



Seasonal variation in the diurnal activity pattern of Eurasian blackbirds (*Turdus merula*) in the forest

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Abstract

Camera traps are increasingly used to estimate the density of animals as well as their activity patterns. As camera traps allow monitoring of animals over long periods of time without disturbance, they are especially useful to observe changes in diurnal activity patterns over time. In ornithology, camera trapping is still in its infancy. To our knowledge, no study has yet investigated the activity pattern of a songbird over the full annual cycle. We used camera traps in the Rammert, a small mountainous forest area near Rottenburg in Southwest Germany to monitor the diurnal activity pattern of forest-dwelling Eurasian blackbirds (*Turdus merula*). As the activity level of animals is known to be affected by day light, we used double-anchoring transformation of day times to account for the variation in sunrise and sunset across the different seasons. By generating activity models, we investigated the pattern of blackbird activity during the four seasons of the year and compared the patterns of male and female birds, respectively. A significant difference between a unimodal activity pattern in spring and a bimodal pattern for the rest of the year was found which might be related to breeding and territorial behaviour in spring. Moreover, we observed that the activity pattern of males and females overlapped greatly but still showed some variation in the number and timing of density peaks.

Keywords Camera traps · Diurnal activity pattern · Seasonal variation

Zusammenfassung

Saisonale Variation der Tagesaktivität von Amseln (*Turdus merula*) im Wald

Kamerafallen werden zunehmend eingesetzt, um die Dichte von Tieren und ihre Aktivitätsmuster zu ermitteln. Da Kamerafallen die Beobachtung von Tieren über lange Zeiträume hinweg ermöglichen, ohne sie zu stören, sind sie besonders nützlich, um Veränderungen in den täglichen Aktivitätsmustern im Laufe der Zeit zu beobachten. In der Ornithologie steckt die Kamerafallennutzung allerdings noch in den Kinderschuhen. Unseres Wissens wurde bisher in keiner Studie das Aktivitätsmuster eines Singvogels über den gesamten Jahreszyklus hinweg untersucht. Wir haben Kamerafallen im Rammert, einem kleinen Mittelgebirgswald bei Rottenburg im Südwesten Deutschlands, eingesetzt, um das tageszeitliche Aktivitätsmuster von waldbewohnenden Amseln (*Turdus merula*) zu beobachten. Da das Aktivitätsniveau der Tiere durch Tageslicht/Photoperiode beeinflusst wird, verwendeten wir eine doppelt verankerte Transformation der Tageszeiten, um

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die Variation von Sonnenaufgang und Sonnenuntergang in den verschiedenen Jahreszeiten zu berücksichtigen. Durch die Erstellung von Aktivitätsmodellen untersuchten wir das Muster der Amselaktivität während der vier Jahreszeiten und verglichen die Muster von männlichen bzw. weiblichen Amseln. Es wurde ein signifikanter Unterschied zwischen einem unimodalen Aktivitätsmuster im Frühjahr und einem bimodalen Muster für den Rest des Jahres festgestellt, was mit dem Brut- und Territorialverhalten im Frühjahr zusammenhängen könnte. Außerdem stellten wir fest, dass sich die Aktivitätsmuster von Männchen und Weibchen stark überschneiden, aber dennoch eine gewisse Variation in der Anzahl und dem Zeitpunkt der Dichtespitzen aufwiesen.

Introduction

Niche partitioning, the process of using the environment in a unique way to enable coexistence of various species, also occurs on the scale of time. The resulting species-specific activity patterns are mostly determined by available illumination and suitability of thermal conditions (Bennie et al. 2014), resulting in a crepuscular, nocturnal, diurnal or cathemeral activity with uni- or multimodal distribution. However, the activity of individuals might be further affected by inter- and intraspecific interactions (Blanchet et al. 2008; Pita et al. 2011; Randler and Kalb 2020), the diurnal activity of prey or predators (Harmsen et al. 2011; Foster et al. 2013); food availability (Boulos and Terman 1980; Orpwood et al. 2006; Pereira 2010) or unfavourable environmental conditions such as weather events or poor light conditions (Fernandez-Duque 2003; Halle and Stenseth 2012).

