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Occupancy and activity rhythms of the Siberian roe deer

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Short title: Activity and occupancy of Siberian roe deer

26 **Abstract**

27

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

42

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

45

46 **Introduction**

47

48 Assessing spatiotemporal behaviour of wildlife is pivotal to design specific management plans,
49 to preserve rare and elusive species and to manage pest species and biological invasions
50 (Srivathsa et al. 2004; Ancillotto et al. 2018; Merson et al. 2019; Mori et al. 2020a). This
51 research field may be challenging, particularly for those species inhabiting impenetrable
52 habitats and remote geographic areas (e.g. De Luca and Rovero 2006; Botts et al. 2020). Camera

53 traps placed for inventories of medium-large mammals in remote study areas (e.g. Augugliaro
54 et al. 2020; Zaccaroni et al. 2020) should provide a wealth of new information (Pamplin 2013;
55 Edward et al. 2018; Mazzamuto et al. 2019), integrating occurrence data very relevant for
56 poorly known, elusive species (Augugliaro et al. 2019; Viviano et al. 2020).

57 The Siberian roe deer *Capreolus pygargus* Pallas, 1771 is a widespread, elusive ungulate
58 species occurring throughout temperate-cold Eurasia, from Baltic countries to the Far East
59 (Argunov 2013; Argunov and Safronov 2013; Lorenzini et al. 2014; Lovari et al. 2016). The
60 current climatic change has promoted its range expansion towards northern latitudes and upper
61 elevations (Argunov and Safronov 2013), although Siberian roe deer tend to select areas at
62 lower elevations with respect to coexisting deer species (Jiang et al. 2006, 2008; Adhikari et al.
63 2016). Little is known on the ecology and behaviour of the Siberian roe deer (Danilkin et al.
64 1995; Danilkin 1996; Jiang et al. 2008, 2009; Adhikari et al. 2016; Lovari et al. 2016). This
65 species inhabits dense forests and forest-steppes up to 3300 m a.s.l. (when permanent ice is
66 absent: Fig. 1); it tends to feed in open habitats where grass cover is abundant, making seasonal
67 movements of up to 200 km between their wintering and breeding ranges in spring, and back
68 in autumn, in groups of up to 500 individuals (Danilkin et al. 1995; Danilkin 1996; Jiang et al.
69 2008; Lovari et al. 2016). However, where larger-sized deer species are present (e.g. *Cervus*
70 *canadensis* Erxleben, 1777, *Cervus elaphus* Linnaeus, 1758, *Alces alces* Linnaeus, 1758), the
71 Siberian roe deer may use sheltered habitats (i.e., forests) in the surroundings of human
72 settlements (Jiang et al. 2008; 2009). Territoriality has only been confirmed in males, before
73 and during the rut, between mid-July and mid-September (Danilkin 1996; Lovari et al. 2016).
74 In the warm months (May-September), females live with their offspring, whereas males are
75 solitary. Conversely in the cold season (October-April), the Siberian roe deer forms mixed
76 groups of up to 20-30 individuals (Argunov and Safronov 2013; Lovari et al. 2016). There is
77 no information on covariates influencing the occupancy of this species. Furthermore, no data

78 on circadian rhythms of the Siberian roe deer are available, despite being reported as a mainly
79 nocturnal species, with peaks at dawn and dusk in the warm season, while being active mainly
80 at dawn during the cold season (Danilkin 1996; Lovari et al. 2016; Tang et al. 2019). In our
81 work, we have aimed to help filling these gaps, by investigating the patterns of activity rhythms
82 of the Siberian roe deer in Central Mongolia, in the warm months, and the relevant effect of
83 moonlight. We also estimated the probability of occupancy of the Siberian roe deer in this area,
84 and the minimum number of camera-trap nights required to reliably assess its local absence.
85 Given the biological requirements of this ungulate (Jiang et al. 2008; Lovari et al. 2016), we
86 expected that occupancy by the Siberian roe deer (*i*) would be influenced by the presence of its
87 main predators (i.e., large carnivores and perhaps the red fox *Vulpes vulpes* Linnaeus, 1758 on
88 fawns) and human / livestock presence; (*ii*) would decrease with increasing slopiness, elevation
89 and distance from forest patches, and that (*iii*) ranging movements of this cervid would be
90 reduced to a minimum in bright full moon nights (Monterroso et al. 2013) to reduce predation
91 risk.

