



*Management and Conservation Article*

# Relative Effect of Food Supplementation and Natural Resources on Female Red Deer Distribution in a Mediterranean Ecosystem

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**ABSTRACT** Supplementary feeding is a widespread game management practice in several red deer (*Cervus elaphus*) populations, with important potential consequences on the biology of this species. In Mediterranean ecosystems food supplementation occurs in the rutting period, when it may change mating system characteristics. We studied the role of food supplementation relative to natural resources in the spatial distribution, aggregation, and mean harem size of females in Iberian red deer (*Cervus elaphus hispanicus*) during the rut. We studied 30 red deer populations of southwestern Spain, 63% of which experienced supplementary feeding. Using multivariate spatial analyses we found that food supplementation affected distribution of females in 95% of the populations in which it occurred. Green meadows present during the mating season acted as an important natural resource influencing female distribution. Additionally, the level of female aggregation and mean harem size were significantly higher in those populations in which food supplementation determined female distribution than in populations in which female distribution did not depend on supplementary feeding. Because female aggregation and mean harem size are key elements in sexual selection, supplementary feeding may constitute an important anthropogenic element with potential evolutionary implications for populations of Iberian red deer.

**KEY WORDS** *Cervus elaphus*, environmental resources, female aggregation, mating system, Mediterranean ecosystems, spatial analyses.

Supplementary feeding of ungulate game species during seasons of low food abundance is a common management practice in many countries of Europe, as well as in North America (Guillett et al. 1996, Gundersen et al. 2004, Putman and Staines 2004). Snow and low winter temperatures compel managers to supply food to deer to maintain their body condition and fecundity, to increase overwinter survival, to reduce damage caused to agriculture and forestry, and to produce trophy antlers (Klein 1985, Putman and Staines 2004). In red deer (*Cervus elaphus*) populations, food supplementation is particularly common and may have important consequences (Smith 2001, Putman and Staines 2004). These consequences can be beneficial, such as enhancing body condition (Putman and Langbein 1992, Kozak et al. 1995) or increasing male antler size (Rossler 1983). They may also not occur (Groot Bruinderink et al. 2000) or even be harmful for deer populations (Smith 2001, Schmidt and Hoi 2002, Miller et al. 2003), vegetation (Smith 2001, Cooper et al. 2006), and other community levels (Côté et al. 2004). Food supplementation is likely not neutral with regard to several physiological, ecological, and evolutionary features of red deer populations.

In Spain, Iberian red deer (*C. elaphus hispanicus*) populations inhabit mostly private hunting estates located in Mediterranean ecosystems. In the regions of Europe with a Mediterranean climate, such as southwestern Spain,

winters are mild and the limiting seasons are summer and early autumn, when drought can severely reduce food availability (Bugalho and Milne 2003, Olea et al. 2005). It is at this time, which includes the rutting period of red deer (normally September), when some managers supply supplementary food (such as maize, alfalfa pellets, or silage) in certain areas. Some managers also seed crops (usually cereals such as oat, barley, or wheat) during spring for animals to graze during summer, and these crops often remain present until autumn. Because distribution of food resources normally determines female movements, food supplementation during the rut may affect the mating system (Emlen and Oring 1977, Carranza 1992, Shuster and Wade 2003). Supplementary food supply increases female aggregation and, consequently, male mating strategies are likely to change from harem defense to resource defense in which they defend territories rather than mobile harems (Carranza et al. 1990, 1995, 1996). Carranza et al. (1996) showed that the shift from harem defense to territory defense strategies occurs when the number of females reaches an average value of 3.5/ha. In addition, female aggregation tends to increase harem size and the degree of polygyny, so food supplementation in Mediterranean areas can also affect sexual selection and can consequently have important evolutionary consequences for red deer populations (Andersson 1994, Sánchez-Prieto et al. 2004).

