**Foraging sexual segregation in a Mediterranean environment:
summer drought modulates sex-specific resource selection**

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1   **ABSTRACT**

2   A large body of studies have linked sexual segregation in dimorphic ungulates with
3   differential resource selection and nutritional requirements of the sexes. However,
4   detailed patterns of sexual dietary preferences have rarely been assessed as
5   keystone mechanisms of sexual segregation. We compared diet and nutritional
6   selection by 3 sex-age classes in the Iberian red deer (*Cervus elaphus hispanicus*
7   Hilzheimer) across reproductive states and according to seasonal fluctuations in
8   resource availability in a Mediterranean environment. Foraging segregation between
9   sexes was found during rut when female/juvenile selection of shrubs was higher than
10   that of males. Observed foraging patterns relate to a stronger selection of nitrogen,
11   tannins and lignin by females and juveniles, and fibres by males. Our findings are
12   associated to the Mediterranean climate, where rut and lactation concur with a
13   shortage period, the particularly dry summer. Foraging segregation between sexes
14   during the rut could be shaped by a conjunction of factors such as the low quality of
15   resources and different fitness enhancement strategies. We highlight both the
16   importance of including the dietary component and providing a temporal framework
17   when documenting ungulate sexual segregation, and the interest of considering
18   regional conditions when addressing management of ungulates with a wide
19   distribution.

20
21   *Key words:* Cervidae, dietary segregation, fecal analysis, feeding ecology, forage
22   selection, sexual dimorphism

1. Introduction

In sexually dimorphic species, males and females often differ in their social affinities, habitat use and activity synchrony. Such sex-specific segregation has been extensively studied (Clutton-Brock et al., 1982; Ruckstuhl, 2007) generating a suite of explanations regarding sexual segregation in ungulates, including differences in body size, digestive physiology, predation risk, reproductive strategies and activity budget (Main et al., 1996; Ruckstuhl, 2007). Two theories have emerged as keystone hypotheses to explain the so-called ecological segregation (Main, 2008): the Foraging Selection Hypothesis (FSH) and the Reproductive Strategy Hypothesis (RSH).

The FSH is based on the Jarman-Bell principle (Demment and Van Soest, 1985), but applied at the intra-specific level. This principle acknowledges that gut capacity increases linearly with body weight while the metabolic weight of homeotherm animals scales to body weight $^{0.75}$, and therefore relative energy requirements decrease and digestion rate increases in mammals with increasing body size. FSH thus predicts that the smaller females and juveniles should display a more selective strategy with preference for highly nutritious and digestible plant material (e.g. Clutton-Brock and Albon, 1989; Shanon et al., 2006; Staines et al., 1982), whereas the larger males should be able to feed on a poorer quality sward while still achieving sufficiently efficient intake rates (Pérez-Barbería et al., 2008; Ruckstuhl and Neuhaus, 2000; Staines et al., 1982). Two opposing mechanisms may be involved in FSH. On the one hand, the Scramble Competition Hypothesis (Illius and Gordon, 1987; Staines et al., 1982) states that FSH outcomes might entail not only resource partitioning between sexes but an indirect competition process, in which females

would displace males from areas with less abundant but highly nutritious forage. The Gastrocentric Hypothesis assumes, instead, that males have evolved differences in food exploitation patterns to avoid intraspecific competition with females and their offspring (Barboza and Bowyer, 2000).

The RSH rests on the different reproductive strategies of each sex, which lead to contrasting optimal foraging behaviours (Main, 2008; Main et al., 1996; Ruckstuhl and Neuhaus, 2000, 2002). In polygynous species, male fitness is mainly determined by body condition, since males need to defeat competitors and in some cases, such as for red deer, keep the largest harem possible (Clutton-Brock et al., 1982; Main et al., 1996). Female fitness, on the other hand, is mainly determined by offspring survival, which is maximized by seeking habitats that provide optimal refuge against predators while sacrificing high quality foraging areas (Clutton-Brock et al., 1982). Traits improving fighting abilities would, therefore, be favoured in males, whilst traits related to foraging efficiency would be more strongly favoured in females (Clutton-Brock et al., 1982). As a result, males have been shown to have higher absolute energy requirements than females, during most of the year (Pérez-Barbería et al., 2008; Staines et al., 1982) and invest a considerable amount of energy, proteins and minerals when growing annual antlers and neck muscles (Landete-Castillejos et al., 2007) and during the rut period (Clutton-Brock et al., 1982; Main et al., 1996). Therefore, they should mainly select high-quality and high-quantity forage areas (Main et al., 1996). Although during lactation females seem to have similar or even higher nutritional requirements than males (Oftedal, 1985), other factors increasing offspring security and satisfying both offspring and mother requirements (such as the presence of water sources) may restrict habitat choice by females (Main et al., 1996).

1 Both the FSH and the RSH are built on allometry and differential fitness between
2 sexes and this presumably affects foraging decisions (Pérez Barbería et al., 2008,
3 Ruckstuhl, 2007). However this dietary component has rarely been assessed as a
4 driving force underlying sexual segregation (Mooring et al., 2005; Post et al., 2001;
5 Schroeder et al., 2010). Particularly, conclusions of foraging preferences of males
6 and females have not been based on actual and simultaneous measurements of
7 available and selected botanical and nutritional parameters, and could therefore be
8 misleading (Main et al., 1996) and limit our availability to test sexual segregation
9 hypotheses.

11 Also, these hypotheses have mainly been tested in northern temperate climates
12 (Clutton-Brock et al., 1982; Festa-Bianchet, 1988; Mooring et al., 2005). But since
13 herbivore reproductive performance is greatly influenced by forage availability during
14 critical periods, latitudinal gradients in seasonal productivity may affect sex-specific
15 resource selection. It is therefore necessary to assess the generality of FSH and
16 RSH across different climatic regions, as hypotheses regarding ecological
17 segregation must incorporate regional environmental conditions (Bonenfant et al.,
18 2004; Bugalho et al., 2001; Main et al., 1996).

