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Occupancy and activity rhythms of the Siberian roe deer

Emiliano Mori[1,*], Maila Cicero[2], Sandro Lovari[3,4], Marco Zaccaroni[5], Silvia Salomoni[6], Andrea Vendramin[7], Claudio Augugliaro[2]

1. Consiglio Nazionale delle Ricerche – Istituto di Ricerca sugli Ecosistemi Terrestri – Via Madonna del Piano 10, 50019, Sesto Fiorentino (FI), Italy. ORCID ID: 0000-0001-8108-795.
2. Wildlife Initiative NGO, Bayangol District, 6th Khoroo, Micro District 10, Ulaanbaatar, 210349, Mongolia. Claudio Augugliaro, ORCID: 0000-0001-9917-709X.
3. Unità di Ricerca in Ecologia Comportamentale, Etologia e Gestione della Fauna– Dipartimento di Scienze della Vita, Università di Siena, Via P.A. Mattioli 4, 53100 Siena, Italy.
4. Maremma Natural History Museum, Strada Corsini, 5, 58100 Grosseto, Italy.
5. Department of Biology, University of Florence, Via Madonna del Piano 8, 50019, Sesto Fiorentino (FI), Italy.
6. World Biodiversity Association Onlus c/o Museo Civico di Storia Naturale, Lungadige Porta Vittoria 9, 37129, Verona, Italy.
7. Università degli studi di Udine - DI4A (Dipartimento di Scienze Agroalimentari, 23 ambientali e animali), via Sondrio 2/A, 33100, Udine, Italy.

*, Corresponding Author. Emiliano Mori, Consiglio Nazionale delle Ricerche – Istituto di Ricerca sugli Ecosistemi Terrestri – Via Madonna del Piano 10, 50019, Sesto Fiorentino (FI), Italy. Email: emiliano.mori@cnr.it

Short title: Activity and occupancy of Siberian roe deer

Abstract

The assessment of spatiotemporal behaviour patterns of wild species is pivotal both for conservation and for management, especially when involving rare or elusive species, or species living in delicate ecosystems, e.g. mountains. The Siberian roe deer *Capreolus pygargus* is a native Asian ungulate, whose ecology is still poorly known, especially on mountain ecosystems. In particular, information on its spatial behaviour and temporal patterns of activity is poor. We have assessed its patterns of circadian rhythms in relation to moon phases, with some conclusions on spatial behaviour in respect to potential predation and slope inclination. Data were collected between August and October 2019, with 35 camera-traps deployed over an area of mountain forests alternated to steppe, in Central Mongolia. Camera trap data were analyzed with occupancy models and kernel smoothers, providing a reliable assessment of the presence of Siberian roe deer, with only 1% of false absence and a very high detection probability. This ungulate showed a bimodal temporal behaviour, with activity peaks at dawn and at early night, irrespective from moon phases. The occurrence of Siberian roe deer was negatively influenced by the presence of large carnivores and by increasing slope steepness.

Keywords: *Capreolus pygargus*; moonlight; mountain ecosystems; predation risk; spatiotemporal behaviour.

Introduction

Assessing spatiotemporal behaviour of wildlife is pivotal to design specific management plans, to preserve rare and elusive species and to manage pest species and biological invasions (Srivathsa et al. 2004; Ancillotto et al. 2018; Merson et al. 2019; Mori et al. 2020a). This research field may be challenging, particularly for those species inhabiting impenetrable habitats and remote geographic areas (e.g. De Luca and Rovero 2006; Botts et al. 2020). Camera traps placed for inventories of medium-large mammals in remote study areas (e.g. Augugliaro et al. 2020; Zaccaroni et al. 2020) should provide a wealth of new information (Pamplin 2013; Edward et al. 2018; Mazzamuto et al. 2019), integrating occurrence data very relevant for poorly known, elusive species (Augugliaro et al. 2019; Viviano et al. 2020).