Camera traps enable researchers to monitor animal behaviour over long time periods with minimal disturbance. The data collected can be used to investigate a variety of research questions ranging from species composition to population size estimates to animal behaviour such as diel activity patterns (Rovero et al. 2013; Fancourt 2016; Krauss et al. 2018; Randler et al. 2020). The number of studies using camera traps increased tremendously over the last years (Zimmermann et al. 2016; Wearn and Glover-Kapfer 2019). However, most studies aimed to capture large mammals, fewer investigated small mammals, and even less studies drew upon reptiles or birds (Burton et al. 2015; Krauss et al. 2018; Richardson et al. 2018; Randler and Kalb 2020). This bias is most likely due to a lower capturing success of small animals by the sensors of most camera traps as they might quickly move out of view before a photo can be taken. Moreover, small species are often hard to identify on images, especially if they are far away from the camera trap or the image quality is low due to e.g. weather or light conditions. Fortunately, there is a growing body of research concerning the sensitivity of camera traps and guidelines to optimise the usage of camera traps for monitoring small mammals and birds (Di Cerbo and Biancardi 2013; Hobbs and Brehme 2017; Randler and Kalb 2018; Dundas et al. 2019). By following the published guidelines (Di Cerbo and Biancardi 2013; Hobbs and Brehme 2017; Randler and Kalb 2018; Dundas

et al. 2019), camera traps can be a powerful tool to observe activity patterns over days, weeks, months and even years as camera traps can collect data on a species presence for prolonged and sustained time periods.

The aim of this study was to investigate the activity pattern of forest-dwelling Eurasian blackbirds (*Turdus merula*, LINNÉ 1758) under natural environmental conditions throughout a whole year using camera trapping in the Rammert (48° 26' 38.0" N 8° 58' 59.5" E), a mainly forested ridge in the Keuper uplands near Rottenburg am Neckar, Southwest Germany. We investigated both the activity patterns of blackbirds throughout the year and sex-specific differences. These sex-specific differences were expected for example due to contrasting behaviour in spring and summer where males spend a considerable amount of time singing on elevated points and females are first building and later, sitting on the nest (Chamberlain et al. 1999; Post and Götmark 2006).

Materials and methods

Camera setup

Basically, the guidelines of Meek et al. (2014) were followed utilising a somehow deliberately biased placement. First, in order to spread the camera traps regularly within the study area, grids were used as a first orientation for choosing the camera trapping places. In a second step, cameras were placed within each grid at focal points to maximise detection (Meek et al. 2014). Trapping success is up to ten times higher when cameras were placed at trails or other structures rather than at random (Kolowski and Forrester 2017). A total of 21 camera traps were placed within 12 different 1 × 1 km large grids distributed in the northern part of the Rammert (Fig. 1). SecaCam Raptor cameras were used, which have been shown to be suitable for detecting small songbirds (Randler and Kalb 2018). To reduce autocorrelation effects (Dormann et al. 2007), cameras were placed in a distance of at least 300 m to each other. As we aimed to study forest-dwelling Eurasian blackbirds, cameras were applied in forested areas, and no camera was placed in the open landscape. Camera traps were placed between 362 and 552 m above sea level.