92

93 **Material and Methods**

94

95 *Study area*

96

97 Our survey was conducted in the Northern Khangai Nuruu National Park (KNNP) (N 46°898';
98 E 101°346') in Orkhon district, Arkhangai province, Mongolia. The sampling area was
99 characterized by mountain forests alternated to steppe, bounded by peaks of over 3000 m a.s.l.
100 in the North and in the West. The mean temperature in the study period was 24.4±3.3°C (mean
101 ± SD), whereas monthly precipitations were 4.9±1.5 mm. The vegetation was stratified
102 following an altitudinal range with the steppe system including Asteraceae, Poaceae,
103 Caryophyllaceae and Fabaceae, up to 2100 m a.s.l. A forest-steppe system dominated by *Larix*

104 *sibirica* Ledeb. and *Pinus sibirica* Du Tour, as well as shrubs such as *Lonicera altaica* (Pall.)
105 Gladkova, *Ribes altissimum* (Turcz.), and *Rosa acicularis* Lindl., occurs between 2000-2700 m
106 a.s.l. Above the upper treeline, a stony mountain tundra occurred with arctic high-mountain
107 species (Klimek and Starkel 1980); mosses and lichens were present in the few peaks over 3000
108 m a.s.l. (Brzeźniak 1977).

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

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

125

126 *Sampling design*

127

128 We set 35 camera traps in 35 locations, between August and the end of October 2018, with no
129 intermediate control. Camera traps were grouped in two clusters with respectively 17 and 18
130 cameras, distant approximately 13 km one another between their closest points (Fig. 2). These
131 two areas were selected as they included the highest number of habitat types in the study area
132 and the highest elevation ranges, from woodlands to alpine meadows, to screes. The minimum
133 distance between 2 cameras was 680 ± 30 m (Rovero and Zimmermann 2016).
134 Cameras were placed on randomly selected cells of a 1 km x 1 km grid created on QGIS 2.18
135 (QGIS Development Team 2018), including forest patches and areas over the tree-line level,
136 depending on their local accessibility. We arrayed the cameras on video-mode, with an average
137 height of 50 cm above the ground (Tobler et al. 2008), on animal trails and forced passages, at
138 elevations ranging between 2065 and 2944 m a.s.l.

139
140 *Occupancy models*

141
142 We counted as one “independent event” all Siberian roe deer videos taken by the same camera
143 trap in less than 30 min; when > 1 roe deer video was recorded by the same camera trap in ≤ 30
144 min, we kept in our dataset only one record, placed in the mid-time between the first and the
145 last video (Viviano et al. 2021). We filled a binary string (1, detection of Siberian roe deer; 0,
146 non-detection) for all camera-trap checks for each camera-trap site (MacKenzie et al. 2006).
147 Occupancy models were calculated by using the package “unmarked” (Fische and Chandler
148 2011) for the software R (version 3.6.1., R Foundation for Statistical Computing, Vienna,
149 Austria: cran.r-project.org). We used the “occu” model-fitting function, which fits occurrence
150 models with no linkage between abundance and detection (Fische and Chandler 2011).
151 As our field work lasted three months, we ran single-season models (MacKenzie et al. 2006).
152 We included the effects of seven environmental variables used as covariates: (i) elevation
153 (metres above sea level); (ii) slope (degrees); (iii) local presence of large carnivores (i.e. the

154 wolverine, the grey wolf and the lynx: 1, detected; 0, not detected); (iv) local presence of the
155 red fox, potential predator of roe deer fawns (1, detected; 0, not detected); (v) local presence of
156 livestock as a proxy of human pressure and as food competitors (1, detected; 0, not detected);
157 (vi) camera trap located in a forest patch (1, yes; 0, no); (vii) aspect (i.e. North-Eastern, North-
158 Western, South-Eastern and South-Western oriented camera traps on mountainsides).

159 We started with a “null” model which does not include covariates for both detectability and
160 occupancy (Mori et al. 2020a). Then, we focused first on the effect of all covariates and their
161 interactions on detectability (p) and, afterwards, on occupancy (ψ) and on both p and ψ , as
162 detectability may affect occupancy, following Luzi et al. (2021). The goodness of each model
163 was assessed through a multi-model inference approach; for each obtained model the AIC_C
164 value was computed. Models were considered as informative and reliable when ΔAIC_C (i.e., the
165 difference between the AIC_C of each model and the lowest AIC_C) was lower than 2 (“top
166 models”: Burnham and Anderson 2002; Mori et al. 2020a). We estimated the minimum number
167 of camera-trap days of activity to reliably infer the absence of the Siberian roe deer through the
168 formula: $N = \ln(\alpha)/\ln(1-p)$, where α represents the probability of type-I error (i.e. 0.05: Reed
169 1996).