Several studies have addressed the effect of food supplementation in red deer (reviewed in Putman and

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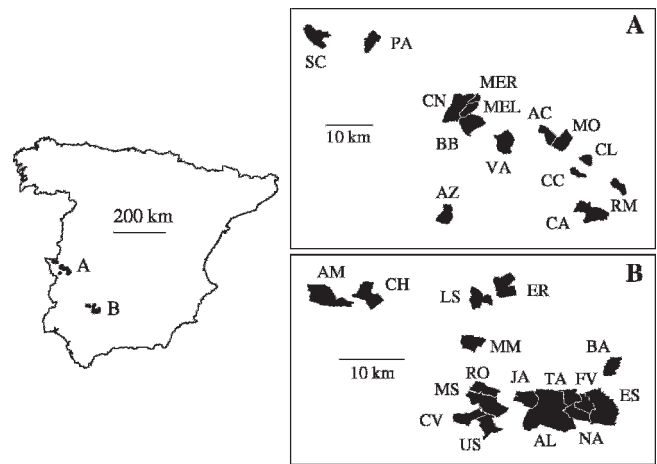
Staines 2004; see Sánchez-Prieto et al. 2004 for Iberian red deer). We focused on the relative importance of food supplementation and natural resources for distribution of red deer females and mean harem size in Mediterranean ecosystems. We first estimated frequency of food supplementation practices in red deer populations of southwestern Spain. We then built predictive models to determine effects of several natural and supplementary resources on female distribution in each studied population. Finally, we determined relative importance of supplementary food in relation to natural resources for female aggregation and mean harem size.

## STUDY AREA

The study area presented 2 types of general vegetation formations: Mediterranean scrubland and open grassland areas called “dehesas” (Olea et al. 2005). Scrubland was composed of species such as oaks (*Quercus ilex*, *Q. suber*), strawberry tree (*Arbutus unedo*), false olive (*Phillyrea angustifolia*), wild olive (*Olea europaea*), and several rockrose species (*Cistus* spp.), among others. Areas covered by Mediterranean scrub and forest constituted refuge zones and, mainly during summer, feeding areas (Rodríguez-Berrocal 1979). Dehesas were mainly covered by grassland and dispersed oak trees. Deer used dehesas as both feeding areas and rutting arenas. Dehesa productivity fluctuated seasonally, and it could be divided into 2 seasons: high and low productivity. Maximum productivity occurred during late autumn, winter, and spring, with presence of oak acorns and green grass. During summer and early autumn (dry season), dehesa productivity fell abruptly (Olea et al. 2005). In this period dehesas consisted mostly of a dry grassland with patches of different quantity or quality. Additionally, there were rich but scattered natural resources. For example, there could be green meadows where the moisture level was sufficient. Also, there could be perennial plants or shrubs such as jointleaf rush (*Juncus holoschoenus*) or wild blackberry (*Rubus ulmifolius*), located on dry or damp stream beds. Lastly, there were ponds that became the water supply for animals in the rutting season. These natural features, together with supplementary feeding, constituted the environmental factors that could influence female red deer distribution during the rut.

We studied the red deer populations of 30 hunting estates in southwestern Spain: 14 in the Extremadura region and 16 in the Andalucía region (Fig. 1). The estates had an average area of 1,211.15 ha ( $\pm 756.39$  ha). Dehesas of these estates, where we focused our field work, had an average area of 320.21 ha ( $\pm 292.21$  ha).

In Mediterranean ecosystems of the Iberian Peninsula red deer density ranged from 0.1 to 1.0 individuals per hectare, averaging around 0.3 individuals per hectare (J. Carranza, University of Extremadura, unpublished data). These high densities could be sustained because of the ecological characteristics of the Mediterranean ecosystems (J. Carranza, unpublished data).



**Figure 1.** Study area and location of the 30 estates within Spain, where we studied the effects of food supplementation on red deer distribution. (A) Estates in Extremadura region studied during 2004. (B) Estates in Andalucía region studied during 2005.