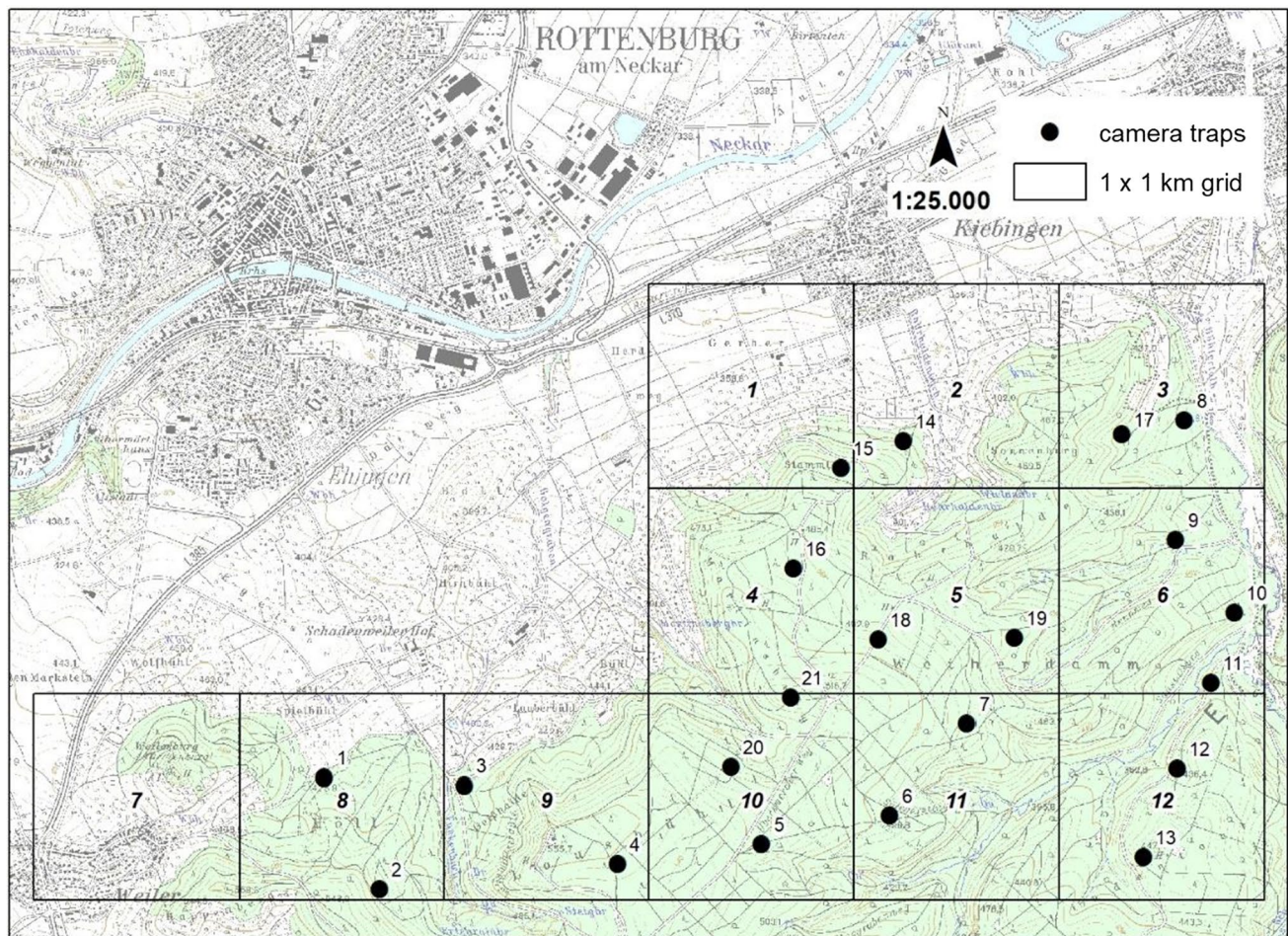


Fig. 1 Locations of the camera traps within the Rammert near Rottenburg

The recording started on the 13th of January 2021 and 17 cameras operated until 19th January 2022, and the rest had to be removed earlier due to technical difficulties. Camera #15 worked well but did not yield any images of blackbirds. Cameras were mounted on trees approximately about 60–80 cm above the ground. The surveyed areas covered different forest types and structural elements, such as dense underwood, small trails, dead wood, openings and grass-covered patches. The forest is formed mainly by *Quercus spec.*, *Picea abies*, *Fagus sylvatica* and *Pinus sylvestris*. All camera traps operated for 24 h/d and collected a series of multiple photos when motion was detected. The starting date of each camera was defined as the date when the camera was deployed in the field. The end date was determined by the end of the survey or the last day the camera was proven to work. The date on the last triggered photo was used as end date. All camera traps were surveyed regularly to switch memory cards and batteries if necessary. The cameras are sensitive enough to take images during twilight and at night, and the cameras have been pretested to show that they are

able to capture thrushes reliably (Randler and Kalb 2018). However, fast-flying birds cannot be recorded reliably by camera traps.

Activity analysis

As animals have to move to trigger a camera trap, we defined activity as movement of Eurasian blackbirds outside of refuges/nest or sleeping places and in front of our cameras (Rowcliffe et al. 2014). We further defined the clock time at which a camera was triggered as activity record. If birds repeatedly triggered the camera without leaving the field of view, only the initial trigger was used and defined as one blackbird event.

To analyse the activity patterns of blackbirds, 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 day length throughout these three-month periods, a time transformation

method suitable for 48.46° latitude was implemented. We transformed the times of the observations within each three-month period with a double-anchoring procedure as described by Vazquez et al. (2019). To apply this transformation to our data, we used the solar time function from the Animal Activity r-package (Rowcliffe et al. 2014; Rowcliffe 2023). The function transforms clock time to solar time anchored to the average sunrise and sunset times for a specific period and location (Rowcliffe 2023). During this transformation, the observation times get transformed into radian time format which is a numeric representation of clock times within the range of $[0, 2\pi]$.

