Contrasting feeding patterns of native red deer and two exotic ungulates in a Mediterranean ecosystem

María Miranda^A, Marisa Sicilia^A, Jordi Bartolomé^B, Eduarda Molina-Alcaide^C, Lucía Gálvez-Bravo^A, Jorge Cassinello^A

^A*Instituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCM, Ciudad Real, Spain*

^B*Grup de Recerca en Remugants, Departament de Ciència Animal i dels Aliments, Universitat Autònoma de Barcelona, Bellaterra, Spain*

^C*Estación Experimental del Zaidín (EEZ-CSIC), Granada, Spain*

Running title: Foraging strategies of native and exotic ungulates

Corresponding author current address:

María Miranda

School of Animal, Plant and Environmental Sciences

University of the Witwatersrand

Private Bag 3

Wits 2050

Johannesburg. South Africa

maria.mirandaroves@gmail.com

maria.miranda@wits.ac.za

Abstract

Context. Ungulates have been widely introduced in multiple ecosystems throughout the world due to their value as food and for sport hunting. The identification of foraging preferences of exotic and native ungulates living in sympatry is, therefore, becoming increasingly important in order to assess potential impacts of introduced animals on the host ecosystem.

Aims. To describe species-specific foraging strategies and infer resource selection overlap between native and exotic ungulates.

Methods. We compare the trophic ecology of three sympatric ungulate species living in a Mediterranean landscape: the native Iberian red deer *Cervus elaphus hispanicus*, and two exotic bovids, the European mouflon *Ovis orientalis musimon* and the aoudad *Ammotragus lervia*. We simultaneously determined herbivore diet through analyses of botanical content in faeces and assessed the nutritional content of these diets.

Key results. Higher selection of shrubs by deer was sustained throughout the year, while bovids showed seasonal shifts in forage selection. Both bovids displayed a selective dietary strategy directed towards a higher overall nutritional quality than that of deer. Divergent exploitation patterns between the studied cervid and bovids might be related to body mass and physiological adaptations to overcome secondary defence compounds of shrubs, and were largely affected by seasonal changes in the nutritional value of available vegetation. Ecological theory suggests that diet overlap should be greater between similar-sized species. Indeed, both exotics showed similar, sometimes overlapping, dietary patterns that could lead to potential competition in the use of resources. Native red deer preferences just showed some overlap with those of exotic mouflon under constrained summer conditions.

Conclusions. Dietary overlap between deer and mouflon and between aoudad and mouflon during limiting summer conditions could entail a potential competitive interaction under more even densities of the study species, since a concurrent habitat overlap between those pairs of species has previously been reported.

Implications. The outcomes of our study suggest the need of an integration of habitat and ungulate management. Management actions in Mediterranean rangelands should be directed towards protecting habitat conditions so that biodiversity is enhanced along with the presence of sustainable communities of large herbivores. Management directed towards ungulates should keep moderate stocking rates and monitor and control introduced and native populations.

Additional key words: exotic species, interspecific interactions, faecal analysis, herbivory, Mediterranean ecosystem, resources selection, trophic ecology, ungulates.

Introduction

Sport hunting and livestock husbandry have caused the introduction of numerous ungulate species outside their native ranges across different ecosystems all over the world (Spear and Chown 2009). The effects of the introduction of exotic species can be divided into horizontal and vertical components. Horizontal effects comprise the interactions with ecologically equivalent species that are native to the host system, and vertical effects refer to interactions emerging between the different trophic levels (Smit *et al.* 2001; Beguin *et al.* 2011).

Horizontal effects of exotic animals on the extant herbivore guild can be measured by examining trophic interactions between herbivores (Bertolino *et al.* 2009). Much ecological research has been devoted to this topic (see Prins and Fritz 2008), with overlap in resource selection as the general outcome from the co-occurrence of exotic and native species (Latham 1999; Mysterud 2000; Dolman and Wäber 2008). However, there is also evidence for beneficial interactions between animals of different origins, in which effects on resources by one species may even increase their supply and quality for another (Gordon 1988).

Quantifying such interspecific trophic interactions relies on the knowledge of seasonal diet selection by each of the interacting herbivore species, and it is broadly accepted that forage selection by wild herbivores may be partly determined by plant-related components (Hanley 1982; Cooper *et al.* 1988; Benschahar and Coe 1992; Baumont *et al.* 2000). Moreover, it has been shown that ungulates may select for a minimum nutrient value in preferred plants (Belovsky 1981) and that the preference for a plant species cannot be associated to any single chemical factor but rather to a trade off between nutrients (proteins, soluble sugars, digestible fibres) and non-nutritive compounds (lignin and condensed tannins) (Cooper *et al.* 1988; González-Hernández *et al.* 2000; Verheyden-Tixier *et al.* 2008). Linking resource selection with its nutritional content would therefore enable a better assessment of horizontal effects of large herbivore introductions in an existing herbivore guild. Despite its ecological importance, the nutritional basis of diet selection in ungulates has been poorly documented.

On the other hand, herbivore-related components may also affect dietary preferences. Previous studies have identified three traits that seem to determine differences in diet selection between sympatric herbivores: (1) taxonomic identity (Gagnon and Chew 2000; Bascompte and Jordano 2007); (2) feeding type (see Hoffmann 1989); (3) body size and related nutritional requirements (Bell 1971; Jarman 1974; Demment and Van Soest 1985; Kingery *et al.* 1996). Taxonomic identity has been suggested to be a secondary factor since

feeding behaviour may not be unique for each animal taxon but for a group of ecologically equivalent herbivore species (Zamora 2000). Regarding feeding types, herbivores are generally classified along a continuum according to browse and grass contents in their diets (see v.g. Hoffmann 1989 and Gagnon and Chew 2000): concentrate selectors, intermediate feeders and grass/roughage eaters. Body size as a possible predictor of dietary preferences rests on the widely accepted Jarman-Bell principle (Bell 1971; Jarman 1974; Demment and Van Soest 1985), which predicts that small ungulates require more relative energy per unit weight and have reduced gut efficiency. They therefore need to be highly selective for food items of a high quality compared to larger species.

Two bovids, the aoudad (*Ammotragus lervia* P.) and the European mouflon (*Ovis orientalis musimon* S.), have been widely introduced in Spain both in natural reserves and private rangelands due to their interest as game (Cassinello *et al.* 2002, 2007; Rodríguez-Luengo *et al.* 2002, 2007). Emerging interspecific interactions with native species that perform a similar role within the host ecosystem are expected (Fandos and Reig 1992; Cassinello *et al.* 2006; Acevedo *et al.* 2007). Native Iberian red deer (*Cervus elaphus hispanicus*, a cervid) is the main big game species in Spain with a wide distribution in the Iberian Peninsula and achieving high densities (over 0.4 individuals/ha) in private estates (Gortázar *et al.* 2000; Carranza 2002, 2007; Acevedo *et al.* 2008). We studied the native Iberian red deer in sympatry with the exotic aoudad and European mouflon in order to disentangle the emerging competition/partition in their use of the feeding resources under Mediterranean climate. More specifically, the study aims to understand the simultaneous effect of the botanical and the nutritional component on trophic interactions between co-occurring native and introduced herbivores. We hypothesized that (1) the nutritional component will provide a significant explanation regarding species-specific foraging patterns of the study herbivores, with a higher nutritive value in diets selected by the smaller ungulate species, and (2) horizontal interactions within the herbivore guild might emerge from aoudad and mouflon introduction. We predicted a higher potential for trophic overlap between the exotic aoudad and mouflon because of their proximity in body sizes, feeding types and taxonomic identity.

Materials and methods

Study area

The study was conducted during 2006 and 2007 in a 724 ha fenced hunting estate located in the province of Ciudad Real in Castile-La Mancha, South Central Spain (38°55'N 0°36'E),

Topography consists of rolling hills with elevation from 650 to 820 m above sea level. The region has a Mediterranean continental climate, which is characterised by summer drought (mean yearly rainfall: 356mm, mean rainfall in August: 7mm), mildly cold winters (mean temperature in January: 5.7°C) and high summer temperatures (mean temperature in July: 25.4°C) (Agencia Estatal de Meteorología 2010).

The study area comprised pastures with scattered holm oaks (*Quercus ilex* L.) and Mediterranean perennial shrubs. The dominant shrub species were *Cistus ladanifer* L., *Phillyrea angustifolia* L., *Rosmarinus officinalis* L., *Quercus ilex* L., various species of *Erica* genus and *Genista hirsuta* V. Browsing was intense leading the community to a late stage of plant succession. Grasses dominated the herbaceous layer, with a smaller proportion of forbs (*Compositae*, *Leguminosae*, *Cistaceae*, *Brassicaceae*). In part of the study area (64 ha in 2006 and 52 ha in 2007), the estate staff planted oat as food for ungulates as well as offering them a daily supplementary concentrate composed of cereals and legumes (1:1). Because the concentrate contained different species depending on the season, its nutritional composition varied across the year (October-March: 9.7 hemicellulose (HC), 7.0 cellulose (C), 3.25 total N; March to October: 11.7 HC, 13.7 C, 3.0 total N, all values expressed as g/100g dry matter).

Three large herbivore species occupied the study area. Iberian red deer are native to the study area whereas European mouflon and aoudad were both introduced as game in 1988. Red deer was also the most abundant species in the study area with approximately 400 individuals (0.55ind/ha), followed by the European mouflon ($\approx$ 60 individuals; 0.08 ind/ha) and the aoudad ($\approx$ 20 individuals; 0.03 ind/ha). The aoudad is original from mountainous and desert areas in the North of Africa and has been successfully introduced in the USA and Spain (Cassinello 1998). The European mouflon is native to Corsica and Sardinia and has been repeatedly introduced in most of Europe since the second half of the nineteenth century (Cugnasse 2000; Markov and Penev 2000; Rodríguez-Luengo *et al.* 2002). Red deer was the heaviest herbivore within the estate (males: 80-160kg, females: 50-100kg, Carranza 2004), followed by aoudad (males: 50-132kg, females: 12-68kg, Cassinello 2002) and mouflon (males 40-60 kg, females 30-40 kg, Bang and Dahlstrom 1974).

