Research Article

Avoidance of fallow deer by roe deer may not be habitat-dependent

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Abstract

Information is scarce on behavioural interference between wild ungulates. In particular, data are lacking on relationships between interference and habitat use. We analysed habitat correlates of behavioural interactions between fallow deer *Dama dama* and roe deer *Capreolus capreolus* at a feeding site, in a Mediterranean area. Previous research has shown that behavioural interference between these deer, with the former dominant over the latter, occurred also through direct aggression. Here we show that, for roe deer, the probability of being displaced by fallow deer did not depend on the habitat where the deer meet. Interspecific encounters, thus interactions, were the most frequent in the habitat selected by roe deer, i.e. the set-aside grassland. In the habitats most used by fallow deer (pastures and crops), roe deer experienced a greater risk of suffering a displacement. The rate of intolerance encounters increased in spring, when habitat overlap occurred because fallow deer intensified the use of set-aside. Our results suggest that, most likely, avoidance of fallow deer by roe deer is not habitat-dependent.

Introduction

In ungulates, ecological interactions have been assessed indirectly (e.g. niche relationships, spatiotemporal comparisons of densities; Focardi et al. 2006; Forsyth and Hickling 1998; Latham 1999). High levels of overlap in the use of resources or inverse numerical trends may develop, suggesting the potential for interspecific competition (Putman, 1996). By contrast, beyond some anecdotal information (Anthony and Smith, 1977; Bartoš et al., 2002; Batcheler, 1960; Danilkin, 1996), data are very scarce on

behavioural interactions, under field conditions (but see Berger and Cunningham 1998; Ferretti et al. 2008, 2011a). In particular, information is still lacking on the relationships between interference interactions, habitat and habitat use of species.

The occurrence of interspecific interference is related to the availability of shared resources (e.g. Eckardt and Zuberbühler 2003; Gese et al. 1996; Sushma and Singh 2006). In seasonal environments (e.g. Mediterranean areas), variations in patterns of resource use could occur throughout months, which may determine seasonal variation in the rate of occurrence of interspecific interference (Ferretti et al., 2011a).

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We analysed the use of open habitats and behavioural interactions between the roe *Capreolus capreolus* and the fallow *Dama dama* deer, in a Mediterranean open area. The roe deer is a small sized cervid (20-30 kg), which feeds on highly energetic vegetation (Andersen et al., 2000; Hofmann, 1989). The density of roe deer appears to be negatively affected by that of other cervid species (red deer *Cervus elaphus*, Latham et al. 1997; muntjac *Muntiacus reevesi*, Hemami et al. 2005; fallow deer, Ferretti et al. 2011a,b; Focardi et al. 2006). The fallow deer is a medium sized cervid (males: 55-85 kg; females: 35-55 kg, in Italy, Boitani et al 2003), who can use energetic food as well as fibrous vegetation (Hofmann, 1989). In captivity, the fallow deer has been reported to be intolerant of red deer (Bartoš et al., 1996) and of spotted deer *Axis axis* (McGhee and Baccus, 2006).

Great densities of fallow deer may reduce habitat quality for roe, leading the latter to a smaller body size and larger home ranges (Focardi et al., 2006). In another Mediterranean area, behavioural interference of fallow to roe deer was documented: the former excluded the latter from feeding sites (Ferretti et al., 2008, 2011a), also using direct aggression (Ferretti, 2011). In both areas, roe deer numbers declined, with an increase of numbers of fallow deer (Ferretti et al., 2011a; Focardi et al., 2006). Ferretti et al. (2011a) showed that behavioural interference was the greatest on roe does in spring (when late pregnancy, births and early maternal care occur), which could explain how fallow deer outcompete roe deer. None of these studies provided data on relationships between habitat and interference.

