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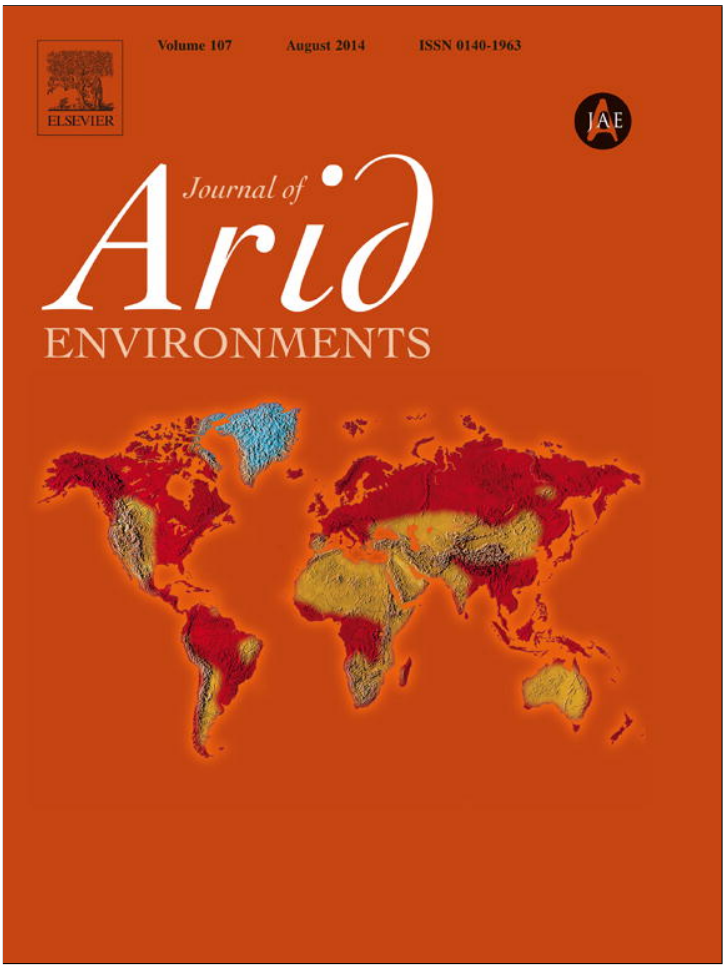

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Guanacos in the Desert Puna: A trade-off between drinking and the risk of being predated

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ABSTRACT

Habitats vary not only in resource availability and quality but also in predation risk, among other factors. The Desert Puna of Argentina comprises two habitats: the shrub steppe and the vegas. The former, the most abundant habitat, is a topographically simple area with unavailable free water and poor food quality; the latter is a very scarce and topographically complex habitat and with water available year round and high quality food. Guanaco relies heavily on vision to detect predators and narrow and complex habitats would be risky. Hence, we expected that guanacos would use the vegas in lowest proportion and would increase the time devoted to vigilance. Guanacos spent more time in the shrub-steppe than in the vegas, where the highest percentage of vigilant guanacos was recorded. A positive and significant relationship between time devoted to foraging and number of animals per herd was observed in both habitats. In the shrub-steppe the opposite was observed for vigilance, whereas in the vegas, no relationship was observed. Despite the low availability of vegas and the high predation risk, they represent a critical habitat for guanacos in the Desert Puna, because they representing the only areas with free water available throughout year for wildlife.

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1. Introduction

Habitats vary not only in availability and quality of resources, but also in terms of diversity and abundance of competitors and parasites, and predation risk for prey animals (Borgnia et al., 2008; Grand and Dill, 1999; Sinclair et al., 2006). Thus, individuals need to make habitat use decisions because they are strongly affected by the presence of predators or the perceived risk of predation and the extent to which they can behaviourally control that risk as well as by the quality of the foraging reward (Crosmary et al., 2012; Grand and Dill, 1999; Lima and Dill, 1990). For example, prey under threat of predation may continue to forage without paying heavy fitness penalties, by selecting feeding sites that facilitate crypsis, quick escape, vigilance or access to refuges (Lima and Dill, 1990). Prey might also adopt foraging strategies that reduce predation risk, such as group vigilance; consequently, the mere presence of predators can force prey to make behavioural choices between vital activities, such as feeding and avoiding contact with predators (Lima and Dill, 1990). Because vigilance increases with increasing predation risk and is partially incompatible with other fitness-enhancing behaviours, such as foraging, there is a trade-off between predation risk and energy gain (Cowlishaw et al., 2004; Crosmary et al., 2012; Lima and Dill, 1990). Nevertheless, studies have suggested that animals can simultaneously forage and be vigilant (Beauchamp, 2003; Lima and Bednekoff, 1999; Makowska and Kramer, 2007). Ruminants would have lower costs associated with feeding than non-ruminant species because they can be vigilant and process food simultaneously when they are in a head-up posture. However, when animals are cropping with their head down they cannot monitor the surrounding environment, and therefore the effectiveness of vigilance appears reduced, probably due to cognitive interference and obstructed views (Fortin et al., 2004; Makowska and Kramer, 2007).