After the transformation, we used the *fitact* function to fit kernel density functions and calculate activity levels for the transformed observation times (Vazquez et al. 2019). Whilst generating these activity models, we used bootstrapping to estimate errors. To obtain sensible confidence intervals despite dealing with low sample sizes for some seasons, we decided to sample from the fitted probability density distribution for the bootstrapping method instead of sampling from our data. We used these models to describe the changes of the activity patterns during the year. To understand more about the differences in activity patterns between male and female blackbirds, we grouped our data by sex and rerun the same computations.

To test for significant differences between all seasons, we first computed an NNTS likelihood ratio test for homogeneity in circular data as proposed by Fernández-Durán and Gregorio-Domínguez (2010). We then computed Watson's two-sided tests of homogeneity to determine the seasons for which differences exist and to detect differences between the sexes for specific seasons. In addition, we used the *overlap* package to determine the overlap of different kernel density estimations by calculating overlap coefficients and generating overlap plots for visualisation (Ridout and Linkie 2009; Meredith and Ridout 2021). We used the “Dhat1” overlap coefficient due to the small sample size (< 75), as recommended by Meredith and Ridout (2021).

All analyses were carried out with RStudio (RStudio Team 2020). Our data and a script to reproduce our results are available on reasonable request from the authors.

Results

Overall, 499 events of blackbirds (definition see above) were photographed by the camera traps. In spring, we recorded 147 blackbirds, 162 during summer, 123 in fall and 67 blackbirds during the winter period (Fig. 2). With one exception in April, we recorded more male than female blackbirds. Appendix Table 1 depicts the recorded observations for each camera trap.

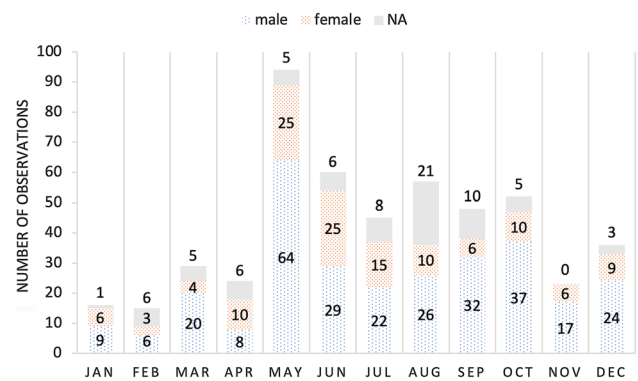


Fig. 2 Total number of observations of *Turdus merula* from January 2021 to January 2022. NA include those pictures, where identification of males or females was not possible due to bad light conditions, image quality or when individuals were incompletely depicted

The camera traps did not record nocturnal activity for blackbirds. As activity starts well before sunrise in all seasons but winter (when activity starts later), we assume a crepuscular–diurnal activity pattern for blackbirds. We found that the activity pattern of Eurasian blackbirds differs significantly throughout the year (Table 1).

Subsequent tests between different seasonal models showed significant differences between all seasons (Table 2).

Within all seasons, we identified 294 males (58.8%), 129 females (25.8%) and in 76 (15.2%) events, the sex of the blackbird could not be identified.

Although there were no significant differences between the raw activity data of both sexes (Appendix Table 2) throughout the seasons, the probability density functions of male and female blackbird activity look different (Fig. 3), and the overlap coefficient between activity is below 1 (Table 3).

Discussion

To our best knowledge, to date, no camera-trap-based study has been conducted to reveal the diurnal activity pattern of songbirds across the full annual cycle. Many factors are known to affect the diurnal activity pattern of animals, including illumination, food availability, brood care, and inter- and intraspecific interactions (Pita et al. (2011), Domononi et al. (2014), Bogdan et al. (2016), Luo et al. (2019)). Therefore, we expected to find a difference in activity patterns between seasons as most of the previously mentioned factors, both biotic or intra- and interspecific relations and abiotic factors, fluctuate during the four seasons in Central Europe. Our study revealed significant differences of activity data between all seasons. Furthermore, in summer, fall and winter, we found a bimodal activity pattern that most

Table 1 Results of NNTS likelihood ratio test for homogeneity for all seasons

M_0	Spring	Summer	Fall	Winter	Combined	$-2\ln(\Lambda)$	d.f	$\chi^2 p$ value
2	-218.719	-243.076	-163.515	-80.419	-735.653	59.861	12	>0.001

