitat structure as well as temperature differs greatly between northern Italy and southwest Germany, the aim of our study was to depict seasonal variation in the diel activity of the red squirrel across a full years' cycle in southwest Germany.

Squirrels show terrestrial and arboreal feeding behavior (Gurnell 1987; Braun and Dieterlen 2005) and preferences change during the year (Holm 1987). Depending on their feeding preference, red squirrels are prone to various predators including goshawk (*Accipiter gentilis*), sparrowhawk (*Accipiter nisus*), tawny owl (*Strix aluco*), red fox (*Vulpes vulpes*), beech marten (*Martes foina*) and pine marten (*Martes martes*). Red fox (*Vulpes vulpes*), European pine marten

(*Martes martes*) and beech marten (*Martes foina*) are present in the study area (Randler 2006; Gottschalk and Randler 2019; Randler et al. 2020) and have been reported to occasionally prey on red squirrels in Europe, including Germany (Storch et al. 1990; Kenward and Hodder 1998; Russell and Storch 2004). Red foxes (*Vulpes vulpes*) are very common mesopredators in Europe with an omnivorous diet that depends on the resources available in their habitat (Braun and Dieterlen 2005; Soe et al. 2017). A main food source of red foxes in Europe are small mammals, including rodents such as the red squirrel (Soe et al. 2017; Castañeda et al. 2022). Telemetry data revealed a mainly nocturnal pattern (Servín et al. 1991; Cavallini and Lovari 1994), but camera trapping showed crepuscular and diurnal activity peaks indicating behavioral plasticity (Monterroso et al. 2014; Díaz-Ruiz et al. 2016; Torretta et al. 2017; Caravaggi et al. 2018; Roy et al. 2019). As foxes partial predate on squirrels, we studied the temporal overlap between the species.

The beech marten (*Martes foina*) and the slighter larger pine marten (*Martes martes*) are similar in weight (about 1.5 kg), size (body length about 700 mm) and diet. Both are generalist omnivores, whereby their diet is known to vary with seasonal and regional food availability (Serafini and Lovari 1993; Padial et al. 2002). However, red squirrels are severely predated by martens (up to 50% of the diet in a Swedish population Storch et al. 1990). Red squirrels in turn have been shown to alter their behavior in response to pine marten scent as they started to avoid feeders, increased vigilance and decreased feeding activity (Twining et al. 2020). Therefore, temporal niche overlap between marten species and red squirrels are studied in relation to the annual cycle.

Martens are mostly nocturnal, but sometimes show diurnal activity (Posillico et al. 1995; Bischof et al. 2014; Monterroso et al. 2014). Roy et al. (2019) monitored the activity pattern of stone martens with camera traps and found them to display nocturnal activity for 85% of their total activity. Posillico et al. (1995) reported seasonal variation in the diurnal activity of three radio-tracked stone martens. In spring and summer animals displayed a bimodal pattern with a small peak at mid-day and a high peak at night whereas in autumn and winter there was an unimodal pattern with almost no diurnal activity. Stone martens in Italy were mainly nocturnal, whereas pine martens showed a cathemeral pattern, but both species showed some variation dependent on the study region (Torretta et al. 2017). The activity of the marten species therefore shows some temporal overlap with the red squirrel's activity. Avoiding or reducing the overlap might be a strategy to avoid predation.

The goals of the study were threefold. First, we wanted to study the diurnal activity of the red squirrel across a full annual cycle and to analyse the patterns across seasons. Second, we were interested in studying differences between the

two distinct color morphs of the red squirrel. Third, by collecting additional data about potential predators, we aimed to study circadian overlap of predators and prey to assess temporal niche. By doing so predators might minimize intraspecific competition over food while maximizing the likelihood to prey on squirrels and their offspring.

