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Locomotor activity pattern of two recently introduced non-native ungulate species in a Mediterranean habitat

Laura CENTORE¹, Damir UGARKOVIĆ², Dino SCARAVELLI³, Toni SAFNER⁴, Karlo PANDURIĆ⁵
and Nikica ŠPREM^{5*}

¹ Georg-August-Universität Göttingen Master of International Nature Conservation M.I.N.C.,
Wilhelm-Weber-Str. 2, 37073 Göttingen, Germany

² Department of Forest Ecology and Silviculture, Faculty of Forestry, University of Zagreb, Svetošimunska
cesta 25, 10000 Zagreb, Croatia

³ Department of Veterinary Medical Sciences, University of Bologna, via Tolara di Sopra 50,
40064 Ozzano dell'Emilia, Bologna, Italy

⁴ Department of Plant Breeding Genetics, Biometrics and Experimentation, Faculty of Agriculture,
University of Zagreb, Svetošimunska cesta 25, 10000 Zagreb, Croatia

⁵ Department of Fisheries, Beekeeping, Game Management and Special Zoology, Faculty of Agriculture,
University of Zagreb, Svetošimunska cesta 25, 10000 Zagreb, Croatia; e-mail: nsprem@agr.hr

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Abstract. The aim of this study was to determine the locomotor activity pattern of European mouflon and axis deer in a Mediterranean habitat on the island of Rab, and to determine the temporal overlap between these two species. Nine cameras with an infrared motion detection system were used to track animal activity over a 12-month period, 24 hours per day. A total of 122082 JPEG photographs were obtained, of which 69273 recorded the presence of the two target non-native ungulate species. The average monthly number of recorded animals varied by sex and season for European mouflon and by season for axis deer. Both species displayed a bimodal activity pattern, with an overlap coefficient of 0.74 for the activity of both species during the entire study period. The results indicate a non-competitive coexistence and similar activity patterns in the studied ungulate species, despite the high overlap coefficient.

Key words: European mouflon, axis deer, camera trapping, overlap, temporal segregation

Introduction

European mouflon (*Ovis aries musimon*), originating from Sardinia and Corsica (ITIS 2016), have been successfully introduced to several European countries, including Croatia (Kusak & Krapinec 2010). Axis deer (*Axis axis*), also known as chital or spotted deer, is native to the Indian subcontinent and introductions were performed worldwide (Duckworth et al. 2015). However, the only two successful introductions in Europe were those in Croatia, on the islands of Brijuni and Rab (Kusak & Krapinec 2010). Both European mouflon and axis deer are present on the Kalifront Peninsula of the island of Rab, where populations were created and maintained for hunting purposes. In this area, seven axis deer were released in 1974, while 41 European mouflons were released in 1998 (Tomljanović 2016). None of the previously

conducted behavioural studies described patterns of coexistence of these two species in the same habitat. In order to do this, a camera trap survey was designed. In recent years, camera trapping has been increasingly used to estimate activity patterns of ungulate species (O'Connell et al. 2011). This method has a range of benefits, as a non-invasive system that provides an abundance of data in short periods of time, at relatively low financial cost (Ridout & Linkie 2008). New analytical methods are emerging from camera trap data that enable scientists to quantify aspects of behaviour, such as locomotor activity pattern (Ridout & Linkie 2008, Oliveira-Santos et al. 2010). Locomotor activity pattern can be an important descriptor of animal behaviour and may reveal ample information about a species (Pagon et al. 2013). In Sardinia and the northern French Alps, European

* Corresponding Author

mouflon show a bimodal activity pattern with two marked peaks near dawn and dusk, separated by a period of low activity (Pipia et al. 2008, Darmon et al. 2014). Axis deer also show a bimodal activity pattern in different geographic regions, such as Hawaii (Graf & Nichols 1966) and India (Tak & Lamba 1984). Apart from this, very few studies have been dedicated to the activity patterns and time budgets of axis deer (de Silva & de Silva 2001). Previous studies on other ungulate species describe a similar bimodal pattern (e.g. European red deer and North American elk, Ensing et al. 2014; European roe deer, Stache et al. 2013).

