Roe and fallow deer: are they compatible neighbours?

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Roe and fallow deer: are they compatible neighbours?

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Abstract The analysis of the relationships between popu-
lation density and habitat features is important to evaluate
the ecological needs of a species, its potential impact on
ecosystems and its interspecific interactions. We analysed
the spatial variation of roe deer *Capreolus capreolus* and
fallow deer *Dama dama* densities in a Mediterranean area
in summer 2007 and winter 2007/2008. Previous research
has shown that fallow deer can actively displace and
exclude roe deer from natural feeding sites. Here we show
that both species have the greatest densities in ecotone
habitats between wood and open fields (abandoned olive
groves and pastures), but with contrasting geographic
patterns. The fallow deer showed the greatest densities in
the central northern part of the study area near to local
historical release sites. The densities of roe deer were great
where fallow deer were rare and low where fallow deer
were abundant. Spatial overlap was great at the habitat
scale, indicating a high potential for competition, but was low
at the plot scale, suggesting that partitioning of space occurred
at a fine scale. Supporting great numbers of deer, the ecotone
areas are crucial for the management of ecosystems. We
suggest that roe deer avoid areas with great densities of fallow
deer and that interspecific interference from the latter affects
the density and distribution of the former both at a fine and at
a large scale.

Keywords Deer · Interspecific interactions ·
Population density · Ungulates

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Introduction

The spatiotemporal variation of densities of wild popula-
tions is an important parameter to evaluate their ecological
needs (Apps et al. 2004) and dynamics (Kruuk et al. 1999;
Forchammer et al. 2002; Angulo et al. 2007), as well as
their potential impacts on ecosystems (Putman and Moore
1998; Stockton et al. 2005). A comparison of densities of
species living in sympatry can help in understanding
interspecific interactions (Latham et al. 1997; Forsyth and
Hickling 1998).

In ungulates, patterns of density and resource use of species
living in sympatry have been analysed (e.g. Jenkins and Wright
1988; Putman 1996; Arsenault and Owen-Smith 2008). Some
studies suggested resource partitioning (e.g. Jenkins and
Wright 1988; Arsenault and Owen-Smith 2008), but overlap
can be great (Putman 1996; Bertolino et al. 2009). Most of
these studies often identified only the potential for competition
(Putman 1996). Linking knowledge on density and habitat
relationships to information on behavioural interactions could
help in understanding the patterns of density and distribution
of species in sympatry (Anthony and Smith 1977), but
relevant information is scarce.

Because of its large distribution range, in sintopy with those of other ungulate taxa, the roe deer *Capreolus capreolus* is a useful model species to study density–habitat relationships as well as interactions with sympatric ungulates (Andersen et al. 1998; Latham 1999). The roe deer is a medium–small-sized cervid (20–30 kg; Andersen et al. 1998) well adapted to the woodfields ecotone as well as to the early succession stages of wood (Gill et al. 1996; Putman 1996; Mysterud et al. 1999). This deer relies on highly nutritious vegetation for survival and reproduction (mating: July–August; births: April–May; Hofmann 1989; Andersen et al. 2000). Habitat selection occurs when high-quality food and vegetation cover are available (Duncan et al. 1998; Tufto et al. 1996). The density of roe deer appears to be negatively affected by that of other cervid species (red deer *Cervus elaphus*, Latham et al. 1997; barking deer *Muntiacus reevesi*, Hemami et al. 2005; fallow deer *Dama dama*, Focardi et al. 2006).

The roe deer shares part of its present distribution range with the fallow deer, a medium-sized cervid (males, 55–85 kg; females, 35–55 kg, in Italy; Boitani et al. 2003), introduced to Europe from Asia Minor, after the Neolithic (Nowak 1991). This deer is well adapted to open habitats (fields, meadows, open wood; Batcheler 1960; Apollonio et al. 1998) and can use highly energetic food as well as fibrous vegetation (Hofmann 1989). In captivity, the fallow deer has been reported to be intolerant of the red deer (Bartoš et al. 1996) and of the spotted deer *Axis axis* (McGhee and Baccus 2006).