170

171 *Pattern of circadian activity rhythms*

172

173 We defined the “activity” as the cumulate period which roe deer spend while “non-sleeping”,
174 regardless of their behaviour (Lashley et al. 2018). For each Siberian roe deer detection, we
175 reported the date and the solar hour of capture directly shown on each file, in a dataset.
176 Circadian rhythms and associated 95% confidence intervals (hereafter, CIs) were computed
177 through the R 3.6.1 package *overlap* (Meredith and Ridout 2014). We removed from our dataset
178 records occurring at the same site within less than 30 min, to limit pseudo-replication (Meredith

179 and Ridout 2014). Each detection kept in the final dataset after this filtering was considered
180 arbitrarily as independent. We tested whether moonlight had an effect on the locomotor activity
181 patterns of the Siberian roe deer by classifying moon phases into four clusters: phase (1) from
182 new moon to $\frac{1}{4}$; phase (2) from $\frac{1}{4}$ to $\frac{1}{2}$; phase (3) from $\frac{1}{2}$ to $\frac{3}{4}$ and phase (4) over $\frac{3}{4}$ and full
183 moon. Then, we performed a chi-squared test on the numbers of detections recorded during
184 each moon phase, to assess if they were uniform throughout the four clusters (Mori et al. 2020a).
185 We performed a Hermans–Rasson test to evaluate whether a random activity pattern was
186 exhibited over the 24 hours (Landler et al. 2019).

187

188 **Results**

189

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

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

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

208

209 **Discussion**

210

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

215 Although the diets of the grey wolf, the wolverine and the Eurasian lynx have not been assessed
216 in this area (where they occur: Zaccaroni et al. 2020), they are predators whose presence may
217 affect the local population density of European (cf. Odden et al. 2006; Van Dijk 2008;
218 Newsome et al. 2016) and that of Siberian (Danilkin 1916; Soyumert et al. 2019; Tan et al. 2019;
219 Balayed-Lyngdoh et al. 2020) roe deer. In China, Tang et al. (2019) showed a low encounter
220 probability between Siberian roe deer and the lynx, suggesting it as a potential predator
221 avoidance tactic by this ungulate and providing support to our results. In contrast, the presence
222 of the red fox (Danilkin 1916; Aanes et al. 1998) was not a significant variable affecting the
223 presence of the Siberian roe deer in Central Mongolia. Fawns of Siberian roe deer are 80%
224 larger than those of the European species and this may prevent foxes to prey easily on them (cf.
225 Hewison and Danilkin 2001, but see Danilkin 1996). Furthermore, the red fox is an inferior
226 competitor of the lynx, and presence of larger predators may lead meso-carnivores to avoid
227 areas and hours where/when the superior predator is present, thus coinciding with roe deer
228 habits (cf. Helldin et al. 2006; Tang et al. 2019, but see Ferretti et al. 2021, and Rossa et al.
229 2021, as to facilitative relationships between the wolf and the red fox). Our models showed also
230 that an increasing degree of declivity limits the occurrence of the Siberian roe deer, in line with

231 our prediction (*ii*). Conversely, forest patches and elevation were not significant variables,
232 possibly because Siberian roe deer are adapting to higher elevation over the treeline as a
233 consequence of climate change (Ross et al. 2021). Most likely, the European roe deer evolved
234 as a glade inhabitant in forested habitats (Lovari et al. 2017), rarely observed beyond the upper
235 treeline (cf. Robin 1975; Mori et al. 2018; Boitani et al. 2003), as their anatomy is not well-
236 adapted to broken terrain or cliffs (Boitani et al. 2003). Accordingly, Siberian roe deer use
237 mountains only in the warm season, i.e. when snow cover is not present, whereas they move to
238 lowlands in the cold months through fixed migration routes (Danilkin et al. 1995; Danilkin
239 1996). Our occupancy models did not show any importance of forest patches for Siberian roe
240 deer occupancy. In North-Eastern China, the Siberian roe deer is a typical species of mature
241 coniferous forests, avoiding sparse scrublands and bare rock areas which do not provide food
242 nor shelter sites (Guo et al. 2017). Adhikari et al. (2016) showed that, in mountainous areas of
243 Jeju Island (South Korea), Siberian roe deer mostly use open areas to feed in the warm months,
244 i.e. areas rich in forbs-climbers and graminoid plants. Although we did not attempt to estimate
245 habitat-selection in our study area, the Siberian roe deer may only use forests (where most
246 photos were taken) as cover to rest, being also active in areas with sparse trees, where their food
247 is most abundant and time required for vigilance is the lowest (see San Josè et al. 1996; Jiang
248 et al. 2008; Adhikari et al. 2016).