## METHODS

### Data Collection

For each estate, using aerial orthophotographs, we mapped the dehesa areas, registering distribution of environmental features such as ponds, streams, and crops. We then confirmed location of these features by in situ observations. For each grassland patch of the dehesas we measured the percentage of plant cover as an index of quantity and the percentage of leguminous plants as a measure of quality, because their high nitrogen content is important in plant-herbivore interactions (Whitehead 2000). We estimated the percentage of grassland cover and percentage of leguminous plants using 25-cm by 25-cm sampling frames divided into 4 quadrants (following Carranza et al. 1990). Grassland characterization took place during spring of 2004 in the estates of Extremadura and in spring of 2005 in Andalucía. Areas with the best grassland patches during spring can attract many individuals that fertilize them, so these areas usually remain as good-quality patches all year (Whitehead 2000). During the rutting season (Sep 2004 in Extremadura, Sep 2005 in Andalucía) we recorded the location of food supplementation sites and green meadows. We digitized all maps and included them in a Geographic Information System (GIS) using ArcView 3.2.

We recorded spatial locations of red deer individuals in September 2004 (in Extremadura) and September 2005 (in Andalucía). In each estate we travelled in the vehicle of the land manager at 10–20 km/hour. Managers continually travel within the estates, so the animals ignored us, which minimized recording the same individual more than once. Peak rut (around 5 days of higher activity) occurred at different dates among populations and years. Within any day, rutting activity was higher at dawn and dusk and lower at midday. Thus, surveys were always performed by  $\geq 2$  observers (at least the manager and a researcher), at sunset (between 1700 hr and 1900 hr solar time), and during peak rut for each population (following managers' advice). We

recorded presence, sex, and age class (yearling and Ad [ $\geq 2$  yr old]) of observed individuals. With these counts we determined the number of females and the sex ratio for each population (we excluded yearling males from all calculations and analyses; Clutton-Brock et al. 1997). Also, with maps, a video camera, and a Global Positioning System (GPS), we georeferenced all individuals observed and included their spatial coordinates in the GIS. Surveys covered the full area the animals used as arenas during the breeding season (following estate manager's information). With this survey methodology we recorded the location of all individuals with potential breeding interactions in a moment of relevant breeding activity for each population.

To assess the possible bias caused by this one-time (i.e., punctual or snapshot) data collection procedure (which was the only one possible for most of the estates), in one population we conducted 5 counts on different days during the rutting period (13, 14, 15, 16, and 22 Sep 2005). These 5 surveys covered the same area in the population and were conducted at the same solar time. In this way we assessed the repeatability of our punctual data collection and compared the results obtained with each of the 30 spatially different surveys.

### Spatial Processing

During the rut, adult males pursue mating rather than feeding, so they are not directly driven by environmental resources (Clutton-Brock et al. 1982). Also, females form matrilineal groups in which calves and subadult females follow adult females (Clutton-Brock et al. 1982), so we based our distribution analyses on the location of adult females ( $>1$  yr old).

We based spatial models on a quadrangular grid defining territorial units. We established grid cell size (scale grain) according to the mean spatial scale of the female distribution patterns for the studied populations, measured using Ripley's K statistic, a second-order analysis based on the variance in the distance between points (Ripley 1981, Dale 1999, Diggle 2003, Pérez-González et al. 2010). This method describes the characteristics of the point distribution pattern over a range of distance scales, estimating the expected number of points within a distance  $t$  of an arbitrary point in the study area. We determined the scale of female distribution by quantifying the Ripley's K function in a range of distances ( $t$ ). To determine if the spatial pattern reached a significant aggregation we used 1,000 Monte Carlo simulations. We also used Ripley's K analysis to estimate female aggregation (Diggle 2003). We implemented Ripley's K analyses and Monte Carlo simulations with ADE-4 (Thioulouse et al. 2001).