Relationships between roe and fallow deer have been object of debate (Batcheler 1960; Putman 1996; Bartoš et al. 2002; Focardi et al. 2006; Ferretti et al. 2008). A partial overlap in the use of resources has been shown (Putman 1996), suggesting the potential for exploitation competition. Inverse numerical trends have also been recorded (Batcheler 1960; Putman and Sharma 1987; Focardi et al. 2006), which may be an effect of independent and inverse reactions to a third factor (Putman 1996; e.g. contrasting reactions to succession changes of wood: Batcheler 1960). Great densities of fallow deer may reduce the habitat quality for roe deer, leading the latter to a smaller body size, larger home ranges and a population decrease (Focardi et al. 2006). Ferretti et al. (2008) showed that fallow deer can actively exclude roe deer from natural feeding sites even through direct aggression. It is unclear whether behavioural interference by fallow deer could affect the density of roe at a large spatial scale.

The aims of our study were: (1) to assess the spatial variation of densities of roe and fallow deer in summer and in winter in an area where active behavioural interference has been shown from the latter to the former (Ferretti et al. 2008; Ferretti et al. in press) and (2) to analyse habitat relationships and spatial overlap between roe and fallow deer.

Methods

Study area

Our study was carried out in the central southern part (6,260 ha) of the Maremma Regional Park (MRP, Central Italy; 42°39′ N, 11°05′ E). The local climate is Mediterranean. Vegetation is composed mainly by Mediterranean sclerophyllic scrubwood (58%) of three main wood types (Mencagli and Stefanini 2008): oakwood, with the prevalence of holm oak *Quercus ilex* trees with a height > 7 m; scrubwood, with the prevalence of holm oak and strawberry tree *Arbutus unedo*, with a height of <7 m; garigue, with bushes (mainly holm oak, rosemary *Rosmarinus officinalis*, juniper *Juniperus* spp., rockrose *Cistus* spp.), with a height of <2 m. Other habitats are pinewood (10%, mainly domestic pine *Pinus pinea*), abandoned olive groves and pastures (partially re-colonized by wood species and bushes, 15%), set-aside grassland (4%) and crops (12%, mainly cereals and sunflower). Evergreen, deciduous and half-woody plants as well as wild forbs and wild graminoids are the most used plant categories by roe deer in our study area (Minder 2006) and preliminary information suggests considerable diet overlap with the fallow deer in scrubwood (Minder in prep.). The availability of food resources for ungulates is generally lower in the scrubwood than in open habitats (Minder 2006).

The local ungulate community includes wild boar *Sus scrofa*, free-ranging cattle and horses, which are locally and irregularly moved through some pastures and part of pinewood. Wild boar density did not influence roe deer presence in sampling plots (Ferretti et al. in press). A study on behavioural interactions between roe deer, fallow deer and wild boar showed that both deer species were rarely displaced by wild boar (roe deer: 22% of 74 interspecific encounters; fallow deer: 13% of 61 interspecific encounters; Ferretti et al. in press). Wild boar density is expected not to affect the densities of our study species. Avoidance of livestock by fallow deer occurred only once in 16 observations and mixed groups were repeatedly seen in other pastures within the MRP (Ferretti et al. in press). No encounter was recorded between roe deer and livestock (Ferretti et al. in press). The predators are the wolf *Canis lupus* and the red fox *Vulpes vulpes* (the latter being a potential predator of young fawns only; Aanes and Andersen 1996). The territory size of wolves is generally more than 100 km^2 (Fuller et al. 2003), suggesting that they use all of our study area (about 63 ha). No study has been published on the local diet of the wolf, but preliminary observations suggest that the fallow deer appears to be the most used prey (Manghi et al. 2006). The red fox is widespread in all our study area, using both wood and open habitats (Cavallini and Lovari 1994). Its diet includes

mainly juniper berries and insects while large mammals are used mainly during the cold season (Cavallini and Lovari 1994). A recent study confirmed a small use of roe deer during their fawning season: roe deer hairs were present in only two scats out of 205 (Coneybeer 2003).