Plant availability

We seasonally recorded plant availability along 50m transects at 20 locations. We defined four seasons according to plant phenology: spring (April, May and June), summer (July,

August and September), autumn (October, November, December) and winter (January, February and March). We distributed transects following a stratified random design, thus placing them according to the availability of three vegetation types: pastures, scrubland and habitat edges. We determined herb availability up to the family level and scrub cover to the species level. We registered vegetation cover in 100 points along transects. We regarded shrubs as available if they had green foliage within an animal's reach ($\leq 2\text{m}$ high).

Botanical content of diet

We estimated resource use by means of microhistological analysis of the cuticle of plant remains in collected faecal samples (Stewart 1967; Putman 1984; Henley *et al.* 2001). We collected a total of 149 fresh faecal samples of the three ungulate species under study during 2006 and 2007 (38 aoudad, 80 deer and 31 mouflon samples), including individuals from different sexes and ages. We obtained the faecal samples across all seasons either from hunted animals or we collected them fresh in the field when an animal was seen defecating. We stored collected samples at -20°C until we processed and analysed them in the laboratory. From each sample, we placed 10 g in a test tube with 5 ml of 65% concentrated NO_3H . We then boiled the test tubes in a water bath for 1 minute. After digestion we added 200 ml of water per sample. We then passed this suspension through 0.5 mm and 0.125 mm sieves. We spread the 0.125 to 0.5 mm fraction on glass microscope slides in a 50% aqueous glycerine solution. We prepared two slides from each sample. We examined the slides under a microscope at $100\times$ to $400\times$ magnifications by viewing a total of 20 fields (2 mm^2) randomly distributed in each slide. We recorded and counted plant fragments in each field of view with a minimum of 100 fragments of identified plant material per slide. We compared epidermal fragments in faeces with a previously prepared reference collection (Cristóbal 2006). We could not assess consumption on supplementary food through microhistological analysis of faeces since we could not observe epidermal remains in the faecal samples.

Nutritional content of diet

To measure the nutritional content of herbivore diets, we harvested leaves and stems of the most ubiquitous and diet relevant shrub species occurring within the site (*Cistus* spp., *Quercus* spp. *Cytisus* spp., *Phillyrea angustifolia*, *Rosmarinus officinalis*, *Genista hirsuta*, *Erica* spp.), as well as a bulk sample of the herbaceous layer. We carried out the sampling during the four seasons at random localities within the study area

We oven-dried the plant samples at 60°C until constant weight, stabilised them at ambient temperature for 48 h and ground them to 1 mm before analysed (AOAC 2005). We carried out all analyses on duplicate samples and we reported results as g/100g dry matter [DM]. We determined DM content by drying to constant weight in a forced air oven at 103°C. We calculated organic matter [OM] content from ash content, which we determined by burning in a muffle furnace for 3 h at 550°C. We performed neutral detergent fibre [NDF], acid detergent fibre [ADF] and acid detergent lignin [ADL] analyses by the sequential procedure of van Soest *et al.* (1991) using an Ankom 220 Fibre Analyser (Ankom 2010). We determined total N by Kjeldahl procedure (AOAC 2005). We determined N bound to ADF by Kjeldahl analysis of ADF residues. We then obtained available N from the difference between total N and N bound to ADF. We determined separately free, protein-bound and fibre-bound condensed tannins using the procedure of Pérez Maldonado and Norton (1996). We calculated total condensed tannins as the sum of the three fractions.

Selection of the botanical and nutritional components

We distinguished three coarse forage categories depending on their growth form: grasses (graminoids), forbs (dicotyledonous herbs) and shrubs (woody plants) (Duncan and Poppi 2008; Iason and van Wieren 1999; van Wieren and van Langevelde 2008). General traits of these categories include a higher cellulose and hemicellulose content for grasses, and a higher concentration of cell contents, plant secondary compounds and N in forbs and woody browses, the latter containing in addition greater proportions of lignin (Owen-Smith 1997; Clauss *et al.* 2008; van Wieren and van Langevelde 2008). We evaluated herbivore diet selection both at the forage category level and at the plant species or family level.

We quantified foraging preferences using the Savage Selectivity Index for each season in order to adjust the seasonal use of each plant species with respect to its relative availability (Savage 1931; Manly *et al.* 2002). This index determines selectivity of a given resource (w_i) by dividing its use (U_i) by its availability (p_i). The Savage index varies from zero (maximum refusal) to infinite (maximum selection), where 1 is the value defining the selection expected by chance. We assessed selectivity for the different nutritional contents according to Verheyden-Tixier *et al.* (2008). We first determined the content of nutrient C in diets (C_d) using the equation (eqn1).

$$(1) C_d = \sum_{i=1}^n D_i \times C_i$$

238

239 where D_i is the proportion of plant i in faeces and C_i is the concentration of nutrient C in plant
 240 i . Once we had determined the nutrient content in diet, we assessed nutrient availability in the
 241 study area; we calculated the content of nutrient C in the available vegetation (C_a) using (eqn
 242 2).

243

$$(2) C_a = \sum_{i=1}^n A_i \times C_i$$

245

246 where A_i is the proportion of plant i in the field transects. We could subsequently calculate
 247 Savage index to determine selection for each nutrient.

248

249 We used the values resulting from Savage Index calculations for forage categories and
 250 nutritional contents as described in this section for all analyses and hereafter we will refer to
 251 them as selection for the botanical and nutritional components, respectively.

252

253 *Statistical analyses*

254 We used linear discriminant functions to test if either diet selection or nutritional selection
 255 discriminated the three herbivore species. We assessed the relative importance of each
 256 independent variable on discriminant functions using the structure coefficients (Garson 2008).
 257 We subsequently used one-way ANOVAs with the discriminant function scores to test the
 258 hypothesis of equal diet or nutrient selection, and used Tuckey HSD for pairwise
 259 comparisons. We performed those ANOVAs only on discriminant function 1, which accounts
 260 for a higher percentage of variance explained and larger statistical significance in classifying
 261 cases into species, compared to discriminant function 2.

262

263 Indicator Species Analysis, originally developed as a method to find indicator species for a
 264 given habitat (Dufrene and Legendre 1997), has been widely used in biology. We applied it
 265 here to assess the relative affinities for different plant taxa by a particular ungulate species. It
 266 takes into account both plant relative abundance and its relative frequency of occurrence in
 267 the different diets. The indicator value obtained ranges from 0, when the plant appears in all
 268 species diets, to 100, when the plant is just present in a single herbivore diet. We ran the

analysis within R environment using the *indval* function from the *indicspecies* package (de Cáceres and Legendre 2009) with 10,000 iterations. We only included in the analyses plant species present in at least 20% of the individual diets.

We applied, when necessary, Box-Cox transformations (Box and Cox 1964) to data in order to meet the assumption of normality and homocedasticity. We carried out all hypotheses testing using non-sequential type III sums of squares, which is appropriate for unbalanced data (Langsrud 2003). We performed analyses using procedures in JMP 6.0.3 (SAS Institute SAS Campus Drive, Cary, North Carolina, USA), SPSS 17.0 packages (SPSS, Chicago IL, USA) and R version 2.12.2 (R Development Core Team 2011).

Results

Selection for the botanical component

Forage category level

Herbivore selection for the botanical components was studied at the forage category level across the different seasons (Table 1, Fig.1).

Linear discriminant analyses (Table 2, Fig. 2) indicated that the cervid differentiated from bovids primarily according to the vegetation layer selected. Red deer feeding habits were consistent for all seasons with a diet selection associated with the shrub layer. However, selection shifts at the forage category level occurred for both bovids throughout the year (Fig. 2). The three herbivores could be discriminated on a plant selection axis during spring ($F_{2,29}=27.38$, $p<0.0001$, $R^2=0.65$) and winter ($F_{2,36}=39.88$, $p<0.0001$, $R^2=0.69$). In spring, aoudad showed the greatest selection for the herbaceous layer while deer selected for shrubs, and mouflon was intermediate in its foraging preferences. During winter, the analysis yielded the greatest degree of separation between mouflon, which selected for the herbaceous layer, and red deer, which selected for shrubs, placing the aoudad in a halfway position within the axis. In summer, the analysis yielded a dissimilarity between deer preferences for the shrub layer and aoudad preferences for herbs ($F_{2,30}=7.66$, $p=0.0021$, $R^2=0.34$), while mouflon overlapped with both red deer and aoudad foraging preferences. In autumn, deer preferentially fed on shrubs, and the foraging response of the two bovids overlapped on the opposite end of the axis being associated with herbaceous forage categories ($F_{2,42}=17.66$, $p<0.0001$, $R^2=0.47$).

Correctly classified cases by the discriminant functions ranged between 72.7 and 87.5% in the analysis of the different seasons.

Plant species or family level

The Indicator Species Analysis highlighted mainly forb taxa and a few shrubs as indicators of aoudad diet along the year (Table 3). Red deer diet, instead, was primarily associated with shrub species: *Pistacia* spp. in spring and *Cistus* spp., *Hallimium ocymoides*, *Quercus* spp. and *Rosa* sp. and *Rubus ulmifolius* in both, autumn and winter. Mouflon autumn and winter diets were associated with herbaceous *Leguminosae*. Winter diet of mouflon was also characterised by other forbs such as *Polygonaceae* and *Umbelliferae* and a single shrub, *Asparagus acutifolius*. Also a shrub genus, *Cytisus* spp., correlates with spring diet of mouflon.

Selection for the nutritional component

Seasonal average nutritional selection was determined for each herbivore species diet (Table 4). Nutrient selection varied across seasons and herbivore species (Table 5, Fig. 3).