The Siberian roe deer *Capreolus pygargus* Pallas, 1771 is a widespread, elusive ungulate species occurring throughout temperate-cold Eurasia, from Baltic countries to the Far East (Argunov 2013; Argunov and Safronov 2013; Lorenzini et al. 2014; Lovari et al. 2016). The current climatic change has promoted its range expansion towards northern latitudes and upper elevations (Argunov and Safronov 2013), although Siberian roe deer tend to select areas at lower elevations with respect to coexisting deer species (Jiang et al. 2006, 2008; Adhikari et al. 2016). Little is known on the ecology and behaviour of the Siberian roe deer (Danilkin et al. 1995; Danilkin 1996; Jiang et al. 2008, 2009; Adhikari et al. 2016; Lovari et al. 2016). This species inhabits dense forests and forest-steppes up to 3300 m a.s.l. (when permanent ice is absent: Fig. 1); it tends to feed in open habitats where grass cover is abundant, making seasonal movements of up to 200 km between their wintering and breeding ranges in spring, and back in autumn, in groups of up to 500 individuals (Danilkin et al. 1995; Danilkin 1996; Jiang et al. 2008; Lovari et al. 2016). However, where larger-sized deer species are present (e.g. *Cervus canadensis* Erxleben, 1777, *Cervus elaphus* Linnaeus, 1758, *Alces alces* Linnaeus, 1758), the Siberian roe deer may use sheltered habitats (i.e., forests) in the surroundings of human settlements (Jiang et al. 2008; 2009). Territoriality has only been confirmed in males, before and during the rut, between mid-July and mid-September (Danilkin 1996; Lovari et al. 2016). In the warm months (May-September), females live with their offspring, whereas males are solitary. Conversely in the cold season (October-April), the Siberian roe deer forms mixed groups of up to 20-30 individuals (Argunov and Safronov 2013; Lovari et al. 2016). There is no information on covariates influencing the occupancy of this species. Furthermore, no data on circadian rhythms of the Siberian roe deer are available, despite being reported as a mainly nocturnal species, with peaks at dawn and dusk in the warm season, while being active mainly at dawn during the cold season (Danilkin 1996; Lovari et al. 2016; Tang et al. 2019). In our work, we have aimed to help filling these gaps, by investigating the patterns of activity rhythms of the Siberian roe deer in Central Mongolia, in the warm months, and the relevant effect of moonlight. We also estimated the probability of occupancy of the Siberian roe deer in this area, and the minimum number of camera-trap nights required to reliably assess its local absence. Given the biological requirements of this ungulate (Jiang et al. 2008; Lovari et al. 2016), we expected that occupancy by the Siberian roe deer (*i*) would be influenced by the presence of its main predators (i.e., large carnivores and perhaps the red fox *Vulpes vulpes* Linnaeus, 1758 on fawns) and human / livestock presence; (*ii*) would decrease with increasing slopeness, elevation and distance from forest patches, and that (*iii*) ranging movements of this cervid would be reduced to a minimum in bright full moon nights (Monterroso et al. 2013) to reduce predation risk.

Material and Methods

Study area

Our survey was conducted in the Northern Khangai Nuruu National Park (KNNP) (N 46°898′; E 101°346′) in Orkhon district, Arkhangai province, Mongolia. The sampling area was characterized by mountain forests alternated to steppe, bounded by peaks of over 3000 m a.s.l. in the North and in the West. The mean temperature in the study period was 24.4±3.3°C (mean ± SD), whereas monthly precipitations were 4.9±1.5 mm. The vegetation was stratified following an altitudinal range with the steppe system including Asteraceae, Poaceae, Caryophyllaceae and Fabaceae, up to 2100 m a.s.l. A forest-steppe system dominated by *Larix* *sibirica* Ledeb. and *Pinus sibirica* Du Tour, as well as shrubs such as *Lonicera altaica* (Pall.) Gladkova, *Ribes altissimum* (Turcz.), and *Rosa acicularis* Lindl., occurs between 2000-2700 m a.s.l. Above the upper treeline, a stony mountain tundra occurred with artic high-mountain species (Klimek and Starkel 1980); mosses and lichens were present in the few peaks over 3000 m a.s.l. (Brzeźniak 1977).