Density estimates

Deer densities were estimated through pellet group counts in summer 2007 (June–August) and winter 2007/2008 (January–March). We used the faecal accumulation rate technique, which is based on the counts of pellet groups accumulated in sample areas during a defined time interval (Mayle et al. 1999). This technique is considered more reliable than faecal standing crop counts (Mayle et al. 1999; Campbell et al. 2004) because it does not imply the use of pellet group decay rates, variable across habitats (in our same study area: Massei et al. 1998), to calculate densities.

There were 196 circular sampling plots (5-m radius) placed through a stratified sampling design (Gregoire and Valentine 2008). We assessed strata according to the main habitat categories: Mediterranean scrubwood, pinewood, abandoned olive groves and pastures, set-aside grassland and crops, as well as local features (see below; Mayle et al. 1999) and differences in deer densities detected through preliminary pellet group counts (Sforzi 2004). Because of that, we divided Mediterranean scrubwood, abandoned olive groves and pastures, as well as crops, in two strata each, respectively, in the north and in the south of our study area, in relation to local deer densities (Sforzi 2004; Table 1). In larger strata (north/south Med. scrubwood and pinewood), we adopted a two-stage strategy. In the first stage, the strata were partitioned into spatial units of different sizes (determined on the basis of natural or man-made edges), easily recognizable on the vegetation map as well as in the field. A sample of units was selected through a sequential (draw-by-draw) sampling with inclusion

probabilities proportional to unit size and avoiding the selection of contiguous units. The use of inclusion probabilities proportional to size was adopted to handle the presence of units with different sizes (Skalski 1994). With equal-sized units, the population variance simply measures the spatial variation of abundance across the area of interest; with different-sized units, the population variance is inflated by the size variation with detrimental effects in the subsequent estimation (Skalski 1994). In turn, the selection of contiguous units was avoided since adjacent units were more alike than units that were far apart, thus giving poor contribution to sample information (Barabesi et al. 1997). In the second stage, plots were placed within selected units by means of tessellation stratified sampling (Cordy and Thompson 1995), also referred to as unaligned systematic sampling (EPA 2002), to provide a more even distribution of plots over the units. We allocated a number of plots to strata proportionally to their size, and seven plots were assigned to each unit. In smaller strata (north/south abandoned olive groves, north/south cultivated fields and set-aside grassland), the first phase was avoided and plots were placed directly on the stratum through the same scheme adopted within the spatial units. The methodological details and theoretical justifications regarding this sampling scheme are given in Fattorini et al. (in press), where unbiased estimators of abundance and conservative estimators of sampling variances are provided for each stratum and for the whole study area. The reliability of this sampling strategy was assessed through nine sampling seasons and through the comparison with direct counts in open areas, which revealed estimates stable between near seasons and agreement among estimates obtained through different methods (Fattorini et al. in press).

On the vegetation map of the MRP (Mencagli and Stefanini 2008), geographic coordinates were assigned to the centre of each selected plot through the ArcView GIS 3.2 ESRI © software. A portable GPS Garmin Etrex was used to find plots in the field. During a first survey, we carefully searched plots for any pellet group, which were later removed from the plot. We marked the centre of each plot through a peg or a tape. Local landmarks were noted down to help plot detection in subsequent surveys. A second survey was conducted after 40 days (according to the local decay rate of deer pellet groups: Massei et al. 1998; Minder 2006) to count pellet groups (more than five pellets, Mayle et al. 1999) in the plots. Pellets of fallow and roe deer were recognized out of shape and size: the former defecates cylindrical pellets, usually with a pointed end and slightly concave at the other, whereas the latter makes small, elongated pellets, rounded at both ends (Mayle et al. 1999). For fallow deer, we used a defecation rate of 25 pellet groups/day (data from our same study area: Massei and Genov 1998). For roe deer, local information on