Nonnegative Trigonometric Sums (NNTS) ratio likelihood test is performed to determine significant differences in activity patterns between spring ($N=147$), summer ($N=162$), fall ($N=123$) and winter ($N=67$). H_0 “There is no significant difference between the combined model and the seasonal models” is rejected

Table 2 Results of Watson two-sample tests for comparing activity (observed) data between seasons

Season	Test statistic	Significance
Spring–summer	0.494	***
Spring–fall	0.213	*
Spring–winter	0.274	**
Summer–fall	0.539	***
Summer–winter	0.865	***
Fall–winter	0.209	*

Watson two-sample test of homogeneity tests are performed to determine significant differences in activity patterns between spring ($N=147$), summer ($N=162$), fall ($N=123$) and winter ($N=67$). Test statistics are calculated and compared to critical values. Critical values are obtained using the asymptotic distribution of the test statistic. Significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

probably reflects underlying basic diurnal rhythms (Santiago-Quesada et al. 2012).

Seasonal differences

For spring, we found a unimodal activity pattern which peaks after noon. Activity starts before sunrise and ends shortly after sunset (Fig. 4). The missing bimodality is conspicuous, and we assume that the longer photoperiod in spring in contrast to the darker winter is reflected in the activity pattern. Different reasons might explain this result. During spring, blackbirds might constantly allocate time to nest building, mating and breeding throughout the day and therefore may not show distinct activity peaks. Moreover, male blackbirds fly to their perches for singing during twilight early in the morning to establish a territory in early March (Hölzinger 1994). Dominioni et al. (2013a) showed that blackbirds from the forest started singing before twilight in the lab. However, the studies are difficult to compare because Dominioni et al. (2013b) studied the onset of song activity of blackbirds experimentally in the lab, whilst our study considered activity pattern under natural conditions, and thus did not explicitly collect data on song. The additional use of audio recording data could compensate for the shortcoming that with our camera trap setting it was not possible to record blackbirds early in the morning during spring, when males are singing up in the tree.

Additionally, in spring, migrating blackbirds may mix up with the residents which may mask the pattern of diurnal activity since migrants may not sing and show a different behaviour than residents, because they have to refuel and restore body fat, or need more time for resting (Randler et al. 2015). Migrating Central European blackbirds have an earlier seasonal timing than northern populations. Thus, migrants from Scandinavia may also occur in our observations later in spring (Main 2002) which may influence the activity pattern in our data. As, there are only few published data about the phenology of the annual spring migration of blackbirds, further studies focussing on the springtime should be applied. Moreover, urban blackbirds have changed their migration behaviour to a residence status in many European regions as a response to climate change (Moller et al. 2014; van Vliet et al. 2009). Here, we studied forest-dwelling blackbirds that may differ from urban blackbirds. In our study, the lowest numbers of blackbirds were recorded between November and April. Thus, one part of the population of the Rammert might leave the forest to winter in urban areas, migrate to more southern regions. Alternatively, blackbirds may fly longer distances within the forest during the winter because territorial behaviour is absent during the winter months, whilst in spring, the birds are more confined to their territories. Bird detection probabilities should be even higher during the winter compared to summer because the camera traps are based on the temperature differences between moving objects and their surroundings, cooler winter days should elicit more photos compared to the warmer summer days (Randler and Kalb 2018). Further studies should address these differences between urban and forest blackbirds. Even differences concerning the activity pattern could be caused by the fact that urban populations start their daily activity earlier (Dominioni et al. 2013a) and show a longer activity period because of artificial lights at night (Russ et al. 2015). Apart from spring, blackbirds showed a clear activity pattern with a bimodal activity, as in many other animals, including humans (Santiago-Quesada et al. 2012).

The cameras detected fewer blackbirds during January and February. This may be caused by a lower density, a lower activity and less movement during that period. Various studies showed that temperature is an important variable concerning metabolism in passerine birds (Dawson and Marsh 1986; Lehikoinen 1987; Cresswell 1998; Swanson

