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Short report

## Intolerance amongst deer species at feeding: Roe deer are uneasy banqueters

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### Abstract

The function of inter-specific interactions in large herbivore assemblies is under debate. We have studied inter-specific interactions between roe and fallow deer on pastures, to assess whether competition between these *Cervidae* occurs through behavioural interference. Roe were displaced by fallow deer (i.e. the former moved away from the latter at a distance of >50 m) in 83% of cases ( $N=127$ ). Ninety-four percentage ( $N=83$ ) of displacement events occurred while roe deer were feeding; in 50% of these cases ( $N=78$ ), roe stopped grazing and left the feeding ground. Even when fallow deer did not show any sign of direct aggression to roe, these moved away from fallow in 72% of cases ( $N=127$ ). Vigilance rate was significantly greater in roe than in fallow deer, irrespectively of the presence of the other species. When roe and fallow deer grazed within 50 m from each other, vigilance rate increased significantly in roe, but not in fallow deer. Roe deer, in a group, were significantly more tolerant of the presence of fallow deer (even in group), than when solitary. Fallow deer seemed to be able to exclude roe deer from feeding sites through behavioural intolerance.

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**Keywords:** Inter-specific competition; Roe deer; Fallow deer

### 1. Introduction

The role of inter-specific interactions in regulating the coexistence of sympatric herbivores is under debate (Arsenault and Owen-Smith, 2002). Apparently, competition seems to be the most frequent relation amongst ungulates (Latham, 1999). In interference competition, a resource is actively disputed; in exploitation competition, individuals deplete the amount of resource left available to others. Strict ecological studies of niche relationships of sympatric species are often unsuitable to identify ongoing competition, but can only identify the potential for it (Putman, 1996). By contrast, even if observable behavioural relationships may sometimes constitute the direct mechanisms involved in competition (Anthony and Smith, 1977), only few studies have assessed the effects of behavioural interactions between wild ungulates (Latham, 1999). Anthony and Smith (1977) observed that desert mule deer *Odocoileus hemionus crooki* were dominant over Coues white-tailed deer *Odocoileus virginianus couesi* in aggressive interactions, in two areas of Ari-

zona. Bartoš et al. (1996) observed that, in semi-captivity, fallow deer *Dama dama* were more aggressive than red deer *Cervus elaphus* at supplemental feeding sites, forcing the latter to leave the sites before the supplemental food was depleted. Contrastingly, Bartoš et al. (2002) observed an increased grazing time for white-tailed deer *Odocoileus virginianus*, fallow deer and red deer when any deer, other than conspecifics, were present or entered the field, suggesting that inter-specific cooperative behaviour may occur between these cervids.

Roe deer *Capreolus capreolus* is a suitable model species to study inter-specific interactions, because of its large distribution and wide overlap with the range of other ungulate taxa (Latham, 1999). Latham et al. (1996) showed that densities of roe and red deer were inversely correlated across 20 Scottish conifer plantation forests and red deer density appeared to influence negatively that of roe deer (Latham et al., 1997). Indigenous roe deer and introduced muntjac *Muntiacus reevesi* showed a high habitat overlap in a pine forest, in England (Hemami et al., 2004, 2005): the density of muntjac increased and outnumbered that of roe deer (Hemami et al., 2005; cf. also Chapman et al., 1993).

Fallow deer is assumed to be a potential competitor for other deer species (because of its grouping behaviour, considerable

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body mass and opportunistic food habits), but relevant information is very scarce (Bartoš et al., 1996, for fallow/red deer interactions).

The nature of relationships between roe and fallow deer is unclear. Some studies found no evidence of competition (Batcheler, 1960; Bartoš et al., 2002). Putman (1996) observed a high overlap in diet and habitat use, as well as an inverse correlation between population sizes of fallow and roe deer across years. Using structural equation models, Focardi et al. (2006) found that, within a study area of 3300 ha, where fallow were locally abundant, roe showed a smaller body size, larger home ranges and a greater inter-specific habitat separation than in other patches of the same area where fallow were scarce. In that area, a crash of the roe deer population occurred early in 2000 (Focardi et al., 2005), whereas the fallow population increased (Focardi et al., 2006). In another area, through pellet group count surveys, Sforzi (2004) found out that the density of roe deer in areas with low density of fallow deer was much greater than in those where the latter was numerous, in woodland. No study could show how competition was acting.