Table 1 Strata partitioning the study area. Strata in the study area and number of plots sampled within each stratum in summer 2007 and winter 2007/2008

Stratum	Area (ha)	N plots
North Mediterranean scrubwood	2,051.1	63
South Mediterranean scrubwood	1,588.5	49
Pinewood	874.2	28
North abandoned olive groves and pastures	442.3	14
South abandoned olive groves and pastures	318.0	10
Set-aside grassland	172.8	6
North cultivated fields	241.3	8
South cultivated fields	572.8	18
Total	6,260.9	196

defecation rate was lacking. Researches on different deer species indicated little variation of defecation rates between different habitats or geographic areas (e.g. fallow deer: Stubbe and Goretzki 1991 in Massei and Genov 1998; Mayle et al. 1996; Massei and Genov 1998; red deer *C. elaphus*: Mitchell and McCowan 1984; Bruno 1996; white-tailed deer *Odocoileus virginianus*: Rogers 1987; Sawyer et al. 1990). We used an estimated value of 20 pellet groups/day (i.e. an average between two sites with different environmental conditions: Mitchell et al. 1985), recommended for roe deer (Ratcliffe and Mayle 1992; Mayle et al. 1999; see also Fattorini et al. in press; Ferretti et al. in press). Defecation rate could vary across seasons since severe variations in climactic conditions (e.g. temperatures ranging from −35°C to 35°C: Rogers 1987) may determine the changes in the feeding activity of deer. Accordingly, the use of a single defecation rate for both winter and summer surveys may constitute a source of bias. Even if we could not exclude an across-season variability of defecation in MRP, the variation is expected to be moderate owing to the moderate climactic changes occurring in our study area (mean monthly temperatures range from 7°C to 24°C and snow is absent).

Habitat relationships

Habitat niche breadths of both deer species were investigated descriptively through the Hurlbert standardized index (H; Krebs 1999) from data collected through pellet group counting surveys in summer and in winter. This index considers differences in availability across habitats, is sensible to the presence of rare habitats and ranges from 0 to 1 (Krebs 1999). We considered the following habitat types: oakwood, scrubwood, garigue (i.e. the three wood types composing Mediterranean scrubwood strata; Mencagli and Stefanini 2008), pinewood, abandoned olive groves and pastures, set-aside grassland, cultivated fields. Considering M habitats, the availability of each of them, denoted by π_i $(i=1,…,M)$, was calculated through the ratio of the total size of the sampling plots fallen in the habitat to the total plot size. Defining O_i the proportion of pellet groups found in the i-th habitat with respect to the total amount of pellet group found in the survey, the index turns out to be (Krebs 1999):

$$H = (B - \pi_{\min})/ (1 - \pi_{\min})$$

where $B = 1/ \sum_{i=1}^{M} (o_i^2/\pi_i)$ and $\pi_{\min} = \min_i \pi_i$. In each season, spatial overlap was assessed through the Pianka index (Pianka 1974). This index ranges between 0 (no overlap) and 1 (complete overlap). Overlap can depend on the spatial scale adopted (Hemami et al. 2004): we calculated spatial overlap at two scales. At the habitat scale, overlap was assessed through the formula (Pianka 1974):

$$P = \sum_{i=1}^{M} o_{iF} o_{iR} / \sqrt{\sum_{i=1}^{M} o_{iF}^2 \sum_{i=1}^{M} o_{iR}^2}$$

where O_{iF} and O_{iR} denote the proportion of fallow deer and roe deer pellet groups in the i-th habitat, respectively. The same index was also assessed at plot scale:

$$P = \sum_{i=1}^{n} o_{iF} o_{iR} / \sqrt{\sum_{i=1}^{n} o_{iF}^2 \sum_{i=1}^{n} o_{iR}^2}$$

where n denotes the total number of plots and O_{iF} and O_{iR} denote the proportion of fallow and roe deer pellet groups in the i-th plot, respectively.