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In areas with high perception of predation risk, animals can aggregate with conspecifics as a behavioural mechanism to reduce such risk (Hamilton, 1971). Individuals in a group can benefit from coordinated group defence, increased predator detection, increased probability of escape or decreased probability of death per encounter (Turner and Pitcher, 1986). Anti-predator vigilance is one of the main behavioural mechanisms that many prey use to avoid being predated, because it allows individuals to detect an approaching predator early and escape from it. However, prey animals often reduce the time available for other activities, such as foraging or mating (Childress and Lung, 2003). Therefore, groups of vigilant individuals can benefit from a collective ability to detect predators sooner than solitary individuals, allowing for reduced levels of individual scanning and increased foraging effort (Elcavage and Caraco, 1983).

In large herbivorous mammals, vigilance is shaped not only by the ingestion process (cropping, chewing and swallowing), but also by perception of elevated predation risk (Fortin et al., 2004). Several studies have shown that the time an individual spends in vigilance can be affected by several factors, including characteristics of the individuals, like sex and age (Elgar, 1989; Marino and Baldi, 2008; Taraborelli et al., 2012; Whittingham et al., 2004) and ecological characteristics, such as visual obstacles that reduce predator detection, distance from refuge, predation risk, group size or spatial separation between group members (Beauchamp, 2003; Li et al., 2009). For these large species, perception of risk increases with increasing structural complexity of habitats in terms of vegetation and topography, because predators are more difficult to be visually detected by prey and can hide more easily, increasing likelihood of attack (Baldi et al., 1997). Therefore, when the optimal habitats for drinking or foraging are also the most dangerous, individuals need to decide where to drink or forage and how much time to allocate to these activities. Thus, they are faced with a trade-off between benefit gain, such as water, and the risk of predation (Crosmary et al., 2012; Fortin et al., 2004; Lima and Dill, 1990).

Guanaco (*Lama guanicoe,* Camelidae) is the largest ungulate present in South America. It is a resource-defence polygynous species, with family groups including one territorial male, females and their offspring (Franklin, 1982, 1983; Puig and Videla, 1995). Guanaco is a social species and there is evidence that both sexes perceive significant anti-predator benefits of group living (Marino and Baldi, 2008). Likewise, it has been suggested that the social behaviour of guanacos would be influenced by ecological variables, such as water or food availability or the presence of predators, such as the puma (*Puma concolor*), which is their most important predator (Franklin et al., 1999; Taraborelli et al., 2012). As other large ungulates, guanaco relies heavily on vision to detect predators. This characteristic would be especially important in open habitats with low vegetation (Sarno et al., 2008), especially considering that foraging and vigilance make up almost 90% of the diurnal activity of guanacos (Marino and Baldi, 2008).

Guanaco is currently distributed from northern Peru to Tierra del Fuego (Argentina and Chile), at altitudes ranging from sea level to 4500 m in the Andes, the most abundant populations being found in the Patagonian steppe and Puna ecoregions (Baigún et al., 2008; Franklin, 1982). In Argentina, the Puna extends along the Andes mountain range, from the border with Bolivia up to the north of Mendoza province (Reboratti, 2005). The driest extreme of this ecoregion is the Desert Puna, characterized by the scarcity of free water due to the absence of rivers and lakes, and annual precipitation below 100 mm. In the Desert Puna, the shrub-steppe is the most abundant habitat; it is a topographically simple area of slight slopes, scarce and low plant cover of xerophytic vegetation, poor quality of trophic resources, unavailable free water, and high bare soil cover. A contrasting environments also present in the Puna are wetlands that originate a characteristic habitat known as vega (Squeo et al., 2006). These sites are topographically complex, with rock outcroppings, dense hydrophytic vegetation and plant of high nutrient content. Vegas are a scarce (>1% of the area) but representing the only areas with free water available throughout year for wildlife (Lara et al., 2007; Sixto, 2003; Squeo et al., 2006) and an important source of food (succulent plants). However, this more complex habitat than the shrub-steppe in terms of vegetation and topography would increase the risk of guanacos of being hunted by puma (Frid and Dill, 2002). The puma hunts by stalking and stealth, relying on vegetation cover (e.g., tall-dense vegetation) and steep topography with large rocks, to approach close enough (20–30 m) to their prey before attack (Bank and Franklin, 1998). As this predator does not chase its prey over long distances, early detection by guanacos can be advantageous because it might reduce predation chances.

