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Source: Folia Zoologica, 66(4) : 267-276

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v66.i4.a9.2017

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Folia Zool. – 66 (4): 267–276 (2017)

Territorial behaviour of male roe deer: a telemetry study of spatial behaviour and activity levels

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Received 11 December 2017; Accepted 13 February 2018

Abstract. The roe deer (*Capreolus capreolus*) is considered a special case of territorial ungulate. This study aimed to contribute to the knowledge of male roe deer territoriality by exploring its spatial use and activity patterns. We divided the territorial period (March-August) into three two-month sampling periods and found that the home range (HR) size of 13 radio-collared males averaged from 47.9 ± 14.5 ha to 109.7 ± 31.9 ha. We classified the spatial behaviour of eight out of the 13 males into three groups and concluded that HR size variation alone did not explain the potential territorial status. Nevertheless, it was indicative of their territorial status when considered along with the bucks' age, spatial movements and activity levels. The activity levels of July-August were significantly lower than the activity levels of March-April. HR size variation of the males monitored significantly contributed to explain the variations in their activity levels. Old bucks were significantly less active than other males, especially during July-August. To sum up, we found an indication of an influence of spatial profiles on activity levels, though a larger sample will be needed in order to better understand differences in age and territorial status, and inter-individual differences in activity.

Key words: activity rhythms, *Capreolus capreolus*, home range, seasonality, territoriality

Introduction

Studies on animal mating behaviour play a crucial role in gaining knowledge on species biology, behavioural ecology, evolution and recruitment. Mating systems are known to be directly linked to sexual selection (Andersson 1994), social organisation (Clutton-Brock 1989), sex-biased dispersal (Lawson Handley & Perrin 2007), and population genetic structure (Miller et al. 2010). The interest of researchers for mating systems and sexual selection in sexually monomorphic species developed later with respect to that for highly dimorphic species (Vanpé et al. 2010). The roe deer (*Capreolus capreolus*), a small-sized cervid species with very low sexual body-size dimorphism, is considered a rather special case of territorial ungulate (Liberg et al. 1998, Vanpé et al. 2009a, b). It adopts the so-called "always stay" territorial strategy (Linnell & Andersen 1998), where males are dominant only locally and they express extremely high site fidelity to their first territory (tenure for consecutive years) with little change of territory borders among the years (Melis et al. 2004). Such territorial strategy with emphasis on high survival and long tenure was called also a "low risk – low gain" strategy (Linnell & Andersen 1998, Melis et al. 2004). Further support for this was provided also by Hoem et al. (2007) with the finding that even in direct fights between two territorial males no territory loss occurred. Further on, the latest research on behavioural ecology and population genetics confirmed that roe deer territorial and reproductive behaviour does not fully conform to the conventional resource defence polygyny strategy (Vanpé et al. 2009b, Debeffe et al. 2014). Indeed, male roe deer access to females was seen to be conditioned by the size and not by the quality of a territory (Vanpé et al. 2009b). Territoriality is a predominantly male mating strategy characterised by male competition, though evidence for female competition and mate choice also exists (Debeffe et al. 2014), as females perform breeding dispersal (Lovari et al. 2008). Moreover, the degree of polygyny was found to be very low (Vanpé et al. 2008), and natal dispersal was not sex-biased (Coulon et al. 2006, Gaillard et al. 2008, Biosa et al. 2015).

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Male roe deer territoriality is a seasonal phenomenon, with territories being established in spring and maintained until the end of the rutting period. For European populations the territorial period was usually reported to last from March to August (Johansson et al. 1995, Johansson & Liberg 1996, Liberg et al. 1998), with mating occurring in July and August. However, not all male roe deer in the population are territorial.

Although yearlings and 2-year old roe deer are physiologically already capable of inseminating females (Sempere et al. 1998), they usually do not participate in the reproduction, because the territorial system of older, dominant males prevents them from copulating through direct harassment resulting in their dispersion (Wahlström 1994, Liberg et al. 1998). Non-territorial males may sometimes use alternative mating tactics, such as wandering around larger areas to find unattended females and behaving in a sub-ordinate manner in the area of a territory holder (Bideau et al. 1993, Liberg et al. 1998).

Species with a distinct breeding season are often highly constrained during this period, spatially as well as in terms of altered activity budgets (e.g. Brivio et al. 2010). In fact, activity rhythms are the result of an inner control system (circadian clockwork), which ensures a timed coordination of life-sustaining activities (Yerushalmi & Green 2009). In ungulates, the mating system is linked to spatial behaviour, which is related to the optimisation process in the acquisition of resources. Likewise, activity rhythms are considered an indication of the capacity to adapt to the current set of environmental and ecological conditions (Scheibe et al. 2009).