Results

Densities

In both seasons, the greatest densities of fallow deer were found in the north abandoned olive groves and pastures (more than 45 individuals/100 ha; Figs. 1a and 2). By contrast, densities were much lower in the corresponding habitats in the south (less than ten individuals/100 ha; Figs. 1a and 2). Densities were intermediate in the set-aside grassland (18–36 individuals/100 ha) and in scrubwood (ten to 20 individuals/100 ha), being 1.3 and 2.1 times greater in the north than in the south in summer and in winter, respectively (Figs. 1a and 2). Densities were low in the pinewood (eight to 12 individuals/100 ha) and in the south cultivated fields (less than seven individuals/100 ha), whereas fallow deer were not found in the cultivated fields in the north (Fig. 1a).

Roe deer showed greater densities in the south than in the north (Fig. 2). Densities were the greatest in the south abandoned olive groves and pastures, as well as in Mediterranean scrubwood (20–34 individuals/100 ha; Figs. 1b and 2). In the corresponding habitats in the north, densities were more than three times lower than in the southern ones (less than eight individuals/100 ha; Figs. 1b and 2). Densities showed medium to low values in the set-aside grassland and in the cultivated fields (four to 12 individuals/100 ha; Fig. 1b). Roe deer were not found in the pinewood (Fig. 1b).

Differences in densities between northern and southern strata did not depend on differences in the proportion of plots sampled in the wood types of Mediterranean scrubwood (oakwood, scrubwood, garigue), which was similar between strata (G-test: $G_{adj}=2.499$, df=2, $P=0.287$).

Fig. 1 Densities estimates (*N* individuals/100 ha ± estimated standard error) of fallow and roe deer in the strata partitioning the study area in summer 2007 and winter 2007/2008
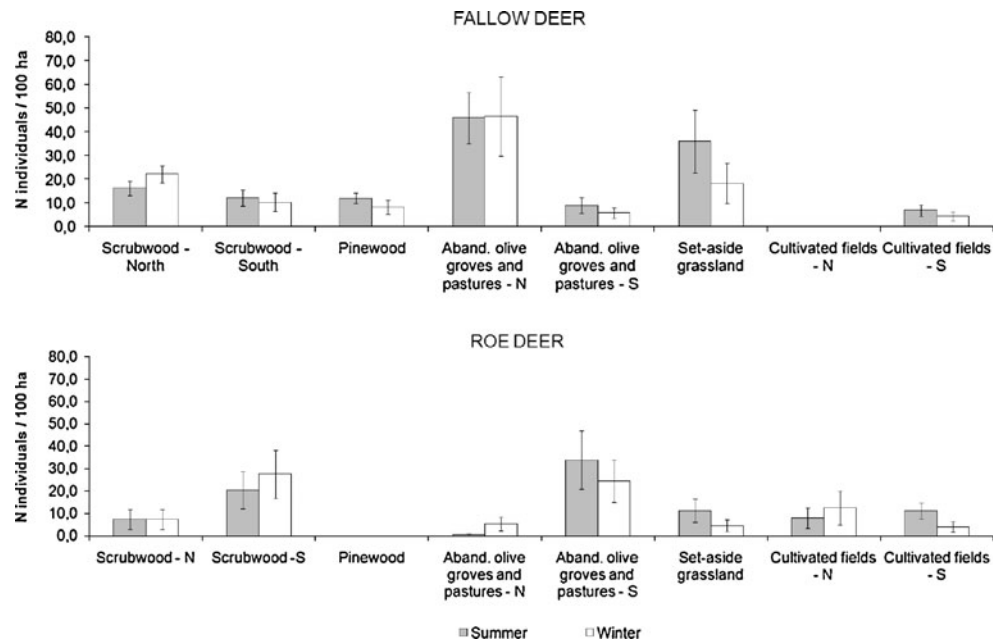
Habitat relationships

The habitat niche breadth of fallow deer was 31% (summer) and 64% (winter) broader than that of roe deer (Fig. 3a). At the habitat scale, the spatial overlap was great (Pianka index=0.79 in summer, 0.82 in winter; Fig. 3b). At the plot scale, the spatial overlap was 5.3 (summer) and 4.3 (winter) smaller than that measured at the habitat scale (Pianka index=0.15 in summer, 0.19 in winter; Fig. 3b).