Vigilance may have a number of functions in obtaining information about the environment (Lima and Dill, 1990); nevertheless, it is clear that predator detection is a major function in many species. We hypothesize that guanaco perceives the vegas as more hazardous than the shrub-steppe because they are more complex habitats; consequently, guanacos should adopt foraging strategies to obtain water or food in a safe manner. Accordingly, our aim was to evaluate the importance of the vegas for guanacos by exploring a) the relationship between amount of time of use and area used in the vegas, and b) the time spent in the different behaviours. We predict that in the vegas, guanaco would reject the close presence of a potential terrestrial predator by increasing agonistic behaviours. In addition, we expect increased vigilance in the vegas at the expense of foraging because the perceived risk is higher than that in the shrub-steppe.

2. Methods

2.1. Study area

The study was conducted in Don Carmelo Multiple Use Private Reserve (hereafter "the Reserve"), a protected area about 40,000 ha, with 10% (4000 ha) being occupied by the shrub-steppe and 0.0025% (0.01 ha) by the vegas (Márquez, 1999). One of highest guanaco densities (4.01–6.00 ind/km^2) in the region is present in the Reserve (Baigún et al., 2008), where human presence is scarce and unusual; hence, it is unlikely that this guanaco population is habituated to humans (Cappa Flavio pers. obs.). The Reserve is located in La Invernada valley, Ullúm department (3000 m a.s.l.; 31° 10'S, 69° 46′ W), San Juan province, Argentina (Márquez, 1999, Fig. 1). The most abundant plant species in the shrub-steppe are shrubs (*Lycium chañar*, *Artemisia mendozana*, *Maihueniopsis glomerata, Adesmia* aff. *horrida*), and grasses (*Stipa* spp.), whereas in the vegas the herb species *Lilaeopsis macloviana*, *Taraxacum officinale*, *Nastanthus agglomeratus, Azorella* spp.; the tall shrub *Adesmia pinnifolia*, are dominant (Lara et al., 2007; Márquez, 1999).

To describe the two habitats in terms of complexity, we used eight 100-m transects per habitat using the intersection line method (Maestre and Escudero, 2009). The vegas were characterized by tall vegetation (mean vegetation height = 44.4 cm; SE = 3.3; maximum height = 215.0 cm); mean proportion of bare soil, shrubs, grass-like vegetation, and rocks was 65.5%, 12.9%, 11.2%, and 10.4%, respectively. Rocks were large blocks with a mean height of 36.4 cm (SE = 4.1), a maximum height of 230 cm, and a mean volume of 0.48 m^3 (SE = 0.3), reaching a maximum volume of 19.3 m^3. The shrub-steppe was dominated by low vegetation (mean height = 13.9 cm, SE = 0.72; maximum height = 40 cm); mean proportion of bare soil, shrubs, and grass-like vegetation was 88%,

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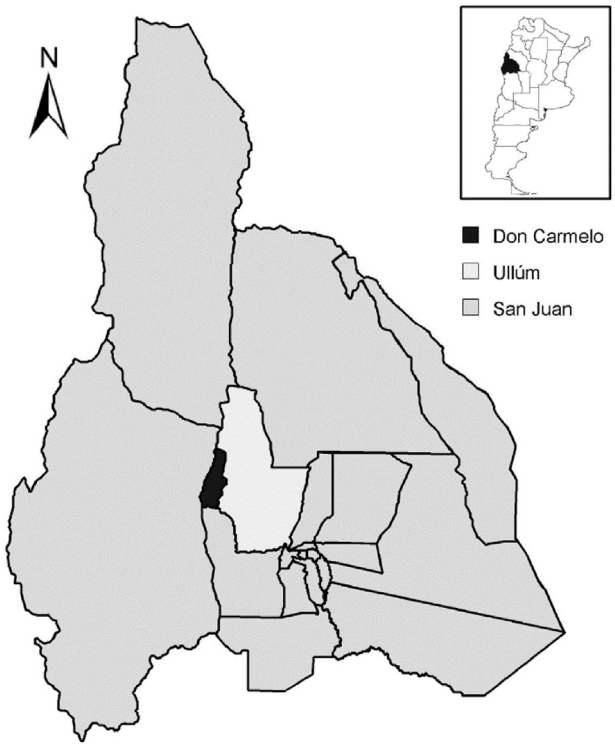

