

Behavioural interference between ungulate species: roe are not on velvet with fallow deer

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Abstract Interference is expected to occur at feeding areas between species with a similar diet, but few studies have tested this idea for wild ungulates. We analysed interactions between fallow deer, European roe deer and wild boar, in three sites, in a Mediterranean area. We expected that interference should be greater between deer than between them and wild boar. We documented the negative effects of behavioural interference by fallow on foraging behaviour of roe deer, under field conditions. Deer species built up 90% interference interactions, with fallow always dominant on roe, also through direct aggression. Although roe deer decreased feeding and increased vigilance levels in proximity (<50 m) of either fallow deer or wild boar, they were displaced significantly more often by the former than by the latter. Fallow deer were neither displaced nor alarmed by roe and rarely by wild boar. No deer species displaced wild boar. Interference was significantly greater on solitary roe deer, especially females, in spring and roe left the feeding ground most often in the smallest site (13 ha). Roe deer avoided areas where the local density of fallow deer was the highest. During our 4-year-study, roe deer density decreased whereas fallow deer numbers increased. Behavioural interfer-

ence may explain how fallow deer outcompete roe deer through spatial exclusion from feeding sites and avoidance of areas with high densities of the former. Fallow deer evolved in semi-arid, relatively poor habitats of Asia Minor: interspecific defence of crucial resources could have developed as a beneficial tactic for its survival.

Keywords Behavioural intolerance · Deer · Interspecific interactions · Ungulates

Introduction

Two species with identical ecological niches should not coexist (Gause 1934). Over an evolutionary scale, species are expected to develop ways to limit competitive interactions, e.g. niche partitioning (Pianka 1974; Schoener 1974). Conversely, species frequently show overlap in the use of resources (Putman 1996; Eckardt and Zuberbühler 2003; Gehrt and Prange 2006). Overlap amplifies the potential for interspecific competition, which may depend on a variety of factors, e.g. availability of a scarce resource or the introduction of alien *taxa* (Hobbs et al. 1996; Arsenault and Owen-Smith 2002; Gurnell et al. 2004; Ahola et al. 2007).

Interactions between species may involve behavioural interference (Birch 1957). Interspecific behavioural interference has been described across multiple *taxa* (insects, Tanner and Adler 2009; fishes, Höjesjö et al. 2005; reptiles, Langkilde and Shine 2005; and birds, Garcia and Arroyo 2004). In mammals, interspecific aggression has been documented mainly in carnivores, affecting population dynamics of the inferior competitors (Palomares and Caro 1999; Donadio and Buskirk 2006, for reviews), and, to a

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much lesser extent, in primates (Eckardt and Zuberbühler 2003; Sushma and Singh 2006). Most carnivores are predators, which may explain why interspecific aggression is frequent in that Order: sixty carnivore species have been involved in about 100 pairwise, species-to-species, aggressive interactions (Palomares and Caro 1999; Donadio and Buskirk 2006), with over 11% species killing other carnivores, but seldom or not feeding on them in 45% of pairwise interactions (Donadio and Buskirk 2006). Most ungulate species are also equipped with potentially lethal weapons. By contrast, comparable information is lacking for wild ungulates: behavioural interference has been rarely seen in the wild (Forsyth 1997) whereas aggression has been recorded mainly in captivity (Bartoš et al. 1996; McGhee and Baccus 2006) or as anecdotal information (Anthony and Smith 1977; Berger 1985; Danilkin 1996; Bartoš et al. 2002).

Predation (Sinclair et al. 2003), density dependence (Bonenfant et al. 2009) and environmental conditions (Coulson et al. 2000) have been shown to influence the population dynamics of ungulates. Even when interspecific competition was suspected to influence numerical trends (Forsyth and Hickling 1998; Focardi et al. 2006), density (Latham et al. 1997), distribution (Anthony and Smith 1977), resource use (Putman 1996) and phenotypic quality (Richard et al. 2010) of sympatric ungulate species, no evidence of active behavioural interference has been provided.

We used the roe deer *Capreolus capreolus* as a model species to address this topic, with an analysis of its interactions with the fallow deer *Dama dama* and the wild boar *Sus scrofa* in a Mediterranean area. The large geographic range of the roe deer, syntopic with other ungulate taxa, makes it suitable to study interspecific interactions (Latham 1999). This small-sized cervid (20–30 kg), well adapted to the wood-field ecotone (Andersen et al. 1998), relies on highly nutritious vegetation for survival and reproduction (mating, July–August and births, April–May; Hoffman 1989; Andersen et al. 2000). The density of roe deer appears to be negatively affected by that of other cervid species (autochthonous: red deer *Cervus elaphus*, Latham et al. 1997; introduced: muntjac *Muntiacus reevesi*, Hemami et al. 2005; cf. also Chapman et al. 1993; fallow deer, 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), well adapted to open habitats (fields, pastures and open wood, Batcheler 1960; Apollonio et al. 1998). This deer can use highly energetic food as well as fibrous vegetation (Hoffman 1989). In captivity, fallow deer have been reported as intolerant of the red (Bartoš et al. 1996) and the spotted deer *Axis axis* (McGhee and Baccus 2006). The wild boar is a suid (males, 80–100 kg; females, 50–70 kg, in Italy; Boitani et al. 2003), with a highly opportunistic foraging behaviour (Massei et al. 1996).