20 The red deer (*Cervus elaphus*) is a sexually dimorphic polygynous ungulate widely
21 distributed in temperate zones, with populations living under different management
22 and environmental regimes. It is therefore an ideal model species for testing the
23 applicability of existing theories regarding sexual foraging segregation in ungulates
24 living in environments of contrasting climate and resource availability patterns
25 (Putman and Flueck, 2011).

Identifying diet and nutritional preferences of both sexes in a deer population within a Mediterranean environment with regards to a temporal framework may provide a novel insight into mechanisms driving sexual segregation.

2. Materials and methods

2.1 Study area

The study was conducted in a fenced hunting estate in the province of Ciudad Real, Castile-La Mancha, central Spain (38°55'N 0°36'E), during autumn 2006 and the following winter and summer. The 724-ha estate is located in a region of Mediterranean-continental climate, characterized by summer drought (mean yearly rainfall: 356mm., mean rainfall in August: 7mm.). The estate is mainly devoted to large ungulate hunting. The semi-free ranging ungulate guild consists of the aoudad (*Ammotragus lervia* Pallas), the European mouflon (*Ovis orientalis musimon* Schreber), wild boar (*Sus scrofa* L.) and the Iberian red deer (*Cervus elaphus hispanicus* Hilzheimer). The latter is the most abundant with around 400 individuals (0.6 deer/ha). High-density deer populations living in fenced estates are common in the central-southern Iberian Peninsula (Bugalho et al., 2001; Lazo et al., 1994).

The plant community has a patchy structure composed of Mediterranean evergreen scrubland and pastures with scattered holm oaks (*Quercus ilex* L.). The dominant shrub species are *Cistus ladanifer* L., *Phyllirea angustifolia* L., *Rosmarinus officinalis* L., *Quercus ilex* L., *Erica* spp. and *Genista hirsuta* Vahl. Annual grasses dominate the herbaceous layer, with a smaller proportion of forbs (mainly Compositae, Leguminosae, Cistaceae and Brassicaceae). In part of the study area (64 Ha in 2006 and 52 Ha in 2007), the estate staff planted oats as food for ungulates as well as

1 offering them a daily supplementary concentrate in troughs. The supplementary
2 concentrate consisted of cereal and legumes in similar proportions and it was
3 supplied in 36 troughs distributed throughout the estate, being most of them located
4 within pastures. Because the concentrate contained different species depending on
5 the season, its nutritional composition varied across the year (October-March: 9.7
6 hemicellulose (HC), 7.0 cellulose (C), 3.25 total N; March to October: 11.7 HC, 13.7
7 C, 3.0 total N, all values expressed as g/100g dry matter).

9 *2.2 Vegetation cover*

10 Plant cover was characterized for each of the study periods along 50 m transects at
11 20 randomly selected locations within 3 differentiated habitats in the study area:
12 pastures, scrubland and habitat edge. The availability of herbs was determined up to
13 the family level and scrub cover to the species level. Vegetation cover was registered
14 in 100 points along transects. Shrubs were regarded as available if they had green or
15 greenish foliage within an animal's reach (≤ 2 m. high).

17 Mediterranean main flowering and growing season concurs with the birth period of
18 red deer (March-May), while summer (June-September) is characterised by droughts
19 and a low availability and quality of resources. A secondary re-growth of vegetation
20 takes place during the autumn rains (late September-December).

22 *2.3 Sex-age class distinction*

23 Deer age was estimated in hunted individuals from the tooth eruption pattern up to 24
24 months (Sáenz de Buruaga et al., 1991) and from histological examinations of
25 incisors for animals older than 24 months (Hamlin et al., 2000). For all analyses,

1 each study animal was assigned to a major sex-age class following the criteria in
2 Carranza (2004). Red deer remain with their mothers until approximately two years of
3 age conforming the nursery groups (does, fawns and yearlings of either sex). At that
4 age, males have been observed to leave the family group, and most females give
5 birth to their calves in their second year. Animals over two years were therefore
6 classified as adults and all animals below two years as juveniles. Since males and
7 females below two years are of approximately the same size, 3 sex-age classes were
8 defined: adult males, adult females and juveniles (including both males and females).

10 *2.4 Diet composition*

11 The botanical components of the diet were determined using microhistological analysis
12 of plant remains in faecal samples (Henley et al., 2001; Stewart, 1967). Faecal
13 samples were collected from hunted deer during three periods corresponding to
14 definite reproductive states in Iberian red deer: reproductive period (September) which
15 corresponds with the male rut and the late lactation period for females; post rutting
16 period (October, November and December) when males are recovering the condition
17 lost during rut, fawns are fully weaned, and females are in early gestation; and finally
18 late gestation (February and March) (Carranza, 2004). A total of 69 fresh faecal
19 samples were collected from all hunted animals, mainly in culls and occasionally in
20 beats during the specified periods: 8 adult females, 8 juveniles, 8 adult males during
21 the rut; 8 adult females, 13 juveniles, 6 adult males during the post-rutting period; and
22 5 adult females, 8 juveniles and 5 adult males during the late gestation. For each
23 animal, sex, age class (adult or juvenile) and body weight were registered. Although
24 fresh scats collected in the field from tracked animals were available, only faeces from
25 hunted deer were used for this study because of the importance of knowing the

individual body weight in order to test segregation hypotheses based on allometric predictions. Since faecal sampling relied on hunting activity, samples could not be collected during the birth period i.e. spring and early summer as this is off-hunting season.

Fresh faeces were frozen after collection and kept at -20°C until further analyses.

From each sample, 10 g were placed in a test tube with 5 ml of 65% concentrated NO_3H . Test tubes were then boiled in a water bath for 1 min. After digestion in NO_3H , samples were diluted with 200 ml of water. This suspension was then passed through 0.5 and 0.125 mm sieves. The 0.125 to 0.5 mm fraction was spread on glass microscope slides in a 50% aqueous glycerine solution. Two slides were prepared from each sample. Slides were examined under a microscope at 100× to 400× magnifications by viewing transects with a total of 20 fields (2 mm²) in each slide. Plant fragments in each field of view were recorded and counted until a minimum of 100 leaf epidermal fragments were identified from each slide. Epidermal fragments in faeces were compared with a previously prepared reference collection (unpublished data). Consumption on supplementary food could not be assessed through microhistological analysis of faeces since it is a concentrate and no epidermal remains could be observed in the faecal samples.