Roe deer are active by day as well as by night, with peaks of activity at twilight (Krop-Benesch et al. 2013, Pagon et al. 2013). Roe deer activity rhythms also vary in relation to biological periods and age classes (Turner 1979). During the territorial period, for example, male roe deer adopt specific behaviours (i.e. marking, patrolling, and defending a territory, male-male aggression; Johansson & Liberg 1996, Melis et al. 2005a), which may be held responsible for the increase in total daily activity levels (Pagon et al. 2013). As yet roe deer territorial behaviour was studied by analysing spatial use patterns (Linnell & Andersen 1998, Melis et al. 2004, 2005a, Lovari et al. 2008, Aiello et al. 2013) and by recording behavioural patterns during the territorial and reproductive periods, such as the territorial barking phenomenon (Reby et al. 1999), the territory marking behaviour (Johansson & Liberg 1996), aggression (Wahlström 1994, Hoem et al. 2007), and mating activities (Melis et al. 2005a). Data on the direct connection between activity levels and territory holding are very scarce. A study carried out by Batard (2010) amounts to the only attempt to combine spatial criteria of territoriality with the evaluation of activity patterns, though male roe deer spatial behaviour and activity levels were investigated during the territory establishment phase only.

The aim of the present study was to contribute to the knowledge of roe deer territoriality by exploring male spatial use and activity patterns during the territorial period and by reporting on the potential interaction between these two behavioural patterns. Vanpé et al. (2009b) reported territory size to be positively linked to breeding success and in general suggested a strong role of territorial status in male mating success. Reproductive activities, on the other hand, are believed to condition seasonal activity levels in roe deer (Krop-Benesch et al. 2013), being both behavioural components (spatial use and activity) linked to life-history cycles. Thus, we predicted that certain spatial profiles could correspond to distinctive activity levels (Prediction 1). Moreover, previous research suggested that the mating system (i.e. seasonal male territoriality) may be an important factor in modifying roe deer activity levels (Pagon et al. 2013). Besides, males were seen to mark their territories and face constant intrusions by other nearby males (especially non-territorial ones) during the whole territorial period (Johansson & Liberg 1996, Hoem et al. 2007). That is why we expected elevated activity at each stage of the reproductive period, both when mating took place and during the territory establishment. So, we predicted that the activity levels would be high and constant throughout the territorial period (Prediction 2).

Material and Methods

Study area

The research was conducted in a mountainous and forested habitat of the Apennines, in the Province of Arezzo, in Tuscany (Central Italy; 11°54′ E, 43°39′ N). The study area consists of about 120 km^2 and is mainly covered by mixed forests (beech *Fagus sylvatica*, silver fir *Abies alba*, Turkey oak *Quercus cerris*, chestnut *Castanea sativa*, black pine *Pinus nigra*, and Douglas-fir *Pseudotsuga menziesii*). An unfenced, protected area (Oasi Alpe di Catenaia – OAC, 28 km^2) is located within the study area. Two ungulate species, roe deer and wild boar (*Sus scrofa*), permanently inhabited the area during the study period. In the study area, grey wolf (*Canis lupus*) and red fox (*Vulpes vulpes*) were the documented natural predators of roe deer. The two canids appeared to prey

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on wild ungulates unevenly, the former preferring medium-sized and large individuals (> 4 months old roe deer), whereas the latter selected younger and smaller prey (roe deer fawns, Bassi et al. 2012). Hunting activities were permanently banned inside OAC, whereas hunting with hounds in battue drives (wild boar) and by shooting from fixed high seats (roe deer) was practiced outside of it (for more details, see Grignolio et al. 2011 and Pagon et al. 2013).

Data collection

Roe deer were captured by means of vertical drop nets during battue drives. They were immobilized, blindfolded, fitted with VHF radio-collars (Televilt, Sweden) with activity sensors and eventually released. For the purpose of this study, we analysed the data on 13 bucks monitored from March to August 2009 (Table 1). Individuals were assigned to age classes on the basis of teeth eruption (yearlings) and teeth wear (which allowed to discriminate prime-aged males from old ones). In the present study, six out of 13 males were estimated to be six years old or older, five males were between two and five years old and two males were yearlings. In some cases, a more precise age estimation was assessed from the cleaned mandible at a later stage. A previous pilot study on the same population based on the section of the first lower molar of more than 300 individuals confirmed that the age classes determined by teeth wear corresponded to the age classes determined by dentin rings (unpublished data).