The aim of our study has been to analyse behavioural interactions between fallow and roe deer in the wild, to investigate whether alleged competition could be assessed through aggressive behavioural interference.

## 2. Materials and methods

Our study was carried out in three open, i.e. with a good visibility, areas of the Maremma Regional Park (Tuscany, Central Italy; 42°39'N, 11°05'E). The local climate is Mediterranean. These areas (15, 26 and 98 ha; from 3 to 9 km apart) included set-aside grassland (cut once or twice/year) and herbaceous crops, bordered by sclerophyllic scrubwood, with prevalence of *Quercus ilex*. A minimum number of 44 roe and 162 fallow deer (estimated as the maximum number of deer seen in the same area during the same session, and by pooling the results among the three areas) visited these areas during the study period. Deer were observed for a total of 328 h, between April 2006 and May 2007, from vantage points, by one observer (F.F.), through a Zeiss 8 × 56 binocular and a Nikon 15–45 × spotting scope, in 2 h sessions, at dawn and dusk.

Deer activities were registered on a portable tape recorder, through focal animal sampling (Lehner, 1996), with sampling bouts of 15 min. Observations started even if only one species was present at the observer's arrival. When both species were present, they were alternatively selected for the initial watching bout. Activities recorded were: *feeding* (grazing or browsing, still 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), *other activities* (cf. San Josè et al., 1996). Frequency of vigilance (number of head-lifts/min) was used as an index of alertness (e.g. Bruno and Lovari, 1989; San Josè et al., 1996; Rucksuthl et al., 2003). Data collection did not occur when the vegetation was higher than 50 cm, i.e. preventing full visibility of roe deer. Because of that, observations were not carried out

(June/September) at one set-aside area, where grass was cut once a year only.

We defined as a “contact” when roe and fallow deer grazed within 50 m from each other (cf. Anthony and Smith, 1977). “Contacts” between roe and fallow deer were recorded through all-occurrence sampling (Lehner, 1996). Starting/ending time of “contact”, group size and activity before/during/after the “contact” were also recorded. A deer was considered displaced by a deer of the other species when: (a) it was chased away, (b) it interrupted its previous activity and moved away (>50 m) from the other deer (c) it avoided the “contact”, i.e. it reached a distance of 50 m from the other deer by alternating short feeding bouts, frequent steps and head-lifts to the other, suddenly 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 deer species by avoiding any close-up. If so, we assumed that roe deer were actively avoiding fallow, not simply moving away because their feeding bout was over. In fact (a) they never grazed in mixed groups with fallow deer, but kept a minimum distance of 20 m from fallow; (b) the “contacts” of category *c* had a short duration (mean = 10.1 min, S.D. =  $\pm 7.1$  min,  $N = 14$ ); (c) roe frequently kept on feeding after reaching a distance of >50 m from fallow (93%;  $N = 14c$  contacts), i.e. they did not move away because their feeding bout was over. We estimated that no displacement occurred if both species moved at a mutual distance of 50 m, without showing any evident variation in behaviour and/or direction of movement. After detection of a “contact”, the activity of both deer was assessed until it ended, i.e. when individuals of either species moved farther than 50 m from each other. When required, distances and relative locations of deer were estimated by using the deer torso length as a reference, as well as known reference points in the landscape, i.e. isolated trees, ditches, rocks, anthropogenic features as fences, paths, strips of cultivated fields and others, detectable on 1:10,000 cm topographic maps (CTR, Regione Toscana, cf. Frid, 1997).

G-Test, adjusted with the Williams correction (Sokal and Rohlf, 1995), has been used to assess whether there were differences between: (a) the frequency of fallow approaches to roe deer (<50 m radius) and that of roe approaches to fallow; (b) likelihood of displacement (i.e. number of displacement events/number of “contacts”) when fallow approached roe deer and that when roe approached fallow deer; (c) the proportion of activities interrupted by a “contact” and that recorded in absence of “contact”, to assess whether harassment was elicited by the sight of a feeding individual of the other species or it was random.