According to the first discriminant function, herbivores were positioned along a nutrient selection axis characterised, during most of the year, by available N and HC and C on one extreme, and tannins, total N and lignin on the opposite end (Fig. 3). Red deer was always closer to the end of the axis associated with a higher tannin and lignin selection. Bovids often appeared closer to the end characterised by available N, C and HC selection. However, discriminant functions revealed a shifting positioning of mouflon and aoudad within the nutrient selection axis throughout the year (Fig. 3).

During spring, the discriminant function segregated the three animal species on a nutrient axis, placing red deer in the extreme defined by tannins, total N and lignin and aoudad in the opposite end associated with HC, C and available N ($F_{2,29} = 23.07$, $p < 0.0001$, $R^2 = 0.61$). Mouflon occupied a halfway position in the nutritional axis. During summer, the nutrient selection of the two bovid species overlapped with HC and C as the most selected nutritional components, while deer preferentially fed on resources containing higher concentrations of N, tannins and lignins ($F_{2,30} = 27.44$, $p < 0.0001$, $R^2 = 0.65$). The first discriminant function scores for autumn revealed a greater degree of similarity of the nutritional components in the diet selected by mouflon and aoudad than those selected by red deer ($F_{2,42} = 34.32$, $p = <$

0.0001, $R^2 = 0.63$). Aoudad and mouflon showed a preference for higher HC, C and available N contents while red deer selected items richer in total N and tannins. During winter all three species were significantly discriminated with regards to nutrient selection ($F_{2,36} = 57.83$, $p < 0.0001$, $R^2 = 0.76$). Red deer selected for higher tannin, lignin and C levels in its diet while mouflon favoured total and available N and HC. Aoudad appeared intermediate in its feeding response. Correctly classified cases by discriminant functions ranged between 81.3 and 93.9% in the analysis of the different seasons.

Discussion

The exotic bovids showed similar foraging strategies that were largely determined by seasonality and differed from those displayed by the native red deer. However, none of the herbivore species-specific traits or the plant-related components were unique predictors of the preferences of the three co-occurring ungulate species. Instead, a range of botanical, nutritional, and herbivore-related factors must be taken into account in order to understand species-specific foraging strategies, and the subsequent interspecific trophic interactions.

Here the taxonomic identity and the nutritional content of selected plants have been simultaneously analysed to allow a better assessment and reasoning of foraging decisions by the study herbivores.

Species-specific foraging strategies

Deer sustained preferences for shrubs throughout the year have been widely reported across Europe (Gebert and Verheyden-Tixier 2001). Regarding the bovid's shifting selection across seasons, Heroldová *et al.* (2007) described the mouflon as an opportunistic feeder, capable of using diverse habitats. Similar physiological and behavioural plasticity has been reported for the aoudad, which should enable diet shifts consistent with available resources, as well as a wide feeding niche (Krysl *et al.* 1980; Piñero and Luengo 1992).

Annual feeding types apparently responded to a pattern in which red deer showed the highest preference for shrubs, aoudad showed the highest preference for grasses and forbs, while mouflon showed an intermediate feeding behaviour. Traditional classifications in feeding types, however, regard mouflon as a grass eater and red deer as an intermediate feeder (Hofmann 1989). Our results suggest that an approach to the classification of ungulate

feeding types cannot be merely focused on chemical (Hofmann 1989) or physical characteristics of forage (Clauss *et al.* 2003). This is because feeding preference seems to be a plastic trait, and thus these classifications should be flexible and take into account temporal and spatial heterogeneity in forage availability. Also, introduced populations may adapt to new conditions and select optimal resources within the available plant array.

Regarding the nutritional component, the consistency of deer preference for lower quality forage throughout the year could be related to a lower selection ability of this animal compared to that of aoudad and mouflon. This agrees with the increased absolute energy requirement and tolerance of low quality food, associated with a larger body size (Jarman-Bell principle, e.g., Demment and van Soest 1985).

On the other hand, our results may imply better developed systems in deer to overcome the typically high contents in tannins of evergreen sclerophyllous shrubs growing in the Mediterranean Basin (Barroso *et al.* 2001; Rogosic *et al.* 2006). Consumption of plants with a high content in chemical defences such as *Pistacia* spp., *Rosa* sp. and *Rubus ulmifolius* by red deer has been previously documented in Spain, France and Portugal (Maillard and Casanova 1995; Garin *et al.* 2001; Bugalho and Milne 2003; Verheyden-Tixier *et al.* 2008). Tannins are known to bind and precipitate plant proteins and carbohydrates resulting in a decreased digestibility (Robbins *et al.* 1987; Scalbert 1991). It has been suggested that, in order to neutralize plant secondary compounds, browsers segregate proline-rich salivary proteins that bind to tannins and negate their detrimental effects (Robbins *et al.* 1987; Austin *et al.* 1989; Hofmann 1989; Clauss *et al.* 2008; van Wieren and van Langevelde 2008). Association of Iberian red deer with chemically defended plants (Glasser *et al.* 2008) seems to be related to their high total N concentration and, very likely, to high soluble sugar contents (Cooper *et al.* 1988; Verheyden-Tixier *et al.* 2008) and their ability to overcome plant chemical defences. Bovids favoured available N intake instead, probably due to a lack of abilities to cope with tannins (Austin *et al.* 1989).

Interspecific trophic interactions between the study species

The divergent exploitation patterns between native and exotic species during most of the year correlates with the Jarman–Bell principle (Demment and van Soest 1985), as indicated above, since smaller bovids showed a selective dietary strategy, which related to overall higher nutritive resources than those selected by larger deer. So coexistence of ecologically similar

species was achieved by means of differing foraging strategies that allowed exotic and native species to occupy non-overlapping trophic niches during most of the year, excluding the summer.

In a guild of naturally co-occurring species, resource partitioning could be expected, since they have co-evolved in sympatry and developed compatible trophic strategies and adaptations to available forage permitting the sharing of common resources (v.g. Jarman and Sinclair 1979). This would explain why species coexist in spite of their similar ecological requirements and roles (May, 1973; Schroener, 1986). Niche competition is instead likely as a result of anthropogenic introductions of species ecologically similar to those present in the native guild (v.g. Schwartz and Ellis, 1981; Putman, 1996; Voeten and Prins, 1999; Mysterud, 2000). In this study, all three species belong to different native ranges so, under this prediction, niche overlap would be likely due to the lack of both previous co-evolution and resource partitioning processes between them. Indeed, the overlap in dietary selection observed for aoudad and mouflon throughout the year and between deer and mouflon during summer, could be explained by this hypothesis but further studies specifically designed to test it are needed.

The observed overlap in selection at the forage category level between deer and mouflon during summer could lead to a potential competition interaction during this period of food shortage. However, overlap in diet selection does not constitute in itself evidence of competition unless it concurs with overlap in habitat use (Putman 1996). A previous study of these populations in our study area suggested, indeed, an overlap between deer and mouflon for the use of cultivated lands and of the scrubland that is close to waterholes (Sicilia 2011). In our study case, however, a competitive interaction between deer and mouflon is not expected since they only overlapped at the forage category selection but mouflon seemed to be searching for shrub species that differ in nutritional composition from those selected by deer (see Fig. 3). Further studies on changes in deer and mouflon population sizes in the absence of hunting activities and under more even densities could help clarify the existence of a potential competition between them.

Regarding the exotic species and according to our predictions, aoudad and mouflon exhibited analogous foraging strategies across the year, and they even overlapped in their foraging preferences during summer and autumn. This outcome could result in an interspecific

competition for resources, especially under summer limiting conditions, which is supported by an overlap in pasture use across the year between these two species, as reported by Sicilia (2011).

Although dietary supplementation adds artificiality to the management of hunting states, in this case it allows a better understanding of the selection for different plant species by herbivores, since it is important for animals to receive a basal diet in order to test preferences under conditions in which nutritional or energetic requirements are satisfied (McArthur *et al.* 2000). Access to feeding areas is not restricted to any species and, furthermore, the two bovids and red deer have been observed to use this artificial source of food, being equally selected by the three study species during periods of food scarcity (Sicilia 2011).

In summary, exploitation patterns within this herbivore guild seem to be a product of body size, taxonomic identity and feeding types, being largely affected by seasonal nutritional changes in vegetation. Tannins and lignin were determinant factors in diet selection by herbivores under Mediterranean climate, since high total N associated with a high lignin and tannin content, which are considered as digestive retardants (Robbins *et al.* 1987; van Soest 1994). As predicted, diet quality of smaller mouflon and aoudad was greater (higher content in available N and highly digestible fibbers and lower in tannins and lignin) than that of deer. Also, as we hypothesised due to their higher similarity in body sizes, taxonomic identity and feeding types, a high trophic similarity occurred between aoudad and mouflon across the year. Overlap in resource use between the native red deer and the exotics only occurred during the resource-limited season (Mediterranean summer) between deer and mouflon.

Management implications

We have here analysed and discussed horizontal effects of the introduction of exotic ungulates on native ungulate populations. Under the light of our results we can suggest a few recommendations regarding the management of sympatric red deer, aoudad and mouflon.

As we have shown, simultaneous introduction of ungulates sharing functional traits such as feeding type and body sizes (aoudad and mouflon in the study case), may lead to a potential competition due to the similitude of their foraging preferences. Also, native red deer preferences overlapped with those of exotic mouflon, in summer. All this could lead to the exclusion of preferred resource use of either native or introduced populations, especially

under high stocking rates and during drought conditions in summer. An integration of habitat and ungulate management is, therefore, crucial according to the outcomes of our study.

Mediterranean rangelands oriented to big game exploitation are predominantly characterised by ungulate confinement within a fenced estate. Management actions in such rangelands should be directed towards protecting habitat conditions so that biodiversity is enhanced along with the presence of sustainable communities of large herbivores. Measures such as cultivating part of the pastures as supplementary grazing to fulfil all of the big game dietary requirements and keep animals in good condition during the limiting summer, might become necessary.