High 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 the study area of Focardi et al. (2006), a crash of the roe deer population occurred (Focardi et al. 2005) whereas fallow numbers increased (Focardi et al. 2006). Ferretti et al. (2008) showed that fallow deer can actively exclude roe deer from natural feeding sites. Information is still lacking on sex/age correlates of behavioural interactions, their spatiotemporal variation, their effects on small scale distribution and density of competitors. We analysed the interactions between roe deer and fallow deer in a Mediterranean area and compared them with those recorded on wild boar. We assessed: (a) behavioural interactions, through direct observations at three natural feeding sites; (b) the effects of the densities of fallow deer and wild boar on the presence/absence of roe deer in sampling plots, through faecal pellet group counts, within the whole study area; (c) the variations in populations densities of roe and fallow deer, throughout our study. We tested the following five hypotheses:

- Hypothesis 1 Both roe and fallow deer are ruminants (*Ruminantia*). They are expected to share resources and show intolerance interactions between them more than with the wild boar that are monogastric *Suiformes* (see Donadio and Buskirk 2006 for similar arguments on carnivores). Only when roe deer are in close proximity of fallow deer, they should reduce the time spent feeding and increase that spent in vigilance. Fallow deer should neither be affected by proximity to roe deer (Ferretti et al. 2008) nor to wild boar, as interference effects are expected to be greater in the smaller species (roe deer) and lower between unrelated species (see Donadio and Buskirk 2006, for carnivores).
- Hypothesis 2 Roe deer are income breeders, and both sexes have high energetic demands because of reproductive costs (Gaillard et al. 1997; Cimino and Lovari 2003): males and females should show similar tolerance levels to fallow deer. Adults should be displaced by fallow deer less frequently than yearlings because the former take part in reproductive activities (Liberg et al. 1998). From yearling size upwards, fallow deer of different sex/age are considerably larger than roe deer, and are expected to have similar probabilities to displace the latter. Roe deer, in groups, should be more tolerant of fallow deer than solitary ones, independent of fallow deer group size

(Ferretti et al. 2008). The probability of a displacement should be lower in winter than in other parts of the year, as roe deer group together in that season (Hewison et al. 1998). The probability of displacement events should also not differ between sites, if avoidance of fallow by roe deer is independent of local features. We expected that, for roe deer, the probability of a displacement by fallow depends only on roe deer sex/age/group size and season.

Competition is expected to arise when the availability of shared resources is scarce (Birch 1957). Roe, when displaced from a food patch, should be forced to abandon the feeding ground where less space is available (i.e. the smaller site), if roe and fallow deer compete for space.

- Hypothesis 3 For herbivores, summer is the limiting season in Mediterranean habitats because the availability of lush vegetation and water is scarce due to the summer drought (Minder 2006, but see also Massei et al. 1997). Thus, interference interactions between deer species should be more frequent in this season than in the others.
- Hypothesis 4 We predicted that behavioural interference should be greater between deer species than between these and the wild boar. The local density of fallow deer should have a negative effect on the presence of roe in sampling plots, both in summer and in winter, if behavioural interference has an effect on small scale distribution of the latter. In contrast, the density of wild boar should not have a negative effect on the presence of roe deer.
- Hypothesis 5 The interference by fallow deer should reduce the density of roe deer, with little or no detectable cost to the former. Throughout our study, we expected a decrease of the density of roe deer and either no change or an increase in the density of fallow deer.

Methods

Study area

Our study was conducted in the Maremma Regional Park (6,260 ha; MRP, Central Italy; 42°39' N, 11°05' E). The

climate is Mediterranean (dry summers; wet autumns and winters), with a mean annual rainfall of 670 mm and a mean annual temperature of 13.2–15.5°C (RDM 2002). Mean seasonal rainfall is 71.6 mm (summer), 143.1 (spring), 202.3 (winter) and 229.1 mm (autumn; RDM 2002), indicating a period of aridity in summer (the limiting period for ungulates, in Mediterranean areas: Massei et al. 1997). Vegetation is composed mainly of Mediterranean sclerophyllic scrubwood (58%) of three main wood types (Mencagli and Stefanini 2008): oakwood, with prevalence of holm oak *Quercus ilex* trees with a height >7 m; scrubwood, with prevalence of holm oak and strawberry tree *Arbutus unedo*, with a height <7 m; garrigue, with bushes (mainly holm oak, rosemary *Rosmarinus officinalis*, juniper *Juniperus* spp., rockrose *Cistus* spp.), with a height <2 m. Other habitats are pinewood (10%: mainly domestic pine *Pinus pinea*), abandoned olive groves and pastures (15%), set-aside grassland (4%) and crops (12%, mainly cereals and sunflower).

Behavioural observations were conducted in three open areas bordered by sclerophyllic scrubwood. The sites were located 3 to 9 km apart, in a straight line. Site A (91.7 ha) included shrub/grassland (82%) and herbaceous crops (18%); sites B (26.3 ha) and C (12.9 ha, i.e. the smallest site) included only shrub/grassland (100%). A minimum number of 44 roe and 162 fallow deer (i.e. the maximum number of deer observed in the same site during the same bout, over our study sites) visited the sites during the study period. Roe deer were more abundant in site C (minimum density, 1.2 individuals (ind)/ha) and showed lower densities in site B (0.4 ind/ha) and in site A (0.2 ind/ha). Fallow deer density was the highest in site B (3.2 ind/ha), intermediate in site C (2.8 ind/ha) and the lowest in site A (0.8 ind/ha). Crops, at site A, were sowed at the beginning of winter (December) and harvested at the end of June (wheat) and August (sunflower) whereas a part of grassland was cut at the beginning of July. In sites B and C, grassland was cut in September 2006 on the first year and in December 2007 on the second year.

Free-ranging cattle (less than 60 individuals) and horses (less than 20 individuals) were irregularly and infrequently moved through part of site A, as well as in other areas within the MRP. Avoidance of these livestock by fallow deer occurred only once in 16 observations and mixed groups were repeatedly seen in other pastures within the MRP. No encounter was recorded between roe deer and livestock.

