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Determining changes in the nutritional condition of red deer in Mediterranean ecosystems: Effects of environmental, management and demographic factors

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ABSTRACT

Monitoring changes in the nutritional status of wild populations is crucial to understanding how species respond to natural or human-mediated variations in food availability and quality. It is a fundamental step for decision-making in wildlife management. Many studies on nutritional ecology still tend to rely on the use of single indicators. Nonetheless, nutrition has multiple interdependent facets that should be combined to better understand how organisms interact with their environment through feeding. Here, data from a large-scale cross-sectional survey conducted between 2010 and 2013 were used to examine the influence of environmental conditions and management practices on the variation of faecal nitrogen content (FN, index of dietary quality) and kidney fat index (KFI, indicator of nutritional condition) in red deer *Cervus elaphus* in the Mediterranean ecosystems of Iberia. Variations in the nutritional indicators in relation to sex, age, faecal fibre contents and faecal counts of lungworm larvae were also analysed. Our results showed that FN levels were statistically and positively correlated with vegetation primary productivity ($P = 0.003$). In contrast, faecal fibre fractions were significantly and negatively correlated with FN concentrations ($P = 0.024$ for hemicellulose, $P < 0.0001$ for cellulose and lignin). Moreover, a negative, marginally significant relationship was found between FN and the average altitude of the study areas ($P = 0.055$). The KFI was statistically higher in females than in males ($P < 0.0001$) and increased with increasing FN levels ($P = 0.01$). Fat stores were also statistically and positively correlated with vegetation productivity ($P = 0.001$) and with the amount of supplementary food provided ($P = 0.04$). The effect of high-quality diets on deer kidney fat deposits was gradually lower as the population density increased ($P = 0.02$). This result was more marked in non-food-supplemented populations. Both FN and KFI were statistically higher during the winter in relation to the autumn ($P < 0.0001$ and $P = 0.005$, respectively). This study shows that FN can be used to monitor and predict changes in the dietary quality, and the KFI in the nutritional status, in red deer in Mediterranean environments, reliably. Since both indicators showed different sensitivity to intrinsic, ecological and management determinants, this research also highlights their value and complementary use when studying populations of large wild herbivores.

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1. Introduction

Nutritional condition (*sensu* Harder and Kirkpatrick, 1994) is a major determinant of animals' performance, influencing diverse aspects of their life history such as growth, reproduction and survival (Barboza et al., 2009) and therefore with consequent implications for population dynamics (Owen-Smith and Mills, 2006). From a physiological perspective, it can be viewed as an outcome of dynamic processes that involve allocation and mobilisation of somatic reserves, which, in turn, are regulated by a combination of intrinsic traits, environmental factors and ecological interactions (Barboza et al., 2009; Parker et al., 2009).

In sexual dimorphic species, such as most wild ungulates, nutritional or energy requirements may vary according to differences in body size and digestive efficiency (Barboza and Bowyer, 2000), activity time (Long et al., 2014), as well as with sex, age, and reproductive status (Forsyth et al., 2005; Santos et al., 2013). Furthermore, pathogens can negatively affect both nutrient metabolism and absorption (Coop and Kyriazakis, 1999; Gálvez-Cerón et al., 2015), therefore increasing the host's nutritional demands and consequently its susceptibility to environmental constraints (Ezenwa, 2004). Likewise, the whole plethora of parasites and/or pathogens may have effects, either independently or in concomitance, on the host's body condition and, subsequently, on several life-history traits (Lello et al., 2005).

Natural populations, inhabiting seasonally changing environments, typically face annual cycles of forage availability and quality, which are strongly influenced by climatic conditions (Rodriguez-Hidalgo et al., 2010). The way animals cope with seasonal nutritional constraints is context-dependent (Moen et al., 2006; Parker et al., 2009), thus highlighting the importance of considering environmental conditions on different geographical scales to understand the nutritional ecology of large herbivores (Martínez-Jauregui et al., 2009). The influence of environmental variation on both diet and nutritional condition of wild ungulates is broadly documented for populations living in northern latitudes (*e.g.*, Cook et al., 2013; Pettorelli et al., 2005a). However, fewer efforts have been made to elucidate how seasonal changes affect the feeding ecology and nutritional condition of wild deer in the Mediterranean ecosystems (Miranda et al., 2012; Rodriguez-Hidalgo et al., 2010), where the summer drought is the most critical factor influencing the availability and nutritive value of forage (Bugalho and Milne, 2003).