We located the roe deer by discontinuous radio-tracking with Wildlife Materials receivers and four-elements hand-held Yagi antennas. The location of each collared individual was obtained by means triangulation of at least three bearings, 8-12 times per month, usually taken from a distance of 100-300 m to reduce bias. We distributed the locations uniformly over the 24 hours and separated consecutive locations by intervals of at least 12 hours in order to avoid temporal and spatial autocorrelation (White & Garrott 1990, Börger et al. 2006). Before the beginning of our research, the accuracy of fixes was validated in the field using test transmitters placed in various habitats, so that the precision of each location was an error polygon of 1 ha. (see also Bongi et al. 2008, Grignolio et al. 2011 for further details about the radio-tracking technique in the study area).

The activity sensors in the VHF transmitters detected movements in any direction. Any head movement triggered a switch that changed the transmitting to a faster pulse rate. The number of pulse-rate changes within a given timeframe can be used to index an animal activity (Coulombe et al. 2006). Field experience with the roe deer showed that its pulse rates may change very dynamically and within short timeframes (Löttker et al. 2009). Therefore, following the approach used in Pagon et al. (2013), we listened to the signals of each collar until 10 pulses recurring at the same rate were counted continuously, so as to distinguish between active (at least 10 consecutive fast-rate pulses) and inactive roe deer (at least 10 consecutive slow-rate pulses) and to avoid recording intermediate situations. Thus, we avoided errors associated with head and comfort movements in resting periods and with otherwise active roe deer keeping their heads still for extended periods (Coulombe et al. 2006). From March to August 2009, we performed 15 activity monitoring sessions, each lasting 24 hours, with an average of eight males monitored per session and the active/inactive status being assigned every 15 minutes.

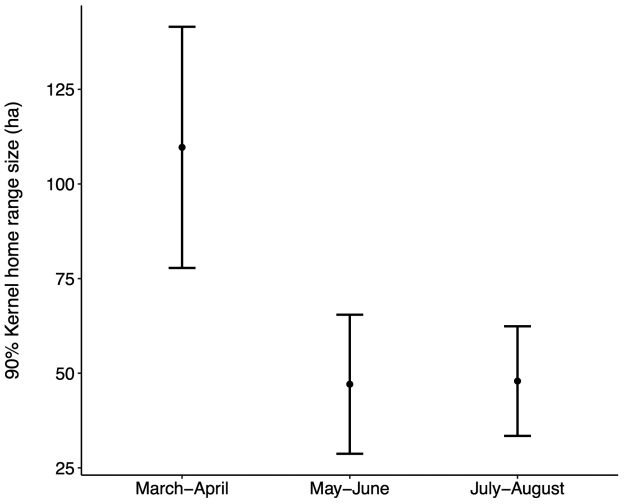


Fig. 1. Mean size (±SE) of bimonthly 90 % Kernel home ranges of 13 male roe deer during the territorial period (from March to August) in 2009 in the North-Eastern Apennines, Central Italy.

Data analysis

Bimonthly home ranges (March-April, May-June and July-August) of each roe deer were calculated by using Ranges VI software (Kenward et al. 2003). Home ranges (HR) were estimated with 90 % and 50 % Kernel method, and with 90 % minimum convex polygon (MCP) method (Börger et al. 2006) with an average of 14 fixes per HR. By using the same software, we calculated the overlap between pairs of neighbouring 90 % Kernel HRs during the same bimonth (overlap of smaller HR over the larger one) and between consecutive HRs for the same male (as overlap of the preceding bimonthly HR over the

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Table 1. Individual age, period of data collection, availability of activity data, bimonthly home range size (both Kernel and MCP method), and cluster of male roe deer from the North-Eastern Apennines, Central Italy, from March to August 2009. MA = March-April, MJ = May-June, JA = July-August, Y = activity data available. For details on cluster analysis, see the text.

Male identity	Age class	Sampling period	Activity data	Home range size (Kernel 90 %)			Home range size (MPC 90 %)			Cluster
				MA	MJ	JA	MA	MJ	JA	
M1	> 6	March-August	Y	25.5	26.1	12.6	13.5	36.0	7.5	B
M2	1	March-August	Y	10.8	31.7	22.4	10.0	17.5	14.0	B
M3	2-5	March-April		17.6			9.0			
M4	1	March-June		59.0	221.0		22.5	320.0		
M5	> 6	March-August		74.2	28.3	14.9	26.5	16.5	6.5	
M6	> 6	March-August	Y	68.9	18.2	22.7	17.0	15.0	12.0	B
M7	> 6	March-August	Y	133.8	77.4	102.7	95.5	38.0	23.0	A
M8	2-5	March-August		341.8	12.8	164.9	141.0	6.5	62.5	
M9	> 6	March-August	Y	133.2	17.7	41.1	81.0	9.0	14.5	C
M10	2-5	July-August				34.8			10.0	
M11	> 6	March-August	Y	126.7	53.2	74.8	56.5	40.5	51.5	A
M12	2-5	March-August	Y	307.7	9.2	13.6	105.5	3.5	6.5	C
M13	2-5	March-August	Y	16.7	22.5	22.7	3.5	13.0	10.5	B

subsequent one). Percentage of vegetation types in each Kernel HR was estimated by using Arc Map 9.2 software (ESRI Inc., Redlands, U.S.A.), and a layer Corine Land Cover (2006 dataset – IV level).