Estimates of spatial and temporal overlaps of locomotor activities between species can be used to describe patterns of coexistence, such as habitat interference (Faas & Weckerly 2010) or food competition (Bartoš et al. 2002). For example, a study conducted in Texas (U.S.A.) showed aggressive and dominant behaviour in axis deer toward white-tailed deer (Faas & Weckerly 2010). An interaction study on two ungulate species in a Mediterranean area showed that roe deer avoided areas with high densities of fallow deer (Ferretti et al. 2008). This interspecific interference affected the density and distribution of the two species at both fine and large scales. Ferretti et al. (2008) also showed that fallow deer can actively exclude roe deer from natural feeding sites through direct aggression. Conversely, European mouflon have shown tolerance to the presence of individuals of other bovid species. Darmon et al. (2012) described the coexistence of European mouflons and chamois

in the northern French Alps. The temporal and spatial partitioning of resources might have positively affected the spatial overlap of the two species, and it was concluded that habitat selection of those two species was not influenced by their coexistence.

Based on the available knowledge, we developed hypotheses that: (i) activity patterns of European mouflon and axis deer on the island of Rab, where they were recently introduced, are similar to those described for other ungulate species, and (ii) the temporal overlap of their locomotor activities is high, since there are no resource limitations in the new habitat. Through the use of a camera-trap survey, the objectives of this study were (i) to identify locomotor activity patterns in European mouflon and axis deer on the island of Rab, and (ii) to determine the degree of temporal overlap between these two species.

Material and Methods

Study area

The study was conducted on 846 ha of the Kalifront Peninsula, located on the northwest side of the island of Rab in Croatia, in the northeastern Adriatic Sea (N 44°47'24", E 14°40'10"; Fig. 1). The study area is a forest ecosystem representing an inclination from 3° to 15° and an altitude from 50 to 94 meters. Annual precipitation is 1087 mm and the average air temperature is approximately 14.7 °C. Scrublands and woodlands of Euro-Mediterranean vegetation represent the typical habitat in the study area, with black ash (*Fraxinus ornus*) and holm oak (*Quercus ilex*) as the dominant plant species. Artificially