Materials and methods

The study was conducted at the Rammert (48°26'38.0"N 8°58'59.5"E), in Baden-Württemberg (southwest Germany), a forest located near Rottenburg between Rangendingen in the southwest and Tübingen in the northeast. The Rammert is between 362 and 552 m above sea level. The Rammert measures about 3200 ha and consists mainly of beech (*Fagus sylvatica*), spruce (*Picea* sp.) and oak (*Quercus* sp.). A total of 21 SecaCam Raptor SC-000-021 cameras (SECACAM, VenTrade GmbH, Germany) were placed in 12 1 × 1 km large grids distributed in the northern

part of the Rammert (Fig. 1). The placement of the cameras followed a stratified random sampling procedure, following the guidelines of Meek et al. (2014) utilizing a somehow deliberately biased placement. To spread the camera traps regularly, grids were used as a first selection for determining camera trapping sites. Further, cameras traps were placed within each grid at focal points to maximize detection (Meek et al. 2014). The study focused on the northern part of the Rammert due to bureaucracy reasons as the installation of camera traps needs to be approved by the landowners and responsible forestry offices. In every grid, we placed at least one camera depending on the area covered by forest. To reduce autocorrelation effects described by Dormann et al. (2007), the distance between cameras was at least 300 m. Because our target species are mainly forest-dwelling, cameras were placed in forested areas, and no camera was placed in the open landscape. Therefore, in some grids only one camera was placed. Following the local vegetation structure, in some grids three cameras were placed. In grid 7 a camera was placed but had to be taken down because the