Demographic factors have also been shown to be important drivers of nutritional condition among ungulates (Stewart et al., 2005). Population densities above the ecological carrying capacity (*sensu* Caughley, 1979) often result in competition for food resources (Stewart et al., 2005), with additional negative impacts not only on plant communities and the nutritive value of vegetation, but also on the whole ecosystem (Blanchard et al., 2003; Côté et al., 2004; Perea et al., 2014). Moreover, the interactive effects between high densities and unfavourable environmental conditions affecting plant productivity may also have profound short- and long-term consequences on the animals' nutritional condition and, ultimately, on the dynamics of wild populations (Rodriguez-Hidalgo et al., 2010; Simard et al., 2010). In recent decades, ecological and socio-economic changes have contributed to a significant increase of deer populations in many temperate regions of the Northern Hemisphere (Apollonio et al., 2010), including in the Mediterranean areas of southwestern Europe (Acevedo et al., 2011). Despite this, few studies have investigated the impact of population densities on the nutritional status and dietary quality of wild deer in this region (Carpio et al., 2015; Torres-Porras et al., 2009).

Management practices can also affect the nutritional condition of large herbivores in numerous ways, either through interventions in the structure and composition of habitats (Simard et al., 2014; WallisDeVries, 1998), or by directly providing supplemental food, a practice traditionally used in areas managed for hunting (Milner et al., 2014; Putman and Staines, 2004). In the Iberian Peninsula, where big game hunting represents an important economic activity (Martínez-Jauregui et al., 2011), supplementary feeding practices are usually related to the maintenance of artificially high population densities and/or production of high-quality trophies. Although management practices are recognised as important factors influencing the nutritional condition of ungulate species, their effects have rarely been studied in detail in wild populations, especially in Mediterranean environments (but see Rodriguez-Hidalgo et al., 2010; Santos et al., 2013).

For wild ungulates, nutrition and condition result from complex interactions with biophysical and social factors (*e.g.*, Parker et al., 2009), which should be considered simultaneously for an overall assessment of their effects. In this study, a large-scale, cross-sectional approach was used in order to assess the influence of environmental factors, population densities and management practices on the dietary quality and nutritional status of red deer *Cervus elaphus* in the Mediterranean habitats of the Iberian Peninsula, during the seasons following the summer (the period of greatest food restriction). The red deer is one of the most widespread ungulates in Iberia. Due to its economic and ecological relevance (Martínez-Jauregui et al., 2011; Smit and Putman, 2011), knowledge of the factors that may affect the nutritional condition of this species is therefore fundamental to developing appropriate management practices. By using two complementary nutritional indicators – faecal nitrogen (FN) as a proxy for dietary quality (Leslie et al., 2008) and kidney fat index (KFI) as an indicator of the amount of energy reserves in an animal's body (Santos et al., 2013) – the following hypotheses were tested: (H1) periods of increased vegetation productivity, which are greatly influenced by accumulated rainfall during the autumn and winter in Mediterranean areas (Rodriguez-Hidalgo et al., 2010), are expected to affect positively both FN and KFI (Blanchard et al., 2003; Hamel et al., 2009; Kucera, 1997); (H2) significant effects of habitat composition and supplementary feeding practices are also predictable, with high-quality habitats and increased forage supply having positive effects on deer nutritional condition (Santos et al., 2013); (H3) high population densities are expected to have a negative effect on deer nutritional condition (Blanchard et al., 2003; Stewart et al., 2005). Finally, the effects of sex, age, faecal fibre fractions and parasite load on the nutritional indicators measured were also considered because of their relevance in studies involving highly sexually dimorphic species, such as the red deer.

2. Materials and methods

2.1. Study areas and red deer populations

The present study was conducted in eight areas which are representative of the Mediterranean environments in the Iberian Peninsula (Fig. 1): *Lombada* National Hunting Area and *Sierra de la Culebra* Regional Hunting Reserve (LSC); *Lousã* Mountain (LOU); *Cubeira* Tourist Hunting Area (CUB); *Negrita Norte* Tourist Hunting Area (NEG); *Doñana* National Park (DN); *Quintos de Mora* (QM); *Montes Universales* Hunting Reserve (RCMU); *Caspe-Fraga* Social Hunting Area (CF). The sampling sites are predominantly characterised by a Mediterranean climate, but show different temperature and precipitation regimes throughout the year (Fig. 1). The types of vegetation and land-use patterns found at each location result from the combination of environmental determinants and land management practices carried out by landowners (public or private entities, or both; Table 1). Red deer densities vary among study areas (Table 1) and reflect the type of management applied. In Iberia, despite the diversity and complexity of scenarios, red deer densities are generally higher on private hunting estates. In most of the populations studied, management objectives are oriented to deer hunting. However, in some areas, those objectives are related to damage and population control. The provision of supplementary food for red deer is a common management practice only in some study sites, especially in private hunting grounds (Table 1).