An increased habitat overlap should determine an increased rate of interference interactions (Donadio and Buskirk, 2006; Sushma and Singh, 2006). Ferretti et al. (2011a) showed that the rate of roe deer displacements, at natural feeding sites, was the most frequent in spring and decreased significantly from summer to winter. This suggests that an increase in habitat overlap occurred when high quality food is available (Minder, 2006; Purser, 1981). Roe deer rely on food intake, rather than fat reserves, for reproduction (Andersen et al., 2000; Hewison et al., 1996): especially in females, a reduced food intake in spring, when pregnancy and lactation occur, can affect reproductive success (McLoughlin et al., 2007; Pettorelli et al., 2005). Events of spatial intolerance by fallow deer are likely to determine a negative effect on feeding roe deer, especially if the latter is displaced by the former from its most used habitat and is forced to use sub-optimal patches for feeding.

We assessed habitat correlates of behavioural interactions between roe and fallow deer in a Mediterranean area and verified whether (i) the probability of occurrence of a roe deer displacement differed across habitats; (ii) interspecific interactions were randomly distributed across habitats or occurred more frequently in a habitat than in the others and (iii) the seasonal variation of the rate of interactions was associated with the seasonal variation of habitat use of our study species. We hypothesized that interference should not depend on habitat features, if competition is determined by avoidance of fallow by roe deer (Ferretti et al., 2008) (hypothesis 1). Roe deer avoid feeding close to fallow deer, whereas the foraging behaviour of the latter is not affected by the proximity of the former (Ferretti et al., 2008, 2011a). Fallow deer are expected to use open habitats irrespective of the presence of roe deer, but the reverse should not be true. Thus, interspecific interactions should occur more often in the habitat the most used by the roe deer than in the others (hypothesis 2) and habitat overlap should depend on the seasonal variation in the habitat use of fallow deer rather than that of roe (hypothesis 3).

Materials and Methods

Study area

Our study was carried out in an open area of the Maremma Regional Park (MRP, Central Italy; 42°39'N, 11°05'E). The local climate is Mediterranean. The area (91.7 ha; Fig. 1) is bordered by Mediterranean scrubwood, with prevalence of holm-oak *Quercus ilex*, and is composed by pastures (54%), set-aside grassland (22%), herbaceous crops (18%: wheat and sunflowers) and sedges (6%). Crops were sowed at the beginning of winter (wheat) or spring (sunflower) and harvested at the end of June (wheat) and August (sunflower). The set-aside grassland was harvested at the beginning of July, in both years of

study. A minimum number of 17 roe deer and 70 fallow deer (i.e. the maximum number of individuals seen during the same observation bout) visited the area during our study. Wild boar *Sus scrofa* also attended this area, whereas free-ranging cattle and horses were irregularly moved through pastures and sedges. Interference interactions were rare between wild boar and deer species, as well between livestock and fallow deer, whereas no encounter was recorded between roe deer and livestock (Ferretti et al., 2011a).
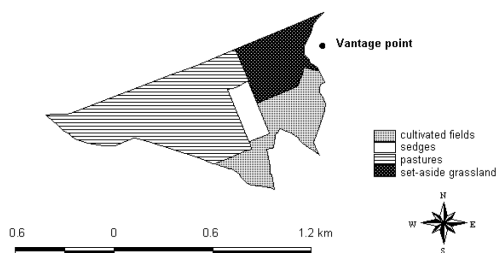

Figure 1 – Study site and location of the vantage point.

Data collection

Behavioural observations were carried out from a vantage point, between April 2006 and May 2008, by the same observer, through a 8×56 Zeiss binoculars and a 15-45× Nikon spotting scope. Data were collected in sessions of two hours, at dawn and dusk, once per week until March 2007, twice per week from April 2007 to May 2008. For both deer species, locations of groups of individuals were recorded at 30 minutes intervals.

We defined as a "contact" when two ungulates of different species were within 50 m from each other (Ferretti et al., 2008). Distances and relative locations of individuals were estimated by using the deer torso length as a reference, as well as known reference points in the landscape detectable on 1:10000 topographic maps (CTR, Regione Toscana; Frid 1997). Interspecific "contacts" were recorded through all-occurrence sampling (Lehner, 1996). An individual was considered as displaced by the other species when: (a) it was chased away, (b) it interrupted its previous activity and moved away (>50 m) from the other species, (c) it avoided the "contact", i.e. it reached a distance of 50 m from the other species by suddenly modifying the direction of its movement after the "contact' started (≥45°, in relation to the location of the other species), as well as reacting to the approach of the other species by avoiding any close-up (cf. Ferretti et al. 2008, 2011a). We estimated that no displacement occurred if both species moved

at a mutual distance of 50 m, without showing any variation in behaviour and/or direction of movement. See Ferretti et al. (2008, 2011a) for further details.