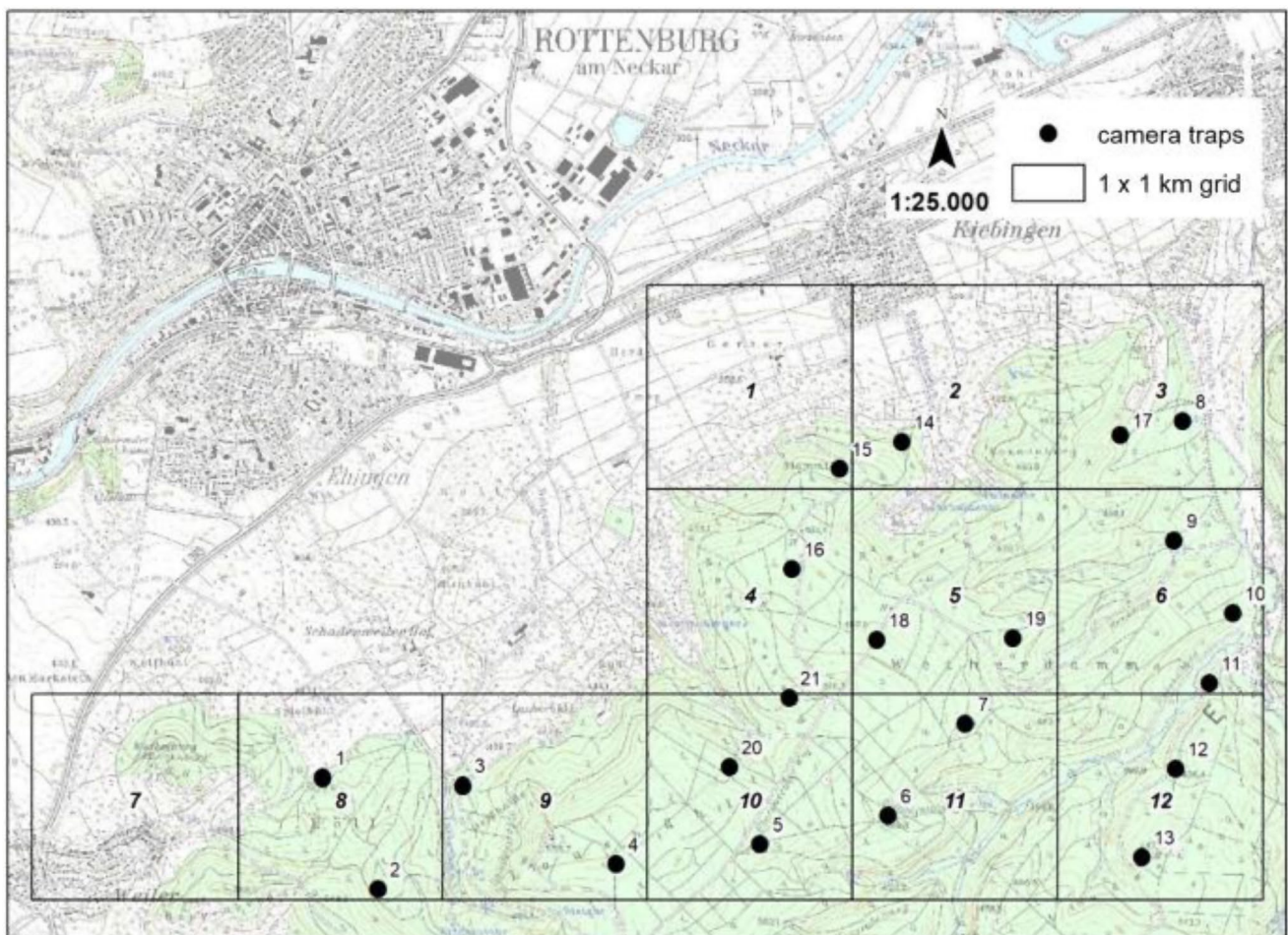


Fig. 1 Locations of the camera traps within the Rammert near Rottenburg. 21 Camera traps (black dots) were placed in twelve (bold numerical numbers) 1 × 1 km large grids throughout the northern part of the Rammert. Figure taken from Schlindwein et al. (2024)

local hunters refused permission to operate a camera trap there.

21 cameras were activated on the 13th of January 2021, but only 17 operated until the end of the study on 19th January 2022. Four cameras stopped working during the study due to technical difficulties. Cameras were mounted on trees approximately about 60–80 cm above the ground. The surveyed areas covered different habitats and structural elements, such as dense underwood, small trails, dead wood, openings and grass-covered patches. All camera traps operated continuously and collected a series of three photos when motion was detected. We used a minimum difference of 5 min to consider the events as different. Camera traps were surveyed every four to twelve weeks to switch memory cards and batteries if necessary. To capture natural conditions, including predator presence, we did not use bait for our camera. All images were studied by trained students from the university of Tübingen, and finally, by XS. In cases of problematic identifications, XS and CR agreed on the identification.

Statistical analysis

To analyze the activity patterns of the three species, we grouped the observations by seasons, namely spring from 1 March to 31 May, summer from 1 June to 31 August, and fall from 1 September to 30 November and winter from 1 December to 28 February. To account for the variation in daylength throughout these three-month periods a time transformation method suitable for the latitude was implemented. We transformed the times of the observations with a double anchoring procedure as described by Vazquez et al. (2019). To apply this transformation to our data we used the `solartime` function from the `Animal Activity R`-package (Rowcliffe et al. 2014; Rowcliffe 2023). The function transforms clock time to solar time anchored to sunrise and sunset times for a given location (Rowcliffe 2022) by returning values in radian time format. In this format every second of a day can be mapped to a numeric value between 0 and 2π (e.g., 12:00 pm equals 43,200 s equals 3.14 rad). The transformation to a numeric time format facilitates complex computations and methods.