We conducted a cluster analysis in order to group males with similar spatial behaviour and test for a relation between the spatial patterns of radio-collared bucks and their activity levels. To describe the spatial profile of each buck and then to assign it to a behavioural cluster, we used the following quantitative factors: HR size 90 % Kernel (ha), HR size 50 % Kernel (ha), overlap between two consecutive bimonthly HRs (90 % Kernel) for each male (%), distance between the centres of two consecutive bimonthly HRs for each male (m), and percentage of vegetation types included in each HR (i.e. deciduous forest, coniferous forest, shrubs, agriculture with natural elements, and grassland). Each of these factors consisted of three values, i.e. one for each of the three bimonths. Thus, together 27 variables were standardised and prepared to enter the clustering algorithm, in different combinations. We used the hierarchical agglomerative and the k-means methods as data classification algorithms. In particular, as for the former, to measure the diversity level between pairs of data we built a matrix of Euclidean distances, which was calculated by using single-linkage, complete-linkage and average-linkage techniques. We applied all these clustering methods so as to obtain a stable result, thus several outcomes were considered to impose successive techniques and to verify the stability of the final result. The results were visualised with dendrograms. One technique and one combination of spatial variables were chosen according to the stability of a given grouping pattern. As the complete activity dataset for the whole territorial period was available for eight males only (Table 1), we included only these individuals in the final cluster analysis and in the subsequent activity data analysis.

In order to detect the link between spatial behaviour clusters and activity patterns, generalised mixed-effects models (GLMM) were fitted to the activity dataset of the eight males roe deer. Activity level was expressed as the proportion of active records out of all the records collected per hour. For the purpose of GLMM modelling, hourly activity data were averaged into four day periods: dawn, daylight, dusk, night. For each session, sunrise and sunset exact times were assessed by using a sunrise/sunset calculator (www.hia-iha.nrc-cnrc.gc.ca/sunrise_adv_e.html), which provided the standard times in the study area (11°52′ E, 43°39′ N). Dawn and dusk periods were considered to start an hour and a half before and to end an hour and a half after the sunrise and the sunset times, respectively. The time periods between dawn and dusk were defined as night and daylight, whose duration varied throughout the year according to the sun cycle (photoperiod).

Mean activity values were arcsin-square-root-transformed in order to satisfy the normality condition (Sokal & Rohlf 1981) and used as a dependent variable in the models. The following predictor

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variables were considered: bimonth (March-April, May-June, July-August), day period (dawn, daylight, dusk, night), cluster (three clusters of spatial use), age class ("1", "2-5", and "≥ 6" years old), percentage of broadleaved forest included in the bimonthly HR, and percentage of shrubs included in the bimonthly HR. Roe deer identity was considered as a random factor in the models to avoid pseudo-replication of data (Machlis et al. 1985).

As all combinations of these variables were found to be biologically justified and their role in roe deer ecology was confirmed by literature (San José et al. 1997, Melis et al. 2005a, b, Pagon et al. 2013, Lovari et al. 2017), we considered all possible combinations of the six predictors in our model selection analysis. Therefore, we produced 64 candidate GLMMs (maximum-likelihood method; Supplementary material, Table S1). Afterwards, model selection procedures were implemented on the basis of Akaike information criterion, corrected for small sample sizes (AICc; Burnham & Anderson 2002, Johnson & Omland 2004, Grueber et al. 2011). According to the minimum AICc criterion, we considered models with $\Delta AICc < 2$ to be essentially as good as the best model (Burnham & Anderson 2002, Symonds & Moussalli 2011). Parameters and variance were estimated from the selected top-ranked models by means of model-averaging technique (Symonds & Moussalli 2011). Statistical analyses were performed using the package "nlme" in R software to implement GLMMs and "MuMIn" for the model selection analysis (R Development Core Team 2014).