Hypotheses 1–3: behavioural observations

Behavioural observations were conducted from vantage points, between April 2006 and May 2008 by the same observer, through 8×56 Zeiss binoculars and a ×15–45

Nikon spotting scope. Data were collected in 2 h sessions, at dawn and dusk once/week until March 2007 and twice/week from April 2007 to May 2008. Activities of roe and fallow deer were recorded on a portable tape recorder, through focal animal sampling (Lehner 1996), with sampling bouts of 15 min. If only one species was present at the observer's arrival, observations started on it. When both species were present, we alternatively selected them for the initial watching bout. The following activities were recorded: feeding (grazing or browsing, standing or in movement), vigilance (the animal lifts its head above the body axis, intently looking at/around and orienting the ears towards the source of disturbance, if any) and other activities (San José et al. 1996).

We defined a "contact" as occurring when two ungulates of different species were within 50 m from each other (Anthony and Smith 1977; Berger 1985). 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 1:10,000 topographic maps (CTR, Regione Toscana; Frid 1997). Interspecific "contacts" were recorded through all-occurrence sampling (Lehner 1996). Starting/ending time of "contact", sex, age, group size and activity of deer before/during/after the "contact" were recorded. The following age classes were considered: adult (≥ 2 years old) and yearling (1 year old) for roe deer and fallow deer females; adult (≥ 5 years old), subadult (2–4 years old) and yearling (1 year old) for fallow deer males; fawns (0 years old) for both species. Age classes were estimated in the field by considering body size, body shape and, for males, the size and development of antlers. After detection of a "contact", deer activities were assessed until it ended (i.e. when individuals of either species moved farther than 50 m from each other). 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 modifying the direction of its movement after the "contact" started ($\geq 45^\circ$, 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 (Ferretti et al. 2008). An individual was considered as excluded from the feeding site when it left the field immediately after being displaced. 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. At site B, we could not collect data during the peak of the vegetation height (>50 cm: June–September 2006; mid-April–December 2007 and 2008) because our visibility of roe deer was impaired. At sites A and C, the vantage points were located at a height which allowed roe deer to be observed even at the

peak of vegetation height (May/June). Whenever an anthropogenic source of disturbance was detected, the time of the beginning/end of disturbance was noted, and data were not collected again until the animals had calmed down. "Contacts" between the deer species and the wild boar were recorded in the second year of study (June 2007/May 2008).

Generalised linear models with binomial errors (Crawley 2007) were used to investigate both the occurrence of displacement/no displacement and that of exclusion/no exclusion, in relation to: (1–2) the sex of the displaced (excluded) and that of the displacing (excluding) species; (3–4) the age class of the displaced (excluded) and that of the displacing (excluding) species; (5–6) the interaction between sex and age for both the displaced (excluded) and the displacing (excluding) species; (7) the species which occupied first the foraging space; (8–9) the group size of the displaced (excluded) and that of the displacing (excluding) species; (10) site; (11) season; (12) the interaction between season and year; (13) the interaction between season and site; (14) the interaction between season and sex of both the displaced (excluded) and the displacing (excluding) species; (15) the interaction between season, sex and age of both the displaced (excluded) and the displacing (excluding) species. For both models, all variables were entered in a global model. The total model of exclusion showed overdispersion (Crawley 2007): the residual deviance was greater than residual degrees of freedom (residual deviance=170.17; residual $df=130$). Thus, we used a generalised linear model with quasi-binomial error (Crawley 2007). Minimum adequate models were estimated by removing the least significant term at each step, starting from the highest level of interactions, until the elimination of terms caused a significant increase in the residual deviance (Crawley 2007). Chi-square deletion tests were used to assess the significance of changes in residual deviance (Crawley 2007).

Hypotheses 4–5: density estimates

Deer densities were estimated at two spatial scales: observation sites and study area. Within each site, in spring (2006–2009), we counted the maximum number of individuals seen at the same time, or differing for sex and/or apparent age. In the whole study area, the faecal accumulation rate (Mayle et al. 1999) was used to assess densities of deer and presence of wild boar in summer 2007, winter 2007/2008 and summer 2009. Pellet group counts have been consistently used from several decades to estimate deer densities in areas with dense vegetation cover and scarce visibility of animals (e.g. Neff 1968; Bailey and Putman 1982; Putman 1984; Mayle 1996; Latham et al. 1997; Campbell et al. 2004). In particular, the faecal