After the transformation we used the `fitact` function to create kernel density estimations of the transformed observation times (Rowcliffe et al. 2014; Rowcliffe 2023). While generating these activity models we used bootstrapping with 999 iterations to estimate errors. In order to obtain sensible confidence intervals despite the small sample sizes for some seasons, we decided to sample from the fitted probability density distribution for the bootstrapping method, rather than sampling from our data. This follows the recommendations of Rowcliffe (2023) for fitting activity models with

small sample sizes. We used these models to analyze the changes of the activity patterns during the year.

To test for significant differences between different models we computed Wald Tests. Additionally, we used the `overlapEst` and `overlapPlot` functions from the `overlap` package to determine the overlap of different activity models by computing overlap coefficients and creating overlap plots for visualization (Ridout and Linkie 2009; Meredith et al. 2014). This coefficient ranges from 0 (no overlap) to 1 (complete overlap). We used the “Dhat1” overlap coefficient due to low sample size in most comparisons (<75) as recommended by Meredith and Ridout (2021). We defined the overlap coefficient D , as low ($D \leq 0.5$), moderate ($0.5 \leq D \leq 0.75$) or high ($D > 0.75$) as following previously published studies (Meredith et al. 2014; Monterroso et al. 2014; Watabe et al. 2021). All analyses were carried out with RStudio (RStudio Team 2020).

Results

Activity pattern of squirrels

The total camera trapping result was 101,916 images, and the effort was 9779 independent events. Camera traps ran on average for 322 days $SD = 73$ days, range 159–371 days. We recorded a total of 978 of either light or dark colored squirrels: 327 in spring, 276 in summer, 271 in fall and 104 in winter. We could identify the color coat in 49% of the observations, 299 were dark and 179 were light. There was no significant difference in activity between the light and dark morphs (all $p > 0.35$).