Fig. 1. Location of "Don Carmelo" Multiple-Use Private Reserve, in the Ullúm department (3000 m a.s.l.; 31° 10'S, 69° 46′ W), San Juan province, Argentina.

5%, and 7%, respectively, and rocks were absent. The mean slope was 35° in the vegas and 5° in the shrub-steppe.

2.2. Experimental design

The study was conducted in the 2007–2008 summer season, in five vegas in the Reserve and five sites in the shrub-steppe, which were randomly selected. Behavioural observations were made from 09.00 to 16.00 h, according to Donadio and Buskirk (2006), Young and Franklin (2004) and our pre-sampling data from the area. We evaluated if guanacos perceived different predation risks in each habitat (vega and shrub-steppe) by simulating a potential predator via the presence of a human. Human presence is often used in studies of flight decisions and risk assessments in mammal and bird species due to the difficulty of observing animal responses to natural predators (Franklin, 1982; Frid and Dill, 2002; Lima and Dill, 1990; Taraborelli et al., 2012). In addition, poaching is an ancestral and current activity, even within some protected areas (Donadio and Buskirk, 2006). In the Reserve, hunting has been banned only recently since its creation in 1993 (Márquez, 1999), so humans are likely considered potential threats by these guanacos. Also, as reported in similar studies (e.g., Taraborelli et al., 2012), guanacos emit alarm calls when they see humans approaching, suggesting that they perceive humans as predators.

Before guanacos arrived at the vega or the shrub-steppe, a human was positioned in the centre of the vega (at the valley bottom) and at a site of the flat shrub-steppe with evidence of guanaco activity (fresh faeces, footprints), to await the arrival of animals; this was defined as the "disturbed situation". The human was always the same person, who was standing so as to be sighted, always wearing brown and green clothing. Frequency of occurrence of alarm calling by guanacos was recorded when the animal approached the human present in the vega or the shrub-steppe at a distance of about 500 m or less. We also recorded the occurrence of alarm calling without human presence. For this, the human was also the same person and was always dressed the same way, but he was squatting so as not to be sighted.

We also evaluated the perceived risk of predation by comparing the rate (frequency/sec) and time spent in different behaviours under undisturbed conditions in both environments. These data were recorded from high sites in the vegas (so that the observer could not be sighted by the animals) whereas in the shrub-steppe, data were collected from a distance of over 900 m to avoid disturbing the animals. Individuals were considered to belong to the same foraging group when they were at a maximum distance of 50 m from one another (Marino, 2010). For each group, we recorded group size and randomly selected one adult for focal sampling. Focal samples were treated as independent samples because we only recorded one adult per herd. Moreover, we sampled different sites on subsequent days to minimize repeated measurements on the same herd. Thus, if repeated observations of the same animal occurred because it was unmarked, a period of at least 20 days elapsed between two consecutive records, avoiding the risk of pseudoreplication. We could not distinguish among family groups, male groups, or mixed groups because the number of herds with young was very low. Our sampling unit was an individual because sex cannot be determined in the field (Franklin, 1983; Pedrana et al., 2009).

