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Trade-offs between food availability and predation risk in desert environments: The case of polygynous monomorphic guanaco (*Lama guanicoe*)

Pablo Acebes*, Juan E. Malo, Juan Traba

Terrestrial Ecology Group-TEG, Departamento de Ecología, Facultad de Ciencias, Universidad Autónoma de Madrid, C/. Darwin, 2, E-28049 Madrid, Spain

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ABSTRACT

Habitat selection by ungulates is determined by the quantity, quality and distribution of trophic resources as well as by predation risk. It may also vary in relation to species-specific reproductive strategies and social organization. The guanaco (*Lama guanicoe*), a highly social and sexually size-monomorphic wild camelid typical of arid lands, is ideal for evaluating behavioural responses of this type, since most studies have done on dimorphic ungulates in temperate environments, where trophic resources are abundant. We recorded the group size and social structure of guanaco during both dry and wet seasons of 2005–2007 in an Argentinean desert, where pumas (*Puma concolor*) are the sole predators. Remote sensing data were used to calculate five variables that reflected trophic availability and terrain morphology for each guanaco group and for an equivalent number of random controls. Habitat use did not differ between types of social groups but differed between seasons. Guanacos used less productive and less steep areas during the breeding season, irrespective of juvenile:adult ratios in the family groups, and larger groups occupied flatter areas. Overall, guanaco habitat selection prioritizes reducing predation risk to the extent that animals occupy areas offering the minimum productivity capable of meeting their energy requirements.

1. Introduction

Populations of large herbivores are generally regulated via top–down mechanisms such as predation (Hopcraft et al., 2010; Sinclair et al., 2003) and by bottom–up constraints in primary production (Hopcraft et al., 2010; McNaughton et al., 1989). Large herbivores may respond to changes in resource availability or predation with behavioural adjustments (Kie, 1999; Sinclair and Arcese, 1995), which may affect demographic parameters (Creel et al., 2007). Such mechanisms operate differently within species according to their type of social organization (Jarman, 1974).

Predation risk effects arise when a prey alters its behaviour in response to predators, and these behavioural responses carry costs. Indeed, risk effects can be larger than direct effects of predation, and can be influential even when the direct rate of predation is zero (Creel and Christianson, 2008). It is generally accepted that selection will favour individuals that optimally balance the benefits of risk reduction against its costs (Lima, 2002). Behavioural responses to reduce predation risk include changes in habitat use (Creel et al., 2005) or in group size (Creel and Winnie, 2005). The response may also differ between sexes: males usually seek habitats which offer high trophic availability, whereas females with offspring select habitats that firstly offer security against predators and secondly provide abundant forage (Main et al., 1996; McCullough, 1999). Thus, habitat selection to maximize reproductive fitness represents a trade-off between maximizing foraging opportunities and minimizing predation risk (Kie, 1999; McCullough, 1999).

The guanaco (*Lama guanicoe* Müller), a highly social medium-sized South American ungulate, is sexually monomorphic in body size and exhibits a resource defence polygyny mating system (Franklin, 1983). Three types of groups may be encountered during the breeding season (González et al., 2006): family groups (i.e. a territorial male with adult females and their offspring), groups of non-territorial males, and solitary territorial males that are seeking or defending a territory without females. Outside the breeding season, guanaco group composition varies according to environmental conditions. Sedentary populations are observed when weather and forage supply is stable, allowing populations to maintain territories all year round (Franklin, 1983; González et al., 2006). However, in areas with particularly snowy winters with a drastic reduction of food availability, guanacos may move to more sheltered areas, losing their territoriality and forming large mixed

* Corresponding author. Tel.: +34 914978916; fax: +34 914978001.
E-mail address: pablo.acebes@uam.es (P. Acebes).

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herds composed of adults of both sexes, juveniles and newborns (Franklin, 1983; González et al., 2006).

Most studies on ungulates have done in temperate ecosystems (Creel et al., 2005; Kunkel and Pletscher, 2000; Pierce et al., 2004; Theuerkauf and Rouys, 2008), but little information about desert ecosystems is available, where resources are extremely scarce and prey may accept higher predation risk. Predators establish a 'landscape of fear' (Laundré et al., 2001) whose topography is determined by the level of predation risk that prey face in different habitat types. When foraging in this landscape, prey will often shift their use from riskier to safer areas which may represent a change to poorer quality habitat, resulting in a decreased diet quality (Hernández and Laundré, 2005). However this behavioural decision might not be faced when safer habitats are of very low abundant forage.

On the other hand, most hypotheses in this field have been tested on dimorphic ungulates, which generally show marked sexual segregation (Main et al., 1996; Ruckstuhl and Neuhaus, 2000), but more studies on monomorphic ungulates are needed. As Ruckstuhl and Neuhaus (2000) emphasized, non-dimorphic species may be ideal to explain sexual differences in habitat use, forage selection, predator avoidance or activity budgets, because body size effects are absent. The guanaco thus becomes an interesting species for analysing the trade-off between resource availability and predation risk as a function of its social organization.