3 coarse forage type categories were considered when testing for differences in seasonal feeding preferences by male, female and juvenile deer. All graminoids were assigned to the grass category; the forb category comprised all dicotyledonous herbs, and woody species were assigned to the shrub category. Plant resources are generally aggregated under these 3 categories since grasses, forbs and shrubs present themselves in very different ways to the foraging herbivore and differ in

1 physical structure and nutritional attributes (van Wieren and van Langevelde, 2008).

2 General nutritional traits of these 3 forage categories include higher cellulose and
3 hemicellulose contents for grasses, and a higher concentration of cell contents, plant
4 secondary compounds and nitrogen in forbs and shrubs, the latter containing in
5 addition greater proportions of lignin (Codron and Brink 2007; van Wieren and van
6 Langevelde 2008).

7 8 *2.5 Nutritional content of the diet*

9 According to previous field observations, we harvested leaves and stems of the most
10 ubiquitous and diet-relevant shrub species occurring in the study site, as well as a bulk
11 sample of the herbaceous layer for nutrient evaluation. Collected shrub species were:

12 *Cistus* spp., *Cytisus* spp., *Erica* spp., *Phillyrea angustifolia* and *Quercus* spp.

13
14 Harvested plant samples were oven-dried at 60°C until constant weight, stabilized at
15 ambient temperature for 48 h and ground to 1 mm before analyses. All analyses
16 were carried out on duplicate samples and results reported as g/100g dry matter. The
17 total dry matter content of each sample was determined by drying to constant weight
18 in a forced air oven at 103°C (AOAC, 2005). Organic matter was determined by
19 ashing samples in a muffle furnace for 3 hours at 550°C (AOAC, 2005). Structural
20 carbohydrates, which constitute the cell wall, were determined according to the
21 sequential procedure of Van Soest et al. (1991) using an Ankom 220 Fibber Analyzer.
22 This procedure first extracts all soluble, largely digestible cell components and
23 separates them from those components whose microbial fermentation requires a
24 longer digestion time, i.e. hemicellulose, cellulose and lignin. The material that
25 remains after this neutral detergent dilution constitutes the neutral detergent fibre

(NDF). Then, after digestion in an acid detergent solution, a residual mainly composed of cellulose and lignin is obtained; this is known as acid detergent fibre (ADF). Acid detergent lignin (ADL), a fraction of the cell wall mainly composed by lignin, is extracted after digestion in SO_4H_2 . HC was estimated as the difference between NDF and ADF, and C as the difference between ADF and ADL. Total N was assessed by Kjeldahl analysis following AOAC (2005). Total N provides a measure of the crude protein available ($\text{total N} \times 6.25 = \text{crude protein}$) which is important for the efficient functioning of rumen microorganisms as well as providing for the N required by the host animal for growth, lactation and reproduction (Landete-Castillejos et al., 2003; Van Soest, 1982). Nitrogen bound to ADF was determined by Kjeldahl analysis of ADF residues. Available nitrogen was calculated as the difference between total nitrogen and nitrogen bound to ADF. Free, protein-bound and fibre-bound condensed tannins were determined following the colorimetric methods described by Pérez Maldonado and Norton (1996). Total condensed tannins were calculated as the sum of these 3 fractions. Lignin and tannins are considered as digestive retardants, the former limiting digestion of HC and C (Van Soest, 1982), and the latter binding and precipitating plant proteins resulting in a decreased digestibility (Robbins et al., 1987).

2.6 Diet and nutrient selection

The proportion of plant species found in deer dung and the nutritional content of the diet are constrained by plant availability. Therefore, the Savage Selectivity Index (Manly et al., 2002) was used in order to adjust the use of each plant species with respect to its relative availability for each study period. 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), 1 being the value defining the selection expected by chance.

Selectivity for the different nutritional components was assessed according to Verheyden-Tixier et al. (2008). The content of nutrient Nt in diets (Nt_d) was first determined using the equation (eqn 1).

$$(eqn 1) \quad Nt_d = \sum_{i=1}^x D_i * Nt_i$$

where D_i is the proportion of vegetation item i in faeces and Nt_i is the concentration of nutrient Nt in item i . Once the nutrient content in diet was determined, nutrient availability in the study area was assessed; the content of nutrient Nt in the available vegetation (Nt_a) was calculated using (eqn 2).

$$(eqn 2) \quad Nt_a = \sum_{i=1}^n A_i * Nt_i$$

where A_i is the proportion of vegetation item i in the field transects. The Savage Index was subsequently calculated to determine selection for each nutrient.

The values resulting from Savage Index calculations for plant categories and nutritional components as described in this section were used for all analyses and hereafter will be referred to as diet selection and nutrient selection, respectively.

2.7 Data analyses

Multivariate analyses of covariance (MANCOVA) were used to simultaneously analyse diet selection of 3 forage categories, grasses, forbs and shrubs. Pillai's trace was applied since it has been widely recommended as a multivariate test statistic (Garson, 2009). In the model, period and sex-age class were used as fixed factors and the Savage Selection Index for each diet category as the dependent variable. To control for the effect of body weight, the residuals from a linear model of body weight against sex-age class were added as a covariate. These residuals were added rather than the raw weights since they reflect the residual effects of body weight after the effect of sex-age class has been accounted for. When significant effects were observed, multiple comparisons were performed by using pairwise t-tests, and p levels were adjusted following the false discovery rate method (Benjamini and Hochberg, 1995).

A Principal Components Analysis (PCA) was carried out on nutrient selection, i.e. Savage indexes calculated for cellulose, hemicellulose, lignin, total and available nitrogen, and tannins. This PCA allowed us to obtain a reduced set of variables that summarize nutritional selection. The correlation matrix between original variables was used. Nutritional principal components were rotated by the varimax normalized procedure, which improved the interpretability of the factors. A MANCOVA similar to that previously described for diet was used to analyse the effects of period, sex-age class and body weight on each nutritional principal component.