On the other hand, management directed towards ungulate populations should keep moderate stocking rates, monitor and control introduced and native populations through annual game counts, and efficient fencing that avoids exotic species expansion over the limits of managed rangelands (Cassinello *et al.* 2004).

Acknowledgments

Authors are very grateful to Y. Fierro for allowing us access to her private hunting estate and facilitating our fieldwork at all times. We are indebted to L. Díaz for statistical advice. F. Dalerum provided very valuable comments on an earlier draft of the manuscript. I. Cristóbal helped out with lab work, and I. Martín, J. Fernández and V. Toledano helped out with nutritional analyses. MM and MS enjoyed PhD fellowships from the Junta de Comunidades de Castilla-La Mancha (JCCM), and the Spanish National Research Council (CSIC, I3P grant), respectively. LGB was supported by a post-doctoral fellowship from Junta de Comunidades de Castilla-La Mancha (JCCM). Financial support was provided by projects PBI-05-010, PREG-07-21, PAI08-0264-1987 (all granted by JCCM) and CGL2007-63707/BOS (granted by Ministerio de Educación y Ciencia and co-funded by the European Regional Development Fund, ERDF).

References

- Acevedo, P., Cassinello, J., Hortal, J., and Gortázar, C. (2007). Invasive exotic aoudad (*Ammotragus lervia*) as a major threat to native Iberian ibex (*Capra pyrenaica*): a habitat suitability model approach. *Diversity and Distributions* **13**, 587–597.
- Acevedo, P., Ruiz-Fons, F., Vicente, J., Reyes-García, A. R., Alzaga, V., and Gortazar, C.

- 507 (2008). Estimating red deer abundance in a wide range of management situations in
508 Mediterranean habitats. *Journal of Zoology* **276**: 37–47.
- 509 Agencia Estatal de Meteorología (AEMT). (2010). ‘Valores climatológicos normales 1979-
510 2000: Ciudad Real’. (AEMET 2010: Madrid.) Available at
511 <http://www.aemet.es/es/elclima/datosclimatologicos/valoresclimatologicos>
512 [?l=4121&dk=clm](http://www.aemet.es/es/elclima/datosclimatologicos/valoresclimatologicos?l=4121&dk=clm) [Verified Apr 2011] [In Spanish]
- 513 Ankom. (2010). ‘Procedures for fibre and *in vitro* analysis’. Available at
514 <http://www.ankom.com>. [Verified April 2011]
- 515 AOAC. (2005). ‘Official Methods of Analysis’ (Association of Official Analytical Chemists,
516 Gaithersburg, MD Chemists: Washington DC.)
- 517 Austin, P. J., Suchar, L. A., Robbins, C. T., and Hagerman, A. E. (1989). Tannins binding
518 proteins in saliva of deer and their absence in saliva of sheep and cattle. *Journal of*
519 *Chemical Ecology* **15**, 1135–1347.
- 520 Bang, P., and Dahlstrom, P. (1974). ‘Collins Guide to Animal Tracks and Signs’. (Collins:
521 London).
- 522 Barroso, F. G., Martínez, T. F., Paz, T., Parra, A., and Alarcón, F. J. (2001). Tannin content of
523 grazing plants of southern Spanish arid lands. *Journal of Arid Environments* **49**, 301–
524 314.
- 525 Bascompte, J., and Jordano, P. (2007). Plant-animal mutualistic networks: The architecture of
526 biodiversity. *Annual Review of Ecology Evolution and Systematics* **38**, 567–593.
- 527 Baumont, R., Prache, S., Meuret, M., and Morand-Fehr, P. (2000). How forage characteristics
528 influence behaviour and intake in small ruminants: a review. *Livestock Production*
529 *Science* **64**, 15–28.
- 530 Beguin, J., Pothier, D., and Côté, S. D. (2011). Deer browsing and soil disturbance induce
531 cascading effects on plant communities: a multilevel path analysis. *Ecological*
532 *Applications* **21**, 439–451.
- 533 Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. *Scientific American* **224**, 86–93.
- 534 Belovsky, G. (1981). Food plant selection by a generalist herbivore: the moose. *Ecology* **62**,
535 1020–1030.
- 536 Benjamini, Y., and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and
537 powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B*
538 **57**, 289–300.
- 539 Benschahar, R., and Coe, M. J. (1992). The relationships between soil factors, grass nutrients
540 and the foraging behaviour of wildebeest and zebra. *Oecologia* **90**, 422–428.

- 541 Bertolino, S., di Montezemolo, N. C., and Bassano, B. (2009). Food-niche relationships
542 within a guild of alpine ungulates including an introduced species. *Journal of Zoology*
543 **277**, 63–69.
- 544 Box, G. E. P., and Cox, D.R. (1964). An analysis of transformations. *Journal of the Royal*
545 *Statistical Society, Series B* **26**, 211–246.
- 546 Bugalho, M. N., and Milne, J.A. (2003). The composition of the diet of red deer (*Cervus*
547 *elaphus*) in a Mediterranean environment: a case of summer nutritional constraint?
548 *Forest Ecology and Management* **181**, 23–29.
- 549 Carranza, J. (2002). *Cervus elaphus* Linnaeus, 1758. Ciervo rojo. In ‘Atlas de los mamíferos
550 terrestres de España’. (Ed. L. J. Palomo and J. Gisbert.) pp. 310–313. (Dirección
551 General de Conservación de la Naturaleza-SECEM-SECEMU: Madrid.) [In Spanish]
- 552 Carranza, J. (2004). Ciervo – *Cervus elaphus*. In ‘Enciclopedia Virtual de los Vertebrados
553 Españoles’. (Ed. L. M. Carrascal and A. Salvador.) (Museo Nacional de Ciencias
554 Naturales: Madrid.) Available at <http://www.vertebradosibericos.org/> [Verified May
555 2010] [In Spanish]
- 556 Carranza, J. (2007). *Cervus elaphus* Linnaeus, 1758. In ‘Atlas y libro rojo de los mamíferos
557 de España’. (Ed. L. J. Palomo, J. Gisbert and J. C. Blanco.) pp. 352–355. (Dirección
558 General para la Biodiversidad-SECEM-SECEMU: Madrid.) [In Spanish]
- 559 Cassinello, J. (1998). *Ammotragus lervia*: a review on systematics, biology, ecology and
560 distribution. *Annales Zoologici Fennici* **35**, 149–162.
- 561 Cassinello, J. (2002). Arrui – *Ammotragus lervia*. In ‘Enciclopedia Virtual de los Vertebrados
562 Españoles’. (Ed. L. M. Carrascal and A. Salvador.) (Museo Nacional de
563 Ciencias Naturales: Madrid.) Available at <http://www.vertebradosibericos.org/>
564 [Verified May 2010] [In Spanish]
- 565 Cassinello, J., Acevedo, P., and Hortal, J. (2006). Prospects for population expansion of the
566 exotic aoudad (*Ammotragus lervia*; Bovidae) in the Iberian Peninsula: clues from
567 habitat suitability modelling. *Diversity and Distributions* **12**, 666–678.
- 568 Cassinello, J., Serrano, E., Calabuig, G., Acosta, P., and Pérez, J.M. (2002). *Ammotragus*
569 *lervia* (Pallas, 1777). Arrui. In ‘Atlas de los Mamíferos Terrestres de España’. (Ed. L.
570 J. Palomo and J. Gisbert.) pp. 338–341. (Dirección General de Conservación de la
571 Naturaleza-SECEM-MIMAM: Madrid.) [In Spanish]
- 572 Cassinello, J., Serrano, E., Calabuig, G., Acosta, P., and Pérez, J. M. (2004). Range expansion
573 of an exotic ungulate (*Ammotragus lervia*) in southern Spain: ecological and
574 conservation concerns. *Biodiversity and Conservation* **13**, 851–866.

- 575 Cassinello, J., Serrano, E., Calabuig, G., Acosta, P., and Pérez, J.M. (2007). *Ammotragus*
576 *lervia* (Pallas, 1777). 'Atlas y libro rojo de los mamíferos de España'. (Ed. L. J.
577 Palomo, J. Gisbert and J. C. Blanco.) pp. 374–377. (Dirección General para la
578 Biodiversidad-SECEM-SECEMU; Madrid) [In Spanish]
- 579 Clauss, M., Kaiser, T., and Hummel, J. (2008). The morphological adaptations of browsing
580 and grazing mammals. In 'The ecology of browsing and grazing'. (Ed. I. J. Gordon
581 and H. H. T. Prins.) pp. 47–88. (Ecological Studies. Volume 195. Springer-Verlag,
582 Berlin Heidelberg: Germany.)
- 583 Clauss, M., Lechner-Doll, M. and Streich, J. (2003). Ruminant diversification as an
584 adaptation to the biomechanical characteristics of forage. A reevaluation of an old
585 debate and a new hypothesis. *Oikos* **102**, 53–262.
- 586 Cooper, S. M., Owen-Smith, N., and Bryant, J. P. (1988). Foliage acceptability to browsing
587 ruminants in relation to seasonal-changes in the leaf chemistry of woody-plants in a
588 South-african savanna. *Oecologia* **75**, 336–342.
- 589 Cristóbal, I. (2006). Dieta invernal de tres especies de ungulados silvestres en un ecosistema
590 mediterráneo. Advanced Diploma Studies dissertation. Universidad de Castilla-La
591 Mancha, Ciudad Real, Spain.
- 592 Cugnasse, J. M. (2000). Mouflon in France. International Mouflon Symposium, 27-29
593 October 2000, Sopron, Hungary.
- 594 De Caceres, M., and Legendre, P. (2009). Associations between species and groups of sites:
595 indices and statistical inference. *Ecology* **90**, 3566–3574.
- 596 Demment, M. W., and Van Soest, P. J. (1985). A nutritional explanation for body size
597 patterns of ruminant and non-ruminant herbivores. *American Naturalist* **125**, 641–672.
- 598 Dolman, P. M., and Wäber, K. (2008). Ecosystem and competition impacts of introduced
599 deer. *Wildlife Research* **35**, 202–214.
- 600 Dufrene, M., and Legendre, P. (1997). Species assemblages and indicator species: the need
601 for a flexible asymmetrical approach. *Ecological Monographs* **67**, 345–366.
- 602 Duncan, A. J., and Poppi, D. P. (2008). Nutritional ecology of grazing and browsing
603 ruminants. In 'The ecology of browsing and grazing'. (Ed. I. J. Gordon and H. H. T.
604 Prins.) pp. 89–116. (Ecological Studies. Volume 195. Springer-Verlag, Berlin
605 Heidelberg: Germany.)
- 606 Fandos, P., and Reig, S. (1992). Problems associated with mouflon and Barbary sheep
607 introductions in Spain. In 'Transactions of the 18th IUGB Congress'. (Ed. B. Bobek,
608 K. Perzanowski and W. Regelin.) pp. 139–140. (Global Trends in Wildlife