The puma, the natural predator of guanacos, is a solitary ambush and stealthy carnivore that relies on vegetation cover and terrain features to approach close enough to their prey before attacking, hiding on bushy vegetation, in steeper gradients or rocky terrain (Bank and Franklin, 1998). As pumas do not chase their prey through long distances, early detection by guanacos can be especially advantageous to increase their likelihood to escape (Marino and Baldi, 2008). It is the sole predator of guanacos in the Northwestern Argentina, where this study was conducted. The area is dominated by sparse shrubland of less than 20% of plant cover, with a very scant and seasonal herbaceous layer growing in the wet season, which together with the greening of the shrub vegetation represents a slight increase in forage availability during this season. The minimum plant cover (i.e. lowest forage abundance) of the area corresponds to habitats located on level flat ground of fine-textured substrates, while steep hard terrain contains taller and denser vegetation cover (Acebes et al., 2010b).

We here use field data and satellite-based methods: (i) to firstly determine the social organization of a small and sedentary guanaco population (Acebes et al., 2010a) in both the breeding and non-breeding seasons over three years; (ii) to evaluate whether social units differ in habitat selection as a function of trophic availability and potential predation risk; and (iii) to determine whether any patterns depend on group size, the number of offspring and the yearling/adult ratio.

In this ecological context we expect to find that: (a) there will be a different habitat selection among types of guanaco social organization: male groups and solitary males will occupy more productive zones than family groups, accepting a higher predation risk given that they do not have calves (more vulnerable to predation) in an attempt to maximize their body condition in order to gain access to reproduction (Main et al., 1996) and; (b) family groups will occupy areas of low predation risk, even if they have a lower productivity, and this tendency will be more pronounced for groups with higher number of offspring and/or higher yearling/adult ratio.

2. Materials and methods

2.1. Study area

The study was carried out in Ischigualasto Provincial Park, in San Juan province, Northwestern Argentina (29° 55′ S, 68° 05′ W), part of the Ischigualasto–Talampaya World Heritage Site together with Talampaya National Park (La Rioja province). The mean altitude is 1300 m a.s.l. The park comprises an area of 60 369 ha. The nearest village is 10 km from the park limit. The climate is dry desert with a mean annual temperature below 18 °C (range −10°–45 °C) and a mean temperature in the hottest month above 22 °C. Mean annual precipitation ranges from 80 to 140 mm, concentrated in summer (November–February).

Monte Desert is the dominant biome (Márquez et al., 2005). The predominant vegetation is sparse shrubland, dominated by species of Zygophyllaceae (*Zuccagnia punctata*, *Larrea* spp. and *Bulnesia retama*), Fabaceae (*Prosopis* spp., *Geoffroea decorticans*, *Cercidium praecox*) and Chenopodiacae (*Atriplex* spp. and *Suaeda divaricata*). Cacti (*Tephrocactus* spp., *Opuntia sulphurea* and *Echinopsis* spp.) and Bromeliads (*Tillandsia* spp. and *Deuterocohnia longipetala*) are also frequent but to a lesser extent (Acebes et al., 2010b).

The puma is the unique predator of guanacos in the area. Throughout its geographic range the puma is commonly associated with forested areas or in dryer more-open regions, generally occurring in habitats with dense understory vegetation and with increased topographic relief (Franklin et al., 1999). During the studied period (2005–2007; 107 field days), evidence from predation of two guanaco calves, some guanaco carcasses and several recent puma tracks and faeces were recorded, and two pumas were sighted by park guards, always in habitats of steep terrain and dense shrub cover, but no puma tracks on open-flat habitats with scant or no vegetation were detected.

2.2. Guanaco data

The field work was conducted in February–March 2005, 2006 and 2007 (wet season), when guanacos breed, and in August 2005 and 2006 (dry season), corresponding to the maximum and minimum abundance of trophic resources respectively, although these differences are not marked (Acebes, unpubl. data). Two researchers with binoculars (10 × 42) surveyed the area by vehicle through line – transects surveys from all the roads and tracks, covering 6700 km in total. Surveys were conducted during day-light hours, travelling at 10–40 km/h. Roads and tracks crossed all habitat types (gradient from bare ground to densest plant cover) and topography (i.e. open-flat, steep or rugged terrain), ensuring that landscape heterogeneity was properly examined. The following were recorded when a solitary guanaco or a herd was sighted: (1) exact geographical location using GPS, a laser range-finder and a precision compass; (2) group size; (3) social and age structure: the number of adult males and females, juveniles (yearlings >1 and <1.5 years old) and yearlings (up to one year old) and; (4) social unit: family group, male group, solitary male or mixed herds. Because of their sociability, large size, bright brown colour and low vegetation, guanacos were easily observed. When animals were too distant for individuals to be identified they were approached on foot until this was possible. Guanaco flight events occurred at a mean distance of 141 m (Malo et al., 2011). The local guanaco population is sedentary and comprised of fewer than 400 individuals (0.38 individuals/km^2, Acebes et al., 2010a), so there was a chance that the same individual or group could be recorded more than once in the same season.

2.3. Habitat characteristics

Habitat variables that could be important to guanaco were obtained from a Landsat 7 ETM + image, acquired on February 26 2002, and from an ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer) digital elevation model (DEM). Both images had a resolution of 30 × 30 m. The Normalised Difference