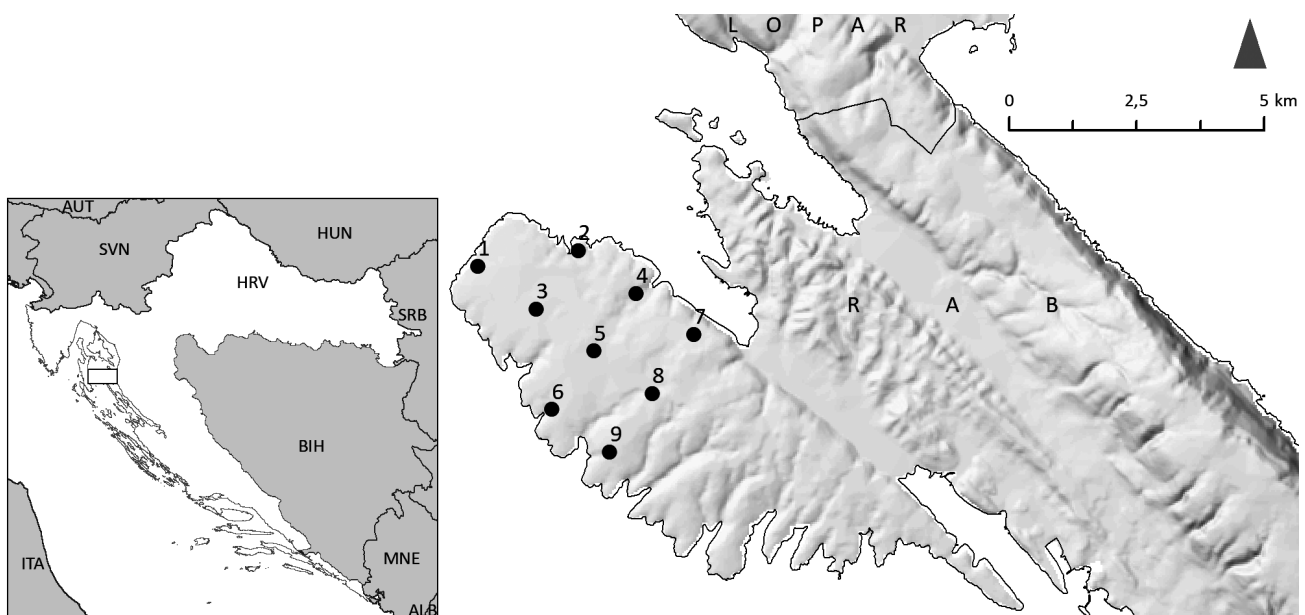


Fig. 1. Study area of the island of Rab in the northeast Adriatic Sea, and Kalifront Peninsula showing the nine camera trap locations.