accumulation rate technique can give reliable results because it does not require the knowledge of the decay rates of pellet groups, which vary greatly between habitats (Mayle et al. 1999; Campbell et al. 2004; Minder 2006, for our study area). We tested the validity of this method of pellet group count, in our study area. A sampling design was assessed and refined across nine sampling seasons (Fattorini et al. 2010). During this study period ($N=8$ years), the sampling design was modified, after each year, to reduce confidence intervals of estimates. Eventually, we obtained stable estimates between the cold and the warm seasons of the same year, with considerably narrow confidence intervals (Fattorini et al. 2010). Our estimates were comparable to those obtained through spotlight and transect counts in open areas where the visibility of deer was high, even in broad daylight, because of low vegetation cover and group living habits of deer (Fattorini et al. 2010). These results showed that, in our study area, the pellet group count (the faecal accumulation rate, Mayle et al. 1999), with the sampling design adopted, provides reliable estimates of deer densities (Fattorini et al. 2010). 196 circular plots (5-m radius) were placed in the study area through a two-stage stratified sampling (Gregoire and Valentine 2008). Each season, a first survey was conducted to remove all pellet groups from plots. A second survey was conducted after 40 days (according to the local decay rate of deer/wild boar pellet groups: Massei et al. 1998; Minder 2006) to count pellet groups (>5 pellets, Mayle et al. 1999) in the plots. Pellets of fallow and roe deer were recognised 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). In the field, less than 0.4% of pellet groups found ($N=2,654$) were dubious, thus discarded. Through this technique, the number of deer in the area is given by the number of pellet groups in the area/(number of days between the surveys $\times$ mean defecation rate) (Mayle et al. 1999). Strata were assessed according to the main habitat categories (Mencagli and Stefanini 2008), as well as local features (Mayle et al. 1999). Differences in deer densities were detected through monitoring surveys (Sforzi 2004). We considered eight strata: north/south Mediterranean scrubwood, pinewood, north/south abandoned olive groves and pastures, set-aside grassland, north/south cultivated fields. In larger strata (north/south Mediterranean scrubwood and pinewood), we adopted a two-stage strategy. In the first stage, strata were partitioned into spatial units (polygons) of different sizes on the basis of natural or man-made edges. A sample of units was selected through 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). The selection of contiguous units was avoided since adjacent units were more alike than farther ones, thus giving poor contribution to sample information (Barabesi et al. 1997). In the second stage, plots were placed within selected units through unaligned systematic sampling (EPA 2002) or tessellation stratified sampling (Cordy and Thompson 1995), to provide an even distribution of plots over the units. We allocated number of plots to strata proportionally to their size, and seven plots were assigned to each unit. In smaller strata, plots were placed directly on the stratum through the same scheme adopted within the spatial units. In summer 2007 and 2009, we estimated the absolute densities of each deer species, to evaluate whether they varied through the sampling period. Methodological details and theoretical justifications regarding this sampling scheme are given in Fattorini et al. (2010), where unbiased estimators of abundance, conservative estimators of sampling variances and confidence intervals are provided. Two geographic coordinates were assigned to plots, to detect the centre of them through a portable GPS Garmin Etrex. The defecation rate could vary between individuals: thus, population means have been used to partly circumvent it (Mitchell et al. 1985; Mayle et al. 1999). For fallow deer, we used a defecation rate of 25 pellet groups/day (in our same study area: Massei and Genov 1998). For roe deer, local information on defecation rate was lacking. 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). We wished to assess the relative variation of population densities rather than actual population densities. The use of defecation rate of roe deer from literature is unlikely to affect our conclusions.

Generalised linear models, with binomial errors, and both fixed and random terms (Crawley 2007) were used to associate the presence/absence of roe deer within the plots to: (1) the number of pellet groups of fallow deer/wild boar in the plots; (2) the proportion of habitat types in 40 ha around the plot (i.e. the seasonal median home range size of roe deer, estimated in our study area through radio-tracking, Börger et al. 2006); (3) the habitat in the plot; (4) the number of habitats in 40 ha around the plot; (5) season; (6) year; (7) the interaction between season and the number of pellet groups of fallow deer/wild boar in the plots; (8) the interaction between season and the habitat in the plot; (9) the interaction between season and the proportion of each habitat type in 40 ha around the plot. Plot identities were entered in the models as random factors, to control for the presence of repeated measures from each plot, in different seasons. The minimum adequate model was estimated through the above procedure (Crawley 2007). We considered

the following habitats: oakwood, scrubwood, garrigue, pinewood, abandoned olive groves and pastures, set-aside, cultivated fields (Mencagli and Stefanini 2008). We conducted the analysis through the vegetation map of the MRP (Mencagli and Stefanini 2008) using ArcView GIS 3.2 (ESRI 1999), SPSS 16.0 (SPSS Inc. 2007) and R 2.9.1 (R Development Core Team 2009). All tests were two-tailed with $\alpha=0.05$.

Results

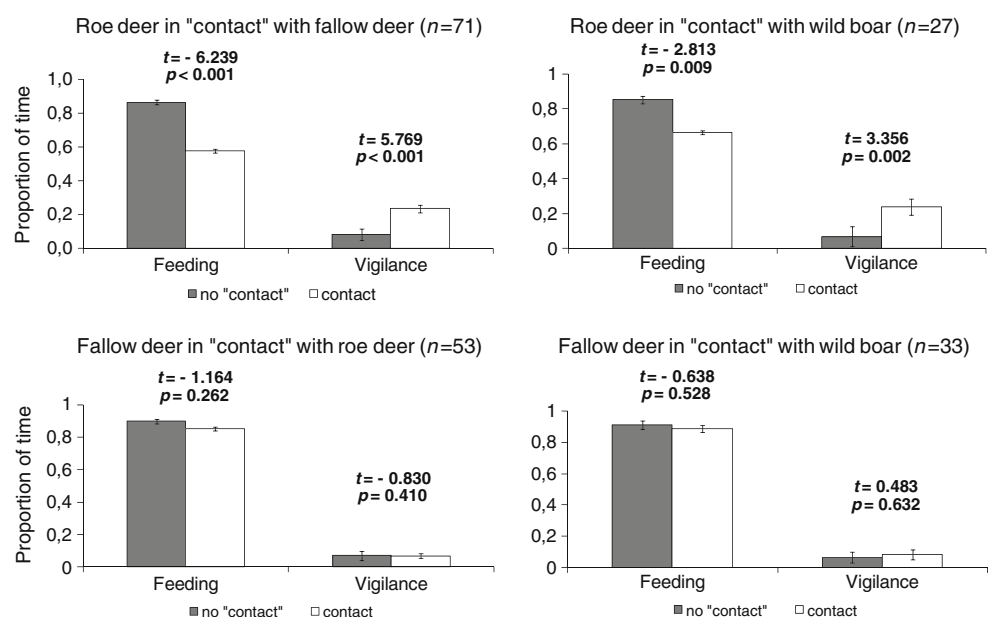
Hypothesis 1 We conducted 768 h of observations during 384 bouts. In partial agreement with our hypothesis, roe deer reduced the proportion of time spent feeding (PTF) and increased the proportion of time spent in vigilance (PTV) when in “contact” with other study species, compared with “no contacts” (Fig. 1). Roe deer showed similar activities both during “contacts” with roe deer and during “contacts” with wild boar (independent t test: $t=0.209$, $df=96$, $p=0.835$ for the PTF; $t=0.611$, $df=96$, $p=0.543$ for the PTV).