The area hosts over 30 mammalian species (Zaccaroni et al. 2020), e.g. the Siberian roe deer, the Siberian ibex *Capra sibirica* Pallas, 1776 and the wapiti *Cervus canadensis* among ungulates. The large carnivore guild includes the grey wolf *Canis lupus* Linnaeus, 1758, the wolverine *Gulo gulo* (Linnaeus, 1758) and the Eurasian lynx *Lynx lynx* (Linnaeus, 1758). A high number of small and meso-carnivore species also occurs, i.e. the Pallas's cat *Otocolobus manul* (Pallas, 1776), the Asian badger *Meles leucurus* Hodgson, 1847, the stoat *Mustela erminea* Linnaeus, 1758, the Siberian weasel *Mustela sibirica* Pallas, 1773, the least weasel *Mustela nivalis* Linnaeus, 1766, the steppe polecat *Mustela eversmanii* (Lesson, 1827), the beech marten *Martes foina* (Erxleben, 1777), the red fox and the corsac fox *Vulpes corsac* Linnaeus, 1768 (Zaccaroni et al. 2020). Amongst meso-carnivores, only the red fox has been recorded as potential predators of roe deer fawns (Danilkin 1996; Aanes et al. 1998).

Herder families live in sparse groups of 5-10 households (i.e., "*ger*": Narangerel 2010). Sheep, goats, horses and yaks were bred throughout the area. The small-sized livestock was guarded by dogs and herders, and it was enclosed in corrals at night. Yaks were free ranging in the grazing area, and brought back to the surroundings of the herder's camp in the evening, whereas horses were left free-ranging round-the-clock.

Sampling design

We set 35 camera traps in 35 locations, between August and the end of October 2018, with no intermediate control. Camera traps were grouped in two clusters with respectively 17 and 18 cameras, distant approximately 13 km one another between their closest points (Fig. 2). These two areas were selected as they included the highest number of habitat types in the study area and the highest elevation ranges, from woodlands to alpine meadows, to screes. The minimum distance between 2 cameras was 680 ± 30 m (Rovero and Zimmermann 2016).

Cameras were placed on randomly selected cells of a 1 km x 1 km grid created on QGIS 2.18 (QGIS Development Team 2018), including forest patches and areas over the tree-line level, depending on their local accessibility. We arrayed the cameras on video-mode, with an average height of 50 cm above the ground (Tobler et al. 2008), on animal trails and forced passages, at elevations ranging between 2065 and 2944 m a.s.l.

Occupancy models

We counted as one "independent event" all Siberian roe deer videos taken by the same camera trap in less than 30 min; when > 1 roe deer video was recorded by the same camera trap in ≤ 30 min, we kept in our dataset only one record, placed in the mid-time between the first and the last video (Viviano et al. 2021). We filled a binary string (1, detection of Siberian roe deer; 0, non-detection) for all camera-trap checks for each camera-trap site (MacKenzie et al. 2006). Occupancy models were calculated by using the package "unmarked" (Fische and Chandler 2011) for the software R (version 3.6.1., R Foundation for Statistical Computing, Vienna, Austria: cran.r-project.org). We used the "occu" model-fitting function, which fits occurrence models with no linkage between abundance and detection (Fische and Chandler 2011).

As our field work lasted three months, we ran single-season models (MacKenzie et al. 2006). We included the effects of seven environmental variables used as covariates: (*i*) elevation (metres above sea level); (*ii*) slope (degrees); (*iii*) local presence of large carnivores (i.e. the wolverine, the grey wolf and the lynx: 1, detected; 0, not detected); (*iv*) local presence of the red fox, potential predator of roe deer fawns (1, detected; 0, not detected); (*v*) local presence of livestock as a proxy of human pressure and as food competitors (1, detected; 0, not detected); (*vi*) camera trap located in a forest patch (1, yes; 0, no); (*vii*) aspect (i.e. North-Eastern, North-Western, South-Eastern and South-Western oriented camera traps on mountainsides).