We generated grids of the established cell size with ArcView 3.2. Using Idrisi Kilimanjaro (Clark Labs, Worcester, MA) we converted all maps to raster format and calculated, for each grid cell, the total number of females and the mean value of the following environmental variables: percentage of vegetation cover (Cover), percentage of leguminous plants (Legum), distance to green meadows (Green mead), distance to ponds

(Ponds), stream beds (Stream), crop lands (Crops), and food supplementation sites (Food supp).

We used spatial distribution of males and females to obtain estimates of distribution of males' breeding success. We used mean harem size ( $H$ ) as an estimation of skewness of male breeding success (Shuster and Wade 2003). We estimated harem size as the number of females within the area of influence of any mature male. To determine the area of influence of each male, we used male spatial positions to create a Dirichlet tessellation based on Thiessen polygons (Okabe et al. 1992, Dale 1999). The Thiessen polygon for an individual can be interpreted as the dominion of this individual (Mithen et al. 1984). During peak rut, females are normally distributed in groups held by a mature male. Holding males expel other males from the area occupied by their female groups (Clutton-Brock et al. 1982). In this case, the harem held by a male is included within the area of influence (the Thiessen polygon) of this male. However, there could be some females that do not belong to any harem. We included females without holding males in the dominion of the nearest male because in the estrous time those females look for the protection of holding males against sexual harassment (Carranza and Valencia 1999).

### Statistical Analyses

We used generalized linear models (GLM) with Poisson distribution and logarithmic link function to build predictive models with the number of females per grid cell as the dependent variable and the environmental variables as independent factors. Generalized linear modeling with Poisson distribution is recommended for count data (Vincent and Haworth 1983, Guisan and Zimmermann 2000). We implemented models with R software (version 2.9.1, <[www.r-project.org](http://www.r-project.org)>, accessed 1 Oct 2009). Prior to modeling, we checked for collinearity between environmental variables using Spearman's rank correlation coefficient. If the correlation between 2 variables was  $>0.7$ , we eliminated one of the variables based on biological significance and expert opinion. Thus, for instance, under high correlation between grassland cover and the percentage of leguminous plants, we used the latter because it has an important ecological effect on ungulate feeding (Whitehead 2000).

To take spatial autocorrelation into account, we included the spatial coordinates in the GLM according to the polynomial form proposed by Borcard et al. (1992):  $x$  coordinate,  $y$  coordinate,  $x^2y$ ,  $xy^2$ ,  $x^3$ , and  $y^3$ . If one of these variables entered a regression model, there was a significant spatial trend not accounted for by the environmental factors we analyzed, which could be attributed to spatial autocorrelation (Legendre 1993, Vargas et al. 2007).

We initially ran the GLM with all non-collinear environmental variables (both natural and supplementary) and spatial coordinates. By using the "step" function in R, we simplified each model based on Akaike's Information Criterion. In the resultant models for each population we considered an environmental factor a resource if it presented the expected relationship with female abundance: we expected grassland cover and percentage of leguminous

**Table 1.** Effects of environmental factors over female red deer distribution in each studied population (Pop) of southwestern Spain. Number of counted females and the estimated slope (from the generalized linear models) of the environmental factors that acted as resources in each population (see Fig 2; Table S2, available at <<http://dx.doi.org/10.2193/2009-130.s1>>). See also Figure 1 for the location of each population. We collected data during the rutting season (Sep 2004 in Extremadura, Sep 2005 in Andalucía).<sup>a</sup>

Pop	F	Food supp	Crops	Green mead	Cover	Legum	Ponds	Streams
AC	128	-6.43				0.54	-38.27	
AL	128	-3.94				7.28		
AM	323	-19.36	-0.90					
AZ	66					4.87	-3.78	
BA	85	-4.88				1.46		
BB	30						-6.39	-9.18
CA	131	-16.34					-0.75	
CH	21	-22.23				2.27		
CL	74					1.59	-1.95	-5.30
CN	86					1.60	-2.69	-3.48
CV	231	-2.74			0.08			
ER	260	-44.04			0.37		-3.97	
ES	150	-2.42				0.46		
FV	193	-1.19						0.77
JA	64	-15.46					-9.40	-4.81
LS	142	-5.94	-46.95					
MEL	17							-4.97
MER	70			-18.19	3.26			
MM	108	-7.07						-0.60
MO	128	-11.28						-0.91
MS	27							-6.94
NA	17				3.84			
PA	34							-1.29
RM	85	-3.15				1.91	-0.81	-1.71
RO	96	-2.50			0.87	1.42		
SC	83		-16.61		1.84			-2.09
TA	79				1.60		-5.23	
US	225	-4.17						-0.22
VA	178	-2.55		-5.46		0.32		