- 609 Management, Krakow 1987. Swiat Press, Krakow-Warszawa: Poland.)
- 610 Gagnon, M., and Chew, A. E. (2000). Dietary preferences in extant African Bovidae. *Journal*
611 *of Mammalogy* **81**, 490–511.
- 612 Garin, I., Aldezabal, A., García-González, R., and Aihartza, J. R. (2001). Composición y
613 calidad de la dieta del ciervo (*Cervus elaphus* L.) en el norte de la Península Ibérica.
614 *Animal Biodiversity and Conservation* **24.1**, 53–63. [In Spanish]
- 615 Garson, G. D. (2008). Discriminant function analysis. Statnotes: Topics in Multivariate
616 Analysis. Available at [http:// faculty.chass.ncsu.edu/garson/pa765/statnote.htm](http://faculty.chass.ncsu.edu/garson/pa765/statnote.htm)
617 [Verified August 2009]
- 618 Gebert, C., and Verheyden-Tixier, H. (2001). Variations of diet composition of Red Deer
619 (*Cervus elaphus* L.) in Europe. *Mammal Review* **31**, 189–201.
- 620 Glasser, T., Landau, S., Ungar, E. D., Perevolotsky, A., Dvash, L., Muklada, H., Kababya, D.,
621 and Walker, J. W. (2008). A fecal near-infrared reflectance spectroscopy-aided
622 methodology to determine goat dietary composition in a Mediterranean shrubland.
623 *Journal of Animal Science* **86**, 1345–1356.
- 624 González-Hernández, M. P., Starkey, E. E., and Karchesy, J. (2000). Seasonal variation in
625 concentrations of fiber, crude protein, and phenolic compounds in leaves of red alder
626 (*Alnus rubra*): Nutritional implications for cervids. *Journal of Chemical Ecology* **26**,
627 293–301.
- 628 Gordon, I.J. (1988). Facilitation of red deer grazing by cattle and its impact on red deer
629 performance. *Journal of Applied Ecology* **25**, 1–9.
- 630 Gortázar, C., Herrero, J., Villafuerte, R., and Marco, J. (2000). Historical examination of the
631 status of large mammals in Aragon, Spain. *Mammalia* **64**, 411–422.
- 632 Hanley, T.A. (1982). The nutritional basis for food selection by ungulates. *Journal of Range*
633 *Management* **35**, 146–151.
- 634 Henley, S. R., Smith, D. G., and Raats, J. G. (2001). Evaluation of 3 techniques for
635 determining diet composition. *Journal of Range Management* **54**, 582–588.
- 636 Heroldová, M., Homolka, M., Kamler, J., Koubek, P., and Forejtek, P. (2007). Foraging
637 strategy of mouflon during the hunting season as related to food supply. *Acta*
638 *Veterinaria Brno* **76**, 195–202.
- 639 Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification
640 of ruminants: a comparative view of their digestive system. *Oecologia* **78**, 443–457.
- 641 Iason, G. R., and van Wieren, S. E. (1999). Digestive and indigestive adaptations of
642 mammalian herbivores to low-quality forage. In 'Herbivores: between plants and

- 643 predators' (Ed. H. Olff, V. K. Brown and R. Drent.) pp. 337–369. (38th Symposium of
644 the British Ecological Society. Blackwell Science: Oxford.)
- 645 Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology.
646 *Behaviour* **48**, 215–266.
- 647 Jarman, P.J., and Sinclair A.R.E. (1979). Feeding strategy and the pattern of resource
648 partitioning in ungulates. In: 'Serengeti: dynamics of an ecosystem'. (Ed. A.R.E.
649 Sinclair and N. Norton-Griffiths.) pp. 130–163. (Chicago University Press: Chicago.)
- 650 Kingery, J. L., Mosley, J. C., and Bordwell, K. C. (1996). Dietary overlap among cattle and
651 cervids in northern Idaho forests. *Journal of Range Management* **49**, 8–15.
- 652 Krysl, L. J., Simpson, C. D., and Gray, G. G. (1980). Dietary overlap of sympatric Babary
653 sheep and mule deer in Palo Duro Canyon, Texas. Technical paper No. T-9-227.
654 College of Agricultural Sciences. Texas Tech University.
- 655 Langsrud, Ø. (2003). ANOVA for unbalanced data: use Type II instead of Type III sums of
656 squares. *Statistics and Computing* **13**, 163–167.
- 657 Latham, J. (1999). Interspecific interactions of ungulates in European forests: an overview.
658 *Forest Ecology and Management* **120**, 13–21.
- 659 Maillard, D., Casanova, J.B., and Gaillard, J.M. (1995). Dynamique de l'abroutissement dû au
660 cerf de Corse (*Cervus elaphus corsicanus*) sur la végétation des enclos du parc de
661 Quenza (Corse). *Mammalia* **59**, 363–372. [In French]
- 662 Manly B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., and Ericsson, W.P.
663 (2002). 'Resource selection by animals. Statistical desingn and analyses for field
664 studies'. (Kluwer Academic Publishers: Amsterdam.)
- 665 Markov, G. G., and Penev, G. (2000). The mouflon (*Ovis ammon* L.) in Bulgaria: History and
666 present status. International Mouflon Symposium, 27-29 October 2000, Sopron,
667 Hungary.
- 668 May, M.R. (1973). 'Stability and complexity in model ecosystems'. (Princeton University
669 Press: Princeton.)
- 670 McArthur, C., Goodwin, A., and Turner, S. (2000). Preferences, selection and damage to
671 seedlings under changing availability by two marsupial herbivores. *Forest Ecology
672 and Management* **139**, 157–173.
- 673 Mysterud, A. (2000). Diet overlap among ruminants in Fennoscandia. *Oecologia* **124**, 130–
674 137.
- 675 Owen-Smith, N. (1997). Distinctive features of the nutritional ecology of browsing versus
676 grazing ruminants. *Zeitschrift fuer Saeugetierkunde* **62**, 176–191.

- 677 Pérez Maldonado, R. A., and Norton, B. W. (1996). Digestion of 14 C-labelled condensed
678 from *Desmodium intortum* in sheep and goats. *British Journal of Nutrition* **76**, 501–
679 513.
- 680 Piñero, J. C. R., and Luengo, J. L. R. (1992). Autumn food-habits of the Babary sheep
681 (*Ammotragus lervia* Pallas, 1772) on La Palma island (Canary Islands). *Mammalia* **56**,
682 385–392.
- 683 Prins, H. H. T., and Fritz, H. (2008). Species diversity of browsing and grazing ungulates:
684 consequences for the structure and abundance of secondary production. In ‘The
685 ecology of browsing and grazing’. (Ed. I. J. Gordon and H. H. T. Prins.) pp. 179–200.
686 (Ecological Studies. Volume 195. Springer-Verlag, Berlin Heidelberg: Germany.)
- 687 Putman, R. J. (1984). Facts from faeces. *Mammal Review* **14**, 79–97.
- 688 Putman, R. J. (1996). ‘Competition and resource partitioning in temperate ungulate
689 assemblies’. (Chapman and Hall: London.)
- 690 R Development Core Team. (2011). ‘R: A language and environment for statistical
691 computing’. (R Foundation for Statistical Computing: Vienna.) ISBN 3-900051-07-0.
692 Available at <http://www.R-project.org> [Verified March 2011]
- 693 Robbins, C. T., Mole, S., Hagerman, A. E., and Hanley, T. A. (1987). Role of tannins in
694 defending plants against ruminants: reduction in dry matter digestion? *Ecology* **68**,
695 1606–1615.
- 696 Rodríguez-Luengo, J. L., Fandos, P., and Soriguer, R. C. (2002). Muflón, *Ovis gmelini* Pallas,
697 1811. In ‘Atlas de los Mamíferos Terrestres de España’. (Ed. L. J. Palomo and J.
698 Gisbert.) pp. 334–337. (Dirección General de Conservación de la Naturaleza -
699 SECER-SECEMU: Madrid.) [In Spanish]
- 700 Rodríguez-Luengo, J. L., Fandos, P., and Soriguer, R. C. (2007). *Ovis aries* Linnaeus, 1758.
701 In ‘Atlas y libro rojo de los mamíferos de España’. (Ed. L. J. Palomo, J. Gisbert, J. C.
702 Blanco.) pp. 371–373. (Dirección General para la Biodiversidad-SECEM –SECEMU:
703 Madrid) [In Spanish]
- 704 Rogosic, J., Pfister, J. A., Provenza, F. D., and Grbesa, D. (2006). Sheep and goat preference
705 for and nutritional value of Mediterranean maquis shrubs. *Small Ruminant Research*
706 **64**, 169–179.
- 707 Savage, R. E. (1931). The relation between the feeding of the herring off the east coast of
708 England and the plankton of the surrounding waters. (Ministry of Agriculture, Food
709 and Fisheries, Series 2, 12:1–88: London).
- 710 Scalbert, A. (1991). Antimicrobial properties of tannins. *Phytochemistry* **12**, 3875–3883.