As expected, fallow deer did not modify their activities when near to other species compared with no “contacts” (Fig. 1). Fallow deer showed similar activities both during “contacts” with roe deer and during “contacts” with wild boar (independent t test: $t=-0.806$, $df=84$, $p=0.423$ for the PTF; $t=-0.319$, $df=84$, $p=0.751$ for the PTV).

Hypothesis 2 In contrast with our hypothesis, roe does were displaced more frequently than bucks or mixed groups, but, as predicted, roe year-

As expected, direct aggression was recorded only during roe–fallow deer “contacts” ($n=31$ fallow–roe aggressions, $n=8$ roe–fallow aggressions; Fig. 2). According to our prediction, roe deer were displaced by fallow deer (79% cases of $n=259$) more frequently than by wild boar (22% cases of $n=74$; G-test, $G_{adj}=80.862$; $df=1$; $p<0.001$; Fig. 2), whereas neither the fallow deer nor the wild boar were ever displaced by roe deer. Roe deer frequently moved away (>50 m) from fallow deer or avoided the “contact” (64% cases; Fig. 2). Direct aggression was rare (fallow–roe, 12% cases; roe–fallow, 3% cases; Fig. 2). A direct approach or a chase was considered as aggressive behaviour patterns. Roe moved away or avoided “contact” with wild boar in 22% cases (Fig. 2). Roe left the feeding ground about half the time (51% cases of $n=187$) when scared by fallow deer, but slightly less frequently when displaced by wild boar (31% cases of $n=16$). Fallow deer were rarely displaced by wild boar (13% of cases of $n=61$) whereas wild boar were never displaced by fallow deer. As we expected, roe and fallow deer showed a similar probability of passive displacement during “contacts” with wild boar (G-test, $G_{adj}=1.654$; $df=1$; $p=0.198$).

Fig. 1 Proportion of time spent feeding and in vigilance (mean $\pm$ standard error) by roe deer (top) and by fallow deer (down) without “contact” compared with those when in “contact” with the other deer species (left) or with the wild boar (right). Differences were assessed with a paired comparisons t test



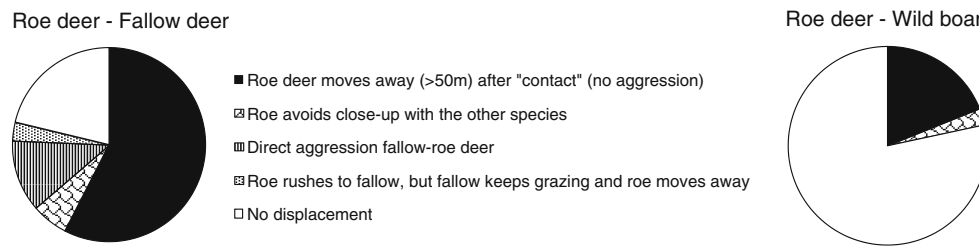


Fig. 2 Interspecific “contacts” between roe and fallow deer ($n=259$, left) and between roe deer and wild boar ($n=74$, right). Fallow deer were never displaced by roe deer and rarely moved away from wild boar (13%; $n=61$), with no aggression. Wild boar were never displaced by deer

lings were displaced more frequently than adults (Table 1). Roe deer were displaced more frequently when solitary than in group, were displaced more frequently by fallow deer males than females and displacements occurred less frequently in winter than in the other seasons (Table 1). In contrast with our hypothesis, roe deer were displaced significantly more often by fallow groups than by solitary individuals (Table 1).

As we expected, roe deer were excluded most frequently from the smallest site, whereas exclusions were frequent in spring and autumn 2007 more than in the same seasons of 2006 (Table 1).

Hypothesis 3 83.4% of fallow–roe deer aggressions occurred in spring, 6.4% both in summer and in autumn and 3.2% in winter ($n=31$). In contrast to our expectations, fallow deer were not more aggressive when forage availability was scarce (i.e. summer; Minder 2006). Pooling data across sites, the rate of displacement (RD: N displacements/h) halved from spring to summer, in both years, and showed a 7- and a 8-fold increase from the first and the second winters to the

following springs, respectively (Fig. 3a). In both years, the RD showed a significant decreasing trend from spring to winter (linear regression analysis, Sokal and Rohlf 1995; 2006: $\beta=-0.230$, $p=0.036$, $R^2=0.929$, $df=2$; 2007: $\beta=-0.118$, $p=0.016$, $R^2=0.968$, $df=2$; Fig. 3b).

Hypothesis 4 Our analysis concerned plots in which at least one species was detected (summer 2007, $n=171$ plots; winter 2007/08, $n=140$ plots; summer 2009, $n=136$ plots). As expected, the local density of fallow deer had a negative effect on the presence of roe deer, particularly in summer compared with winter (Table 2). The mean number of pellet groups/plot of roe deer showed a 4.1- and a 5.4-fold decrease from plots without pellet groups of fallow deer to those with one pellet group, in summers 2007 and 2009, respectively, but only a 2.4-fold decrease in winter (Fig. 4).