<sup>a</sup> Food supp: food supplementation sites; Crops: crop lands; Green mead: green meadows; Cover: percentage of vegetation cover in the grassland patches; Legum: percentage of leguminous plants in the grassland patches; Streams: stream beds.

plants to be positively related with female abundance; we expected distances to green meadows, ponds, stream beds, crop lands, and food supplementation sites to have a negative coefficient. Finally, we compared female density, female aggregation, and mean harem size between the populations in which female distribution was and was not related to food supplementation sites.

## RESULTS

The mean value of female spatial pattern scale ( $\lambda^*$ ) was 49.5 m ( $\pm 5.82$  m). Therefore, we used a grid cell size of 50 m by 50 m as spatial modeling units. In all the estates females showed an aggregated distribution (1,000 Monte Carlo simulations,  $P < 0.05$  for all the estates). Using distribution data from surveys on different days did not significantly change the results for the population tested (see Table S1, available at <<http://dx.doi.org/10.2193/2009-130.s1>>).

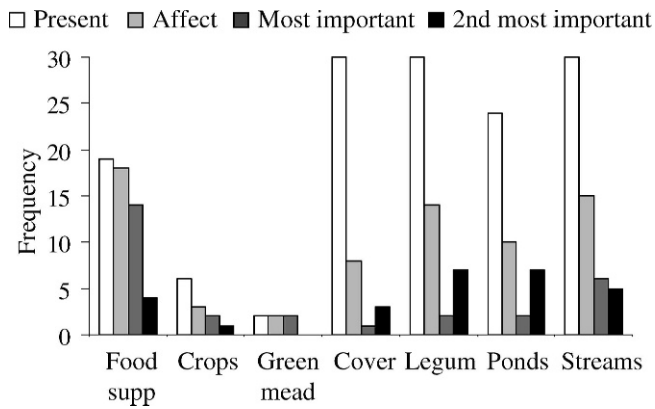
Results for the GLM showed a variety of models (see Table S2, available at <<http://dx.doi.org/10.2193/2009-130.s1>>). For 29 of the 30 estates (96.7%)  $\geq 1$  analyzed environmental variable was associated with the number of females per grid cell (Table 1; see also Table S2, available at <<http://dx.doi.org/10.2193/2009-130.s1>>). In the only estate for which no environmental variables were related to female distribution

(CC in Table S2) the number of counted females (26) was low relative to the other populations.

Food supplementation occurred in 19 (63.3%) of the 30 estates (Fig. 2). In 18 (94.7%) of the estates where it occurred, food supplementation significantly affected female distribution, and in 16 of these estates it was the most important factor (Table 1; Fig. 2). Crop lands occurred in 6 estates (20%) and were associated with female distribution in 3 of them (Table 1; Fig. 2). Presence of green meadows was the most important resource in the 2 estates in which it occurred (Table 1; Fig. 2). The remaining environmental factors (Cover, Legum, Ponds, and Streams) occurred more frequently but acted as significant resources in <50% of cases (Table 1; Fig. 2). These models allowed the display of predicted values for each estate (see supplemental figures, available at <<http://dx.doi.org/10.2193/2009-130.s1>>).