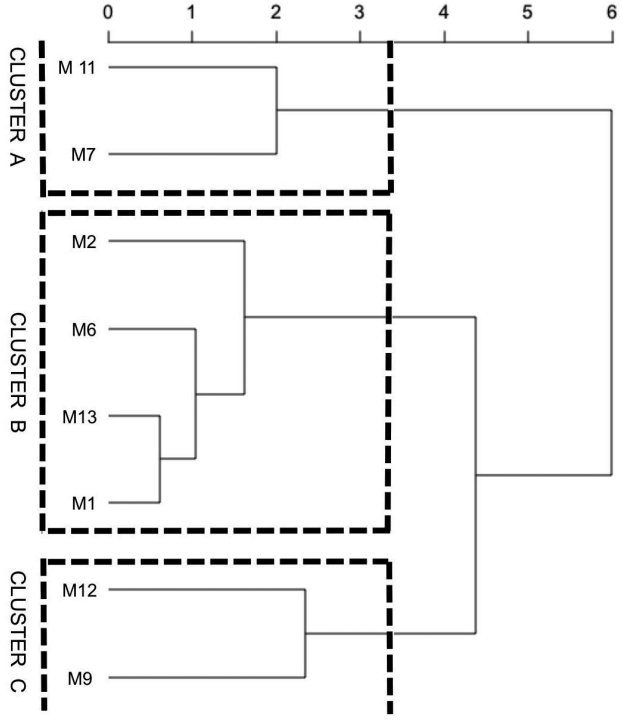


Fig. 2. Dendrogram resulting from cluster analysis with six spatial variables (see the text for more details) for eight males roe deer by means of the complete-linkage hierarchical clustering. Dataset of male roe deer from the North-Eastern Apennines, Central Italy, from March to August 2009.

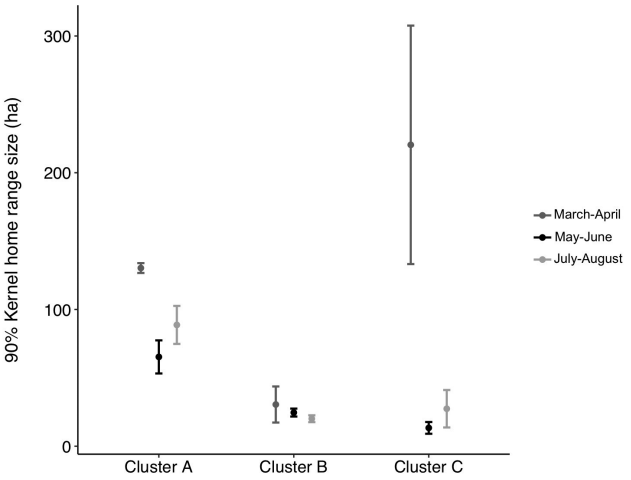


Fig. 3. Mean size (±SE) of bimonthly 90 % Kernel home ranges of eight males roe deer from the North-Eastern Apennines, Central Italy, which were classified into three clusters according to their home range sizes by means of the complete-linkage hierarchical clustering.

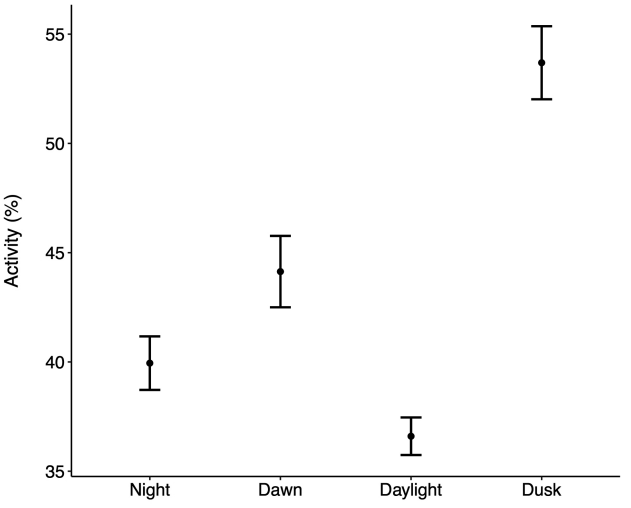


Fig. 4. Activity levels (mean ± SE) of eight males roe deer during four day periods (night, dawn, daylight, dusk) in the period from March to August 2009, from the North-Eastern Apennines, Central Italy.

Results

The HR sizes were calculated for 13 radio-collared male roe deer for the three bimonths (i.e. temporal progress of the territorial period, starting with the territory establishment phase and ending with the reproduction phase) during the 2009 territorial period. The largest HR sizes were measured in March-April (Fig. 1) and averaged 109.7 ± 31.9 ha (mean ± SE; n

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Table 2. Model-averaged coefficients (β), adjusted standard error (SE) and coefficients' intervals (β ± SE) obtained from the confidence set of six models (see Supplementary material, Table S1) explaining activity variation of eight males roe deer from the North-Eastern Apennines, Central Italy, from March to August 2009. *Statistically significant predictors.