The proportion of set-aside grassland and that of abandoned olive groves and pastures in the home range determined a favourable effect on roe deer presence (Table 2). In winter, the proportion of

Table 1 Factors affecting the probability of passive displacement and the probability of passive exclusion of roe deer in “contacts” with fallow deer

Interaction	Variable	<i>B</i>	Standard error	<i>p</i>
Displacement	Roe deer sex (males)	−1.059	0.456	0.020
	Roe deer sex (mixed groups)	−1.757	0.686	0.010
	Fallow deer sex (males)	0.989	0.399	0.013
	Roe deer age (yearling)	1.574	0.790	0.046
	Fallow deer group size	0.113	0.050	0.024
	Roe deer group size	−0.785	0.393	0.046
	Season (winter)	−2.941	1.103	0.008
	Intercept	3.378	1.094	0.002
	Site (C)	1.296	0.432	0.001
	Season (Autumn)×Year (2007)	2.423	1.156	0.038
Exclusion	Season (Spring)×Year (2007)	1.072	0.508	0.036
	Intercept	−1.321	0.432	0.003

Effects estimated through generalised linear models with binomial (displacement) and quasi-binomial (exclusion) errors. Model of roe deer displacement: displacement=1 and no displacement=0 and model of roe deer exclusion: exclusion from the field=1 and persistence in the field=0

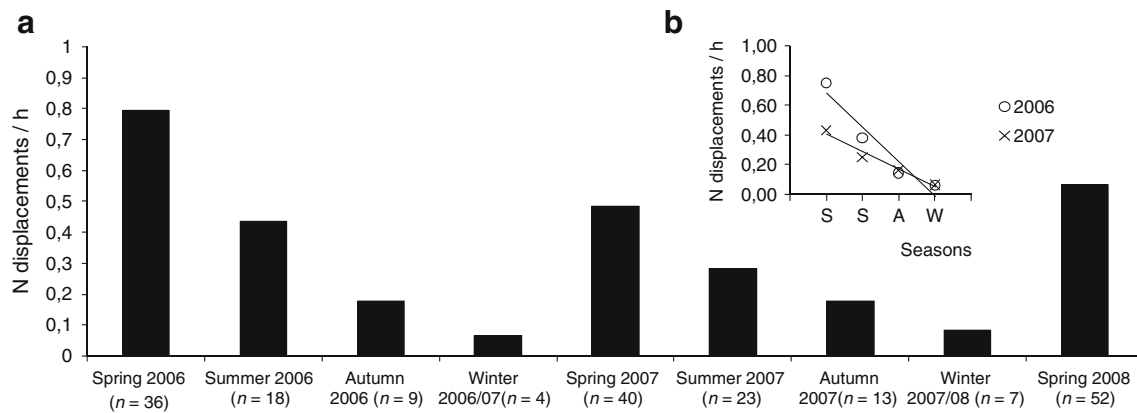


Fig. 3 **a** Seasonal variation of the rate of displacements (RD) by fallow deer to roe. In parentheses, the number of displacement events recorded in each season; **b** linear regressions of seasonal RD, in 2006 and in 2007

cultivated fields in the home range, as well as that of set-aside, i.e. arable land in this season, had a negative effect on roe presence, with respect to summer (Table 2).

Hypothesis 5 From 2006 to 2009, the number of roe deer sightings in spring (RDNS) decreased by 44%, whereas that of fallow deer (FDNS) increased by 41%. This pattern was observed in each site (site A, RDNS decreased by 65% and FDNS increased by 33%; site B, RDNS decreased by 27% and FDNS increased by 34%; site C, RDNS decreased by 33% and FDNS increased by 88%; Fig. 5a). Variation of the number of roe deer sightings in spring (i.e. number of sightings in spring minus number of sightings in the previous spring, for each site) was significantly and inversely correlated to the rate of interference interactions in the previous spring (Spearman's

rank correlation coefficient: $r_s = -0.797$; $p = 0.010$; $n = 9$). That is, a large number of interference interactions was followed by a decrease in the numbers of roe deer sightings.

In the whole study area, the summer density of roe deer decreased by 24.0% from 2007 (10.7 ind/100 ha $\pm$ 4.9 ind/100 ha; 0.90 confidence intervals) to 2009 (8.2 ind/100 ha $\pm$ 3.4 ind/100 ha; 0.90 confidence intervals; Fig. 5b). In contrast, the summer density of fallow deer increased by 12.9% from 2007 (14.4 ind/100 ha $\pm$ 2.8 ind/100 ha; 0.90 confidence intervals) to 2009 (16.3 ind/100 ha $\pm$ 2.7 ind/100 ha; 0.90 confidence intervals; Fig. 5b). Differences were significant for both species (Wilcoxon's test, conducted between the plots sampled in both seasons: $z = -2.525$; $p = 0.012$, for fallow deer and $z = -2.242$; $p = 0.025$, for roe deer).

Table 2 Factors affecting presence/absence of roe deer in 5 m radius sampling plots

Variable	B	Standard error	p
Fallow deer density	-2.069	0.260	0.000
Fallow deer density $\times$ season (Winter)	1.006	0.237	0.000
Prop. set-aside/HR	11.102	3.297	0.003
Prop. set-aside/HR $\times$ season (Winter)	-6.757	2.441	0.005
Prop. cultivated fields/HR $\times$ season (Winter)	-4.616	1.723	0.007
Prop. abandoned olive groves/HR	7.199	3.245	0.027
Prop. oakwood/HR	6.672	3.172	0.035
Intercept	-4.451	3.265	0.173

Effects estimated through generalised linear models with binomial error and both fixed and random effects. Plot identities were entered as random factors. Analyses concerned plots where at least one species was detected ($n = 441$ plots). The final model included the not significant effects of the habitat in the plot, the proportion of cultivated fields, that of garrigue and that of scrubwood in the home range ($p > 0.05$)