Data analysis

Habitat use was assessed, on each season (spring: March-May; summer: June-August; autumn: September-November; winter: December-February), as the proportion of observations in a habitat over the total number of observations recorded in that season.

Selection ratios (w_i) and Bonferroni-adjusted 95% confidence intervals (Manly et al., 2002) were calculated, at the seasonal scale, to assess the selection of open habitats of both deer species:

$$w_i = \frac{o_i}{\pi_i} \qquad (1)$$

where o_i = number of observations in the habitat i / total number of observations; π_i = availability of habitat i. Confidence intervals were calculated through the formula:

$$w_i = \pm \alpha 2 n s e(w_i) \qquad (2)$$

where $se(w_i) = \sqrt{\frac{o_i(1-o_i)}{u_i \pi_i^2}}$, with u_i = total number observations in the habitat i.

Intervals containing the value 1 indicate that the habitat is used proportionally to its availability. Intervals with the lower limit > 1 indicate selection, whereas those with the upper limit < 1 indicate avoidance (Manly et al., 2002).

Habitat overlap between the deer species was assessed, on each season, through the Pianka index (Pianka, 1973):

$$P = \frac{\sum_{i=1}^{N} O_{iF} O_{iR}}{\sqrt{\sum_{i=1}^{M} O_{iF}^2 \sum_{i=1}^{M} O_{iR}^2}} \qquad (3)$$

where O_{iF} and O_{iR} denote the proportion of fallow deer and roe deer locations in the i-th habitat, respectively. The G-test, adjusted with the Williams correction (Sokal and Rohlf, 1995), was used to assess differences between: (a) the probabilities of displacement (N displacements / N "contacts') across habitats; (b) the number of displacement events recorded in each habitat and that expected on the basis of their size and (c) the number of displacement events recorded in each habitat and the number of roe deer locations in that habitat. For each habitat, we calculated an index of roe deer displacement risk, dividing the proportion of displacements observed in that habitat by the proportion of roe deer sightings recorded there. We assessed the relationships

Table 1 – Relative size of each habitat with respect to the total study area and number of contacts, number of displacements, proportion of roe (RDS) and fallow deer (FDS) sightings (N sightings in that habitat/N tot sightings, for each species) and displacement risk (N displacements/N roe deer sightings) in each habitat.

Habitat	Relative size	N contacts	N displacements	Prop. RDS	Prop. FDS	Displacement risk
Crops	0.18	22	17	0.15	0.26	1.53
Sedges	0.06	0	0	0.04	0.00	0.00
Pastures	0.54	21	19	0.08	0.57	3.25
Set-aside	0.22	41	37	0.72	0.17	0.71

between the seasonal rate of displacement events (N displacements/h), the seasonal habitat overlap and habitat use, for both species, through the Spearman's rank correlation coefficient (Sokal and Rohlf, 1995).

Statistical analyses were carried out through Microsoft® Excel add-in PopTools (Hood, 2006) and SPSS 16.0 Inc.© software. Tests were two-tailed.

Results

We recorded 84 fallow-roe deer "contacts". Roe deer were displaced 73 times (87% cases), whereas fallow deer were never displaced by roe (cf. Ferretti et al. 2011a). As expected (hypotheses 1), the probability of displacement did not differ across habitats (G-test: G_{adj} = 2.069, df = 3, p = 0.355). The number of displacements recorded in each habitat was different from that expected on the basis of both habitat size (G-test: G_{adj} = 21.319, df = 3, $p<0.001$) and number of sightings of roe deer (G-test: G_{adj} = 14.424, df = 3, p = 0.003). Displacements occurred most frequently in set-aside grassland (51% cases; N = 73), where 72% of roe deer sightings occurred (N = 1313; Tab. 1; hypothesis 2). Twenty-six percent and 23% of displacements occurred in pastures and crops, respectively, where roe deer were observed 8% and 15% times, respectively (Tab. 1). Thus, for roe deer, the displacement risk was the greatest in pastures (3.25), intermediate in crops (1.53) and the lowest in the set-aside (0.71).