- Schroener, T.W. (1986). Resource partitioning. In: 'Community ecology, pattern and process'. (Ed. J. Kikkawa and D.J. Anderson.) pp.91–126 (Blackwell:Oxford.)
- Schwartz, C. C., and Ellis, J. E. (1981). Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. *Journal of Applied Ecology* **18**, 343–353.
- Shaffer, J. P. (1995). Multiple hypothesis-testing. *Annual Review of Psychology* **46**, 561–584.
- Sicilia, M. (2011). Ecología y comportamiento de ungulados en simpatria en un ambiente mediterráneo: interacciones entre especies nativas y exóticas de interés cinegético. PhD dissertation. Universidad de Castilla-La Mancha, Spain.
- Smit, R., Bokdam, J., den Ouden, J., Olff, H., Schot-Opschoor, H., and Schrijvers, M. (2001). Effects of introduction and exclusion of large herbivores on small rodent communities. *Plant Ecology* **155**, 119–127.
- Spear, D., and Chown, S. L. (2009). Non-indigenous ungulates as a threat to biodiversity. *Journal of Zoology* **279**, 1–17.
- Stewart, D. R. M. (1967). Analysis of plant epidermis in faeces: a technique for studying the food preferences of grazing herbivores. *Journal of Applied Ecology* **4**, 83–111.
- Van Soest, P. J., Robertson, J. B., and Lewis, B. A. (1991). Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* **74**, 3583–3597.
- Van Soest, P. J. (1994). 'Nutritional ecology of the ruminant'. (Cornell University Press: Ithaca, New York.)
- Van Wieren, S., and van Langevelde, F. (2008). Structuring herbivore communities: the role of habitat and diet. In 'Resource ecology: Spatial and temporal dynamics of foraging'. (Ed. H. H. T. Prins and F. Van Langevelde.) pp. 237–262. (Springer: The Netherlands.)
- Verheyden-Tixier, H., Renaud, P. C., Morellet, N., Jamot, J., Besle, J. M, and Dumont, B. (2008). Selection for nutrients by red deer hinds feeding on a mixed forest edge. *Oecologia* **156**, 715–726.
- Voeten, M.M., and Prins, H. H. T. (1999). Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* **120**, 287–294.
- Zamora, R. (2000). Functional equivalence in plant-animal interactions: ecological and evolutionary consequences. *Oikos* **88**, 442–447.

Table 1. Diet content in coarse forage categories (%) for each animal species and season

Season	Herbivore	Grass		Forb		Shrub	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
spring	red deer	21.33	1.81	37.71	4.33	40.96	5.31
	E. mouflon	25.32	1.22	39.94	3.61	34.73	4.37
	aoudad	28.26	1.38	51.86	1.71	19.86	1.34
summer	red deer	24.39	3.12	26.32	2.33	49.29	4.66
	E. mouflon	17.77	2.32	31.00	3.50	51.22	5.65
	aoudad	21.95	0.86	41.77	1.16	36.27	2.00
autumn	red deer	23.68	1.62	15.19	1.15	61.12	2.42
	E. mouflon	34.87	1.68	22.54	2.35	42.59	2.83
	aoudad	36.12	2.05	12.80	0.58	51.08	2.09
winter	red deer	21.34	0.88	9.96	0.46	68.70	0.97
	E. mouflon	33.49	1.43	13.21	0.46	53.30	1.67
	aoudad	27.85	1.27	12.00	0.63	60.14	1.42

Table 2. Summary of discriminant functions developed to distinguish aoudad, mouflon and red deer selection on forage categories

% explained variance (%var.), canonical correlation (Can.Corr.)

Season	Function	Eigenvalue	%var.	Can.Corr.	Wilks λ	χ^2	df	P-value
Spring	1	1.89	84.7	0.81	0.26	37.93	6	< 0.001
Spring	2	0.34	15.3	0.50	0.75	8.22	2	0.016
Summer	1	0.51	94.4	0.58	0.64	12.83	6	0.046
Summer	2	0.03	5.6	0.17	0.97	0.86	2	0.65
Autumn	1	0.88	82.0	0.69	0.45	31.58	6	< 0.001
Autumn	2	0.19	18.0	0.40	0.84	6.90	2	0.032
Winter	1	2.22	96.4	0.83	0.29	43.70	6	< 0.001
Winter	2	0.084	3.6	0.28	0.92	2.82	2	0.24

Table 3. Indicator values (%) for taxa present in seasonal diets of red deer, European mouflon and aoudad

Figures in bold indicate significance as calculated by the *fdr* method for multiple hypothesis testing (Benjamini and Hochberg 1995; see also Shaffer 1995)

Season	Herbivore	Plant taxa	Indicator value	P-value
Spring	Red deer	<i>Pistacia spp.</i>	55.82	0.02
Spring	E. mouflon	<i>Cytisus spp.</i>	43.48	0.04
Spring	Aoudad	<i>Globularia alypum</i>	50.00	0.01
Spring	Aoudad	Herbaceous Compositae	47.37	< 0.001
Spring	Aoudad	Herbaceous Polygonaceae	73.94	< 0.001
Summer	Aoudad	Herbaceous <i>Umbelliferae</i>	57.08	0.02
Autumn	Red deer	<i>Cistus spp./H. ocymoides</i>	40.57	< 0.001
Autumn	Red deer	<i>Quercus sp.</i>	40.06	0.002
Autumn	Red deer	<i>Rosa/Rubus</i>	47.78	0.003
Autumn	E. mouflon	Herbaceous Cistaceae	44.45	0.036
Autumn	E. mouflon	Herbaceous Compositae	45.87	0.002
Autumn	E. mouflon	Herbaceous Leguminosae	53.21	0.03
Autumn	Aoudad	<i>Erica spp.</i>	48.93	0.01
Autumn	Aoudad	<i>Globularia alypum</i>	54.54	0.01
Autumn	Aoudad	Herbaceous Liliaceae	51.22	0.006
Autumn	Aoudad	Herbaceous Umbelliferae	92.20	< 0.001
Winter	Red deer	<i>Cistus spp./H. ocymoides</i>	38.63	< 0.001
Winter	Red deer	Herbaceous <i>Caryophyllaceae</i>	27.78	0.04
Winter	Red deer	<i>Quercus spp.</i>	41.56	< 0.001
Winter	Red deer	<i>Rosa sp./Rubus ulmifolius</i>	59.1	< 0.001
Winter	E. mouflon	<i>Asparagus acutifolius</i>	54.55	< 0.001
Winter	E. mouflon	Herbaceous Leguminosae	77.89	< 0.001
Winter	E. mouflon	Herbaceous <i>Liliaceae</i>	40.16	0.05
Winter	E. mouflon	Herbaceous Poaceae	40.51	< 0.001
Winter	E. mouflon	Herbaceous Polygonaceae	43.01	0.009
Winter	E. mouflon	Herbaceous Umbelliferae	46.23	0.009
Winter	Aoudad	Herbaceous Compositae	52.13	< 0.001
Winter	Aoudad	<i>Osyris alba</i>	54.18	< 0.001

786 **Table 4. Summary statistics of seasonal nutritional content of plants (g/100g dry matter) consumed by red deer, European mouflon and aoudad**

787 Average and standard error are provided. Dry matter (DM), organic matter (OM), hemicellulose (HC), cellulose (C)

Season	Herbivore	DM		OM		HC		C		Lignin		Available N		Total N		Tannins	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Spring	Red deer	35.20	0.71	94.50	0.33	23.24	0.40	24.55	0.94	9.66	0.48	0.91	0.02	1.25	0.01	11.84	0.77
	E. mouflon	34.21	0.54	93.60	0.47	23.59	0.25	25.63	0.57	9.18	0.24	0.94	0.00	1.24	0.01	11.40	0.68
	Aoudad	32.63	0.16	94.58	0.16	24.53	0.08	27.70	0.18	8.55	0.08	0.93	0.00	1.20	0.00	8.94	0.22
Summer	Red deer	73.12	1.57	94.97	0.14	20.41	0.33	31.69	1.18	13.54	0.29	0.56	0.01	0.89	0.02	8.91	0.47
	E. mouflon	73.10	1.90	94.94	0.17	20.49	0.45	31.72	1.41	13.85	0.38	0.54	0.01	0.89	0.03	8.71	0.59
	Aoudad	78.99	0.73	94.40	0.06	21.80	0.14	35.96	0.55	12.62	0.08	0.51	0.01	0.80	0.01	7.37	0.17
Autumn	Red deer	41.82	0.51	94.08	0.19	21.94	0.38	27.01	0.68	10.66	0.19	0.95	0.00	1.27	0.01	16.41	0.55
	E. mouflon	39.05	0.47	93.07	0.17	24.02	0.32	30.77	0.59	9.61	0.16	0.96	0.00	1.25	0.00	13.21	0.49
	Aoudad	40.92	0.30	93.60	0.10	23.08	0.22	28.98	0.39	10.68	0.13	0.93	0.00	1.25	0.00	14.22	0.33
Winter	Red deer	39.68	0.31	93.03	0.11	17.68	0.05	15.91	0.05	13.04	0.12	1.46	0.02	1.84	0.02	19.10	0.37
	E. mouflon	34.79	0.49	91.39	0.18	18.32	0.09	15.40	0.05	11.59	0.22	1.76	0.03	2.07	0.02	15.59	0.47
	Aoudad	36.95	0.43	92.15	0.14	17.97	0.06	15.61	0.10	12.47	0.20	1.63	0.02	1.97	0.02	16.86	0.28

788

Table 5. Summary of discriminant functions developed to segregate aoudad, European mouflon and red deer forage selection according to its nutritional traits
 % explained variance (%var.), canonical correlation (Can.Corr.)