When necessary, Box-Cox transformations (Box and Cox, 1964) were applied to data in order to meet the assumption of homocedasticity. All hypotheses testing were

carried out using non-sequential type III sums of squares, which is appropriate for unbalanced data (Langsrud, 2003). Analyses were performed using SPSS 17.0 package (SPSS Inc., Chicago IL) and R version 2.10 (R Development Core Team, 2009). Type III sum of squares were calculated in R using the Car package (Fox, 2009).

3. RESULTS

3.1 Shifts in forage selection across periods

There was a significant interaction effect between period and sex-age class on dietary selection by deer ($F_{12,153} = 2.9$, $P = 0.001$) (Table 1). During the rut, males selected significantly more grasses and forbs compared to both females and juveniles ($P < 0.01$), and significantly less shrubs ($P < 0.0001$) (Fig. 1). There were no significant differences ($P > 0.10$) in diet selection outside the mating season.

3.2 Differing nutritional preferences between deer classes

The average nutritional content of diet was determined for each period and deer class (Table 2). The PCA yielded two main nutritional axes that accounted for 94.5% of the original variation in nutrient selection (Table 3). The first component (NUT 1) consisted of cell contents, i.e. available and total N on one extreme, and cellulose on the other extreme of the axis (factor loadings higher than 0.7 were considered, Garson 2011). The second component (NUT2) consisted of tannins and cell wall constituents. Nutrients showing positive loadings on this axis were lignin and tannins while factors loading negatively on the axis included hemicellulose. There was a significant ($P < 0.001$) interaction effect of period and sex-age class on NUT1 and NUT 2 scores (Table 4). For NUT 1, during the rut, males exhibited a lower

1 preference for available and total N and higher for cellulose compared to both
2 females and juveniles ($P < 0.0001$, Fig. 2a). There were no differences between sex-
3 age classes for NUT 1 values in neither the post rutting period nor during late
4 gestation ($P > 0.5$). As for NUT 2, there were, similarly, significant differences
5 between males and both females and juveniles during the rut ($P < 0.0001$) but not
6 outside the mating period ($P > 0.3$) (Fig. 2b).

8 **4. DISCUSSION**

9 We report foraging differences and overlaps between sexes in Iberian red deer
10 across reproductive states and seasons that may contribute to the understanding of
11 sexual segregation patterns in dimorphic ungulates within semi-arid ecosystems. We
12 simultaneously assessed botanical and nutritional preferences of three sex-age
13 classes in Iberian red deer across reproductive periods. Under high densities in a
14 Mediterranean ecosystem, dietary and nutritional preferences of Iberian red deer
15 significantly differed between males and females/juveniles during the rut, whereas no
16 differences were detected between sex-age classes during the post rutting period
17 and late gestation. Dissimilar foraging behaviour between classes corresponds with
18 the least favourable time in terms of food resource quality and availability. By
19 quantifying actual foraging and nutritional preferences, we provide a necessary
20 insight into the mechanisms underlying the dietary-related hypotheses of sexual
21 segregation in dimorphic ungulates i.e., the FSH and the RSH.

22
23 The main segregation hypotheses consider sexual divergence in resource selection a
24 consequence of allometry between sexes, but the majority of studies do not include
25 individual body mass as a variable in the model (Mooring et al., 2005; Shannon et al.,

2006). Here we found, as expected, significant between-class differences in body weight. However, intra-class allometry did not have an effect on any of the analyzed dietary parameters. Body size, hence, seemed to play a role only when differences are large (see Illius and Gordon, 1987), such as those found between red deer sexes.

Analyzed dietary and nutritional components showed similar patterns for females and juveniles, so that they could be considered as a unique group from a dietary point of view. This is consistent with observations on red deer elsewhere, where deer segregate during most of the year into 2 types of groups: male groups and nursery groups (Clutton-Brock et al., 1982). Some studies have even considered each sex as a distinct ecological species (Shannon et al., 2006). In our study area, segregation in terms of diet selection between male and females/juveniles occurred during the least favourable period in terms of resources availability and quality, i.e. the late summer or rut. During that period, females and juveniles exhibited, compared with males, a higher selection for shrubs, which are mostly evergreen species and offer a key resource (*sensu* Scoones, 1991) that remains as good quality forage during the harsh Mediterranean summers (Bugalho and Milne, 2003). Males preferred grasses and forbs instead, which are senescent during this season. This behaviour would correlate with the Jarman Bell principle (Demment and van Soest, 1985) that predicts that larger animals can subsist on lower quality bulk food because their larger rumino-reticular volume makes them more efficient at assimilating fibres and because of their lower relative metabolic requirements. Foraging behaviour observed in the current study agrees with results for both male and female trophic patterns from another high density Mediterranean estate, where stags used a less suitable

1 area dominated by *Cistus* spp. and dry grasses whereas females fed in areas with a
2 more nutritious woody plant supply, during the summer (Lazo et al., 1994).

3 The results regarding foraging preferences during the rut seem, therefore, to be in
4 accordance with the Foraging Selection Hypothesis (FSH), in which the smaller
5 females and juveniles are predicted to selectively feed on high protein and highly
6 digestible forage, while larger males subsist on high fibre forage (see v.g. Clutton-
7 Brock and Albon, 1989; Long et al., 2009). However, the present study does not
8 evaluate the actual subsistence of males based on that low-quality diet so our data
9 cannot fully support the FSH hypothesis. Also, as our results are based on feeding
10 preferences, we are not able to deduce whether the Scramble Competition
11 Hypothesis or the Gastrocentric Hypothesis provide an explanation for the observed
12 preferences. Additional data on habitat use and activity patterns are needed to infer
13 potential competitive interactions between sexes.