The area covered during vehicular surveys did not differ between the estates in which female distribution was not related to food supplementation (Without Food Supp estates;  $\bar{x} \pm SE = 290.15 \pm 97.13$  ha) and those in which it was (With Food Supp estates;  $\bar{x} \pm SE = 301.84 \pm 75.50$  ha; Table 2). Female density (no. of F divided by the area covered in the vehicle) was not different between Without Food Supp estates ( $\bar{x} \pm SE = 0.22 \pm 0.26$  F/ha) and With Food Supp estates ( $\bar{x} \pm SE = 0.85 \pm 0.20$  F/ha), although there was a trend towards higher density in With





**Figure 2.** Importance of each resource on female red deer distribution in southwestern Spain. Plot shows the number of estates in which each environmental factor is present (Present), the number of estates in which each factor acted as a resource for females (Affect), the number of estates in which each factor acted as the most important resource (Most important), and the number of estates in which each factor acted as the second most important resource (2nd most important). Food supp: food supplementation sites; Crops: crop lands; Green mead: green meadows; Cover: percentage of vegetation cover in the grassland patches; Legum: percentage of leguminous plants in the grassland patches; Streams: stream beds. Data collected during the rutting season (Sep 2004 in Extremadura, Sep 2005 in Andalucía).

Food Supp estates (Table 2). Female aggregation was significantly higher in With Food Supp estates ( $\bar{x} \pm SE = 28.54 \pm 5.24$  F within  $t^*$ ; Table 2; Fig. 3) than in Without Food Supp estates ( $\bar{x} \pm SE = 3.42 \pm 6.74$  F within  $t^*$ ). Mean harem size was significantly higher in With Food Supp ( $\bar{x} \pm SE = 4.25 \pm 0.27$  F/harem; Table 2;

Fig. 3) estates than in Without Food Supp estates ( $\bar{x} \pm SE = 2.70 \pm 0.35$  F/harem). Additionally, the sex ratio (M:F) was not different between Without Food Supp estates ( $\bar{x} \pm SE = 0.67 \pm 0.10$ ) and With Food Supp estates ( $\bar{x} \pm SE = 0.50 \pm 0.08$ ; Table 2).

Food supplementation affected female distribution mainly at the local scale. Thus, the number of females within 50 m of the main resource was higher in the estates where this resource was food supplementation than in the remaining estates (Fig. 4).

## DISCUSSION

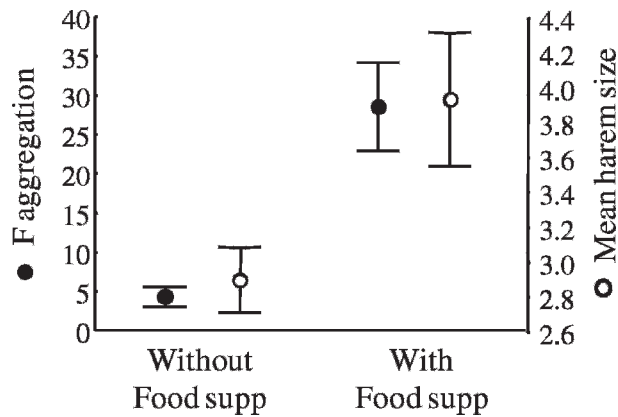
We found that food supplementation occurred in 19 of 30 estates. Moreover, when it occurred, food supplementation almost always determined female distribution and was frequently the most important resource. Also, food supplementation was associated with high levels of female aggregation and high mean harem size. Therefore, food supplementation in red deer populations in southwestern Spain has become a management activity with a high impact on mating system features.