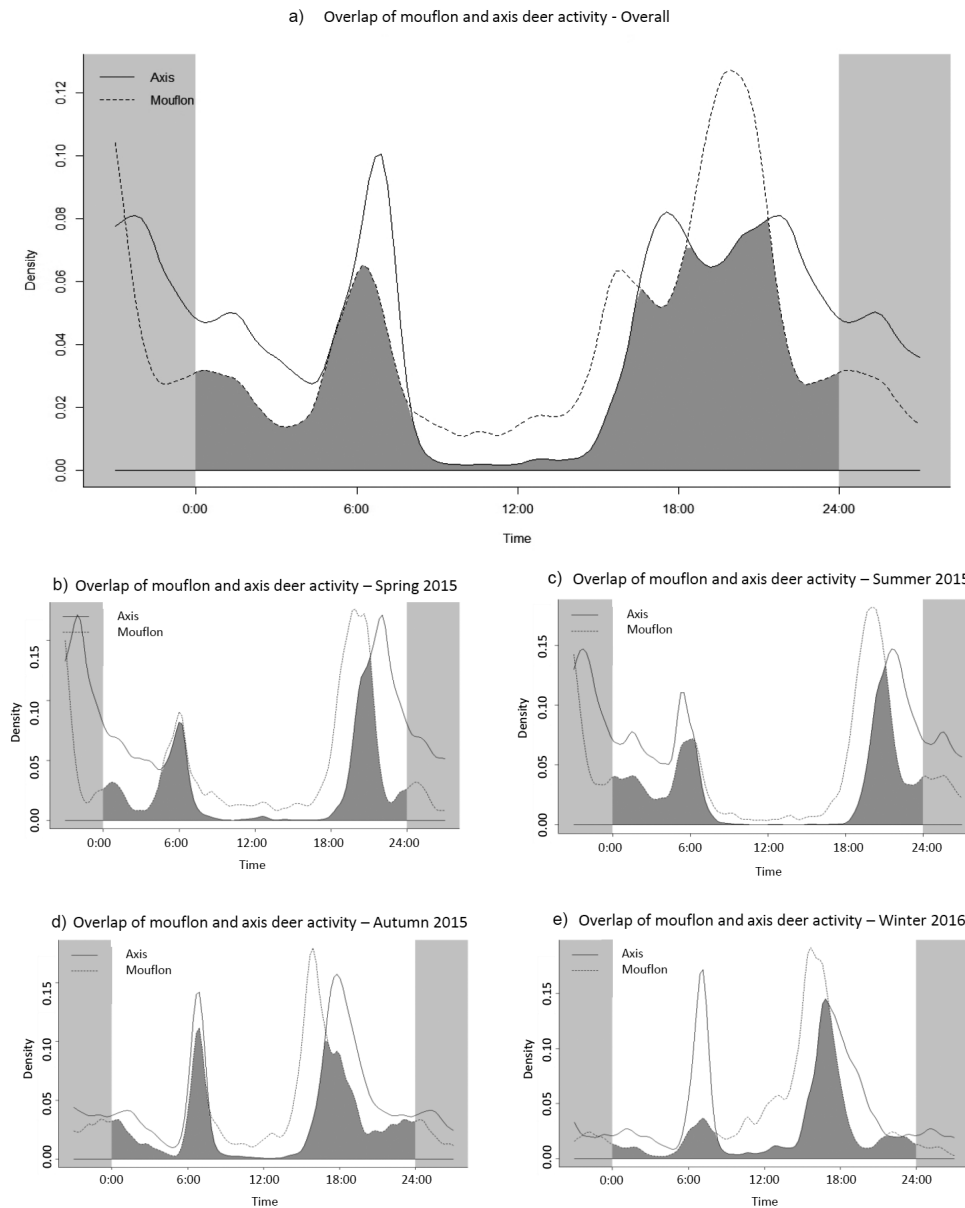


Fig. 2. Kernel density estimates (1.5 smoothing factor) of daily activity distributions for the European mouflon and axis deer in Kalifront Peninsula during: a) overall study period, b) spring: April-June, c) summer: July-September, d) autumn: October-December, e) winter: January-March.

established stands are less common: Aleppo pine (*Pinus halepensis*), stone pine (*Pinus pinea*), and maritime pine (*Pinus pinaster*) (Ugarković & Ugarković 2013).

Numbers of individuals of the two ungulate species present in the study area during the 2015/2016 season as estimated by official game management plans were: European mouflon – total $n = 103$; juvenile = 23, yearling = 22, adult = 58; axis deer – total $n = 78$; juvenile = 15, yearling = 14, adult = 49 (Tomljanović 2016). The estimation method reported in the official game management plan was: (i) twice a year (spring and autumn) counts by 10 observers that independently carried out observations three times continuous

(evening, morning, evening) from 10 station posts (towers). The official estimated sex ratio was 1:1.3 for European mouflon, and 1:1.1 for axis deer (Tomljanović 2016). In addition to these ungulate species, other mammals also coexist in the area, such as European hare, *Marten* spp., and *Rattus* spp.

Data collection and analysis

Camera-trapping was conducted over a 12-month period, 24 h/day, from 1 April 2015 to 31 March 2016 (365 trap-days). Three cameras types were used with infrared detection: 1 Wildlife Innovationc, Spypointc (t) (model: 2 Iron-1, 1 PROX and 1 HD 12), Moultriec (model: 2 MFH-DGS-D55IR, 1 MCG-12589), and 1

Table 1. Counts and proportions of photo captures of European mouflon and axis deer in the island of Rab from 1 April 2015 to 31 March 2016: N – number of captured animals with identified species and sex, percentage of sex – percentage of captured animals in each sex*season cell in relation to the total number of animals of the same sex and species, percentage of season – percentage of animals in each sex*season cell in relation to the column total (season), percentage of species – percentage of animals in each sex*season cell in relation to the total number of identified animal of the same species.

European mouflon		Spring	Summer	Autumn	Winter	Row Total
M	N	5811	13230	7910	4686	31637
	percentage of males	18.4 %	41.8 %	25.0 %	14.8 %	44.7 %
	percentage of season	44.4 %	41.6 %	61.5 %	35.7 %	
	percentage of species	8.2 %	18.7 %	11.2 %	6.6 %	
F	N	7266	18543	4962	8424	39195
	percentage of females	18.5 %	47.3 %	12.7 %	21.5 %	55.3 %
	percentage of season	55.6 %	58.4 %	38.5 %	64.3 %	
	percentage of species	10.3 %	26.2 %	7.0 %	11.9 %	
Season Total		13077	31773	12872	13110	70832
		18.5 %	44.9 %	18.2 %	18.5 %	
<hr/>						
Axis deer		Spring	Summer	Autumn	Winter	Row Total
M	N	3816	8806	12080	9061	33763
	percentage of males	11.3 %	26.1 %	35.8 %	26.8 %	51.7 %
	percentage of season	57.2 %	48.3 %	59.4 %	45.1 %	
	percentage of species	5.8 %	13.5 %	18.5 %	13.9 %	
F	N	2854	9416	8273	11049	31592
	percentage of females	9.0 %	29.8 %	26.2 %	35.0 %	48.3 %
	percentage of season	42.8 %	51.7 %	40.6 %	54.9 %	
	percentage of species	4.4 %	14.4 %	12.7 %	16.9 %	
Season Total		6670	18222	20353	20110	65355
		10.2 %	27.9 %	31.1 %	30.8 %	