Season	Function	Eigenvalue	%var.	Can.corr.	Wilks λ	χ^2	df	P-value
Spring	1	1.60	66.8	0.78	0.22	40.69	12	< 0.001
Spring	2	0.79	33.2	0.67	0.56	15.46	5	0.009
Summer	1	1.83	92.7	0.80	0.31	32.32	12	0.001
Summer	2	0.15	7.3	0.36	0.87	3.72	5	0.59
Autumn	1	1.72	82.3	0.80	0.27	49.92	10	< 0.001
Autumn	2	0.37	17.7	0.52	0.73	11.95	4	0.018
Winter	1	3.21	91.2	0.87	0.18	57.25	12	< 0.001
Winter	2	0.31	8.8	0.49	0.76	9.07	5	0.11

Figure captions

Fig. 1. De Finetti diagram of seasonal selection by the study animals on the different forage categories. Selectivity indexes on grass, forbs and shrubs have been scaled so that their sum equals 1. Seasonal selection is reported for the three study animals: red deer (circles), aoudad (squares), European mouflon (diamonds), and for four seasons: spring (white filling), summer (black filling), autumn (half lined), winter (grey filling).

Fig. 2. Relative position of the study species along a space determined by the two discriminant functions calculated for selection on forage categories. Discriminant scores are plotted for each season. Multivariate means for each species are shown surrounded by ellipses that correspond to a 95% confidence limit for the mean. The direction of the variables in the canonical space is shown by arrows emanating from the grand mean, according to the structure coefficients. HC=hemicellulose, C=cellulose.

Fig. 3. Relative position of the study species along a space determined by the two discriminant functions calculated for selection on the nutritional components. Discriminant scores are plotted for each season. Multivariate means for each species are shown surrounded by ellipses that correspond to a 95% confidence limit for the mean. The direction of the variables in the canonical space is shown by arrows emanating from the grand mean, according to the structure coefficients. HC=hemicellulose, C=cellulose.

Fig. 1.

Fig. 2.

Fig. 3.

School of Animal, Plant & Environmental Sciences

The Biology of a Changing World: Conserving African Biodiversity

Private Bag 3, Wits 2050, South Africa • Enquiries Tel: +27 (0)11 717-6404 • Fax: +27 (0)11 403-1429
E-mail: apesinfo@gecko.biol.wits.ac.za

12 December 2011

Re: revised version of the manuscript WR 11146

Dear Dr Boutin,

Please find enclosed the revised version of our manuscript entitled “*Contrasting feeding patterns of native red deer and two exotic ungulates in a Mediterranean ecosystem*” for consideration for publication in Wildlife Research (note that the manuscript title has been changed according to the reviewer 1’s suggestion).

The manuscript has been previously submitted and you invited us to send a revised version where a number of comments from you and two anonymous reviewers should have been adequately addressed. Both reviewers and yourself agreed that the manuscript is well written, has interesting outcomes, and fits the scope of Wildlife Research, but showed a main concern on our prediction on co-evolutionary terms regarding the dietary selection of the study animals. This hypothesis and its discussion have been removed and the issue is just mentioned briefly in the discussion in the current version of the manuscript. Please find below this and the rest of issues risen by the reviewers and how we have addressed them.

Thank you for your positive review of the manuscript and your valuable comments.

I look forward to hearing from you.

Sincerely and on behalf of my co-authors,

María Miranda García-Rovés
maria.miranda@wits.ac.za
maria.mirandaroves@gmail.com

Associated Editor

Comments

I concur with both reviewers in that this is a well-written and interesting study on the interaction between exotic and native species of herbivorous mammals. However, as pointed out by the reviewers there are some weaknesses, which although not serious, should be properly addressed by the authors and detailed in the cover letter accompanying a revised version of their manuscript. In particular, both reviewers and myself found little ground for the coevolutionary prediction. It is indeed a big leap to make such claims without specific data, so this should be toned down probably to a suggestion in the discussion section.

We have reformulated our hypotheses in abstract (line 52-55) and introduction (line 96-110) and we now just mention the co-evolutionary hypothesis briefly in the discussion (see current lines 409-421).

Review 1

Comments

The paper 'Foraging strategies within a guild of native and exotic ungulates' is excellent in its relevant field of study. The paper is very well written and presented some important findings regarding foraging strategies of sympatric cervid and bovids.

Thank you.

Title: the paper title doesn't signify the study species or study site. It is more likely a running title.

We have changed it to: "Contrasting feeding patterns of native red deer and two exotic ungulates in a Mediterranean ecosystem"

Line 47: 'Deer higher selection for shrubs compared to that of mouflon and aoudad was sustained throughout the year, while bovids showed seasonal shifts in forage selection.' May be changed to 'Higher selection of shrubs by deer species was sustained throughout the year, when bovids showed seasonal shifts in forage selection'.

fixed

Line 50: 'study' may be changed to studied

fixed

Line 58: 'Deer-mouflon and aoudad-mouflon dietary overlap' may be changed to Dietary overlap between deer and mouflon and aoudad and mouflon.

fixed nearly as suggested: dietary overlap between deer and mouflon and between aoudad and mouflon

Line 122: Native Iberian red deer (*Cervus elaphus hispanicus*, a cervid) is the main big game species in Spain with a wide distribution in the Peninsula and achieving high densities in the private estates. What is the high density and how do you define high density?

Data on population densities for all study animals have been added in the "Study area" section under "Materials and Methods", and an indication of what is considered high density and a new reference have been included in the introduction (lines 119-120). The study by Mitchell and Crisp (1981) in upland habitats

in Scotland considers 34 deer/ km² as exceptionally high densities for red deer. Iberian red deer under Mediterranean conditions instead, is generally considered under high densities when there are more than 40 individuals /km² (Lazo et al. 1994; Acevedo et al. 2008; Carranza 2011;), the density in the study area being 55 individuals/ km². These high-density populations have been found in South-central Spain when intense management measures such as fencing and supplementation are implemented (Acevedo et al., 2008).

Acevedo, P., Ruiz-Fons, F., Vicente, J., Reyes-García, A. R., Alzaga, V., and Gortazar, C. (2008).

Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. Journal of Zoology, 276: 37-47.

Carranza, J. (2004). Ciervo – Cervus elaphus. In Enciclopedia Virtual de los Vertebrados Españoles (L. M. Carrascal and A. Salvador, eds). Museo Nacional de Ciencias Naturales, Madrid. <http://www.vertebradosibericos.org/>

Lazo, A., R.C. Soriguer, and P. Fandos. (1994) Habitat use and ranging behavior of a high-density population of Spanish red deer in a fenced intensively managed area. Applied Animal Behaviour Science 40:55–65.

Mitchell, B., and Crisp, J.M. (1981) Some properties of Red deer (Cervus elaphus) at exceptionally high population-density in Scotland. Journal of Zoology 193:157-169.

Line 128: spelling mistake 'hypothesied' may be changed to hypothesized.

Fixed

Line 135: the lack of a history of coevolution. Appropriate literature may be provided here.

We have removed the co-evolutionary prediction and only raise this issue briefly in the discussion, as suggested by both referees and the editor (see current lines 409-421 and comments to referee 2).

Line 171: It is not clear on which basis authors selected 20 transects of 50 meter and why the transects are randomly distributed? Why transects are not stratified or placed in grids? Is 1000 meters (20 X 50m) sampling in ~8 km² (724 ha) study area appropriate? Provide supporting literature.

Transect locations actually respond to a stratified design in which they were randomly placed according to the availability of three habitats: habitat edge (25.6 ha; 3 transects), pastures (229 ha; 11 transects;) and scrubland (469.1 ha; 6 transects). This has been clarified in the text (see current lines 171-173).

Due to high homogeneity within the three habitats we believe that the number of transects placed in each of the habitats was appropriated to measure species availability. No new shrub species or herbaceous families were found when recording new transects for studies developed after the one presented here. Transects initially measured 100m but no significant difference was found in the identity and cover of plant species when compared with transects measuring 50m, and were thus reduced in length.

Line 185: It is not mentioned in the paper that the authors have collected the faecal samples right in the time of defecation. Hence it is unclear how the faecal samples were collected from individuals from different sexes and ages.

Faecal samples were collected either from individuals seen defecating or from hunted individuals. In the former case we identified three main sex-age classes (male, female, and juvenile of either sex) by direct observations. In hunted individuals, age could be more precisely estimated from the tooth eruption pattern up to 24 months (Sáenz de Buruaga et al. 1991) and from histological examinations of incisors for animals older than 24 months (Hamlin et al. 2000). We have clarified this in the text (line 182-183).

Hamlin, K.L., D.F. Pac, C.A. Sime, R.M. Desimone, and G.L. Dusek. (2000). Evaluating the accuracy of ages obtained by two methods for Montana ungulates. Journal of Wildlife Management 64:441–449.

Sáenz de Buruaga, M., A.J. Lucio, and J. Purroy. (1991). Reconocimiento de sexo y edad en especies cinegéticas. Diputación Foral de Navarra, Vitoria, Spain.

Line 215: Appropriate reference may be added for Kjeldahl procedure.
added (line 212)

Line 296: I believe 'scrub layer' would be shrub layer.
fixed

Line 306: The sentence is not clear, may be restructured.

We have reworded and moved this sentence to the methods section since it applies to all discriminant analyses performed (lines 259-261). We used one-way ANOVAs with the discriminant function scores to test the hypothesis of equal diet or nutrient selection. Those ANOVAs were just performed on the scores of discriminant function 1 which is the one that explains a higher proportion of the variance when classifying the different cases into our dependent categorical variable (species).

Line 394: the reference 'Bartolme et al. 1998' was found in the list of references.
reference removed, it is not relevant here.