Discussion

The abundance of pellet groups in a habitat may not be a function of the number of individuals or of time spent in that place because defecation rates may depend on activity (Collins and Urness 1981; Mitchell et al. 1983). On the other hand, pellet group counts can help in estimating the relative habitat use in comparison with other methods (radio-tracking: Loft and Kie 1988; Edge and Marcum 1989; direct observation: Leopold et al. 1984) and have been used from several decades in various contexts (Neff 1968; Putman 1984; Latham et al. 1997; Hemami et al. 2005).
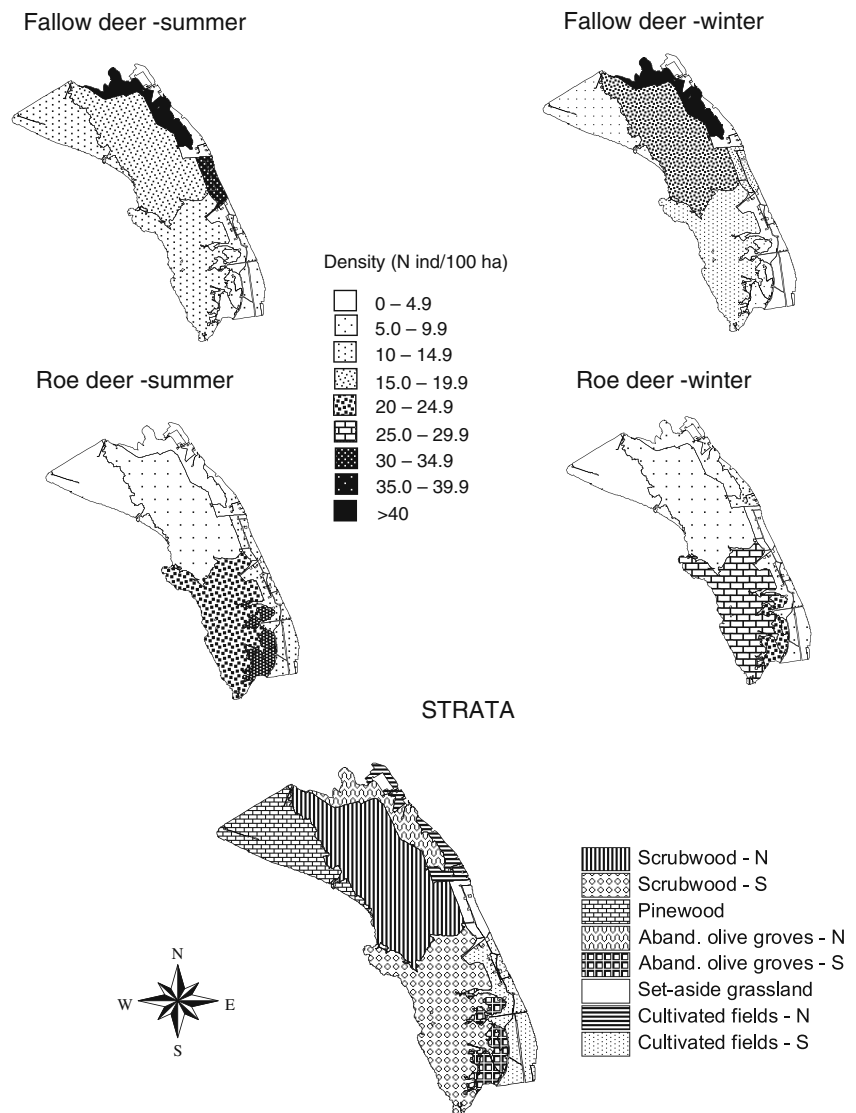
The greatest densities of both the roe and the fallow deer were found in the abandoned olive groves and pastures, although a contrasting pattern was recorded between northern and southern strata (Figs. 1 and 2). These habitats, at the boundary between wood and open fields, are mostly covered by bushes, interspersed with pastures, providing food and cover to deer species. Ecotone areas are an optimal habitat for deer, determining high reproductive success (Miyashita et al. 2008; McLoughlin et al. 2007) and

great densities (Wahlström and Kjellander 1995; Hemami et al. 2005).