Primos Truthc cam 35. Nine cameras were placed throughout the study area, at 50 to 100 cm above ground level, with a default focus distance of 5 m, and were checked twice monthly to download photos and check battery status. The distance between cameras was 1000 m and each camera represented an area of approximately 90 ha. Each camera was placed based on a systematic net grid of 1000 × 1000 m, where each camera was placed at each intersection of the grid. The time lag between successive photo-captures was set to 5 min and for every capture event, the cameras took one photograph (JPEG).

All collected photographs were filtered according to the ability to clearly identify the captured species, and only photographs satisfying this criterion were used in the analyses. Each individual animal captured in each capture event (photograph) was treated as a single observation (data point), and the temporal distribution of observations of each species was used to represent their daily activity budgets. Furthermore, the sex of each recorded animal was identified where possible, and it was marked as unknown if it was not possible

to determine from photo. Photographs were divided into seasonal components based on characteristics of Mediterranean climate/habitat: spring (from April to June), summer (from July to September), autumn (from October to December), and winter (from January to March). The significance of the effects of season, sex and their interaction season*sex on the mean monthly counts of recorded and identified animals was tested using a general linear model. Both predictors were considered as fixed factors, and GLM was fitted using lm function from base R (R Development Core Team 2013), using syntax: `lm(monthly_count~sex+season+sex*season)`. Due to the requirements of the algorithm used to estimate overlap, time of capture was converted to radians (ranging from 0 to 2π), representing a circular random variable with underlying binomial density. Circular normal distributions were fitted using the von Mies Kernel (Meredith & Ridout 2014) over different time frames: seasonally, i.e. April-June, July-September, October-December and January-March, to account for variations in species-specific life cycles and in food

availability; and for the entire study period, from 1 April 2015 to 31 March 2016. Based on the simulation performed by Ridout & Linkie (2008), a number of different smoothing parameters (between 0.5 and 2) were plotted against the original data points. For the presented activity curves, a 1.5 smoothing factor value was chosen, based on visual inspection. To estimate the differences in locomotor activity patterns between axis deer and European mouflon, `overlapEst()` function from 'overlap' package (Meredith & Ridout 2014) was used and the coefficient of overlap calculated between the Kernel density estimation curves in a pairwise manner, over the entire study period. The coefficient values ranged from 0 (no common activity) to 1 (identical activity) and were represented by a single nonparametric estimator (Δ_1), considered as the best estimator to describe activity agreement between the probability distributions of European mouflon and axis deer (cf. Ridout & Linkie 2008). The chosen estimator (Δ_1) best describes activity overlap when the smallest sample has ≤ 50 data points, regardless of the number of data points in the larger samples (Meredith & Ridout 2014). The confidence interval for each coefficient was calculated using a bootstrap method implemented in functions `bootEst()` and `bootCI()` from 'overlap' package with 10000 samples generated from a representative sample of the population (Clemons & Bradley 2000). Statistical analyses were performed using R 3.0.2 (R Development Core Team 2013).

Results and Discussion

The camera trapping dataset allowed for the detection of daily activity patterns of European mouflon and axis deer, and their seasonal variations. During the 12-month study period, 122082 JPEG photographs were collected, of which 71582 were analysed. Captures included 69273 photographs with ungulates species in the photos (European mouflon and axis deer), and 2727 non-target species photographed (34 *Marten* spp.; 1057 European hares; 71 domestic animals (dogs and cats); 292 humans (tourists and forest workers); and 1273 *Rattus* spp.).