Squirrels were diurnal in all seasons (Fig. 2), but activity patterns differed significantly among seasons (all Wald tests $p < 0.036$, Table 1). In spring, squirrel activity was bimodal with an increased activity around noon followed by a lower peak in the afternoon. During summer, there was a trimodal activity pattern with an activity peak after sunrise, before noon and in the afternoon. In contrast, only one peak after sunrise was visible during fall and winter, followed by a soft (fall) or steep activity decline (winter). Moreover, winter activity started later and ended sooner than during fall. In all seasons, squirrel activity began shortly before sunrise and ended before sunset. The longest activity was recorded in summer.

Activity overlap of squirrel and fox

Squirrel and fox activity showed a low overlap across all seasons. The overlap was higher during spring ($D = 0.44$) and summer ($D = 0.45$) than in fall ($D = 0.24$) and winter ($D = 0.19$) (Fig. 3).

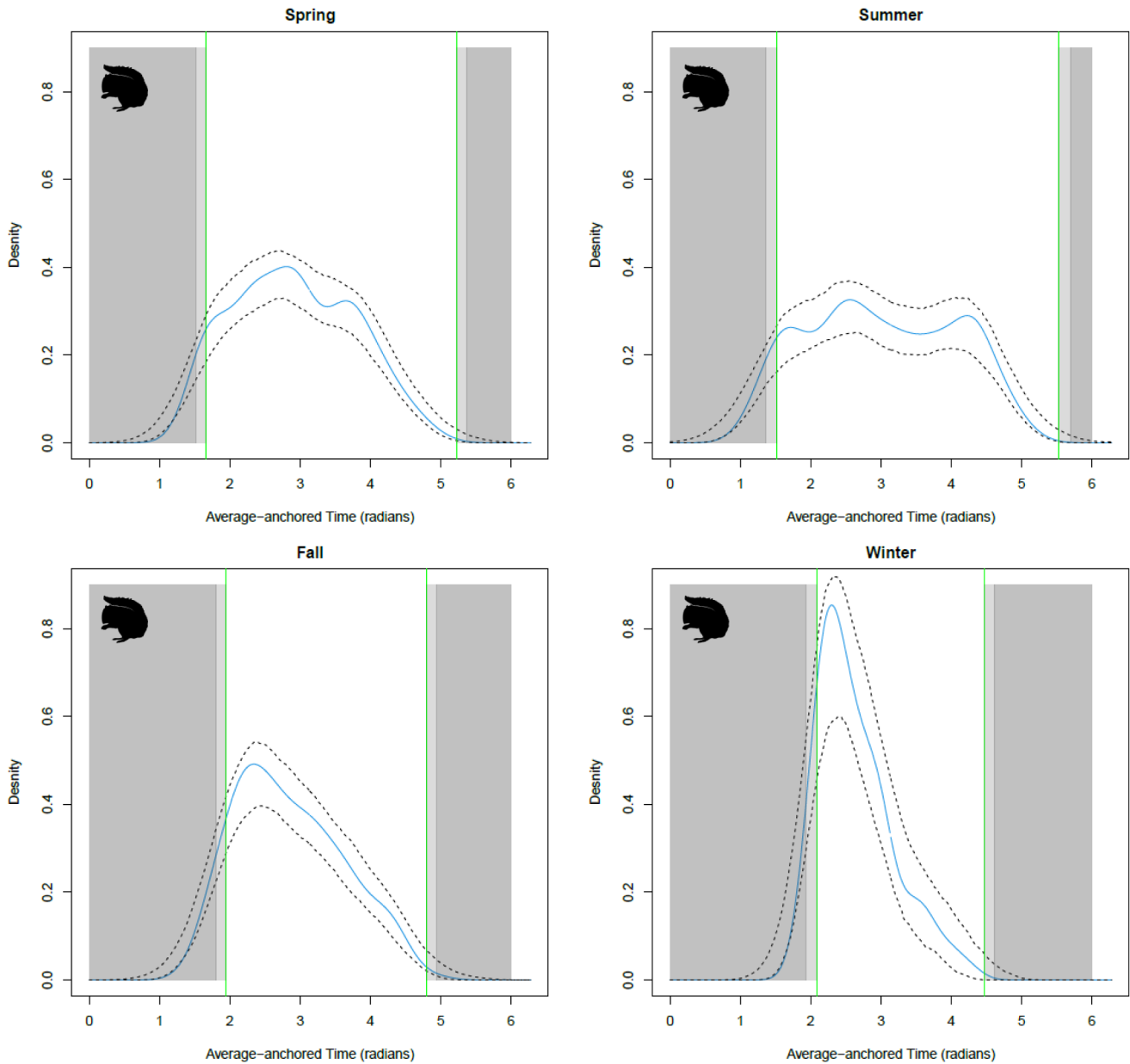


Fig. 2 Squirrel diurnal activity pattern in spring, summer, fall and winter. Activity patterns are illustrated as probability density functions (PDF) dependent on average anchored times. Diurnal activity for each season is illustrated by fitted Von Mises kernel distributions (blue lines, including 95% confidence intervals (dashed lines)). The light grey bars

indicate the average times for civil dawn respectively civil dusk for the observed season. The dark grey bars indicate average night hours. The green lines indicate the average sunset and sunrise times. Times are in radian time format within the range of $[0, 2*\pi)$

Table 1 Difference between seasonal squirrel activity

Seasons	Difference	SE	W	<i>p</i>
Spring - Summer	-0.092	0.042	4.714	0.030
Spring - Autumn	0.072	0.035	4.379	0.036
Spring - Winter	0.210	0.033	40.364	0.001
Summer - Autumn	0.164	0.043	14.663	0.001
Summer - Winter	0.302	0.042	52.481	0.001
Autumn - Winter	0.137	0.034	16.555	0.001

Activity overlap of squirrel and marten

Squirrel and marten activity showed a low overlap during all seasons except summer where activity overlap was modest ($D=0.52$). The overlap was highest in summer, followed by spring ($D=0.33$) and fall ($D=0.24$) and lowest in winter ($D=0.19$) (Fig. 4).