		β	Adjusted SE	β – SE	β + SE	
Intercept		0.480	0.166	0.314	0.646	*
Bimonth	May-June	–0.014	0.024	–0.037	0.010	
	July-August	–0.038	0.021	–0.059	–0.017	*
Day Period	daylight	–0.072	0.020	–0.092	–0.053	*
	dusk	0.106	0.020	0.086	0.126	*
	night	–0.039	0.020	–0.059	–0.019	*
Cluster	C	0.055	0.042	0.013	0.097	*
	B	0.077	0.042	0.035	0.119	*
Age class	2-5	0.189	0.070	0.119	0.258	*
	≥ 6	0.111	0.060	0.051	0.171	*
% broadleaf forest		0.002	0.001	0.001	0.003	*
% shrubs		0.009	0.004	0.006	0.013	*

= 12, range from 10.8 to 341.8 ha) when estimated by 90 % Kernel method and 48.5 ± 13.4 when using 90 % MCP method (Table 1). In May-June the average Kernel HR size measured 47.1 ± 18.4 ha (n = 11, range from 9.2 to 221.0 ha), and in July-August 47.9 ± 14.5 ha (n = 11, range from 12.6 to 164.9 ha; Table 1). The highest percentage of vegetation type included in bimonthly HRs was deciduous forest (73.1 ± 6.1 % in March-April, 85.6 ± 5.1 % in May-June, 83.9 ± 5.8 % in July-August), while the lowest percentage was assigned to grassland (0.3 ± 0.1 % in March-April, 0.2 ± 0.2 % in May-June, 0.3 ± 0.2 % in July-August). Those adult males that were monitored throughout the entire territorial period (n = 9), showed a high degree of site fidelity, as all their reproductive HRs (July-August) were found in the same area of their March-April HRs. The average overlap between two consecutive bimonthly HRs of an individual male was 69.7 ± 4.9 % (n = 27 overlaps, nine males; range from 8.0 to 100 %). As most radio-collared males occupied neighbouring areas, we managed to assess a decrease in the overlap among neighbouring HRs as the territorial period progressed. During the three bimonths, we recorded 22 events of overlapping bimonthly HRs for eight adult males. For March-April HRs, the average overlap between the neighbouring areas was 18.2 ± 3.7 % (range from 0 to 71.4), whereas it dropped to 5.7 ± 2.8 % in May-June (range from 0 to 48.7), and reached 8.8 ± 3.6 % in July-August (range from 0 to 56.3).

Once a consistent pattern of buck allocations to spatial clusters was obtained, the most parsimonious combination of variables that produced the same result was a set of home range variables. Three bimonthly 90 % and three bimonthly 50 % Kernel HR sizes were enough to produce three distinct and consistent male groups on the basis of the complete-linkage hierarchic clustering (Fig. 2) and the k-means method with k = 3. Cluster A included two old bucks (age class "≥ 6" years; M7 and M11; Fig. 2, Table 1), whose average HR size was 130.3 ± 3.6 ha in March-April, 65.3 ± 12.1 ha in May-June and 88.7 ± 13.9 ha in July-August (Fig. 3). Cluster B included four bucks (Fig. 2, Table 1): a yearling (M2), a prime-aged buck (M13) and two older bucks (M1 and M6). This group was characterised by very stable HR sizes, which were quite small during all three bimonths (March-April: 30.5 ± 13.2 ha, May-June: 24.6 ± 2.9 ha, July-August: 20.1 ± 2.5 ha; Fig. 3). Cluster C included two bucks, a prime-aged buck (M12: age class "2-5" years) and an older buck of nine years (M9: such precise age was available on account of three recaptures). These two bucks had much smaller HRs during the May-June and July-August bimonths if compared to the bucks of cluster A. Their average HR size was 220.4 ± 87.2 ha in March-April, 13.4 ± 4.3 ha in May-June and 27.4 ± 13.7 ha in July-August (Fig. 3).

From the candidate set of 64 GLMMs (Table S1), fitted to activity data, we identified a confidence set of six models (ΔAICc < 2, in bold in the Table S1), which were used in the final parameter estimation (Table 2). The confidence set of models included all six predictors: day period, cluster, bimonth, age class, percentage of broadleaved forest and percentage of shrubs in the HR.

According to the predictions of the multi model-based inference, the bimonths only exerted a slight influence on the bucks' activity. In particular, activity levels during the last bimonth (July-August: 42.1 ±

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1.1 %), which included the reproductive period, were significantly lower than activity levels during the first bimonth (March-April: 45.7 ± 1.6 %, β = –0.038, SE = 0.021), i.e. during the territory establishment phase. No difference between the activity levels of March-April and May-June (44.6 ± 1.3 % of the time active) was found (β = –0.014, SE = 0.024).