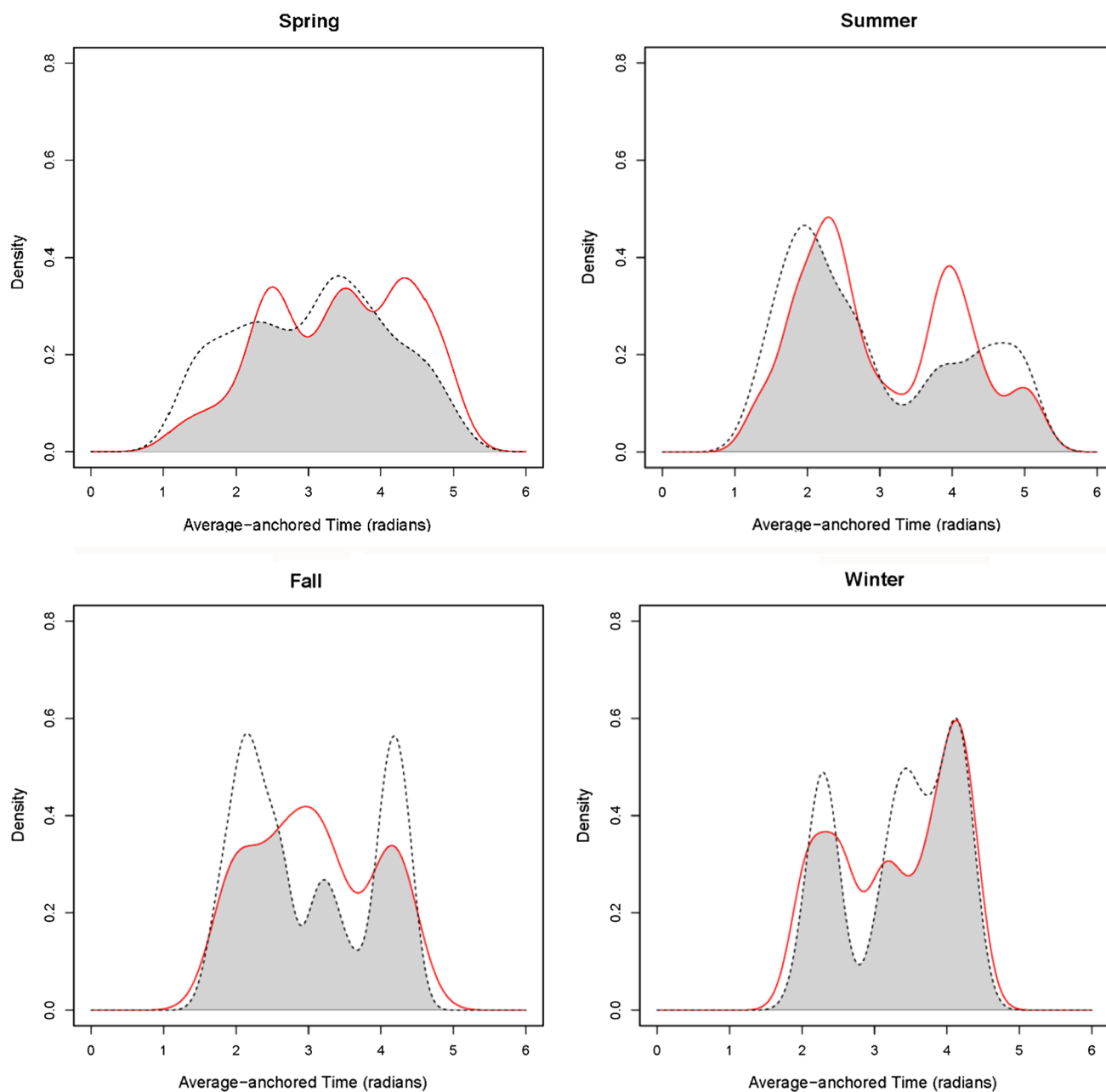


Fig. 3 Fitted kernel density curves showing daily activity of male (black dotted line) and female (red line) Eurasian blackbirds during different seasons. The shaded area indicates the overlap of the density estimates

Table 3 Overlap of activity models for every season between male and female blackbirds

Season	Overlap coefficient	95% Confidence interval
Spring	0.846	[0.717–0.950]
Summer	0.837	[0.721–0.943]
Fall	0.797	[0.660–0.910]
Winter	0.873	[0.716–0.990]

The overlap coefficient ranges from 0 to 1, where 1 represents a perfect overlap of two fitted kernel density curves

and Olmstead 1999; Gosler 2002; Rogers and Reed 2003). In addition to temperature, the shorter photoperiod during winter season also seems to be an important factor affecting foraging because of the time available for feeding (Haftorn 1989; Steinmeyer et al. 2010; Stuber et al. 2015; Schlicht and Kempenaers 2020). However, differences in activity patterns between seasons can be the result of behavioural responses to environmental conditions to which the birds are exposed (temperature, precipitation, etc.). Thus, those patterns may not be related to an underlying circadian rhythm. To test the