The fallow deer reached its greatest densities in the central northern part of our study area, whereas the roe deer showed the opposite pattern (Figs. 1 and 2). This pattern should not depend on differences in habitat between northern and southern strata because the proportion of plots sampled in the wood types of Mediterranean scrubwood was not significantly different. As to the fallow deer, this pattern may be explained because of historical reasons: in MRP, fallow deer were introduced to the northern part of our study area. The last release of individuals dates back to the mid 1960s of the twentieth century when, presumably, less than 30–40 fallow deer inhabited the park (G. Anselmi, MRP Agency, personal communication). Most likely, fallow deer have colonized our northern strata before the southern ones. In 2001–2003, more than 15–20 individuals/100 ha and less than five to six individuals/100 ha were estimated in the northern and in the southern scrubwood, respectively (Sforzi 2004), whereas 16–22 individuals/100 ha and ten to 12 individuals/100 ha were estimated in 2006–2008 (Fattorini et al. in press; this study). The large standard errors of estimates in 2001–2003 and the variations in the sampling design in 2006–2008 (Fattorini et al. in press) complicate comparisons between the periods but, apparently, fallow deer numbers have increased in the southern strata.

As to roe deer, the most used plants in their diet in the scrubwood (*Q. ilex*, *A. unedo*, *R. officinalis*; Minder 2006) are largely present both in the north and in the south of our study area but in the pinewood (Minder 2006; Mencagli and Stefanini 2008) where this deer was not detected. In this habitat, the understorey is composed mainly by species

Fig. 2 Spatial variation of the densities of fallow deer and roe deer within the strata partitioning the study area and location of strata (*down*)

Fallow deer -summer

Fallow deer -winter

Density (N ind/100 ha)

☐ 0 – 4.9
⊡ 5.0 – 9.9
▦ 10 – 14.9
▦ 15.0 – 19.9
▦ 20 – 24.9
⊞ 25.0 – 29.9
▦ 30 – 34.9
▦ 35.0 – 39.9
■ >40

Roe deer -summer

Roe deer -winter

STRATA

N
W ⊕ E
S

▦ Scrubwood - N
▦ Scrubwood - S
▦ Pinewood
▦ Aband. olive groves - N
▦ Aband. olive groves - S
☐ Set-aside grassland
▦ Cultivated fields - N
⊡ Cultivated fields - S

of which few are used or avoided by this deer: mastic *Pistacia lentiscus*, juniper (both *Juniperus oxycedrus* and *Juniperus phoenicea*) and myrtle *Myrtus communis* (Minder 2006; Mencagli and Stefanini 2008). In north scrubwood and abandoned olive groves, the relative scarcity of roe deer should not depend on the lower availability of palatable species than in the southern strata. Most likely, in these

habitats, fallow deer have been living at densities greater than 15–20 individuals/100 ha from at least one decade (Sforzi 2004). The former is expected to have a broader diet than roe deer (Hofmann 1989) and could also eat plants selected by the latter (Putman 1996). In the Mediterranean scrubwood, food offer is low (Minder 2006) and even moderate densities of fallow deer may have a negative effect