We collected 1313 locations of roe deer groups and 867 locations of fallow deer groups. The roe deer selected the set-aside grassland in each season (Tab. 1a). Pastures were avoided, whereas crops and sedges were used irregularly, with a general avoidance/no selection pattern (Tab. 2a).

The fallow deer changed its use of open habitats across seasons. The set-aside grassland was used proportionally to its availability or selected in spring-summer, when the vegetation reaches the peak of development and height, and avoided in the other seasons (Tab. 2b). Crops were used proportionally to their availability or selected from winter to summer, after the sowing of wheat or sunflower, and avoided in autumn, after the harvesting (Tab. 2b). Pastures were used irregularly in spring-summer, but selected in autumn-winter (after both the crops and the set-aside grassland had been harvested; Tab. 2b). Sedges were generally avoided (Tab. 2b). Habitat selection has not been estimated for winter 2006/07, because of a small sample size. In both years of study, habitat overlap increased in spring and decreased from summer to winter (Fig. 2) and the displacement rate varied across seasons, consistently with habitat overlap (r_s = 0.717, N = 9, p = 0.030; Fig. 2; cf. Ferretti et al. 2011a).

The seasonal variation of habitat overlap was directly associated to the selection of set-aside grassland by fallow deer (Spearman's rank correlation: r_s = 0.810; N = 8; p = 0.02; Fig. 2), and it was inversely related to the selection of pastures (r_s = -0.762; N = 8; p = 0.03), independently from the habitat selection of roe deer ($p>0.10$). Behavioural interference appeared to depend on habitat selection of fallow deer, not on that of roe deer (hypothesis 3).
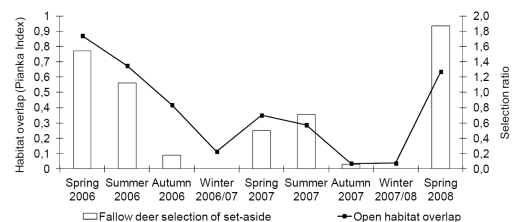
Figure 2 – Seasonal variation of habitat overlap between roe and fallow deer (Pianka Index) and of the selection ratio of set-aside by fallow deer.

Table 2 – Selection of open habitats by roe (a) and fallow deer (b), estimated through selection ratios (Manly et al., 2002) and 95% Bonferroni confidence intervals. +: habitat selected; -: habitat avoided; 0: no selection. For fallow deer, the indices were not calculated in winter 2007/08, because of the small sample size.

(a) Habitat	Spring 2006	Summer 2006	Autumn 2006	Winter 2006/07	Spring 2007	Summer 2007	Autumn 2007	Winter 2007/08	Spring 2008
Crops	0	+	0	0	-	0	-	-	-
Sedges	0	+	0	-	-	-	-	-	-
Pastures	-	-	-	-	-	-	-	-	-
Set-aside	+	+	+	+	+	+	+	+	+
N obs.	132	195	122	80	122	177	171	142	172

(b) Habitat	Spring 2006	Summer 2006	Autumn 2006	Spring 2007	Summer 2007	Autumn 2007	Winter 2007/08	Spring 2008
Crops	0	+	-	0	0	-	0	0
Sedges	-	-	-	0	-	-	-	-
Pastures	-	-	+	0	+	+	0	-
Set-aside	0	0	-	0	0	-	-	+
N obs.	78	180	62	55	162	93	56	173

Discussion

Information is very scarce on behavioural interference between ungulate species (but see Berger and Cunningham 1998; Ferretti et al. 2011a). In particular, no data are available on relationships between interactions, habitat and habitat use of species. We found out that the probability of roe deer displacements by fallow deer did not depend on the habitat where they meet (our hypothesis 1), interspecific interference was more frequent in the most used habitat by the subordinate species (i.e. the roe deer) than in the other habitats (our hypothesis 2) and that habitat overlap, thus the occurrence of interference interactions, was correlated with seasonal changes of habitat use of the dominant species (i.e. the fallow deer; our hypothesis 3).