249 Both the European roe deer (Bonnot et al. 2019; Ossi et al. 2020; Viviano et al. 2021; Zanni et
250 al. 2021) and the Siberian roe deer are mainly crepuscular, i.e. their activity locomotor patterns
251 significantly peak at dawn and dusk. Our results confirm the results of Tang et al. (2019), which
252 showed that ranging movements of the Siberian roe deer are defined by heliophany (including
253 sunrise and sunset times). The roe deer seems to shape its activity to limit encounters with its
254 main local predators, e.g. the lynx and the wolf (Soyumert et al. 2019; Tang et al. 2019; Bonnot
255 et al. 2020; Mori et al. 2020b). Bonnot et al. (2020) showed a remarkable plasticity in European

256 roe deer diel activity in relation to spatiotemporal variation of mortality/predation risks. This
257 flexibility was also suggested for populations of Siberian roe deer (Jiang et al. 2008; Tang et al.
258 2019). This small cervid species shows a limited capacity of the rumen and a fast digestion,
259 requiring frequent feeding bouts (Cederlund 1981; Danilkin 1996). This feature may explain
260 why roe deer activity patterns do not show a single peak, but two peaks of activity/day
261 alternated with resting in cover. An effect of moon phases was also expected, as most prey
262 species tend to avoid bright moonlight nights to limit encounter probabilities with their
263 predators (Lima 1998; Monterroso et al. 2013). Prugh and Golden (2014) reported that the trend
264 in ungulate activity with respect to moon phases is still poorly studied, and it may change with
265 species and adapt to local ecological conditions. Nocturnal activity of mostly-diurnal species
266 peaks in brightest nights (Carnevali et al. 2016; Brisbane and van den Burg 2020), as their
267 visual acuity is fundamental for orientation. Instead, ungulate species with mostly crepuscular
268 and cathemeral activity may decrease predation risk by moving to cover at night, thus limiting
269 their visibility to predators, without avoidance of bright moonlight (Wronski et al. 2006; Prugh
270 and Golden 2014). Consistently, our results showed that, despite the local presence of several
271 large carnivores, the activity rhythms of Siberian roe deer were independent from moon phases,
272 thus not fulfilling our prediction (*iii*). In fact, Pagon et al. (2013) detected no effect of moon
273 phases on the activity rhythms of the European roe deer. Being active at dawn and dusk might
274 thus represent a strategy to avoid both diurnal and nocturnal local predators (cf. Soyumert et al.
275 2019; Bonnot et al. 2020; Mori et al. 2020b).

276 Besides individual behaviour (Stache et al. 2013), human activities (e.g hunting pressure and
277 livestock breeding) may shape the spatiotemporal behaviour of wild ungulates (Douglas 1971;
278 De Boer et al. 2004; Scillitani et al. 2010; Bonnot et al. 2013; Zbyryt et al. 2018). Jiang et al.
279 (2008) reported that Siberian roe deer seem to resent human disturbance, much more than
280 coexisting Manchurian wapitis *Cervus canadensis xanthopygus* Milne-Edwards, 1867,

281 therefore occurring mostly far from human settlements. Ecological studies on European roe
282 deer have shown that hunting pressure increases vigilance levels, with consequent shifts of
283 feeding sites to cover (Benhaiem et al. 2008) and of activity rhythms (Bonnot et al. 2020).
284 Hunting Siberian roe deer is allowed in Mongolia by the National Law on Hunting of May
285 2000, between the 1st of August and the 1st of December. However, our study area was included
286 in a National Park, where hunting is forbidden (cf. Art. 18, Law on Special Protected Areas of
287 Mongolia), although some poaching may have occurred. In our study area, the temporal
288 behaviour of the Siberian roe deer coincided with that of the European roe in sites where human
289 disturbance is the lowest (Bonnot et al. 2020; Mori et al. 2020b). In our study area, the presence
290 of a single human was detected only once (Zaccaroni et al. 2020).
291 Our data refer only to roe deer activity in the warm season, i.e. they cover the birth and mating
292 periods: two rather special biological phases of roe deer (Melis et al. 2005; Bongi et al. 2008;
293 Lovari et al. 2008). Information on activity rhythms in the cold season, with a much longer
294 night-duration, could yield different results. In particular, the activity of large predators seems
295 to occur mainly at night (Soyumert et al. 2019; Tang et al. 2019; Bonnot et al. 2020; Mori et al.
296 2020b), thus leading potentially to an even greater impact on the activity rhythms of Siberian
297 roe deer, in the cold season.

298

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300

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303

304 **Author contributions**

305

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

310

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312

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314

315 **Conflict of interest statement**

316

317 No potential conflict of interest was reported by authors.

318

319 **Compliance with ethical standard**

320

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

323

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551 **Tables**

552

553

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

557

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

558

559

560 **Figure Legends**

561

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

563

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

566

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

570