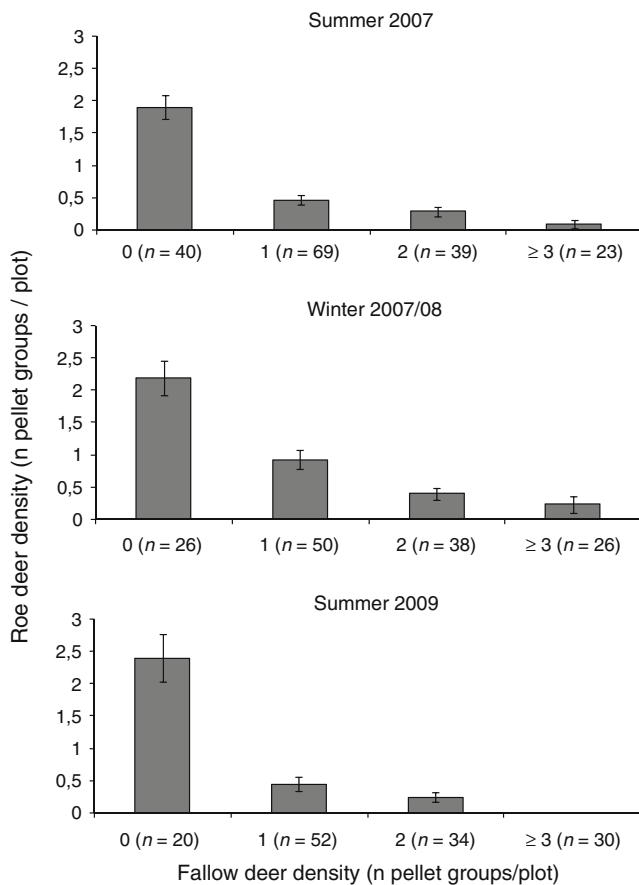


Fig. 4 Number of pellet groups/plot (mean $\pm$ standard error) of roe deer in plots with different numbers of fallow deer pellet groups, in summer 2007, in winter 2007/08 and in summer 2009. In parentheses, the number of plots

Discussion

So far, no study has shown the effects of behavioural interference on foraging behaviour, distribution and density of competitors among ungulate species (but see Berger and Cunningham 1998, for a record of aggressive interactions between African elephants and black rhinos). Over an evolutionary time scale, the pressure of predation on wild herbivores (Sinclair et al. 2003) has probably selected for the development of mutual antipredator strategies rather than competitive behaviour patterns (Sinclair 1985). We have shown that interference may also be strong between wild herbivores. Interference may be greater between taxonomically related species than between more divergent *taxa* (carnivores, Donadio and Buskirk 2006; primates, Sushma and Singh 2006). The roe and the fallow deer are both ruminants and are expected to show a greater overlap in resource use between them than with wild boar, which may explain why interference was higher between them than with the wild boar.

Roe females were displaced by fallow deer more often than roe males and mixed groups and yearlings were

displaced more often than adults (Table 1). Adult roe males defend territories in spring-summer consistently from year to year (Liberg et al. 1998). Territorial males have much greater mating opportunities than non-territorial ones (Liberg et al. 1998; Vanpé et al. 2009). This selective pressure may have lead roe bucks to tolerate a lower food intake in the presence of a competitor (the fallow deer), as well as a high risk of interspecific aggression. Alternatively, roe females could avoid the contact with fallow deer to reduce the risk of an aggression, with injuries of their fawns, who are very small in their first weeks of life (less than 2.5 kg of weight, at birth, with a post-natal growth rate of 113–155 g/day; Andersen et al. 1998).

The probability of displacement events between deer species did not differ across sites (Table 1). Avoidance of fallow deer by roe deer appeared not to be density dependent, even if the latter were displaced more frequently by fallow groups than by solitary individuals (Table 1). Withdrawing (passive exclusion; displacement rate) of roe deer from feeding grounds was observed most often in the smallest site than in the other sites (Tables 1–2), suggesting

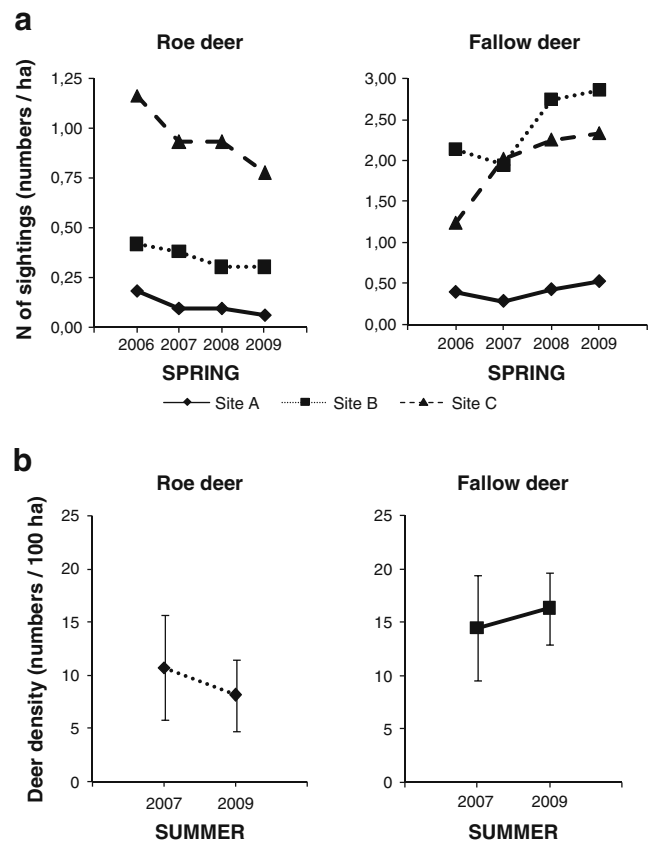


Fig. 5 **a** Number of sightings, in spring, of roe and fallow deer, in three observation sites, between 2006 and 2009; **b** summer densities (mean $\pm$ 0.90 confidence intervals) of roe and fallow deer, in the whole study area, estimated through pellet group counts

that roe and fallow deer interfere for foraging space with the latter dominant over the former.