The greatest probability of recording competitive interactions amongst deer occurs at feeding. Because of that, data collection was concentrated in open habitats, i.e. where deer forage and where interactions can be easily detected, at dawn and dusk (when roe deer are most active, Danilkin 1996). Roe deer avoided fallow deer independently from the habitat type they attended. Fallow deer show aggressive behaviour to a variety of other deer species (in captivity: to red deer, Bartoš et al. 1996, to spotted deer, McGhee and Baccus 2006; in the wild: to roe deer: Ferretti et al. 2008, 2011a; occasionally, to white-tailed deer *Odocoileus virginianus*, Bartoš et al. 2002), which could explain the remarkable avoidance reactions of roe deer.

In the area where our study site was located, Börger et al. (2006) found out that home ranges of roe deer, including a majority of set-aside grassland, were smaller than those with other habitats, suggesting that the set-aside provides rich food and cover, as well as bed sites for fawns, in spring. In a larger study area, including woodland, roe deer concentrated on the set-aside parts of their home ranges (Ferretti et al., 2011a). Our data showed a marked use of set-aside also in summer, after harvesting. In this season, territorial behaviour may lead males to tolerate the removal of vegetation cover in their home ranges (Cimino and Lovari, 2003). Females may keep using this habitat in summer because of the presence of hedges and ditches, rich of uncut vegetation. Although our vantage point was located at a height which allowed deer to be observed even at the peak of vegetation height (May/June), the use of set-aside grassland by the roe deer may have been underestimated, in spring-summer. In all seasons, roe deer used mainly the set-aside grassland (about 44-92% of locations, in spring: Tab. 1, 2), suggesting that a potential low detection probability in this habitat did not affect our conclusions. The fallow deer used mainly pastures, throughout the year, whereas the use of crops and set-aside appeared to depend on alternative resources (food and vegetation cover) from winter, i.e. after sowing,

to late summer, i.e. before harvesting (Tab. 2).

Interspecific interactions may vary across seasons in relation to the spatiotemporal availability of resources (Arsenault and Owen-Smith, 2002). The rate of interactions between roe and fallow deer increased in spring (see Ferretti et al. 2011a). In May, the development of vegetation in the set-aside grassland reached its peak, providing food and cover. Throughout the year, this habitat was the most used one by roe deer, but its usage by fallow deer increased in spring, overlapping with the habitat of the former. On the other hand, for roe deer, the displacement risk was 2.1 and 4.6 times greater in pastures and crops (the habitats most used by the fallow deer: Tab. 1, 2) than in the set-aside, respectively. Thus, interference between fallow and roe deer occurred when (i) the former invaded the habitat niche of the latter or (ii) roe deer used alternative habitats, where the risk of interspecific encounters, thus displacements, increased.

In a large study area (i.e. more than 6000 ha), including our study site, pellet group count surveys and direct counts showed that (i) the densities of roe deer were great where those of fallow deer were rare and low where those of fallow deer were abundant (Ferretti et al., 2011b); (ii) the probability of presence of roe deer significantly decreased with increasing fallow deer density, controlling for the effects of habitat variables (Ferretti et al., 2011a); (iii) roe deer numbers decreased between 2006 and 2009, whereas fallow deer densities increased (Ferretti et al., 2011a). Crucial reproductive activities take place in spring, e.g. late pregnancy, births, early maternal cares and male territoriality (Liberg et al., 1998). Reproductive success of roe deer depends mainly on environmental conditions, in spring-summer (McLoughlin et al., 2007; Pettorelli et al., 2005). Even if causal relationships between behavioural interference by fallow deer and decrease of roe deer are still to be proven (e.g. exploitation competition cannot be ruled out), frequent events of spatial intolerance by fallow deer are also most likely to determine a negative effect on feeding roe deer, e.g. through stress and alteration of feeding patterns (Ferretti et al., 2011a). Presumably, the costs of leaving the set-aside grassland are not negligible when energy requirements of roe deer are the greatest (Andersen et al., 2000; Gaillard et al., 1993), considering that the use of alternative open habitats could increase the risk of interspecific encounters, i.e. displacements, with fallow deer.