14 Sex-dependent traits other than body weight might, however, provide further insights
15 in order to understand the observed foraging segregation during the rut. Two ultimate
16 and non-exclusive mechanisms have been suggested within the framework of the
17 Reproductive Strategy Hypothesis (RSH) that could help explaining this *a priori* non-
18 efficient male foraging behaviour. The first potential explanation states that evolved
19 sexual differences in reproductive strategies may have led to the observed outcome.
20 During the mating season, male red deer invest time and energy in mating strategies
21 in order to maximize their reproductive success (Clutton Brock et al., 1982) and this
22 behaviour prevents them from allocating resources into the search of high quality
23 foraging areas. The second plausible explanation within the RSH predictions for
24 rutting male “inefficient” foraging was provided by Carranza (1995) where males

1 would be displaying territorial behaviour during the rut, defending a territory (the
2 pastures) that, although of no nutritional value at that time, will considerably increase
3 its forage quality and attract the females in late September, after the first rains. The
4 landscape in the study area is a mosaic with two kinds of patches: pastures
5 (containing grasses, and forbs on a lower proportion) and scrubland (mainly
6 evergreen shrubs). Male selection for grasses during the rut could imply a
7 preferential use of pastures and support red deer territoriality. However, this needs to
8 be confirmed with further data on habitat use. Male Iberian red deer have also been
9 shown to defend routes of females to feeding sites and artificial food sources i.e.
10 troughs that attract the females during this limiting season and facilitate the defence
11 of a harem (Carranza, 2004; Carranza et al., 1996).

12
13 As for females, their selection of resources that provide a higher nutritional return
14 probably responds to lactation and nursing demands during this time of the year
15 (Barboza and Bowyer, 2000; Landete-Castillejos et al., 2003). However, female
16 reproductive success relies not only on a good quality diet but also on a promotion of
17 their offspring's welfare through a reduction in predation risks (Bonenfant et al., 2004;
18 Long et al., 2009; Main, 2008). In our study area, despite the lack of natural
19 predators, human hunting activity takes place all year round except in spring. So, in
20 contrast to the trade off that females face in northern climates between choosing a
21 habitat that either maximizes high quality forage intake or "predator" avoidance (Main
22 et al., 1996), our study animals could simultaneously optimize both factors that
23 concur in the same habitat during the Mediterranean rut, i.e. in scrubland. Data on
24 habitat use are necessary to test this potential preference of females for shrublands.

Therefore, RSH seems to provide the most likely explanation for the different dietary preferences observed for male and female Iberian red deer during rut.

Regarding the post rut and late gestation periods, an unexpected overlap in dietary selection was observed between sexes. This outcome contradicts results obtained in other areas where red deer are present (Bonenfant et al. 2004; Clutton-Brock et al. 1982) as well as general segregation assumptions for dimorphic polygynous ungulates that predict dietary sexual segregation outside the mating season (Main et al. 1996; Ruckstuhl and Neuhaus 2002). FSH fails to explain the lack of a continued dietary segregation, since differential forage use would be expected under the assumption of distinct nutritional requirements and digestion capacity of both sexes. Moreover, the higher absolute biomass requirements of males would not be achieved if they fed on the same resources as big nursery groups, because of competition effects under high animal densities (Main et al., 1996). As a result, and under limiting conditions, males would select a less suitable resource in order to avoid intraspecific competition and to maximize their absolute energy gain (Barboza and Bowyer, 2000). These trophic differences would arise whenever conditions are limiting, however, in the Mediterranean climate the autumn (post-rut) is a growing season and as suggested by Barboza and Bowyer (2000) and Perez-Barbería et al. (2008), trophic segregation is unlikely in the absence of resource constraints. Male and female diet overlap in this period is probably due to the need to restore body reserves lost during the rut and lactation, the substantial re-growth of herbs and shrubs that takes place during this rainy period, and the availability of ripe holm oak acorns, which constitute an important proportion of deer diet during this period (Rodríguez Berrocal, 1978; Soriguer et al., 1994). This overlap in resource use would not necessarily prevent

male consumption of greater amounts of the shared resources in order to fulfil their high energy requirements during the post rutting period (Clutton Brock et al., 1982). The overlap in diet selection between sex-age classes outside the breeding season would therefore support the RSH predictions of male diet being of similar or even superior quality than that of females when high-quality forage is readily available (Main, 2008).

The area in which the study was undertaken, as well as many of the game estates in Mediterranean Spain, is under intense management measures that could differentially affect sexes leading to altered foraging patterns. Regarding hunting practices, kills are not aimed at a specific sex-age class (i.e. adult males) but are evenly spread across the three sex-age classes considered (see section 2.4). So the presence of this “predation pressure” would equally impact male, female and juvenile habitat use and foraging patterns. As for the supplementary concentrate in the study site, it is provided daily in troughs in order to enhance deer survival and reproduction rates and promote trophy sizes and quality. Although this common practice adds artificiality to the management of southern Iberian hunting estates, it allows a better visualization of the different plant species selection as 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). In the study area, equal and free access to artificial food for the 3 study classes is ensured during most of the year through the specific architecture of certain troughs that allows exclusive access to females and juveniles (with bars that impede feeding to animals holding antlers). Moreover, our observations confirmed that trough use did not differ between males, lactating and non-lactating females at any time of the year (Sicilia, 2011).

1 Therefore, since all deer sex-age classes have access to available supplementary
2 food, significant differences in plant selection suggest that sex-specific resource
3 selection is taking place in the study area.

4
5 Both this and other studies (e.g. Long, et al., 2009; Main, 2008; Ruckstuhl, 2007)
6 suggest that several environmental and behavioural variables interact with season
7 and reproductive status to shape sexual segregation in ungulates. Therefore, it is
8 difficult to identify one single factor that explains temporal dietary overlap and
9 segregation between deer sexes. In this study, the contrasting fitness strategies held
10 by the two sexes together with their seasonal nutritional requirements seemed to
11 explain the observed foraging and nutritional selection in the study population.
12 Nevertheless, data on spring resource preferences and habitat use by red deer in
13 Mediterranean environments are needed to further test these hypotheses.

14
15 Finally, we would like to stress that our findings must be interpreted under the
16 conditions driving Mediterranean resource availability. The widely accepted
17 hypothesis (FSH and RSH) can be applied to Mediterranean climatic conditions to a
18 certain extent, but some important aspects should be taken into consideration, such
19 as the asynchrony between high food availability and high energy requirement
20 periods for animals. Mediterranean climates are characterized by a summer drought
21 that implies significant food shortages during July, August and September for red
22 deer in the study area. This period of low resource availability corresponds with the
23 period of the highest energy needs, since males are storing energy and gaining
24 weight in preparation for rut and females are nursing their offspring (Barboza and
25 Bowyer, 2000; Landete-Castillejos et al., 2000). We have shown here how we need

1 to adapt the generally accepted hypotheses of ecological segregation to the
2 particular conditions of a Mediterranean area, where RSH can explain the dietary
3 segregation during the nutritional constraints in the rutting period. Furthermore,
4 Iberian red deer have been found to differ in activity patterns, home range (Carranza
5 et al., 1991), group size dynamics (Carranza and Valencia, 1992), and reproductive
6 strategies (Carranza et al., 1996) when compared to northern and central European
7 populations (see also, Putman and Flueck, 2011).