A total of 84572 European mouflon from 32411 photographs and 74653 axis deer from 36862 photographs were recorded as active in front of the camera traps. During the entire study period, 55 % of recorded and identified European mouflon and 48 % of recorded and identified axis deer were females (Table 1). The difference between counts of male and female individuals was significant for European mouflon ($F = 6, p = 0.026$), but not significant for axis deer ($F = 0.28, p = 0.603$).

The number of recorded animals was dependent on the season for both species ($F = 36.92, p < 0.001$ for European mouflon; $F = 10.18, p < 0.001$ for axis deer). European mouflon presented the highest detection during summer (~45 %), whereas an even distribution of animals was recorded in all other seasons (~18 % each season) (Table 1). The number of recorded axis deer was lowest in spring (~10 %), with an even distribution of animals recorded in all other seasons (~30 % each season).

The interaction `sex*season` was significant only for European mouflon ($F = 5.42, p = 0.009$ for European mouflon; $F = 1.49, p = 0.256$ for axis deer). Sex ratios of recorded European mouflon varied by season, with the highest ratios of recorded females in summer ($F = 11.87, p = 0.003$) and winter ($F = 5.85, p = 0.028$), while the axis deer did not show large variation by season (Table 1).

Over the entire study period, both European mouflon and axis deer showed a bimodal activity pattern (Fig. 2). European mouflon had a more distinct bimodal activity pattern (typical of bovids; Darmon et al. 2012, Brivio et al. 2016), while axis deer showed bimodal activity patterns with some rise and fall in locomotor activity during the day, which is a typical behavioural pattern of cervids (Náhlík et al. 2009, Krop-Benesch et al. 2013). Furthermore, European mouflon showed a higher activity during the day and lower activity throughout the night. The first (morning) peak was estimated between 06:00 and 08:00, and the second (evening) peak from 19:00 to 21:00 (Fig. 2a). A study of Sardinian mouflons (Pipia et al. 2008) identified two daily peaks with similar levels of activity, as opposed to the differing degrees of activity for the two peaks from this study, i.e. the activity recorded in the morning peak was substantially lower than the evening peak. A similar bimodal activity pattern of European mouflon has been documented elsewhere (Bourgoin et al. 2011), even in the presence of other bovids such as chamois (Darmon et al. 2014). Darmon et al. (2014) suggested that the daily activity pattern might have facilitated the coexistence between European mouflon and chamois. For European mouflon, activity levels emphasize the greater sensitivity of the species to extreme temperatures, as they show a stronger decrease in activity than in axis deer during thermally stressing hours (i.e. night in winter and day in summer, Bourgoin et al. 2011). A bimodal pattern of European mouflon activity was observed in this study during spring, summer, and autumn (Figs. 2b-d), while in winter, the activity of this species was most pronounced in late afternoon

and was lower at other times of day (Fig. 2e). It can be assumed that this behaviour is linked to the different seasonal temperatures and light/dark cycles throughout the year, as described in the seasonal activity patterns of mouflon on Sardinia (Pipia et al. 2008). The seasonal changes recorded in Pipia et al. (2008) were linked to biological events, such as the presence of lambs. However, in this study it was not possible to distinguish females with or without lambs using camera traps.