Our data showed that interference between roe deer and fallow deer did not depend on the type of open habitat attended. Furthermore, for the roe deer, the probability of being excluded from a meadows tends to increase with decreasing size of the meadow (Ferretti et al., 2011a). This strongly suggests that interference could occur also in small openings in forested areas, where the presence of fallow deer may lead to the exclusion of roe deer. One could expect that beneficial effects of environmental improvements (e.g. clearings in the wood) for roe deer could be vanished by the presence of fallow deer. Thus, any strategy for improving the conservation of populations of roe deer, in sympatry with fallow deer, should not rely solely on forest management (cf. above). The culling – or even attempted eradication – of fallow deer could be an indirect conservation measure for the roe deer.

Very little is known on behavioural interference in ungulates. Our results require confirmation from study areas with different habitat composition and configuration, but, in our study site, the probability of roe displacements by fallow deer did not depend on the habitat where they meet.

References

Andersen R., Gaillard J.M., Linnell J.D.C., Duncan P., 2000. Factors affecting maternal care in an income breeder, the European roe deer. J. Anim. Ecol. 69:672–682.

Anthony R.G., Smith N.S., 1977. Ecological relationships between mule deer and white-tailed deer in Southeastern Arizona. Ecol. Monogr. 47:255–277.

Arsenault R., Owen-Smith N., 2002. Facilitation versus competition in grazing herbivore assemblages. Oikos 97: 313–318.

Bartoš L., Vankova D., Miller K.V., Siler J., 2002. Interspecific competition between white-tailed, fallow, red and roe deer. J. Wildl. Manage. 66: 522–527.

Bartoš L., Vankova D., Siler J., Losos S., 1996. Fallow deer tactic to compete over food with red deer. Aggr. Behav. 22: 375–385.

Batcheler C.L., 1960. A study of the relations between roe,

red and fallow deer, with special reference to Drummond Hill forest, Scotland. J. Anim. Ecol. 29: 375–384.

Berger J., Cunningham C., 1998. Behavioural ecology in managed reserves: gender-based asymmetries in interspecific dominance in African elephants and rhinos. Anim. Conserv. 1: 33–38.

Boitani L., Lovari S., Vigna Taglianti A., 2003. Fauna d'Italia, vol. XXXVIII, Mammalia III, Carnivora - Artiodactyla. Calderini, Bologna.

Börger L., Franconi N., Ferretti F., Meschi F., De Michele G., Gantz A., Coulson T., 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. Am. Nat. 168: 471–485.

Cimino L., Lovari S., 2003. The effects of food or cover removal on spacing patterns and habitat use in roe deer, *Capreolus capreolus*. J. Zool. 261: 299–305.

Danilkin A.A., 1996. Behavioural ecology of Siberian and European roe deer. Chapman and Hall, London.

Donadio E., Buskirk S.W.. 2006. Diet, morphology, and interspecific killing in Carnivora. Am. Nat. 167: 524–536.

Eckardt W., Zuberbühler K., 2003. Cooperation and competition in two forest monkeys. Behav. Ecol. 15: 400–411.

Ferretti F., 2011. Interspecific aggression between fallow and roe deer. Ethol. Ecol. Evol. 23: 179–186.

Ferretti F., Sforzi A., Lovari S., 2008. Intolerance amongst deer species at feeding: roe deer are uneasy banqueters. Behav. Process. 78: 487–491.

Ferretti F., Sforzi A., Lovari S., 2011a. Behavioural interference between ungulate species: roe are not on velvet with fallow deer. Behav. Ecol. Sociobiol. 65: 875–887.

Ferretti F., Bertoldi G., Sforzi A., Fattorini L., 2011b . Roe and fallow deer: are they compatible neighbours? Eur. J. Wildl. Res. 57: 775–783.

Focardi S., Aragno P., Montanaro P., Riga F., 2006. Interspecific competition from fallow deer *Dama dama* reduces habitat quality for the Italian roe deer *Capreolus capreolus italicus*. Ecography 29: 407–417.