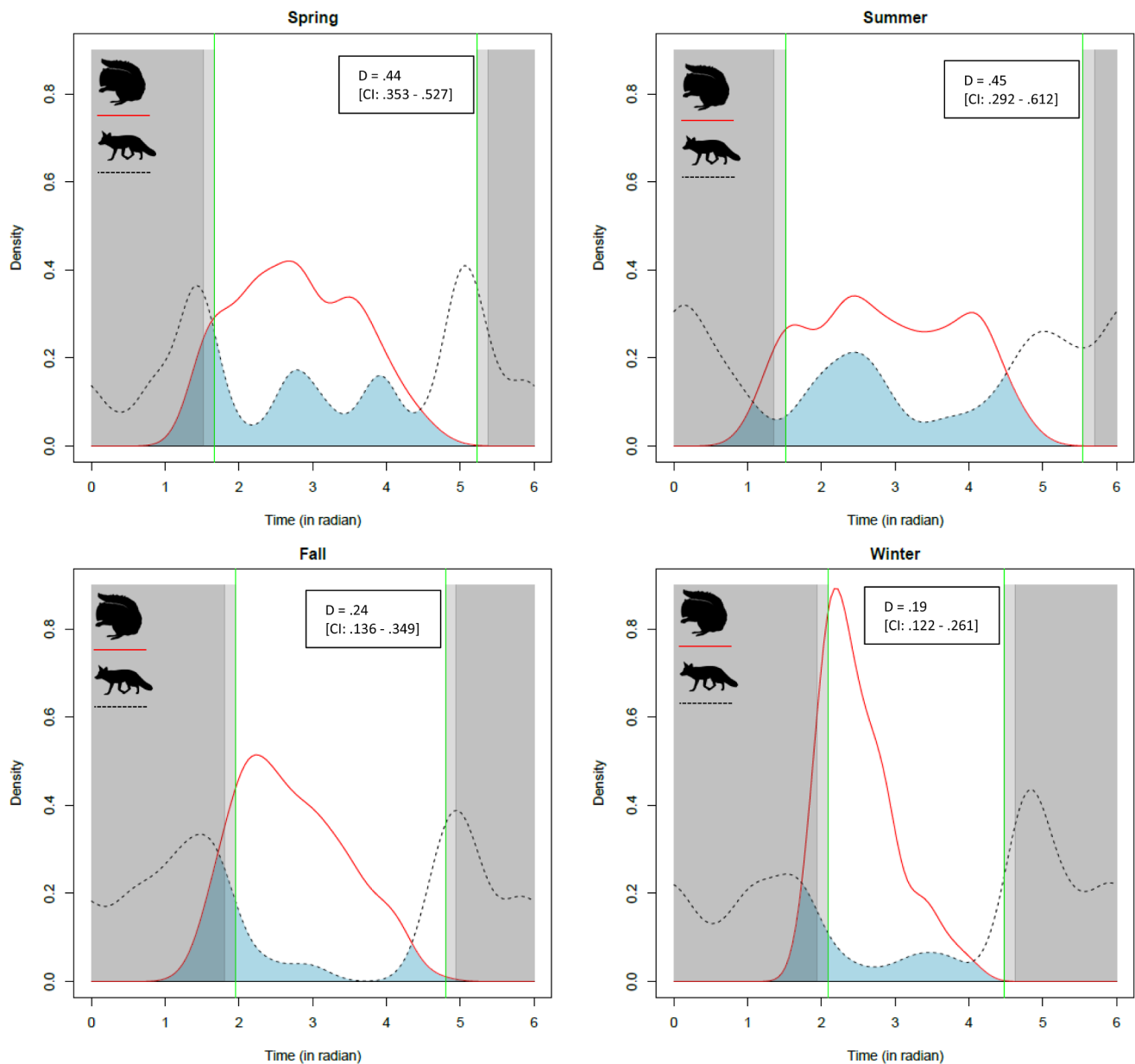


Fig. 3 Temporal overlap between Squirrel (red line) and Fox (black line). The lightblue shaded area indicates the overlap of the density estimates, exact values and 95%-confidence intervals are stated within the figures. The light grey bars indicate the average times for civil

dawn respectively civil dusk for the observed season. The dark grey bars indicate average night hours. The green lines indicate the average sunset and sunrise times. Times are in radian time format within the range of $[0, 2*\pi)$

Discussion

We investigated the diel activity pattern of red squirrels and mammalian predators, red fox and martens in the Rammert, Rottenburg am Neckar, Germany. Based on previous studies, we expected squirrels' activity to differ from those of its predators as well as a difference in activity pattern throughout the seasons.

We found red squirrels to be diurnal in all seasons which is in line with previous findings (Ikeda et al. 2016; Steen

and Barmoen 2017; Caravaggi et al. 2018). Their activity pattern is commonly described as unimodal during winter and bimodal from spring to autumn, with an activity drop during the hottest hours of the day (Gurnell 1987). However, some authors observed unimodal activity in winter, peaking between 9 and 11 am and ceasing in the afternoon, and a bimodal pattern in summer (Tonkin 1983; Wauter and Dondt 1987; Steen and Barmoen 2017). In contrast, squirrels in Italy and Ireland consistently showed a bimodal activity pattern throughout the year (Wauters et al. 2002;