Line 406: the sentence 'Deer association with chemically defended 407 plants seems to be related to their high total N concentration and, very likely, to high soluble sugar contents and deer ability to overcome plant chemical defences.' May be changed to 'Association of Iberian red deer with chemically defended plant seems to be related to their high total N concentration and, very likely, to high soluble sugar contents and their ability to overcome plant chemical defences.'
fixed

Line 413: 'At a seasonal scale, native deer could be?' may be changed to 'At a seasonal scale, selection of

native deer could be'.

fixed

Line 415: 'mouflon overlapped with deer preferences' may be changed to 'mouflon overlapped with the preferences of deer'.

This sentence has been removed when reducing discussion length.

Line 435-443: the present study doesn't have any relevance with the model developed by Illiua and Gordon (1987). Hence, there is no need of mentioning this model here. Line 435-443 may be removed.

Reference to Illius and Gordon model has been removed.

Line 452: the word 'visualization' may be changed to 'understanding'

fixed

Line 475-478: 25 years of assemblage means coexistence for more than five generations. The sentence 'interspecific ecological roles and resource partitioning are not likely to be established' is not making any sense. Land mammals are kin learner. They learn about surrounding environment, competitor species, resource utilization through their experience and lineage. This study is too little to say about this. The lines 475-478 may be removed.

removed

Line 495-502: the present study doesn't have any relevance for recommending Mosaic habitat management. Hence this part may be removed.

removed from discussion and abstract

In general, this paper is well established documenting the foraging strategies of native and exotic ungulates species. But I would suggest authors to test the resource selection by these species following Ivlev's index (Ivlev 1961) or Jacob's Index (Jacob 1974) which are newer methods than Savage selectivity Index. Authors can easily enumerate the percentage availability of each plant species weighted by proportion of nutrition, and compare with the percentage utilization derived from faecal sample analysis by each ungulate species. The dietary overlap between these species can be measured through Pianka's Index, which is much simpler to the readers.

Selectivity indices measure the utilization of the different resources (habitat, food types, etc) in relation to their availability in the environment, and differ in the algorithm used to calculate the electivity from use and availability. Cock (1978) and Lechowicz (1982) presented indice's comparisons. Jacobs modified forage ratio, Ivlev electivity index, and Savage index (also known as Ivlev forage rate) have been shown to essentially have the same advantages and weaknesses (Lechowicz 1982). Moreover, Lechowicz (1982) showed in an empirical analysis that the various indices of feeding selection based on the forage ratio

measures differed in value but gave similar ranks in preferences order. He concluded that those three indices provide useful assessments of resource selection and are applicable when comparing feeding patterns.

Ivlev electivity index's main advantage is the fact that values range from +1 (selection) to -1 (refusal), being this a more comprehensible scale than that obtained when applying Savage selectivity index. Both Jacob and Savage indices have the same unwieldy scales: 0 to 1 showing refusal and 1 to infinite indicating selection. However the latter index allows testing its statistical significance with a Chi-square test (Manly, 2002) after applying an adjustment of the p-value for multiple testing. Statistical testability of Savage index is the reason why we (see Miranda et al. 2010) and other authors (Caro et al. 2008, 2011; Escudero et al. 2011; Gómez et al. 2001, Rosin et al. 2011) have recently applied it.

Pianka's index (Pianka 1973) is a commonly used measure that allows us to calculate an assessment of the degree of dietary overlap. However, if this overlap measure is to be interpreted in any meaningful way, it is necessary to have a measure of what might be expected if the resources were used at random, for instance, by a randomization analysis (Plumptre 1996; López et al. 2009). We instead believe that a diet comparison based on a discriminant analyses entails more interesting outcomes. We have accompanied it by figures in which overlapping circles can be easily interpreted by readers as dietary overlap. Moreover, linear discriminant analyses also identify the importance of the different plant categories/nutrients according to which selection by different species partitions/overlaps. This approach has been previously used by, for instance, Bagchi and Sankar (2003) and Voeten and Prins (1999) at an habitat level with discriminant function scores considered as the 'resource utilization functions'.

Bagchi, S., Goyal, S.P., and Sankar, K. (2003) Niche relationships of an ungulate assemblage in a dry tropical forest. *Journal of Mammalogy* 84: 981-988.

Caro, J., Ontiveros, D., and Pleguezuelos, J.M. (2011) The feeding ecology of Bonelli's eagle (*Aquila fasciata*) floaters in southern Spain: implications for conservation. *European Journal of Wildlife Research*, 57:729-736.

Cock, M.J.W. (1978) The assesment of preference. *Journal of Animal Ecology*, 47:805-816.

Escudero, G., Navedo, J.G, Piersma, T., Goeij, P., and Edelaar, P. (2011) Foraging conditions 'at the end of the world' in the context of long-distance migration and population declines in red knots. *Austral ecology*, doi: 10.1111/j.1442-9993.2011.02283.x

Gómez, J.M., Hódar, J.A., Zamora, R., Castro, J., and García, D. (2001) Ungulate damage on Scots pines in Mediterranean environments: effects of association with shrubs. *Canadian Journal of Botany* 79: 739-746.

Lechowicz, M.J. (1982) The sampling characteristics of electivity indices. *Oecologia* 52: 22-30.

López, J.A., Scarbotti, P.A., Medrano, M.C. & Ghirardi, R. 2009. Is the red spotted green frog *Hypsiboas punctatus* (Anura: Hylidae) selecting its preys? The importance of prey availability. *Revista de Biología Tropical*. 57: 847-857.

Manly B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., and Ericsson, W.P. (2002). 'Resource selection by animals. Statistical desingn and analises for field studies'. (Kluwer Academic Publishers: Amsterdam.)

- Miranda, M., Díaz, L., Sicilia, M., Cristóbal, I., and Cassinello, J. (2011) Seasonality and edge effect determine herbivory risk according to different plant association models. *Plant Biology* 13: 160-168.
- Pianka, E.R. 1973. The structure of lizard communities. *Ann. Rev. Ecol. Syst.* 4, 53-74.
- Plumptre, A. 1996. Modelling the impact of large herbivores on the food supply of mountain gorillas and implications for management. *Biological Conservation*, 75: 147-155.
- Rosin, Z.M., Olborska, P., Surmacki, A., and Tryjanowski, P. (2011) Differences in predatory pressure on terrestrial snails by birds and mammals. *Journal of Biosciences* 36:691-699.
- Voeten, M.M., and Prins, H.H.T. (1999) Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* 100: 287-294.

Review 2

Comments

General comments:

I found this study very interesting, investigating interactions (mainly food preferences) between native (deer) and two exotic bovids in mediterranean Spain. The diet analyses are thorough, the statistical treatment correct, and the conclusions obtained very reasonable. The English righting is quite good for non-native speakers, even though there are a few raw passages.

Thank you

In addition, the results section is rather redundant with the discussion section; wherein what was already discusses is re-discussed. As a consequence, the paper is rather long and slightly repetitive. Finally, I think that the issue of coevolution explaining resource partitioning among the three species is relatively naive. I am not sure there is a formal ecological hypothesis stating that coevolved herbivores will be more dissimilar in diet use than coevolved ones. In this particular case, none of the species concerned have coevolved (the two bovids come from different parts of the world and are not sympatric except at the study site, where they were introduced only 25 yr ago). Yet, the native deer exhibits strong preference for browsing in forested terrain, while the two bovids are grazers in open areas. The only season when the three species have the same plant preferences is during the hot and low-productive summer, when deer dare to come in the open to eat whatever is available. Competition among these species in summer? Perhaps, but not demonstrated. Indeed the two bovids number quite small in comparison to the deer population. Apart from all this, I could hardly pencil anything in, because I found the paper well written and essentially convincing. Below come a few specific comments

Discussion has been reduced in length. We have reformulated our hypotheses and we now just mention the

coevolutionary hypothesis briefly in the discussion, as a suggestion (lines 409-421).

Competition in resource use by deer and mouflon is not demonstrated in this paper, we just wish to highlight the fact that, potentially and under more even distributions of the study species, the observed overlap in diet selection jointly with a previously reported overlap in habitat use in the study area could lead to competition between the study animals. We have made some changes in the abstract and discussion where we just suggest the possibility of a potential competitive interaction under specific conditions that need further studies (lines 56-59 and 429-434).

Abstract:

OK, with a few orthographic or typographical errors.

Style has been improved in the abstract

Material and methods

Study area: elevation is not reported.

Added (line 136)

Reminder of M&M quite well explained, although rather long as a section.

Given the interest of the combination of both botanical and nutritional analyses, as well as the importance of detailing our approach to calculate selection indexes, we believe that the exhaustive M&M section is required for a full understanding of the techniques used.

Discussion:

Line 368 reads strange! 'the mouflon as an opportunistic feeder whose optimal habitat is diverse.' If something is optimal, one tends to think that there is a more preferred habitat.

Changed

In general, this discussion is interesting but rather redundant with information already presented in the results, which render it a little bit too long.

Changed. We have reduced the discussion in four hundred words and avoided speculations based on the coevolutionary explanations, as suggested by both referees and the editor.

References:

Very exhaustive. But I miss a reference to the classical work of Gary Belovsky on nutrient and energy acquisition of moose in North America.

Reference included (lines 86-88)

Table 2: I should like to know how exactly 'non significant' is in this table

We added p-value

Table 5: I should like to know how exactly 'non significant' is in this table

We added p-values

Fig. 1: I think these diagrams have a name. De Finelli's?

Yes, De Finetti. We have added this term in the figure caption.

Fig. 2: In the version I received, these graphs are too thin! Discriminant in panel 1 left is in low case, while in the others it is not.

Fig 3: In the version I received, these graphs are too thin!

Graphs of Figures 2 and 3 are a modified output of JMP 6 software. We are submitting them with a few changes over the previous ones. Graphs quality seems good in our computers but please let us know if further changes are considered necessary.