Forsyth D.M., Hickling G.J., 1998. Increasing Himalayan tahr and decreasing chamois densities in the eastern Southern Alps, New Zealand: evidence for interspecific competition. Oecologia 113: 377–382.

Frid A., 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. Anim. Behav. 53: 799–808.

Gaillard J.M., Delorme D., Jullien J.M., 1993. Effects of cohort, sex, and birth date on body development of roe deer, *Capreolus capreolus* fawns. Oecologia 94: 57–61.

Gese E.M., Stotts T.E., Grothe S,. 1996. Interactions between coyotes and red foxes in Yellowstone National Park, Wyoming. J. Mammal. 77: 377–382.

Hemami M.R., Watkinson A.R., Dolman P.M., 2005. Population densities and habitat associations of introduced muntjac *Muntiacus reevesi* and native roe deer *Capreolus capreolus* in a lowland pine forest. For. Ecol. Manage. 215: 224–238.

Hewison A.J.M., Angibault J.M., Bideau E., Vincent J.P., Boutin J., Sempéré A., 1996. Annual variation in body composition of roe deer. Can. J. Zool. 74: 245–253.

Hofmann R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78: 443–457.

Hood G.M., 2006. PopTools version 2.7.5. http://www.cse.csiro.au/poptools.

Latham J., 1999. Interspecific interactions of ungulates in European forests: an overview. For. Ecol. Manage. 120: 13–21.

Latham J., Staines B.W., Gorman M.L., 1997. Correlations of red *Cervus elaphus*. and roe *Capreolus capreolus*. deer densities in Scottish forests with environmental variables. J. Zool. 242: 681–704.

Lehner P.N., 1996. Handbook of Ethological Methods. Cambridge University Press, Cambridge.

Liberg O., Johansson A., Andersen R., Linnell J.D.C., 1998. The function of male territoriality in roe deer. In: Andersen R., Duncan P., Linnell J.D.C., (Eds.). The European roe deer: the biology of success. Scandinavian University Press, Oslo. 221-256.

MacArthur R.H., Pianka E.R., 1966. On optimal use of a patchy environment. Am. Nat. 100: 603–609.

Manly B.F.J., McDonald L.L., Thomas D.L., McDonald T.L., Erickson W.P., 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer, Boston.

McGhee J.D., Baccus J.T., 2006. Behavioural interactions between axis and fallow deer at high-value food patches. Southwest. Nat. 51: 358–367.

McLoughlin P.D., Gaillard J.M., Boyce M.S., Bonenfant C., Messier F., Duncan P., Delorme D., Moorter B., Said S., Klein F., 2007. Lifetime reproductive and composition of the home range in a large herbivore. Ecology 88: 3192–3201.

Minder I., 2006. Adaptive parameters of the diet of roe deer in a coastal Mediterranean area. PhD Thesis. University of Siena, Siena.

Pettorelli N., Gaillard J.M., Yoccoz N.G., Duncan P., Maillard D., Delorme D., Van Laere G., Toïgo C., 2005. The response of fawn survival to changes in habitat quality varies according to cohort quality and spatial scale. J. Anim. Ecol. 74: 972–981.

Pianka E.R., 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4: 53–74.

Purser D.B., 1981. Nutritional value of Mediterranean pastures. In: Morley F.H.W. (Ed.). Grazing animals. Elsevier, Amsterdam. 159–177.

Putman R.J., 1996. Competition and resource partitioning in temperate ungulate assemblies. Chapman and Hall, London.

Putman R.J., Sharma S.K., 1987. Long term changes in New Forest deer populations and correlated environmental change. Symp. Zool. Soc. Lond. 58: 167—79.

Schoener T.W., 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369–404.

Sokal R., Rohlf F.J., 1995. Biometry, 3rd ed. W.H. Freeman and Company, New York.

Sushma H.S., Singh M., 2006. Resource partitioning and interspecific interactions among sympatric rain forest arboreal mammals of the Western Ghats, India. Behav. Ecol. 17: 479–490.

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