To evaluate the rate (frequency/sec) and time spent in different behaviours, we continuously recorded behaviours of one adult per herd during 10 min or less if it went out of sight, but we only considered the observations that lasted at least 3 min (Marino, 2010). When we finished with focal sampling, we performed scan sampling of the group to evaluate its size and structure. Scans lasted from 2 to 10 s, depending of the herd size and cohesion. Thus, we quantified behaviour through focal and scan samplings (focal-continuous and scan-instantaneous records, Lehner, 1998) using a video camera with a 60× optical zoom and 12 × 25 binoculars. We used the focal sampling method to assess time budgets allocated to different behaviours at the individual level, and scan sampling to obtain information on behaviours of all members of the group (Lehner, 1998). We identified seven behavioural categories based on others studies on guanacos (Franklin, 1982; Marino and Baldi, 2008; Taraborelli et al., 2012): maintenance (grooming, defecating and urinating), lying down (animals were lying with their legs underneath the body), vigilance (animals were standing with the head and neck upright, ears erect and aiming directly at the stimulus or the approaching threat), foraging (animals were standing or walking slowly with the head below the shoulder height, usually handling food), moving (guanacos were displacing from their original location), alarm calling (guanacos emitted loud and sharp shouts, typically lasting 1–3 s, which were initially high-pitched and ended lower-pitched. These animals have ears pressed caudally against the head, and during the call, the head is elevated and the nares are wide open), and drinking (animals were standing with the head down). We quantified time spent in and frequency of each behavioural unit.

2.3. Statistical analysis

Alarm calling frequency was compared between habitats (vegas and shrub-steppes) using a binomial test (Zar, 1999) only in the disturbed situation. To compare the percentage of animals performing different behaviours in each habitat (data from scan-instantaneous), we used the test of difference between two proportions (Zar, 1999). We only used vigilance, foraging, moving, lying down and drinking because the other categories (maintenance and alarm calling) had a very low frequency. To compare percentages of time allocated to different behaviours and rates (frequency of

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behaviour/sec) between the vegas and the shrub-steppe, we used data from focal sampling and we could only use vigilance and foraging behaviours because the other categories had a very low frequency for statistical analysis. The analyses were performed using generalized linear models because the response variable was fitted to a Poisson distribution (link = log). For these analyses we compared two behaviours (vigilance and foraging) between the vegas and the shrub-steppe only for the undisturbed situation; for the disturbed situation we were not able to obtain data from the shrub-steppe because animals detected us from a far distance. We used number of animals per group as a covariate for all tests. Statistical analyses were performed using Statistic Software (version 7.0). In addition, we used the Spearman rank correlation coefficient to evaluate the effect of group size on percentage of animals being vigilant and foraging in the two habitats; in this case, we added foraging and drinking because both behaviours require a position of the animal that would reduce visual detection (head-down posture) and therefore animals would be more vulnerable to attacks from predators (Sarno et al., 2008).

3. Results

We devoted the same amount of time to observations and data collection of the undisturbed and disturbed situations in the vegas and the shrub-steppe (4800 min for each habitat in each situation; total sampling effort: 19,200 min), and used the same methodology for data collection. We made 73 focal observations and 49 scans during sampling of the undisturbed situation, and 34 focal observations and 26 scans in the disturbed situation. However, focal sampling represented 9.2% (441 min/4800 min) of total sampling time in the shrub-steppe in the undisturbed situation, whereas at the vegas, it amounted to only 3.5% (168 min/4800 min) of the total sampling time.

With respect to alarm calling, we found that guanacos only used this alarm call in the vegas with human presence (88 neighing of guanacos in the vegas vs. 0 in the shrub-steppe, binomial test, $p < 0.001$). The analysis of scan samples showed that the highest percentage of vigilant guanacos was found in the vegas, whereas in the shrub-steppe the behavioural categories with the highest percentage were foraging and lying down. Animals drinking were only recorded in the vegas (Fig. 2). According to the analysis of focal samples, the time allocated to the behaviours by guanacos differed between habitats. Guanacos were significantly more vigilant in the vegas than in the shrub-steppe ($\chi^2 = 425.53$; $df = 1$; Log-likelihood = −781.60; $p < 0.001$; covariate $p < 0.001$), whereas the opposite was found for time spent foraging ($\chi^2 = 862.63$; $df = 1$; Log-likelihood = −1469.34; $p < 0.001$, Fig. 3). The same pattern was found for rate of foraging and vigilance in both habitats (foraging: $\chi^2 = 5.68$; $df = 1$; Log-likelihood = −69.18; $p < 0.05$; and vigilance: $\chi^2 = 30.91$; $df = 1$; Log-likelihood = −89.23; $p < 0.001$, Fig. 3).

Mean group size was 6.55 ± 0.94 and 4.82 ± 0.90 for the shrub-steppe and the vegas, respectively. Guanacos showed a positive and significant relationship between time devoted to foraging and number of animals per herd in both habitats (shrub-steppe: $r_s = 0.50$, $N = 51$, $p < 0.001$; vega: $r_s = 0.55$, $N = 22$, $p < 0.01$); the opposite was observed for time spent in vigilance in the shrub-steppe ($r_s = -0.460$, $N = 51$, $p < 0.001$); however, there was not a significant relationship between group and time in the vegas ($r_s = 0.036$, $N = 22$, $p = 0.873$, Fig. 4).