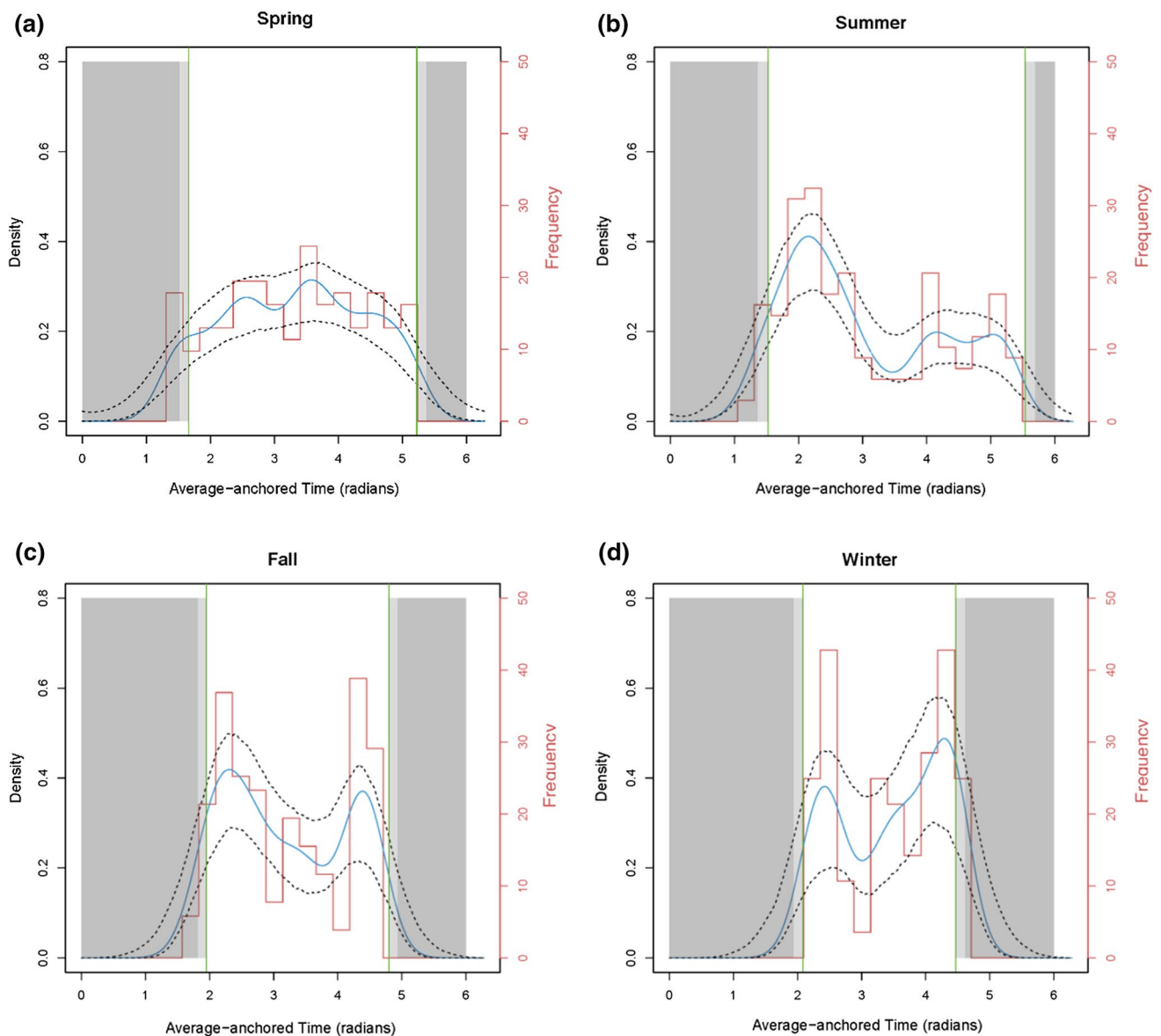


Fig. 4 Blackbird diurnal activity pattern for spring (a), summer (b), fall (c) and winter (d). The step function depicts the frequency of black bird observations, i.e. the transformed raw data per time interval (red line). Our activity model consists of von Mises kernel distribution fitted to raw data (blue lines) with 95% confidence inter-

val (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 lines indicate the average sunset and sunrise times. Times are in radian time format within the range of $[0, 2*\pi]$

underlying circadian rhythms, experiments are needed on a seasonal basis by exposing the animals to constant dim light conditions across the different seasons.