Despite the high importance of food supplementation sites, natural factors also acted as resources associated with female distribution, although with lower frequency and importance (Fig. 2). Green meadows were the natural factor with the highest relative importance in female distribution. Green meadows are poorly represented in Mediterranean ecosystems during the rutting season because of the dry climatic conditions (Bugalho and Milne 2003, Olea et al. 2005). However, when green meadows are present, they

**Table 2.** Comparison between populations in which female red deer distribution was and was not determined by food supplementation sites in southwestern Spain. Table shows the type of comparison (Dependent), the analysis used (Analysis), and the model results. We collected data during the rutting season (Sep 2004 in Extremadura, Sep 2005 in Andalucía).<sup>a</sup>

Dependent	Analysis	Effect	df	F	P
Area	ANOVA	Intercept	1	23.156	<0.001
		Region	1	2.353	0.138
		Food supp	1	0.009	0.925
		Region × Food supp	1	0.496	0.488
		Error	25		
Density	ANOVA	Intercept	1	10.253	0.004
		Region	1	1.905	0.180
		Food supp	1	3.587	0.070
		Region × Food supp	1	1.489	0.234
		Error	25		
Female aggregation	ANOVA	Intercept	1	14.029	0.001
		Region	1	0.053	0.820
		Food supp	1	8.660	0.007
		Region × Food supp	1	0.054	0.818
		Error	25		
Mean harem size	General linear model	Intercept	1	109.922	<0.001
		Sex ratio (covariate)	1	13.048	0.001
		Region	1	1.509	0.231
		Food supp	1	5.525	0.027
		Region × Food supp	1	0.292	0.594
		Error	24		
Sex ratio	ANOVA	Intercept	1	89.017	<0.001
		Region	1	2.960	0.098
		Food supp	1	1.989	0.171
		Region × Food supp	1	0.008	0.928
		Error	25		

<sup>a</sup> Region: Extremadura or Andalucía; Food supp: populations in which female distribution was not determined by food supplementation sites or populations in which female distribution was determined by food supplementation sites; Sex ratio: M:F.



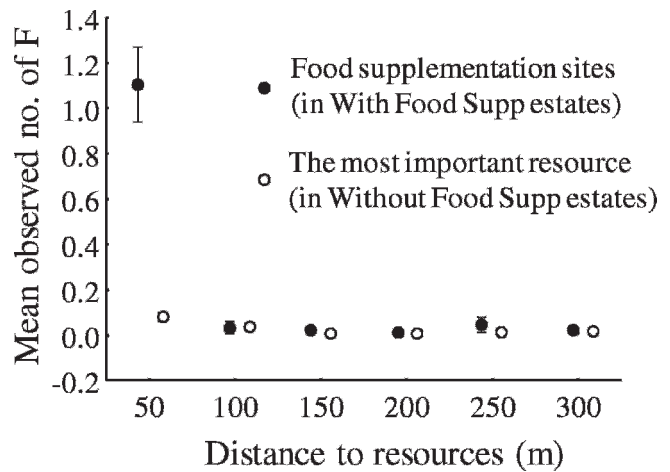
**Figure 3.** Female red deer aggregation and mean harem size in southwestern Spain under different situations. Without Food Supp: populations in which female distribution was not determined by food supplementation sites. With Food Supp: populations in which female distribution was determined by food supplementation sites. Plot shows means and standard errors (see Table 1). Data collected during the rutting season (Sep 2004 in Extremadura, Sep 2005 in Andalucía).

affect the red deer mating system, and in our results they appeared, when present, as the most important environmental factor influencing female distribution (see also Carranza et al. 1990, 1996).

Collection of data on distribution of individuals based on one-time observations can bear an important random component. However, variation in the results of different measurements within the same population was low and presented similar predictive models for female distribution (see Table S1, available at <<http://dx.doi.org/10.2193/2009-130.s1>>).

The measure we used for female aggregation depended on the density of females in the population. Food supplementation could increase female aggregation by increasing female density through, for instance, increased survival or local immigration (Putman and Staines 2004). We found a trend towards higher female density in estates where female distribution was associated with food supplementation, although the effect was not consistent among estates and regions and did not reach significance. In contrast, female aggregation was consistently and significantly higher in estates where female distribution was associated with food supplementation. Therefore, the main effect of food supplementation in our populations was the local female aggregation at estates offering food supplementation. Beyond 50 m from feeding sites the number of females tended to be zero (Fig. 4).