4. Discussion

The complexity of habitats seems to affect their use by guanacos and such differential use could be related to habitat availability and perceived risk of predation. The vegas are a topographically heterogeneous habitat that only occupies 1.05 ha in the Reserve and has high vegetation quality and water availability year round (Lara et al., 2007; Sixto, 2003; Squeo et al., 2006). The time recorded in these sites was 2.6 times lower (considering the undisturbed situation) than the total sampling time in the shrub-steppe. The latter habitat covers 4000 ha and is characterized by a simple topography, with slight slopes and xerophytic vegetation of low height and quality. Foraging animals need to select among habitats or foraging sites that differ in both energy expenditure and mortality risk due to predation (Gilliam and Fraser, 1987). Ungulates and large mammals spend less time in environments rich in resource quantity and quality but with high predation risk (Frid and Dill, 2002). Habitat use by guanacos in the Desert Puna represents the outcome of a trade-off between resource acquisition and avoidance of predators in risky habitats such as the vegas. This habitat has large rocks and dense and tall vegetation where the puma, the principal predator of guanacos, can hide. The puma is a solitary hunter that stalks its prey, and guanacos might have reduced probability of early detection in these habitats.

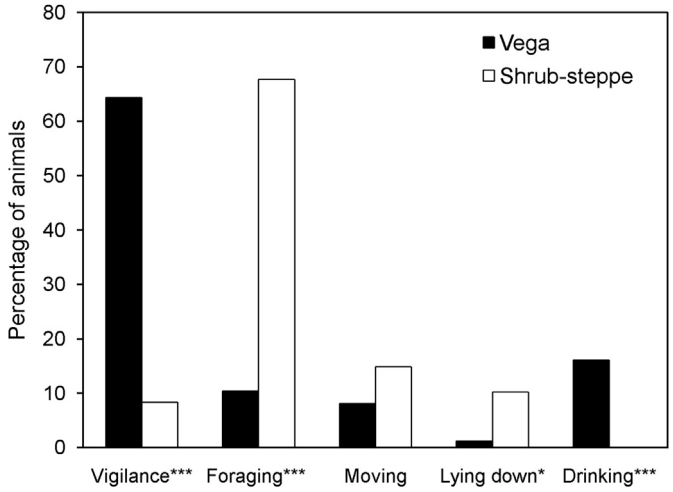

Fig. 2. Percentage of guanacos exhibiting different behaviours in the undisturbed situation in the two sampled habitats: vega and shrub-steppe (scan sampling data). The total number of sampled individuals was 424. Asterisks indicate statistical significant difference (test of difference between two proportions): ***$p < 0.0001$ and *$p < 0.01$.

During our observations guanacos only neighed in the vegas when the human subject was present; however, this alarm call was never recorded in the shrub-steppe in the disturbed situation. According to Franklin (1982), this alarm call is made by males and females when a potential predator (e.g., Andean foxes, *Lycalopex culpaeus*, mountain lions, *Puma concolor*, mountain cats *Lynchailurus pajeros*, or man, *Homo sapiens*) is sighted. In the vegas, habitat complexity might reduce probability of detection and increase predation risk. Therefore, guanacos could use danger call as social transmission of the detection of predator to warn other group members of potential danger. Accordingly, the vegas appear as a valuable habitat for guanacos because despite the disturbance (i.e., human presence) and the emission of alarm calls (alarm calling), they used this habitat almost in a similar proportion to that in the undisturbed situation (4.5% and 3.5% of time, respectively). These habitats are considered the "oases" of the Puna, with water and high biomass and vegetation cover year round and with plant species usually of relatively high nutritional content (Puig et al., 2011). On the other hand, in the shrub-steppe (a flat habitat), guanacos would be able to detect a predator early and keep away from danger, as indicated by our results; indeed, we did not record