9 In sum, this study highlights both the importance of measuring not only the spatial
10 and social components but also a dietary component and providing a temporal
11 framework when documenting ungulate sexual segregation, and the interest of
12 incorporating regional climatic conditions when addressing management of ungulates
13 with a wide geographic distribution.

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6. REFERENCES

- AOAC, 2005, Official Methods of Analysis. 18th ed. Association of Official Analytical Chemists, Gaithersburg, MD Chemists, Washington DC.
- Barboza, P.S., Bowyer, R.T., 2000. Sexual segregation in dimorphic deer: A new gastrocentric hypothesis. *Journal of Mammalogy* 81, 473-489.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B* 57, 289-300.
- Bonenfant, C., Loe, L.E. , Mysterud, A. , Langvant, R. , Stenseth, N.C. , Gaillard, J.M., Francois, K., 2004. Multiple causes of sexual segregation in European red deer: enlightenments from varying breeding phenology at high and low latitude. *Proceedings of the Royal Society, Series B* 271, 883-892.
- Box, G.E.P., Cox, D.R., 1964. An analysis of transformations. *Journal of the Royal Statistical Society, Series B* 26, 211-246.
- Bugalho, M.N., Milne, J.A., 2003. The composition of the diet of red deer (*Cervus elaphus*) in a Mediterranean environment: a case of summer nutritional constraint? *Forest Ecology and Management* 181, 23-29.

- 1 Bugalho, M.N., Milne, J.A. , Racey, P.A., 2001. The foraging ecology of red deer
(*Cervus elaphus*) in a Mediterranean environment: is a larger body size
advantageous? Journal of Zoology 255, 285-289.
- 2 Carranza, J., 1995. Female attraction by males versus sites in territorial rutting red
deer. Animal Behaviour 50, 445-453.
- 3 Carranza, J., 2004. Ciervo - *Cervus elaphus*. In Enciclopedia Virtual de los
Vertebrados Españoles (A.Salvador and J. Cassinello, eds). Museo Nacional
de Ciencias Naturales, Madrid. Retrieved 16/09/2011 from
<http://www.vertebradosibericos.org/>
- 4 Carranza, J., Detrucios, S.J.H. , Medina, R. , Valencia, J., Delgado, J., 1991. Space
use by red deer in a Mediterranean ecosystem as determined by radio-
tracking. Applied Animal Behaviour Science 30, 363-371.
- 5 Carranza, J., Fernandez-Llario, P., Gomendio, M.,1996. Correlates of territoriality in
rutting red deer. Ethology 102, 793-805.
- 6 Carranza J., Valencia, J., 1992. Organización social del ciervo en habitat
mediterráneo. Miscellanea Zoologica 16, 223-232.
- 7 Clutton-Brock, T.H., Albon, S.D., 1989. Red deer in the Highlands. Blackwell
Scientific Publications, Oxford.
- 8 Clutton-Brock, T.H., Guinness, F.E., Albon, S.E., 1982. Red Deer. Behaviour and
ecology of two sexes. Edinburgh University Press, Edinburgh.
- 9 Codron, D., Brink, J.S., 2007. Trophic ecology of two savanna grazers, blue
wildebeest *Connochaetes taurinus* and black wildebeest *Connochaetes gnou*.
European Journal of Wildlife Research 53: 90-99.
- 10 Demment, M.W., Van Soest, P.J., 1985. A nutritional explanation for body size
patterns of ruminant and non-ruminant herbivores. American Naturalist 125,

641-672.

Festa-Bianchet, M., 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* 75, 500-506.

Fox, J., 2009. Car: Companion to Applied Regression. R package version 1.2-16. <http://CRAN.R-project.org/package=car>.

Garson, G.D., 2011. Factor analysis, from Statnotes: Topics in Multivariate Analysis. Retrieved 01/03/2011 from <http://faculty.chass.ncsu.edu/garson/pa765/statnote.htm>

Garson, G.D., 2009. Multivariate GLM, MANOVA and MANCOVA, from Statnotes: Topics in Multivariate Analysis. Retrieved 01/03/2011 from <http://faculty.chass.ncsu.edu/garson/pa765/statnote.htm>.

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

Henley, S.R., Smith, D.G., Raats, J.G., 2001. Evaluation of 3 techniques for determining diet composition. *Journal of Range Management* 54, 582-588.

Illius, A.W., Gordon, I.J. 1987. The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* 56, 989-999.

Landete-Castillejos, T., Estévez, J.A., Martínez, A., Ceacero, F., Garcia, A., Gallego, L., 2007. Does chemical composition of antler bone reflect the physiological effort made to grow it? *Bone* 40, 1095-1102.

Landete-Castillejos, T., Garcia, A., Gómez, J.A., Gallego, L., 2003. Lactation under food constraints in Iberian red deer *Cervus elaphus hispanicus*. *Wildlife Biology* 9, 131-139.