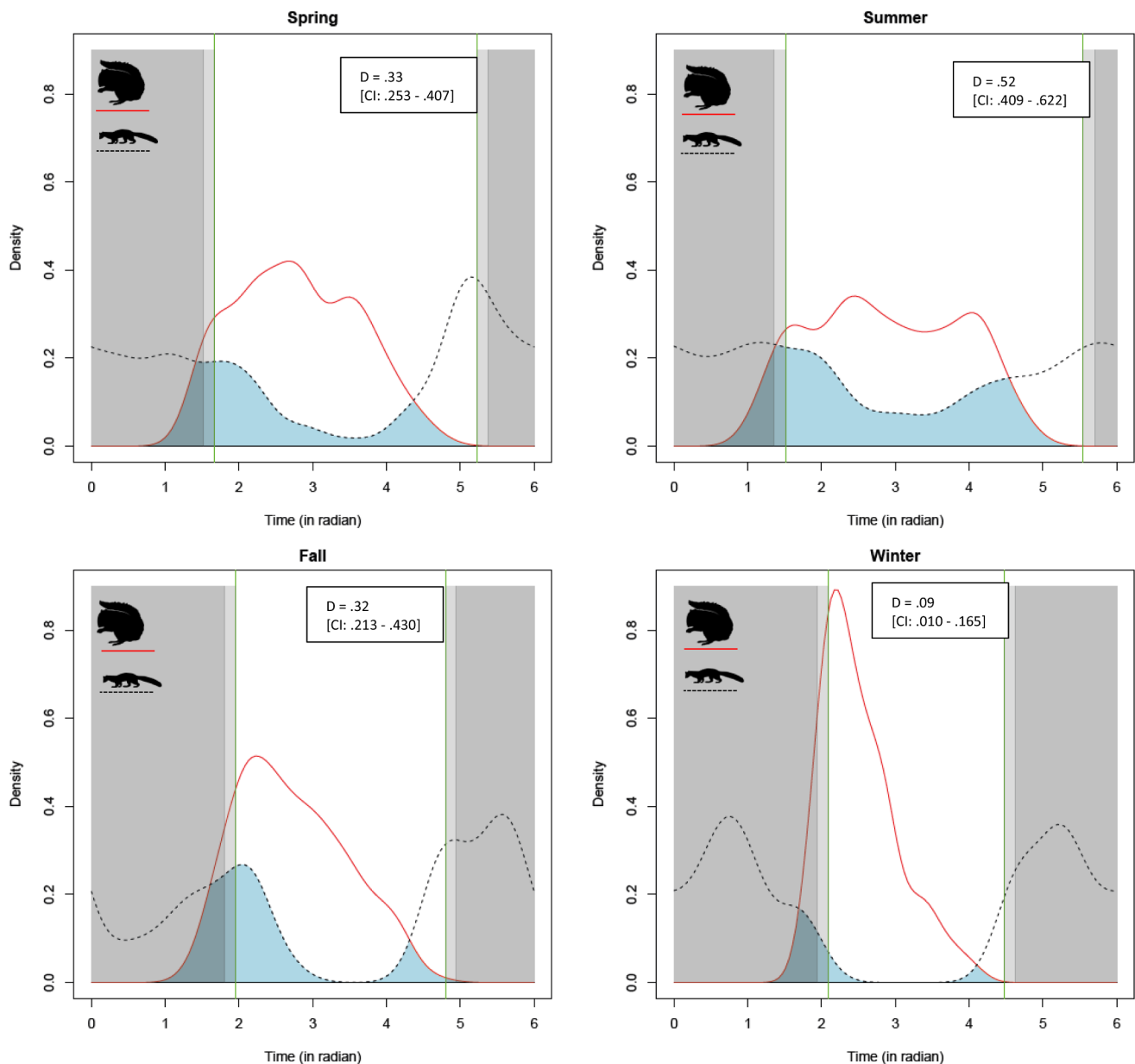


Fig. 4 Temporal overlap between Squirrel (red line) and marten (black line). The lightblue shaded area indicates the overlap of the density estimates, exact values and 95%-confidence intervals are stated within the figures. The light grey bars indicate the average times for civil

dawn respectively civil dusk for the observed season. The dark grey bars indicate average night hours. The green lines indicate the average sunset and sunrise times. Times are in radian time format within the range of $[0, 2*\pi)$

Caravaggi et al. 2018). Di Cerbo and Biancardi (2013) also investigated the activity pattern of small arboreal mammals in Italy. For red squirrels, they found a trimodal pattern in summer, with peaks in the morning and late afternoon and a third peak around midday. The pattern became bimodal in fall and unimodal in winter. Our findings coincide with these studies as we also found such seasonal variation in the activity pattern. The daylight length in winter is shortest, thus, the activity pattern may be more condensed into a uni-modal pattern and driven by energy saving demands.

Spring and fall have an equivalent daytime length, but patterns look differently, which cannot be explained by photoperiod. The difference between spring and fall might arise from the caching of food which is more important during fall. Our results are further in line with findings by Wauters and colleagues who reported higher activity peaks in the morning compared to afternoon during winter, spring and fall, but equal patterns during summer (Wauter and Donnd 1987; Wauters et al. 1992, 2002). We observed the most squirrels in spring, when food is scarce and they spend a

lot of time on the ground, visiting food caches to eat or to move the caches. In addition, young squirrels start to leave the nest and explore their habitat, which probably accounts for another large part of the observations (Bosch and Lurz 2011). In summer and fall, squirrel activity might shift to the treetops, and therefore were not recorded by our camera traps. This might continue until winter, when our activity records were lowest, as there are probably enough conifer seeds left in the trees and so the squirrel might be more active in the upper layer of the forest and caches are rarely visited (Bosch et al. 2020). Wauter and Dondt (1987) attribute up to 90% of nutrition to pine seeds. In spring the active period progressively expanded in the morning and throughout the afternoon which has also been reported by Wauter and Dondt (1987). During summer when natural daylight is available the longest, squirrel activity was the longest, with a total of 18 h. In fall and winter accompanying shorter daylight periods, the activity durations also to about eight hours. Thus, our study shows that a year-round study of the full annual cycle is helpful to address activity patterns. Nevertheless, further research is needed to disentangle the different patterns.