Fig. 3 **a** Habitat niche breadth (standardized Hurlbert index) of roe and fallow deer, in summer and winter. **b** Spatial overlap between roe and fallow deer, in summer and in winter, estimated through the Pianka index at the habitat and at the plot scale
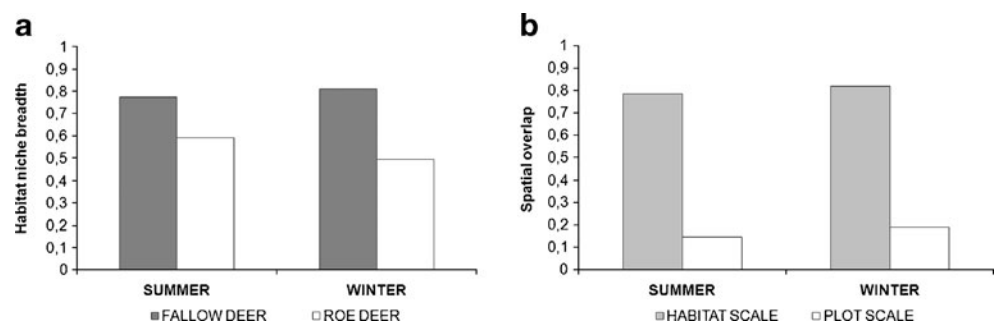
on densities of roe deer. Accordingly, especially in summer, medium to high densities of fallow deer had a strong negative effect on the probability of roe deer presence in sampling plots even considering the effects of habitat (Ferretti et al. in press). We suggest that, in the north scrubwood and abandoned olive groves, medium to high densities of the former could determine low densities of the latter. Fallow deer may have not completed the colonization of the southern part of the MRP, which could contribute to explain the greater densities of roe deer in the southern strata.

Other studies showed inverse numerical trends between populations of these deer species with a decrease of roe and an increase of fallow deer numbers (Putman and Sharma 1987; Focardi et al. 2006). A similar pattern has been recently recorded also in our study area, with an increase in both the number of fallow deer sightings in open areas and fallow deer density and an opposite trend for the roe deer between 2006 and 2009 (Ferretti et al. in press). In our study area, active behavioural interference by fallow to roe deer has been documented, with the former being dominant over the latter in about 80% interspecific encounters, suggesting that fallow displace roe deer at natural feeding sites (Ferretti et al. in press; Ferretti in press). Interference was greater on roe deer females in spring (Ferretti et al. in press), i.e. when pregnancy and lactation occur and a reduced food intake can affect reproductive success (Pettorelli et al. 2005; McLoughlin et al. 2007).

The fallow deer showed a broader habitat niche in comparison to the roe deer (Fig. 3a). This could be due to a different foraging behaviour: the roe deer usually selects vegetation poor in fibre and rich in cell content, whereas the fallow deer can exploit food rich in fibre as well as high-quality vegetation (Hofmann 1989). Alternatively, this pattern may be explained by behavioural interference (Ferretti et al. 2008): roe deer may contract their distribution in areas with great densities of fallow to reduce the probability of interspecific encounters. Spatial overlap between our study species was high at the habitat scale, suggesting a great potential for competition, but decreased markedly at the plot scale (Fig. 3b), suggesting that partitioning of space occurs at a finer resolution. Similar results were also found in sympatric roe deer and muntjac in a forest of Great Britain (Hemami et al. 2004). In our study area, the probability of presence of roe deer was low in areas with great densities of fallow deer (Ferretti et al. in press). Our results suggest that behavioural interference by fallow deer may affect the small-scale distribution of roe, which avoids areas with great densities of the former.

Densities of livestock can negatively affect those of wild ungulates through the depletion of food resources (Baldi et al. 2001; Madhusudan 2004; Mishra et al. 2004). Interspecific negative effects of densities have been suggested also

for wild ungulates (Putman 1996; Forsyth and Hickling 1998; Focardi et al. 2006), although the mechanisms of interactions are unclear. Our data suggest that the density of the superior competitor negatively affects density, habitat use and distribution of the inferior competitor. This negative effect is probably determined by behavioural avoidance of the former by the latter (Ferretti et al. 2008; Ferretti et al. in press). Wild ungulates are often elusive species and behavioural interactions are difficult to observe. Their role in determining ecological relationships between large herbivores has not been assessed but for anecdotal records (Anthony and Smith 1977; Forsyth 1997). We suggest that behavioural interactions could have an important role in shaping relationships between sympatric ungulates, leading to changes on density, habitat use and distribution of competing species both at fine and at large scales.

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