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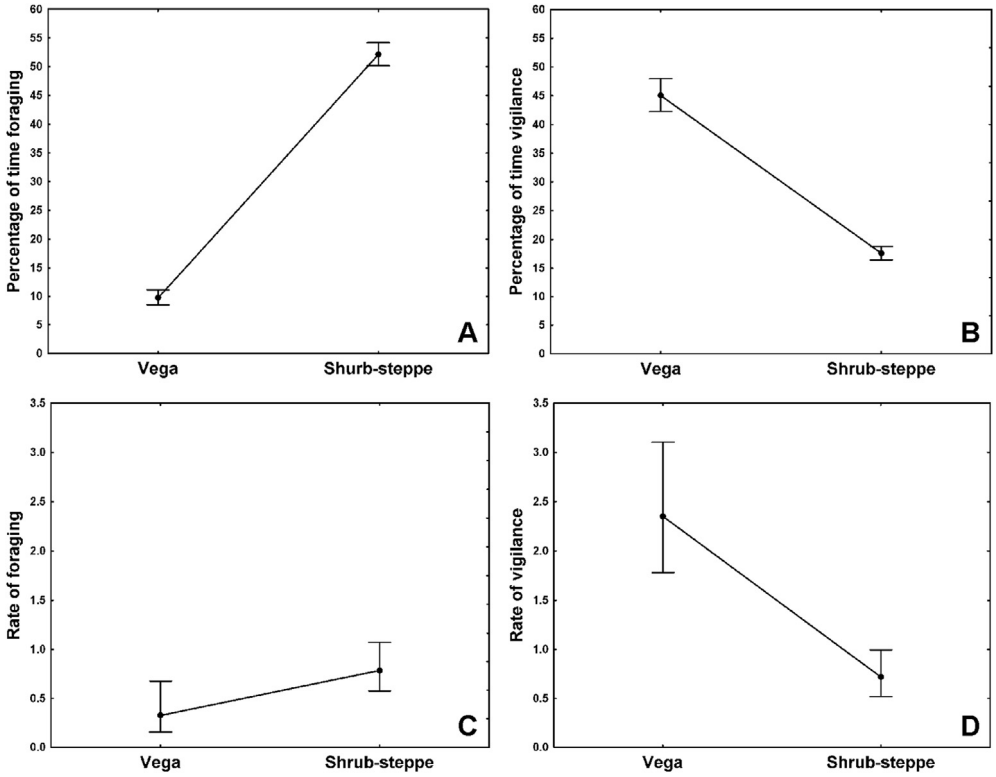

Fig. 3. Generalized linear models (Poisson distribution, link = log) for the percentage of time spent foraging (A, $p < 0.001$) and vigilant (B, $p < 0.001$), and rate of foraging (C, $p < 0.05$) and vigilant (D, $p < 0.001$) in both habitats (focal sampling data). Means ± standard errors (SE) are represented.