Likelihood of displacement, arcsine transformed, was related to fallow and roe group size through a partial correlation coefficient (Sokal and Rohlf, 1995). Differences in frequency of vigilance across species and across the same individual during and before/after contact were tested by the *t*-test and the *t*-test for paired comparisons, after log transformation of data (Sokal and Rohlf, 1995). Statistical analyses were carried out using the Microsoft® Excel add-in PopTools (Hood, 2006) and SPSS 9.0 software (Norusis, 1998). All tests were two-tailed.

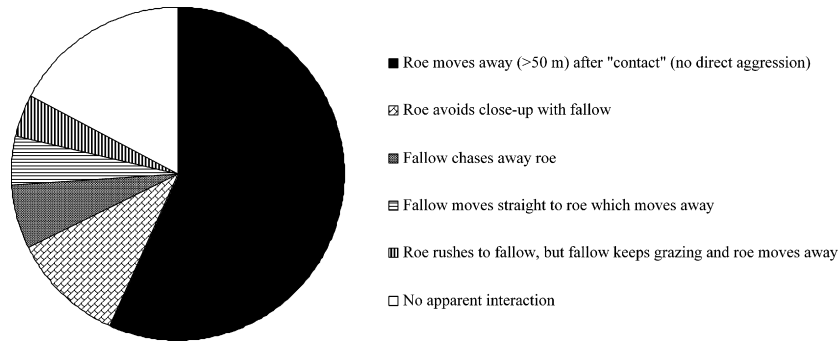


Fig. 1. Interspecific “contacts” between roe and fallow deer ( $N=127$ ).

### 3. Results

One hundred and twenty seven roe/fallow deer “contacts” were observed (0.4 contacts/h; mean duration of each “contact” = 5.0 min; S.D. =  $\pm 5.4$  min; Fig. 1). Fallow approached roe deer more frequently than roe did to fallow (75% of times,  $N=110$ ;  $G$ -test:  $G$  adj = 27.567, d.f. = 1,  $P < 0.001$ ), suggesting that roe deer avoided feeding near a fallow. Very often roe were displaced by fallow deer (83% of cases), whereas roe never displaced fallow deer (Fig. 1). Likelihood of displacement did not depend on which deer occupied first the feeding site: roe were displaced 85% of times when fallow approached them and 89% of times when they approached fallow deer ( $G$ -test:  $G$  adj = 0.272,  $P > 0.05$ ).

Ninety-four percentages of 83 displacement events occurred while roe deer were feeding; in 50% of these cases ( $N=78$ ), roe stopped grazing and abandoned the feeding ground. The proportion of activities of roe deer, interrupted by fallow deer, were not significantly different from those occurring in absence of “contact” (feeding = 88%; other = 12%,  $N=37$ .  $G$ -test:  $G$  adj = 2.176,  $P > 0.05$ ). Direct aggression (fallow deer–roe deer and, even more, roe deer–fallow deer) was rare (Fig. 1). Even when fallow deer did not show any sign of direct aggression to roe, the latter quickly moved away or avoided any close-up in 72% of cases ( $N=127$ , Fig. 1).

Roe deer, in a group, tolerated the presence of fallow deer better than when solitary. Likelihood of displacement was inversely correlated to roe deer group size, after controlling for fallow group size (partial correlation coefficient =  $-0.701$ ,  $P < 0.001$ ,  $N=22$ ), but it was not associated to fallow group size, after controlling for roe group size (partial correlation coefficient = 0.321,  $P > 0.05$ ,  $N=22$ ).

Vigilance rate was significantly greater in roe than in fallow deer (1.7 times greater than that of fallow deer,  $t$ -test:  $t = 8.924$ , d.f. = 74,  $P < 0.001$  during “contacts”; 3.4 times greater than in fallow,  $t = 3.369$ , d.f. = 74,  $P = 0.001$  with no “contact”). Alertness levels increased 2.6 times in roe deer during “contacts”, but they did not in fallow (Fig. 2,  $t$ -test for paired comparisons:  $t = 9.193$ , d.f. = 33,  $P < 0.001$  for roe;  $t = 1.523$ , d.f. = 41,  $P > 0.05$  for fallow), suggesting that disturbance was not mutual.