The two major activity peak estimates for axis deer were focused in the early morning (between 07:00 and 09:00) and evening (between 17:00 and 23:00), while midday activity was avoided year around (Fig. 2a). During spring and summer (Figs. 2b, c), the activity of axis deer increased and became well distributed over the course of the day; while autumn (Fig. 2d) and winter (Fig. 2e) reveal two marked peaks of concentrated activity. There are few studies on activity patterns in axis deer that describe higher activity during dawn and dusk, in both the cold and hot seasons, such as in India (Tak & Lamba 1984) and Hawaii (Graf & Nichols 1966). According to de Silva & de Silva (2001), axis deer showed activity throughout the day, and movement was observed during the night. However, in the present study, axis deer seemed to avoid activity and movements throughout the day. Night movements seem to be more frequent during spring and summer, as Dave (2008) observed in axis deer in India. Similar locomotor activity patterns were found in other cervids, such as red deer and roe deer. Red deer showed a bimodal activity pattern with peaks at dawn and dusk (Náhlik et al. 2009, Pépin et al. 2009). Náhlik et al. (2009) also described a drop in dawn activity in winter, similar to the results for axis deer in the current study. Roe deer have presented high activity during dusk, with reduced diurnal activity (Krop-Benesch et al. 2013). Due to similar daily patterns over all seasons, the overlap coefficient between two ungulate species throughout the entire study period was 0.744 (CI = 0.739-0.752). Overlap of the daily patterns was less pronounced in spring (0.557, CI = 0.546-0.568) and winter (0.576, CI = 0.567-0.585) than in summer (0.629, CI = 0.622-0.636) and autumn (0.654, CI = 0.645-0.663). All estimated overlap coefficients can be interpreted as non-random, since they were within bootstrap confidence intervals (Meredith & Ridout 2014).

Behavioural indirect interactions between ungulate species are typically low (Bartoš et al. 2002, Šprem et al. 2015). These patterns agree with the theoretical

models of the cost of fighting versus resource value, where animals are expected to increase aggression in relation to the value of the disputed resource and probability of injury (Ferretti et al. 2015). However, in the case of this study area, the resources are not limited and therefore the animals have no need for competition. Coppice and maquis are the most common degradation stages of holm oak forests on the island of Rab. Since stump plant sprouts have more main shoots than a seed plant, stump plants contain higher biomass. Namely, when browsing, animals move from plant to plant, trying to use as little energy as possible for feeding. Therefore, they feed mainly on the shoots from stumps, which require a lower investment in effort (Krapinec 2002). In central Spain, the number of seedling and young plants of holm oak is very low (51.2-85.0 pcs/ha), which differs significantly compared to the forest stands on the island Rab (Plieninger et al. 2004). According to Oršanić et al. (2011), large numbers of natural holm oak seedlings and young plants were recorded on the Kalifront Peninsula, which can be attributed to favourable climatic factors influencing the yield on the island. A large number of seedlings was obtained in coppice (480000-1190000 pcs/ha). Hence the resources in this study area should not be described as limited. Since there are no known predators in the area and human activity is moderate only during summer (tourists), predator avoidance strategy is an unlikely driver of the recorded activity of both species. For example, the overlap coefficient between two ungulate species (chamois and wild boar) in a habitat where predators were present (grey wolf and brown bear) was 0.43 (Šprem et al. 2015). In the study area, the annual hunting bag was: 20 European mouflons (juvenile 2, yearling 6 and adults 12) and 6 axis deer (yearling 2 and adults 4). Sex ratios in the hunting bag for European mouflon is 0.94:1 and for axis deer 0.86:1 in favour of males. The hunting technique is stalking, distributed year round (depending on hunting season), and therefore hunting is not a likely driver of the daily activity patterns observed (Sunde et al. 2009).

Although there is a high general overlap of activity patterns between the two species, the minor differences in activity patterns can be attributed to species-specific endogenous rhythms (foraging/ruminating; Hofmann 1988) or other parameters, such as preference for different native habitats, different sensibility to environmental conditions such as thermoregulation (Bourgoin et al. 2011), or adverse climatic conditions (Brivio et al. 2016). For example,

thermoregulation could play an important role in the variation of activity patterns of roe deer in different seasons (Pagon et al. 2013). However, Stache et al. (2013) demonstrated that in roe deer, the behaviour of one individual strongly influences the activity pattern of the population. This is due to the temperaments of individuals that cause high deviation in the population activity pattern. Darmon et al. (2014) showed that the temporal and spatial differentiation of resources allows for the coexistence of two sympatric species such as European mouflons and chamois. Therefore, to better understand the coexistence of these two species on the island of Rab, further analysis using

GPS collaring should be conducted. The comparison between the results of a GPS study with the current camera trapping study would provide substantial evidence for the coexistence of the two species.

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