We started with a "null" model which does not include covariates for both detectability and occupancy (Mori et al. 2020a). Then, we focused first on the effect of all covariates and their interactions on detectability (p) and, afterwards, on occupancy (ψ) and on both p and ψ, as detectability may affect occupancy, following Luzi et al. (2021). The goodness of each model was assessed through a multi-model inference approach; for each obtained model the AIC_C value was computed. Models were considered as informative and reliable when ΔAIC_C (i.e., the difference between the AIC_C of each model and the lowest AIC_C) was lower than 2 ("top models": Burnham and Anderson 2002; Mori et al. 2020a). We estimated the minimum number of camera-trap days of activity to reliably infer the absence of the Siberian roe deer through the formula: $N = \ln(\alpha)/\ln(1-p)$, where α represents the probability of type-I error (i.e. 0.05: Reed 1996).

Pattern of circadian activity rhythms

We defined the "activity" as the cumulate period which roe deer spend while "non-sleeping", regardless of their behaviour (Lashley et al. 2018). For each Siberian roe deer detection, we reported the date and the solar hour of capture directly shown on each file, in a dataset. Circadian rhythms and associated 95% confidence intervals (hereafter, CIs) were computed through the R 3.6.1 package overlap (Meredith and Ridout 2014). We removed from our dataset records occurring at the same site within less than 30 min, to limit pseudo-replication (Meredith and Ridout 2014). Each detection kept in the final dataset after this filtering was considered arbitrarily as independent. We tested whether moonlight had an effect on the locomotor activity patterns of the Siberian roe deer by classifying moon phases into four clusters: phase (1) from new moon to ¼; phase (2) from ¼ to ½; phase (3) from ½ to ¾ and phase (4) over ¾ and full moon. Then, we performed a chi-squared test on the numbers of detections recorded during each moon phase, to assess if they were uniform throughout the four clusters (Mori et al. 2020a). We performed a Hermans–Rasson test to evaluate whether a random activity pattern was exhibited over the 24 hours (Landler et al. 2019).

Results

Our final dataset included 55 records of Siberian roe deer from a total of 7/35 camera trap sites (Fig. 1), with 23.6% records in forest edges and 76.4% in forest areas: no roe deer was recorded in steppe and on bare rocks beyond the upper tree line.

We obtained 1% of false absence, i.e. the percentage of sites in which the Siberian roe deer was actually found (naïve estimate=0.20) was only 1% smaller than the estimate of proportion of occupied sites ψ (0.21). The top model obtained ($\Delta AIC_C < 2$: Table 1) assumed that the occupancy by the Siberian roe deer was a function of both slope and presence of large carnivores, with a very high value for the parameter w_i (98%: Table 1). The effect of both covariates was negative (coefficient $\beta \pm SE$, presence of potential predators = -1.38 ± 0.42; slope = -1.59 ± 0.27), thus indicating that sites where potential predators were not recorded and characterised by a lower degree of declivity were more likely to be occupied by the Siberian roe deer, with respect to those where large carnivores were recorded. The effects of all the other environmental variables included in our models were not significant. The detection probability (p) was high for the best selected model (69%). According to our results, four camera-trap days are required to reliably infer the local absence of the Siberian roe deer.

A non-random activity pattern was exhibited round-the-clock, peaking at dawn and early night (Hermans–Rasson test: R = 74.70; *p* = 0.02: Fig. 3). Activity of Siberian roe deer appeared independent from moon phases ($\chi^2 = 0.53$, df = 3, *p* = 0.08).

Discussion

Our models, valid for the warm season only, showed a strong negative relationship between presence and detection of Siberian roe deer and detection of large carnivores, thus fulfilling our prediction (*i*). We are aware of the limitations related to our small sample size, and further data are needed to assess the Siberian roe deer behaviour throughout the whole year.