In the Mediterranean area, summer droughts are the limiting factor (Massei et al. 1997), through forage scarcity, whereas the availability of forage is greatest in spring (Minder 2006). Aggression is often linked to the availability of essential but scarce resources (Gese et al. 1996; Eckardt and Zuberbühler 2003; Sushma and Singh 2006). Competition may be predicted to be stronger in summer, when competitors are expected to defend sparse food patches, and weaker in the food-rich spring. We observed a quite different pattern: roe–fallow deer intolerance interactions were most frequent in spring (Fig. 3), whereas intolerance encounters were least numerous in winter (Tables 1 and 2). Both deer species may compete for the best food patches in spring. Optimal foraging theory (MacArthur and Pianka 1966; Schoener 1971) predicts that species should narrow their niches, concentrating on the richest food patches, when resources are not limiting, whereas they should expand their niches and use other food patches when resources are limiting. This behaviour, which has been observed in other ungulates (review in Sih and Christiansen 2001), should increase the number of interspecific encounters (i.e. interference interactions) in spring. In winter, roe deer aggregate (Hewison et al. 1998) and in a group they are more tolerant of fallow deer than when solitary (Table 1; Ferretti et al. 2008), which may explain why displacement events were less numerous in that season (Table 1). Roe deer rely on food intake, rather than fat reserves, for reproduction (Hewison et al. 1996; Andersen et al. 2000): especially in females, a reduced food intake in spring, when pregnancy and lactation occur, can affect reproductive success (Pettorelli et al. 2005; McLoughlin et al. 2007).

In our sampling plots, the presence of roe deer was strongly negatively affected by the local density of fallow deer (Table 2). The comparison of densities or patterns of distribution of sympatric species may suggest the existence of interspecific competition, controlling for the effects of other environmental variables (e.g. Latham et al. 1997; Ritchie et al. 2009, for non-ungulate herbivores). This approach does not explain the biological mechanism behind interactions. Our data showed that fallow deer can actively exclude roe from feeding sites. Not surprisingly, presence and density of roe deer have been shown to be negatively affected by high fallow deer densities (Focardi et al. 2006; our data). The negative effect of the density of fallow deer on that of roe deer was more pronounced in summer (i.e. the limiting season; Massei et al. 1997), when the mating season of the latter occurs (Liberg et al. 1998). In winter, group living may make roe deer relatively tolerant of fallow deer where the density of the latter is moderate (Table 1). The set-aside

grassland and the abandoned olive groves and pastures had a favourable effect on roe deer presence in our sampling plots (Table 2). Habitat selection occurs when natural resources are abundant, e.g. high-quality food and vegetation cover (Andersen et al. 1998). Abandoned olive groves, between wood and open fields, are mostly covered with bushes, interspersed with pastures, providing food and cover to roe deer. In a part of our study area (MRP), Börger et al. (2006) found out that home ranges of roe deer with a majority of set-aside were smaller than those with other habitats, suggesting that set-asides provide rich food and cover.

Could interference by fallow negatively affect the numbers of roe deer? Inverse numerical trends have been reported for roe and fallow deer, with decreasing roe numbers (Batcheler 1960; Putman and Sharma 1987; Focardi et al. 2006). These trends may be interpreted as independent reactions of roe and fallow deer to a third factor (Putman 1996; e.g. habitat modification, Batcheler 1960). We observed a reduction of roe deer and an increase of fallow deer numbers in our study area. Number of sightings in all observation sites also followed the same pattern. In our study area, with the sampling strategy adopted, the faecal accumulation rate (Mayle et al. 1999) has been shown to be reliable to estimate deer densities (Fattorini et al. 2010), suggesting that our estimates actually reflected a reduction of roe deer density and an increase of fallow deer numbers, at the population scale. The numerical reduction of roe deer in the observation sites might be the result of a decreasing attractiveness of these sites because of the presence of fallow deer, and the former might simply have used different meadows through the time. On the other hand, we observed that: (1) the proximity of fallow deer determined decreased foraging levels and increased vigilance in roe deer; (2) fallow deer actively displaced and excluded roe deer from feeding grounds; (3) interference was particularly frequent when the latest stages of pregnancy, births and early maternal care of roe deer occur (i.e. spring); (4) the density of fallow deer negatively affected small scale distribution and density of roe; (5) as the number of fallow deer sightings increased, the numbers of roe deer sightings decreased (Fig. 5); (6) a great number of interference interactions was followed by a decrease in the number of roe deer sightings. 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). On the other hand, frequent events of spatial intolerance by fallow deer are also likely to determine a negative effect on feeding roe deer, e.g. through stress and alteration of feeding patterns. Interference and exploitation may be complementary processes, with fallow deer depleting food resources at sites vacated by roe deer.

In captivity, fallow deer males exhibited strong aggression towards similar-sized spotted deer *Axis axis* and the larger red deer at feeding sites (McGhee and Baccus 2006; Bartoš et al. 1996). At feeding sites in the wild, fallow deer have exhibited aggressiveness to the similar-sized white-tailed deer *Odocoileus virginianus* (Bartoš et al. 2002) and to the smaller roe deer (this study). In an area of Spain, red deer females avoided meadows heavily used by fallow deer (Carranza and Valencia 1999).

Why should fallow deer be intolerant of the presence of other deer species, in feeding contexts? In the Mid-Pleistocene, this species colonised Central and, in particular, Southern Europe from Asia (Stuart 1991). There, this warm-adapted deer was abundant on the F-Eemian (Kurtén 1968), but, at the end of the Würm glaciations, it was found only in the semi-arid habitats of Asia Minor (Kurtén 1968), until man brought it back to Southern Europe on the Neolithic (Boitani et al. 2003). Presumably, the defence of crucial resources from competing deer species was an evolutionary strategy that helped the fallow deer to survive in relatively poor habitats.

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Ethical standards The experiments carried out complied with the current laws of Italy.

Conflict of interest The authors declare that they have no conflict of interest.

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