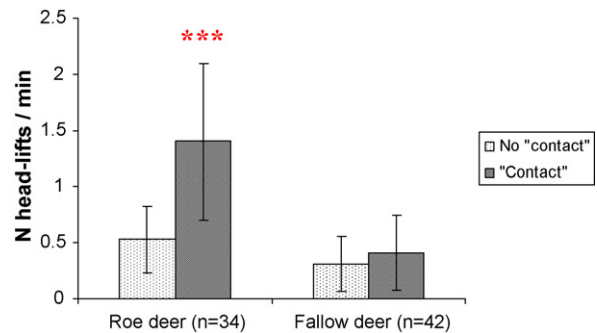


Fig. 2. Frequency of vigilance (mean  $\pm$  S.D.) of roe and fallow deer with no “contact” and during “contacts”. \*\*\* $P < 0.001$ , paired- $t$ -test.

### 4. Discussion

Competition between herbivores may depend on the number of species involved, their behavioural characteristics, population densities, spatio-temporal variation in availability and distribution of resources (Arsenault and Owen-Smith, 2002). In evolutionary terms, competitive interactions between species are expected to be minimal in wild assemblies (Putman, 1996). Fallow deer were introduced to Europe by man, after the Neolithic, from Asia Minor (Nowak, 1991). Thus, potential for competition with roe deer may be particularly strong because they have not shared a common evolutionary history.

Relationships between roe and fallow deer are unclear, as well as contradictory (Batcheler, 1960; Putman, 1996; Bartoš et al., 2002; Focardi et al., 2006). Focardi et al. (2006) suggested that fallow deer affected roe deer reproductive performance by reducing habitat quality through grazing. However, no data on the mechanism involved in alleged competition were provided. The roe deer is a concentrate selector (Hoffman, 1989), i.e. adapted to process high quality forage, easily digestible, rich in plant cell contents. The fallow deer has been termed as an intermediate feeder (Hoffman, 1989), i.e. adapted to process fibrous food, but also using a mixed diet through opportunistic foraging. Thus, the latter could also eat plants selected by the former (Putman, 1986).

Our study suggests that fallow deer can displace roe deer, when the two species use natural feeding sites at the same time. Likelihood of displacement was reduced when roe deer were in

group. This is not surprising, since group living has frequently a calming effect on ungulate behaviour (Lian et al., 2007). Roe deer group together in the cold season, while they are solitary in spring–summer, when births and mating take place. In the first year of our research, 59% of displacements occurred in spring ( $N=74$  feeding interruptions, April 2006–March 2007). As income breeders (Andersen et al., 2000), allocating a high energy expenditure to reproduction (Gaillard et al., 1993), roe deer should be mostly dependent on environmental conditions (thereby food) in spring and summer, the critical period for roe deer survival (Gaillard et al., 1997). Therefore, competition may be particularly strong when roe deer have high energetic demands because of reproductive activities.

We recorded some direct aggression to roe deer (11%), although more frequently roe deer quickly moved away before any aggressive interaction (Fig. 1). Roe approached fallow deer much less frequently than fallow did to roe deer and alertness levels increased during “contacts” only in roe deer (Fig. 2), which sometimes repeatedly barked to fallow. Thus, spatial exclusion between roe and fallow deer seems to be determined by avoidance of the former from the latter, although roe deer could withdraw from “contacts” because of previous events of direct aggression by fallow deer (Fig. 1). Wild boar *Sus scrofa* did not seem to elicit the same strong avoidance reaction in roe deer (10% withdraws of roe deer;  $N=41$  cases, roe deer and wild boar in the same meadow, unpublished data).

Bartoš et al. (1996) reported high aggressiveness levels of fallow deer to red deer at supplemental feeding sites. We recorded a strong interference of fallow to roe deer: fallow prevented roe from using pastures, also exhibiting direct aggression, irrespectively of which deer occupied that space first. 50% of times, roe stopped feeding and left the field, when disturbed. Roe deer rely on food intake rather than fat reserves for reproduction (Andersen et al., 2000). In this species, a reduced food intake, depending on the part of the year, e.g. in springtime, in the last stages of pregnancy, affect the reproductive success (Pettorelli et al., 2005; McLoughlin et al., 2007). Interference from fallow deer may cause a reduced food intake in roe because of the abandonment of the feeding ground, feeding in not preferred food patches and/or, possibly, food depletion by fallow deer at sites left by roe. We suggest that this may contribute to explain the inverse demographic trends, as well as density patterns, described elsewhere (Batcheler, 1960; Putman, 1996; Focardi et al., 2006; Sforzi, 2004).

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