Although the diets of the grey wolf, the wolverine and the Eurasian lynx have not been assessed in this area (where they occur: Zaccaroni et al. 2020), they are predators whose presence may affect the local population density of European (cf. Odden et al. 2006; Van Dijk 2008; Newsome al. 2016) and that of Siberian (Danilkin 1916; Soyumert et al. 2019; Tan et al. 2019; Balayed-Lyngdoh et al. 2020) roe deer. In China, Tang et al. (2019) showed a low encounter probability between Siberian roe deer and the lynx, suggesting it as a potential predator avoidance tactic by this ungulate and providing support to our results. In contrast, the presence of the red fox (Danilkin 1916; Aanes et al. 1998) was not a significant variable affecting the presence of the Siberian roe deer in Central Mongolia. Fawns of Siberian roe deer are 80% larger than those of the European species and this may prevent foxes to prey easily on them (cf. Hewison and Danilkin 2001, but see Danilkin 1996). Furthermore, the red fox is an inferior competitor of the lynx, and presence of larger predators may lead meso-carnivores to avoid areas and hours where/when the superior predator is present, thus coinciding with roe deer habits (cf. Helldin et al. 2006; Tang et al. 2019, but see Ferretti et al. 2021, and Rossa et al. 2021, as to facilitative relationships between the wolf and the red fox). Our models showed also that an increasing degree of declivity limits the occurrence of the Siberian roe deer, in line with our prediction (*ii*). Conversely, forest patches and elevation were not significant variables, possibly because Siberian roe deer are adapting to higher elevation over the treeline as a consequence of climate change (Ross et al. 2021). Most likely, the European roe deer evolved as a glade inhabitant in forested habitats (Lovari et al. 2017), rarely observed beyond the upper treeline (cf. Robin 1975; Mori et al. 2018; Boitani et al. 2003), as their anatomy is not well-adapted to broken terrain or cliffs (Boitani et al. 2003). Accordingly, Siberian roe deer use mountains only in the warm season, i.e. when snow cover is not present, whereas they move to lowlands in the cold months through fixed migration routes (Danilkin et al. 1995; Danilkin 1996). Our occupancy models did not show any importance of forest patches for Siberian roe deer occupancy. In North-Eastern China, the Siberian roe deer is a typical species of mature coniferous forests, avoiding sparse scrublands and bare rock areas which do not provide food nor shelter sites (Guo et al. 2017). Adhikari et al. (2016) showed that, in mountainous areas of Jeju Island (South Korea), Siberian roe deer mostly use open areas to feed in the warm months, i.e. areas rich in forbs-climbers and graminoid plants. Although we did not attempt to estimate habitat-selection in our study area, the Siberian roe deer may only use forests (where most photos were taken) as cover to rest, being also active in areas with sparse trees, where their food is most abundant and time required for vigilance is the lowest (see San Josè et al. 1996; Jiang et al. 2008; Adhikari et al. 2016).

Both the European roe deer (Bonnot et al. 2019; Ossi et al. 2020; Viviano et al. 2021; Zanni et al. 2021) and the Siberian roe deer are mainly crepuscular, i.e. their activity locomotor patterns significantly peak at dawn and dusk. Our results confirm the results of Tang et al. (2019), which showed that ranging movements of the Siberian roe deer are defined by heliophany (including sunrise and sunset times). The roe deer seems to shape its activity to limit encounters with its main local predators, e.g. the lynx and the wolf (Soyumert et al. 2019; Tang et al. 2019; Bonnot et al. 2020; Mori et al. 2020b). Bonnot et al. (2020) showed a remarkable plasticity in European roe deer diel activity in relation to spatiotemporal variation of mortality/predation risks. This flexibility was also suggested for populations of Siberian roe deer (Jiang et al. 2008; Tang et al. 2019). This small cervid species shows a limited capacity of the rumen and a fast digestion, requiring frequent feeding bouts (Cederlund 1981; Danilkin 1996). This feature may explain why roe deer activity patterns do not show a single peak, but two peaks of activity/day alternated with resting in cover. An effect of moon phases was also expected, as most prey species tend to avoid bright moonlight nights to limit encounter probabilities with their predators (Lima 1998; Monterroso et al. 2013). Prugh and Golden (2014) reported that the trend in ungulate activity with respect to moon phases is still poorly studied, and it may change with species and adapt to local ecological conditions. Nocturnal activity of mostly-diurnal species peaks in brightest nights (Carnevali et al. 2016; Brisbane and van den Burg 2020), as their visual acuity is fundamental for orientation. Instead, ungulate species with mostly crepuscular and cathemeral activity may decrease predation risk by moving to cover at night, thus limiting their visibility to predators, without avoidance of bright moonlight (Wronski et al. 2006; Prugh and Golden 2014). Consistently, our results showed that, despite the local presence of several large carnivores, the activity rhythms of Siberian roe deer were independent from moon phases, thus not fulfilling our prediction (*iii*). In fact, Pagon et al. (2013) detected no effect of moon phases on the activity rhythms of the European roe deer. Being active at dawn and dusk might thus represent a strategy to avoid both diurnal and nocturnal local predators (cf. Soyumert et al. 2019; Bonnot et al. 2020; Mori et al. 2020b).