Female distribution was significantly aggregated in all estates, independent of the resulting model. Female aggregation is naturally related to a polygynous mating system (Emlen and Oring 1977). As a consequence of female aggregation, males can monopolize several females in harems (Shuster and Wade 2003). However, food supplementation generated female aggregation and harem sizes not observed with natural factors. In polygynous mating systems, spatial aggregation of females and distribution of males' breeding success are key elements in sexual selection



**Figure 4.** Effects of the distance to main resources on female red deer distribution in southwestern Spain. Mean and 95% confidence intervals of the observed number of females within each 50-m interval are shown. Without Food Supp: populations in which female distribution was not determined by food supplementation sites. With Food Supp: populations in which female distribution was determined by food supplementation sites. Data collected during the rutting season (Sep 2004 in Extremadura, Sep 2005 in Andalucía).

(Andersson 1994). Food supplementation is a new circumstance in Iberian red deer biology (around 6–10 generations) that may affect the opportunity for selection and evolution in populations subjected to game management.

New circumstances can generate rapid evolution of populations in which genetically based phenotypic change takes place at a high rate (Thompson 1998, Hairston et al. 2005). Such evolutionary changes have been observed within a few generations (Singer et al. 1993), within one generation (Grant and Grant 1995), or even within one season (Via and Shaw 1996). New situations created by supplementary feeding might produce behavior-related phenotypic changes in Iberian red deer populations. Excessively high female aggregations during the breeding season might increase the frequency of antagonistic interactions among males and the probability of sexual harassment, as well as changes in male mating strategies (Clutton-Brock et al. 1982; Carranza et al. 1990, 1995, 1996; Sánchez-Prieto et al. 2004). This new scenario might generate new selective optima in the evolution of Iberian red deer populations, with potential consequences on behavior and anatomic structures implicated in mating system and sexual selection (Emlen and Oring 1977, Andersson 1994, Kruuk et al. 2002, Shuster and Wade 2003).

Another potential consequence of supplemental feeding is related to changes in genetic diversity and nonadditive genetic components. Female aggregation and mean harem size may increase variance in male mating success, which might reduce effective population size, with possible consequences for genetic diversity throughout generations (Nunney 1993, Briton et al. 1994, Falconer and Mackay 1996, Frankham et al. 2002, Shuster and Wade 2003). However, female aggregation could also favor processes that maintain genetic diversity. For red deer in Spain, Pérez-González et al. (2009) showed that the level of polygyny was

positively associated with a higher transmission of genetic variability by the paternal lineage compared with the maternal lineage, which was likely related to the advantage of heterozygous males in the competition for mates (Meagher et al. 2000, Slate et al. 2000). Additionally, aggregation of individuals at certain areas may favor female mate choice for dissimilar males, which has been shown to occur in Iberian red deer (Carranza et al. 2009). We are just starting to understand some of these processes in red deer populations and we are yet unable to say how supplementary feeding might affect them.

Supplementary feeding of Iberian red deer during the rut is a recent management activity and may be increasing due to worsening climatic conditions in these areas. Studies on climate change predict an increase of drought periods in Mediterranean areas (Intergovernmental Panel on Climate Change 2007). Scarcity of precipitation will decrease resource availability for deer populations during the rut and managers may tend to increase the frequency and intensity of food supplementation (Bugalho and Milne 2003, Olea et al. 2005, Torres-Porras et al. 2009). The study of new selective pressures caused by food supplementation is an important issue with potential evolutionary consequences for Iberian red deer populations.

## MANAGEMENT IMPLICATIONS

Food supplementation during the summer and early autumn is a common practice in Mediterranean ecosystems and may be unavoidable in some circumstances to maintain deer densities and economic yield and to reduce the impact of deer on shrub vegetation. However, it is increasingly necessary to consider potential evolutionary effects of management practices in wild populations (Sutherland 2000). Supplementary feeding should be avoided when possible. When necessary, its effects should be minimized by spatially dispersing supplementary food throughout the area of the estate to prevent excessive female aggregation.

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