Bucks showed significantly different activity levels among day periods, with the highest activity levels at dusk (53.7 ± 1.7 %, Fig. 4), and significantly lower levels at dawn (44.1 ± 1.6 %, β = 0.106, SE = 0.020). In turns, the latter were significantly higher than nocturnal activity levels (39.9 ± 1.2 %, β = –0.039, SE = 0.020) and daylight levels (36.6 ± 0.9 %, β = –0.072, SE = 0.020; Fig. 4).

We also detected an influence of spatial clusters on activity levels. The two older bucks (M7, M11) of cluster A, which had the largest HRs during the period from May to August, were significantly less active (40.5 ± 1.4 %) than the males of the other two clusters (cluster C: β = 0.055, SE = 0.042; cluster B: β = 0.077, SE = 0.042).

Finally, our analyses indicated that HR vegetation composition influenced the bucks' activity levels, which slightly increased as the percentage of both broadleaved forest and shrubs in their HRs increased (forest: β = 0.002, SE = 0.001; shrubs: β = 0.009, SE = 0.004), though such increase was almost negligible.

Discussion

Some of the males monitored showed much larger HR sizes during the first bimonth than during the following ones. Unlike previous findings on other Italian populations of roe deer (e.g. Aiello et al. 2013), the territory establishment phase in our study site did not appear to start at the beginning of March for all males, but most likely at a later stage of the March-April bimonth. Adult male site fidelity throughout the territorial period was clearly expressed by the high degree of overlap among the three bimonthly HRs for the same male. This high degree of site fidelity confirmed previous findings on Italian roe deer populations (Melis et al. 2004). Moreover, bimonthly HR size was a sufficient measure to classify male roe deer into three consistent groups. The most numerous cluster (cluster B), including four males (M1, M2, M6, M13, see Table 1), held the most consistent HRs through bimonths, with very similar sizes for all bimonths and, therefore, very low HR size variation. As for the HR sizes of cluster C, including an old (M9) and a prime-aged male (M12), these were quite similar in May-June and July-August, and much larger in the first bimonth. Conversely, cluster A, including two old males (M7, M11), held the largest HRs of all during the last two bimonths (May-August). This suggested that the males belonging to the first two clusters (B and C) might be territorial, while the males of the cluster A wandered on much larger space, possibly implying their non-territorial status. However, prior to drawing such conclusions, male age obviously needed to be considered beside their spatial behaviour. Although expressing the same pattern of HR use, while the prime-aged male (M13) and the two older males (M1, M6) from the most numerous cluster (B) were most likely territorial, the yearling (M2) was definitely not, according to literature (Wahlström 1994, Liberg et al. 1998, Debeffe et al. 2012). In fact, the yearling restricted its movements on the territory of another radio-collared prime-aged buck, adopting a subordinate, low-profile behaviour by showing very low activity levels (data not shown). Wahlström (1994) already reported the adult buck aggression toward yearlings, which results in yearlings avoiding bucks as well as in the dispersal of the most mature yearlings.

Comparable spatial behaviour observed for the cluster C (M9, M12) was reported in the literature for young males (Melis et al. 2005b) or first-year territory establishers, seasonally migrating and older roe deer (Johansson & Liberg 1996). Thus, we may assume that the two bucks in the cluster C were most likely territorial, though they did not succeed in establishing their territories as early as the adult males from the previously described cluster.

Based on the interpretations of the other two clusters, May-June and July-August HR size of the two older males from the cluster A (one of them was already around 13 years old, M7) was up to five times larger than the HR size of the other two clusters. We may suppose that they were most likely nomadic, thus failing to defend their own territory. In support of the idea, the radio-telemetry fixes showed they wandered vastly over the reproductive territories of other radio-collared bucks. Indeed, old males often become nomadic since they cannot hold their territories anymore (Liberg et al. 1998), which is associated with their failure to maintain large antlers (Vanpé et al. 2009a).

On the basis of our results, we may conclude that the HR size variations during the territorial period are not a sufficient measure to directly ascertain the territorial status of the males monitored. Beside HR size, combinations of other indices such as age, precise locations and spatial territorial structure of all the males monitored played a decisive role in explaining territorial status. Moreover, we also found that the

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spatial behaviour (i.e. HR size variations) of the males monitored significantly contributed to explain the variations in their activity levels. In particular, the two old males from cluster A showed significantly lower activity levels than the rest of the males. As previously discussed, their large HRs, together with their locations, were indicative of a non-territorial status, which we may directly connect to their lowest activity levels, especially during the last bimonth (Supplementary material, Fig. S1). Indeed, during July-August their activity decreased until reaching the same activity levels of the yearling. However, the latter largely limited its movements on the territory of one buck only, whereas the two nomadic old males wandered widely around several territories, while keeping very low activity levels, likely to avoid territorial residents and confrontations.