Besides individual behaviour (Stache et al. 2013), human activities (e.g hunting pressure and livestock breeding) may shape the spatiotemporal behaviour of wild ungulates (Douglas 1971; De Boer et al. 2004; Scillitani et al. 2010; Bonnot et al. 2013; Zbyryt et al. 2018). Jiang et al. (2008) reported that Siberian roe deer seem to resent human disturbance, much more than coexisting Manchurian wapitis *Cervus canadensis xanthopygus* Milne-Edwards, 1867, therefore occurring mostly far from human settlements. Ecological studies on European roe deer have shown that hunting pressure increases vigilance levels, with consequent shifts of feeding sites to cover (Benhaiem et al. 2008) and of activity rhythms (Bonnot et al. 2020). Hunting Siberian roe deer is allowed in Mongolia by the National Law on Hunting of May 2000, between the 1st of August and the 1st of December. However, our study area was included in a National Park, where hunting is forbidden (cf. Art. 18, Law on Special Protected Areas of Mongolia), although some poaching may have occurred. In our study area, the temporal behaviour of the Siberian roe deer coincided with that of the European roe in sites where human disturbance is the lowest (Bonnot et al. 2020; Mori et al. 2020b). In our study area, the presence of a single human was detected only once (Zaccaroni et al. 2020).

Our data refer only to roe deer activity in the warm season, i.e. they cover the birth and mating periods: two rather special biological phases of roe deer (Melis et al. 2005; Bongi et al. 2008; Lovari et al. 2008). Information on activity rhythms in the cold season, with a much longer night-duration, could yield different results. In particular, the activity of large predators seems to occur mainly at night (Soyumert et al. 2019; Tang et al. 2019; Bonnot et al. 2020; Mori et al. 2020b), thus leading potentially to an even greater impact on the activity rhythms of Siberian roe deer, in the cold season.

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Author contributions

CA conceived the study; EM and SL conducted literature search and performed the analysis for the review; MC, MZ, SS, AV and CA collected field data. EM, SL and CA led manuscript writing. All authors contributed critically to the draft and gave final approval for submission. Data supporting this study are available in the main text.

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Conflict of interest statement

No potential conflict of interest was reported by authors.

Compliance with ethical standard

All procedures were conducted without animal handling and with no disturbance to them, in line with all national and international laws on animal and wildlife wellness.

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Tables

Table 1. Summary of the five parameter estimates for the occupancy. Models are ranked according to the AIC_C, w_i (Akaike weight), ψ (occupancy probability), p (detectability), SE (standard error), N (sample size estimate). The best selected model is shown in bold.

Model	AIC_C	ΔAIC_C	w_i	ψ (SE)	p (SE)	N
ψ (“slope + presence of large carnivores”)p(“.”)	**307.30**	**0.00**	**0.98**	**0.21 (0.07)**	**0.74 (0.12)**	**4**
ψ (“presence of large carnivores”)p(“elevation”)	317.54	10.24	0.01	0.11 (0.03)	0.32 (0.21)	4
ψ (“slope”)p(“.”)	338.17	12.12	0.01	0.10 (0.03)	0.30 (0.17)	5
ψ (“.”)p(“.”)	347.22	15.04	0.01	0.12 (0.02)	0.31 (0.24)	5

Figure Legends

Figure 1. Camera-trapped Siberian roe deer and environmental features of the study area.

Figure 2. Location of the study area (inset map), location of camera traps and occurrences of Siberian roe deer.

Figure 3. Circadian rhythms of the Siberian roe deer, expressed as Kernel density estimate of activity throughout the 24-h cycle (N = 51 independent records). Blue lines represent bootstrapped estimates of activity patterns; dashed black lines represent 95 % CIs.