Sex differences

Besides changing abiotic factors, the activity pattern of blackbirds might further be affected by sex. However, a limitation of our study was that we could not identify the sex of blackbirds in 15.2% of all individuals, which is mostly owed to the occurrence of blackbirds around sunrise and sunset.

In dark ambient conditions, the camera traps switch from colour to black and white photographs and use an infrared flash (blacklight), making it difficult to identify the sex of the individuals pictured. To solve this problem, camera traps with white flash could be used, but since this kind of flash is likely to severely disturb the animals, this practice could have a detrimental effect on the photo yield if the camera location is avoided as a result of the flashing at night (Henrich et al. 2020).

In passerines, the foraging patterns of males and females are known to differ as male foraging heights are often

correlated with male song perch heights, whereas those of females are related to nest heights (Holmes 1986; Randler et al. 2010). Such differences in foraging behaviour could also result in different activity patterns captured by camera traps. Indeed, the study of (Post and Götmark 2006) revealed that female blackbirds foraged more and at lower heights than males.

The comparison of the activity pattern of males and females in our study revealed an overall large overlap of activity. However, males were active earlier than females in spring. During spring, males defend their territory vigorously against male intruders by singing on song posts and directly by territorial conflicts (own observations) which increases the chances of being trapped by a camera. Females, on contrast are breeding on the nest during this time of the day and therefore were recorded less. In summer, both sexes are more active before noon, that is, when the temperature is lower and humidity is higher, both beneficial to foraging earthworms. In fall, males show two distinct peaks in the morning and afternoon as well as one smaller peak right at noon, whereas females were most active around noon. Both sexes are more active in the afternoon in winter. A more extensive survey on individually marked blackbirds or a telemetry study might reveal the relationships between activity patterns and the effect of different factors, like predation risks, energy needs or parental investment throughout the year (Chamberlain et al. 1999; Post and Götmark 2006).

Limitations and methodological implications

The main disadvantage for camera trapping is that activity data is only collected for behaviour displayed in front of the camera traps, for example, foraging in leaf litter when the camera is placed accordingly. Other behaviour occurring out of view, such as singing on perches above the camera angle, will not be recorded and therefore not be included in the resulting activity profiles. This issue can partly be addressed by placing camera traps in all environments relevant to the respective species. Another problem was that sex determination and even determination between females and juveniles were not always possible due to image quality reasons. This is expected to be a smaller problem in the future as optical equipment has been continuously improved in recent years. A detailed result of an individual activity pattern could rather be achieved using invasive methods, such as radiotelemetry and automated bases stations using radio-frequency identification (RFID). For example, passive integrated transponders (PIT tags) can be read by RFID antennas, and these data can be automatically sampled, e.g. during feeder visits, and also, radio-tagging can be used (Santiago-Quesada et al. 2012; Hillemann et al. 2019; Randler 2021). Some recent studies used an array of digital radio-receiving stations (Gotwald et al. 2019; Karwinkel et al. 2022). On the one hand,

the automated techniques have a high quality of activity data collection and allow individual identification, which is usually not the case for camera trapping. On the other hand, radio-tagging and radiotelemetry require the desired animal to be captured at least once, which might affect the normal behaviour and therefore, recorded activity. Furthermore, radio signals can be disturbed in dense forest areas and radio-receiving stations needs intensive maintenance.

A combination of both non-invasive methods, audio recordings and camera traps would likely reveal the most insights about the activity pattern of a certain species. The potential of camera traps to quantify approximate activity patterns of songbirds without the need to catch birds in the field is quite high because it does not need a permission/licence and it is also characterised by cheap devices, little workload in comparison to catching and fitting transmitters, and not time-consuming in acquisition.

Conclusion

Our study shows that camera trap surveys are useful to determine the activity pattern across all seasons of small songbirds such as the Eurasian blackbird. Camera traps can thereby be a useful tool to survey the activity pattern of a species over long time periods to identify possible changes in activity within day and season.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-023-02096-2>.

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Data availability The data used for this research is available from the corresponding author on reasonable request.

Declarations

Conflicts of interest The authors declare no conflict of interest.

Animal ethics This was an observational study and required no formal ethic application.

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