Conversely, cluster C showed the highest activity levels. The youngest buck (M12) kept the highest activity levels not only during the territory establishment phase, but also on a later phase, until August, likely because it was holding the territory for the first time. As suggested also by Batard (2010), the buck probably did not know the neighbours and the area yet and thus might have been forced to remain highly active due to the high number of interactions with other unfamiliar males. In support of this conjecture, Johansson & Liberg (1996) reported that first-year-territory holders showed higher intensity of marking than the neighbouring males which were present also in previous years and thus already knew each other.

Subsequently, activity levels tended to decrease as the territorial period progressed (Prediction 2 not confirmed). The highest male roe deer activity levels in our study area were recorded during the first bimonth. The decreased activity during the July-August bimonth was likely a consequence of the changes in the context of territorial and reproductive behaviour. Indeed, since the roe deer is an income breeder (Andersen et al. 2000), it is highly unlikely that such changes would occur in the usual ruminant feeding-resting rhythms. Accordingly, Batard (2010) proposed that bucks may avoid continuous high-activity states due to territorial behaviour by concentrating the highest energy expenditure in certain periods only. Both in the present research and in Batard (2010), the high-activity phase (March-April) corresponded to the period of territory establishment. This is also consistent with the theory of "low cost – low gain" tactic for roe deer proposed by Linnell & Andersen (1998): males invest relatively little energy during the mating season, and defend the same territory over several seasons. Indeed, high fidelity to territorial sites is connected to little costs, as site familiarity increases foraging efficiency, improves predator detection ability, reduces costs of aggression and combating with neighbours, though such long (multi-year) tenure implies a low annual investment in mating (Linnell & Andersen 1998, Melis et al. 2004, Melis et al. 2005a). Our findings are in line with this theory as bucks' activity levels during the reproductive period were lower than those recorded during the territory establishment phase (Fig. S1).

We suppose that this phenomenon may be linked to the need for male roe deer, as income breeders, to restore their energy promptly during periods of high-activity states. In March-April, i.e. the phase of their major activity, the spring forest green-up begins, thus offering food resources at their peak of protein content. Thus, the territory establishment phase, i.e. when most energy is spent, coincides with the period of prime-quality food resources in terms of protein content, before the vegetation starts to build its fiber load.

To check for the effects of the above-mentioned variables – which were the focus of the present study – we also added other variables to the models, particularly those which were seen to have an effect on roe deer behaviour in previous research (Pagon et al. 2013) and literature (Georgii & Schröder 1983, Johansson & Liberg 1996, Cimino & Lovari 2003, Melis et al. 2004, 2005a, b, Saïd & Servanty 2005, Saïd et al. 2009, Aiello et al. 2013, Lovari et al. 2017). Thus, we managed to better check for variability and obtained robust results on the relationship between male roe deer activity levels and spatial use. We thus confirmed that roe deer show higher activity levels during dusk hours (Pagon et al. 2013); secondly, we found increasing levels of activity with increasing percentage of woodland in the HR. As woodland is thought to be an important source of food resources (San José et al. 1997, Lovari et al. 2017) for roe deer, the finding seems worth further investigation. To sum up, we demonstrated that the link between spatial profiles and activity levels during the territorial period exist (Prediction 1 confirmed), though our conclusions are only based on a small sample. Further research on a larger sample may support our findings on roe deer territoriality.

Acknowledgements

We thank the Province of Arezzo and its staff for their logistic support and help during the capture sessions. We are indebted to all researchers and students who helped us during the fieldwork. C. Polli and G. Falceri edited the English version of this article. We are grateful to E. Mori for his constructive and helpful comments on the first draft of this manuscript.

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Supplementary online material

Fig. S1. Activity levels (mean ± SE) of three male roe deer groups from the North-Eastern Apennines (grouped according to their spatial behaviour) in three bimonths during the territorial period, from March to August 2009.

Table S1. Model selection based on linear mixed models explaining the variation in male roe deer activity levels from the North-Eastern Apennines, Central Italy, from March to August 2009. Empty space: term not included in a given model; BF: broadleaved forests; df: degrees of freedom; log Lik: log likelihood; AICc: corrected Akaike information criterion; ΔAICc: difference in the AICc value between a given model and the most parsimonious one; w: Akaike weight. Models are ordered by ascending AICc values, with the confidence set of six models at the top of the list in bold (http://www.ivb.cz/folia_zoologica/supplemetarymaterials/pagon_et_al._fig._s1,_table_s1.docx).

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