One of research objectives aimed to investigate differences in activity between color morphs. A study in Red Squirrels of northern Italy showed a relationship between the frequency of color morphs and habitat features (Wauters et al. 2004). The frequency of black morphs increased with the proportion of spruce and density of tree, suggesting a selective advantage of black coloration in such habitats. We also detected a higher percentage of black (62,6%) than red morphs (37,4%) in our study area mainly consisting of beech, spruce and oak. Hence, black coloration might indeed be advantageous in our study location due to variance in concealment from predators (Caro and Konecny 2021). Nonetheless, coloration did not differ in activity pattern indicating, temporal niche partitioning is not used to counterbalance possible disadvantages in predation risk due to coloration.

Activity of red squirrel and red fox showed only a low overlap in all seasons, but the overlap was higher in spring and summer than during fall and winter, which can be explained by the decreased day-time activity of foxes in the colder seasons. Red squirrels can produce offspring twice a year (February–April and May–August) and offspring start to leave the nest 40–45 days after birth (Lurz et al. 2005). Hence, during early spring and summer, foxes have an increased chance to prey on young squirrels which might lead to an increased daytime activity and higher activity overlap with squirrels during this time compared to fall and winter. In September and October, the activity of another possible prey item in the study area, the fat dormouse, increases around dusk and dawn, compared to July (Randler

and Kalb 2021). Therefore, foxes might enhance hunting success by shifting activity from daytime to dawn and dusk.

Marten activity showed a modest overlap with squirrel activity in summer but was low in all other seasons. Like foxes, martens may enhance their chance to prey on squirrel offspring by shifting their activity to daylight hours. Indeed, variation in squirrel consumption by martens has already been reported depending on their relative abundance but most studies focused on wintertime (Zielinski et al. 1983; Storch et al. 1990; De Marinis and Masseti 1995). Hence, future studies are needed to investigate the proportion of squirrels in the diet of martens across all seasons, and, on the other hand, predation upon squirrels might be studied in more detail from the squirrels' perspective. In sum, we suppose that the activity pattern of the red squirrel is not mainly dominated or predicted by its mammalian predators.

Conclusion

Camera trapping seems to us a useful tool to monitor red squirrel activity. This is evident from the fact that we get similar results than previous studies which did not use camera traps. The overlap between squirrels and the two predators, marten, and fox, was low in all seasons, which coincides well with the relative proportion of squirrels in the diet of these predators.

Camera traps placed up in trees and radio-tagging could be helpful methods to receive more reliable data regarding possible activity patterns in treetops. The unimodal peak in winter observed in our study may be a result from individual differences in activity patterns. Wauters et al. (1992) reported bimodal activity during winter for individual squirrels, but a unimodal pattern at the population level as individual peaks did not always coincide. Further, the weight of the animal, an important factor whether females get into oestrus (Braun and Dieterlen 2005), was shown to affect diurnal activity and suggests some hierarchies concerning feeder visitations (Bosch et al. 2015). Moreover, as there are personality differences in red squirrels (Uchida et al. 2020), these individual differences may also influence daily activity (Thomas et al. 2018) and varying peak expressions may diffuse the observed patterns. Since we did not mark squirrels, it is not possible to disentangle individual activity patterns from patterns on the population level in our study.

Limitations

It was impossible but would be an interesting aspect to study squirrel activity in the absence of the two predator species. However, in our study area this is not possible due

to high densities of foxes and martens. Moreover, we were not able to analyze the activity patterns of pine and stone marten separately, which might mask differences in temporal activity between these two species. Future studies might therefore further investigate the activity of pine and stone martens in relation to interspecific competitors as well as prey species in Germany.

Acknowledgements Not applicable.

Author contributions Conceptualization, CR, TG; methodology, CR, TG, JD; Data collection (field), CR; formal analysis, JD; investigation, CR, XS; data curation, JD, XS; writing NK, XS, CR, TG. All authors have read and agreed to the published version of the manuscript.

Funding This study received no external funding. Open Access funding enabled and organized by Projekt DEAL.

Declarations

Ethical approval This was an observational study and requires no formal ethic application.

Conflict of interest The authors declare no conflict of interest.

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