- 1 Landete-Castillejos, T., Garcia, A. , Molina, P., Vergara, H. , Garde, J., Gallego, L.,
2 2000. Milk production and composition in captive Iberian red deer (*Cervus*
3 *elaphus hispanicus*): effect of birth date. Journal of Animal Science 78,2771-
4 2777.
- 5 Langsrud, Ø., 2003. ANOVA for Unbalanced Data: Use Type II Instead of Type III
6 Sums of Squares. Statistics and Computing 13,163-167.
- 7 Lazo, A., Soriguer, R.C., Fandos, P., 1994. Habitat use and ranging behavior of a
8 high-density population of Spanish red deer in a fenced intensively managed
9 area. Applied Animal Behaviour Science 40, 55-65.
- 10 Long, R.A., Rachlow, J.L., Kie, J.G., 2009. Sex-specific responses of North American
11 elk to habitat manipulation. Journal of Mammalogy 90, 423-432.
- 12 Main, M.B., 2008. Reconciling competing ecological explanations for sexual
13 segregation in ungulates. Ecology 89, 693-704.
- 14 Main, M.B., Weckerly, F.W., Bleich, V.C., 1996. Sexual segregation in ungulates:
15 New directions for research. Journal of Mammalogy 77, 449-461.
- 16 Manly, B.F.J., McDonald, L.L., McDonald, T.L., Ericsson, W.P., 2002. Resource
17 selection by animals. Statistical design and analyses for field studies, second
18 ed. Kluwer Academic Publishers, Amsterdam, The Netherlands.
- 19 McArthur, C., Goodwin, A., Turner, S., 2000. Preferences, selection and damage to
20 seedlings under changing availability by two marsupial herbivores. Forest
21 Ecology and Management 139,157-173.
- 22 Mooring, M.S., Reisig, D.D., Osborne, E.R., Kanallakan, A,L., Hall, B.M., Schaad,
23 E.W., Wiseman, D.S., Huber, R.R., 2005. Sexual segregation in bison: a test
24 of multiple hypotheses. Behaviour 142, 897-927.

- 1 Oftedal, O.T., 1985. Pregnancy and lactation, in: Hudson, R., White, R.G. (Eds.),
2 Bioenergetics of Wild Herbivores. Boca Raton, CRC Press, Florida, pp. 215-
3 238
- 4 Pérez-Barbería, F.J., Pérez-Fernández, E., Robertson, E., Álvarez-Enríquez, B.,
5 2008. Does the Jarman-Bell principle at intra-specific level explain sexual
6 segregation in polygynous ungulates? Sex differences in forage digestibility in
7 Soay sheep. *Oecologia* 157, 21-30.
- 8 Pérez Maldonado, R.A., Norton, B.W., 1996. Digestion of 14 C-labelled condensed
9 from *Desmodium intortum* in sheep and goats. *British Journal of Nutrition* 76,
10 501-513.
- 11 Post, D.M., Armbrust, T.S., Horne, E.A., Goheen, J.R., 2001. Sexual segregation
12 results in differences in content and quality of bison (*Bos bison*) diets. *Journal*
13 *of Mammalogy* 82, 407-413.
- 14 Putman, R.J., Flueck, W.T., 2011. Intraspecific variation in biology and ecology of
15 deer: magnitude and causation. *Animal Production Science* 51, 277-291.
- 16 R Development Core Team, 2009. R: A language and environment for statistical
17 computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-
18 900051-07-0, URL <http://www.R-project.org>.
- 19 Robbins, C.T., Mole, S., Hagerman, A.E., Hanley, A., 1987. Role of tannins in
20 defending plants against ruminants: reduction in protein availability. *Ecology*
21 68, 98-107.
- 22 Rodríguez Berrocal, J. ,1978. Introducción al estudio y valoración de recursos
23 forestales y arbustivos para el ciervo, en el área ecológica de Sierra Morena:
24 I. Estudio de la dieta del ciervo. *Archivos de zootecnia* 27: 1-10.

- 1 Ruckstuhl, K.E., 2007. Sexual segregation in vertebrates: proximate and ultimate
2 causes. Integrative and Comparative Biology 47, 245-257.
- 3 Ruckstuhl, K.E., Neuhaus, P., 2000. Sexual segregation in ungulates: a new
4 approach. Behaviour 137,361-377.
- 5 Ruckstuhl, K.E., Neuhaus, P., 2002. Sexual segregation in ungulates: a comparative
6 test of three hypotheses. Biological Reviews 77, 77-96.
- 7 Sáenz de Buruaga, M., Lucio, A.J., Purroy, J., 1991. Reconocimiento de sexo y edad
8 en especies cinegéticas. Diputación Foral de Navarra, Vitoria, Spain.
- 9 Schroeder, C.A., Bowyer, R.T., Bleich, V.C., Stephenson, T.R., 2010. Sexual
10 segregation in Sierra Nevada bighorn sheep, *Ovis canadensis sierrae*:
11 ramifications for conservation. Arctic, Antarctic and Alpine Research 42, 476-
12 489.
- 13 Scoones, I., 1991. Wetlands in drylands: key resources for agricultural and pastoral
14 production in Africa. Ambio 20, 366-371.
- 15 Shannon, G., Page, B.R., Duffy, K.J., Slotow, R., 2006. The role of foraging
16 behaviour in the sexual segregation of the African elephant. Oecologia 150,
17 344-354.
- 18 Sicilia, M., 2011. Ecología y comportamiento de ungulados en simpatria en un
19 ambiente mediterráneo: interacciones entre especies nativas y exóticas de
20 interés cinegético. Ph.D. dissertation, Universidad de Castilla-La Mancha,
21 Ciudad Real, Spain.
- 22 Soriguer, R.C., Fandos, P., Bernáldez, E. & Delibes-Serna, J.R., 1994. El Ciervo en
23 Andalucía. Junta de Andalucía, Seville.
- 24 Staines, B.W., Crisp, J.M., Parish, T., 1982. Differences in the quality of food eaten
25 by red deer (*Cervus elaphus*) stags and hinds in winter. Journal of Applied

1 Ecology 19, 65-77.

2 Stewart, D.R.M., 1967. Analysis of plant epidermis in faeces: a technique for studying
3 the food preferences of grazing herbivores. Journal of Applied Ecology 4, 83-
4 111.

5 Van Soest, P.J., 1982. Nutritional Ecology of the Ruminant, second ed. Cornell
6 University Press, New York.

7 Van Soest, P.J., Robertson, J.B., Lewis, B.A., 1991. Methods for dietary fiber, neutral
8 detergent fiber, and nonstarch polysaccharides in relation to animal nutrition.
9 Journal of Dairy Science 74, 3583-3597.

10 Van Wieren S., van Langevelde, F., 2008. Structuring herbivore communities: the
11 role of habitat and diet, in: Prins, H.H. Tvan Langevelde, ., F. (Eds.), Resource
12 ecology: Spatial and temporal dynamics of foraging. Springer, Netherlands,
13 pp. 237-262.

14 Verheyden-Tixier, H., Renaud, P.C., Morellet, N., Jamot, J., Besle, J.M., Dumont, B.,
15 2008. Selection for nutrients by red deer hinds feeding on a mixed forest edge.
16 Oecologia 156, 715-726.

Figure captions

Figure 1. Selection of the 3 main forage categories (mean $\pm$ SE) by adult females

(circles), juveniles (triangles) and adult males (squares) across study periods.

Statistical analyses were conducted on the transformed values of variables, but

original values are shown in the figures

Figure 2. Mean scores $\pm$ SE extracted for a) principal component NUT 1 and b)

principal component NUT 2, for each period and sex-age class (females=circles,

juveniles=triangles and males=squares)

Table 1. Results of MANCOVA explaining the effects of period, sex-age class and residual body weight (Body weight res) on grass, forb and shrub selection. *F* approximate value (*F* approx), degrees of freedom (*df*1 and *df*2) and *P*-level (*P*) are reported.

Effect	<i>F</i> approx	<i>df</i> 1	<i>df</i> 2	<i>P</i>
Body weight res	0.3	3	49	0.83
Period	6.8	6	100	<0.001
Class	0.5	6	100	0.83
Body weight res * period	0.5	6	100	0.80
Body weight res * class	0.6	6	100	0.76
Period * class	2.9	12	153	0.001
Body weight res * period * class	0.5	12	153	0.89

Table 2. Nutritional content in deer diet for each period and sex-age class (g/100g DM). Means $\pm$ SE are provided for DM dry matter, OM organic matter, HC hemicellulose, C cellulose, lignin, total nitrogen, available nitrogen and tannins.

period	class	DM	OM	HC	C	Lignin	Total N	Available N	Tannins
rut	adult	69.57 $\pm$ 0.68	95.30 $\pm$ 0.06	19.77 $\pm$ 0.18	29.17 $\pm$ 0.62	14.17 $\pm$ 0.16	0.95 $\pm$ 0.01	0.58 $\pm$ 0.01	9.89 $\pm$ 0.31
	juvenile	68.50 $\pm$ 1.16	95.38 $\pm$ 0.10	19.40 $\pm$ 0.32	28.18 $\pm$ 1.05	14.46 $\pm$ 0.31	0.96 $\pm$ 0.02	0.58 $\pm$ 0.01	10.24 $\pm$ 0.38
	adult male	83.58 $\pm$ 2.72	94.03 $\pm$ 0.25	22.59 $\pm$ 0.55	39.45 $\pm$ 1.94	11.65 $\pm$ 0.39	0.74 $\pm$ 0.04	0.49 $\pm$ 0.02	5.93 $\pm$ 0.87
post-rut	adult	42.39 $\pm$ 0.63	94.28 $\pm$ 0.22	21.56 $\pm$ 0.43	26.31 $\pm$ 0.77	10.94 $\pm$ 0.26	1.27 $\pm$ 0.00	0.94 $\pm$ 0.01	17.04 $\pm$ 0.48
	juvenile	42.34 $\pm$ 0.40	94.29 $\pm$ 0.13	21.59 $\pm$ 0.24	26.38 $\pm$ 0.42	10.90 $\pm$ 0.17	1.28 $\pm$ 0.00	0.94 $\pm$ 0.00	16.93 $\pm$ 0.24
	adult male	41.37 $\pm$ 1.57	93.97 $\pm$ 0.61	22.18 $\pm$ 1.25	27.45 $\pm$ 2.23	10.32 $\pm$ 0.53	1.28 $\pm$ 0.02	0.96 $\pm$ 0.01	16.17 $\pm$ 1.88
late gestation	adult	39.49 $\pm$ 0.29	92.95 $\pm$ 0.09	17.74 $\pm$ 0.03	15.93 $\pm$ 0.10	12.89 $\pm$ 0.09	1.85 $\pm$ 0.01	1.48 $\pm$ 0.02	18.37 $\pm$ 0.40
	juvenile	39.11 $\pm$ 0.20	92.84 $\pm$ 0.06	17.77 $\pm$ 0.04	15.88 $\pm$ 0.05	13.33 $\pm$ 0.13	1.87 $\pm$ 0.01	1.50 $\pm$ 0.01	18.79 $\pm$ 0.29
	adult male	40.79 $\pm$ 0.91	93.44 $\pm$ 0.32	17.49 $\pm$ 0.16	15.92 $\pm$ 0.15	13.33 $\pm$ 0.36	1.78 $\pm$ 0.04	1.38 $\pm$ 0.06	20.34 $\pm$ 1.08

Table 3. Factor loadings of each of the nutritional variables on the axes extracted by principal component analysis. Range of measured selection over the 6 analyzed nutrients is also provided (MIN: minimum; MAX: maximum).

Nutritional variables	NUT1	NUT2	MIN.	MAX.
Hemicellulose	0.48	-0.85	0.82	1.18
Cellulose	0.93	-0.35	0.68	1.28
Lignin	0.46	0.81	0.73	1.45
Tannins	0.07	0.97	0.59	2.56
Available N	-0.93	-0.35	0.62	1.30
Total N	-0.97	-0.08	0.74	1.27
Eigenvalue	3.12	2.55		
Explained variance (%)	51.93	42.52		

Table 4. Results of MANCOVA explaining the effects of period, sex-age class and residual body weight on nutritional components NUT1 and NUT2. *F* approximate value, degrees of freedom and *P*-level are reported.

Effect	<i>F</i> approx	<i>df</i> 1	<i>df</i> 2	<i>P</i>
Body weight res	0.66	2	50	0.52
Period	21.22	4	102	<0.001
Class	0.63	4	102	0.64
Body weight res * period	0.84	4	102	0.50
Body weight res * class	0.31	4	102	0.87
Period * Class	6.35	8	102	<0.001
Body weight res * period* class	0.97	8	102	0.46

Highlights:

- We compared diet and nutrient selection for 3 sex-age classes in Iberian red deer.
- Foraging sexual segregation was found during the resource-limiting rut.
- Low resource quality and contrasting factors affecting reproductive success of both sexes might explain observed differences during rut.

Figure

Fig. 1

Figure

Fig. 2