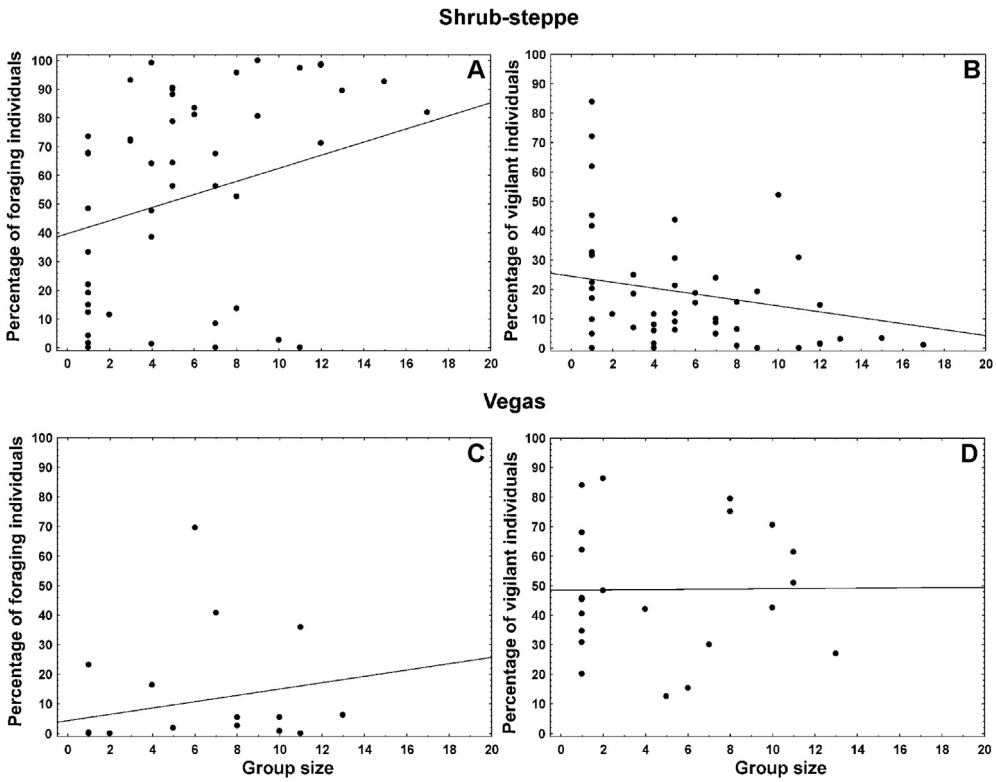

Fig. 4. Effect of group size evaluated with Spearman's correlation coefficients in two habitats from focal sampling data: shrub-steppe (A, $r_s = 0.50$, $N = 51$, $p < 0.001$; B, $r_s = -0.460$, $N = 51$, $p < 0.001$) and vegas (C, $r_s = 0.55$, $N = 22$, $p < 0.01$; D, $r_s = 0.036$, $N = 22$, $p = 0.873$).

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guanacos in the disturbed situation in this habitat because they could see us from a long distance (more than 800 m).

Our results support the assumption that the vega is a valuable resource, although it represents a risky habitat for guanacos. This is because the highest percentage of the total number of animals observed in this site was found vigilant; however, despite the hazard, animals are forced out into exposed areas most likely in search of water. Thus, unlike expected guanacos used the shrub-steppe more extensively to obtain food despite its poor quality, probably because of the lower risk posed in these open and flat habitats. Studies on other guanaco populations (Puig et al., 2011) and on the related wild camelid, the vicuña (*Vicugna vicugna*), found that those animals fed on succulent species that occur in the vegas and their edges rather than in the steppe (Borgnia et al., 2008). In a study comparing the diet of guanaco at sites with and without vegas (Puig et al., 2011), grasses were found to be preferred and shrubs were avoided. These authors stated that high plant cover as well as the considerable dietary proportions of species present exclusively in the vegas and their edges, such as grass-like plants and several grasses, shows the relevance of the vegas for guanaco feeding. In addition, vicuña selects the vegas for foraging; indeed, the vegas are considered the optimal foraging habitat for vicuñas due to the high food quality, whereas the steppe is regarded as a sub-optimal habitat (Borgnia et al., 2008). The selection of succulent plants present in the vegas was related to a higher protein content than that of plants that occur in the dry steppe (Borgnia et al., 2008; Cajal, 1989; Puig et al., 2011). In our study, the low percentage of guanacos of the same herd found feeding in the vega is consistent with the assumption that this habitat would be perceived as risky by guanacos (Makowska and Kramer, 2007). Another fact that supports this idea is that guanacos were always seen drinking in intermittent and short bouts (F. Cappa pers. obs.).

As habitats vary not only in availability and quality of resources but also in predation risk, decisions concerning habitat use are strongly affected by the presence of predators or the perceived risk of predation (Grand and Dill, 1999; Lima and Dill, 1990). As the vega is a valuable habitat in terms of water and food (Sixto, 2003), we expected that guanacos would spend more time foraging and drinking in the vegas if energy intake were the main component of the foraging decision. However, results are consistent with a foraging–predation risk trade-off, in which the time guanacos spend vulnerable to attack would be a major component of foraging decisions. These vegas are obstructed habitats with steep and complex topography that affects foraging decisions, such as an increase in vigilance, as suggested for another guanaco population (Baldi et al., 1997) and for other species (Whittingham et al., 2004). In visually obstructed habitats, predators may be hidden behind rocks and vegetation, increasing actual predation risk (Arenz and Leger, 1997). Therefore, foraging animals frequently change their pattern of vigilance when they move from a patch with a clear view to another with a relatively obstructed view. Animals get an anti-predatory benefit from feeding in open habitats because the low structural complexity provides them with wide availability of means of escape and refuge sites in the field (Baldi et al., 1997). In the present study, habitat complexity affected foraging behaviour, and therefore guanacos spent more time foraging in the shrub-steppe, where topographic complexity is low and vegetation is short (not exceeding 50 cm). The shrub-steppe was perceived by guanacos as the lowest predation risk habitat, affecting the time devoted to vigilance and foraging. This result is consistent with findings reported for other guanaco populations by Bank et al. (2003) and Young and Franklin (2004), who found that open spaces were most widely used and that guanacos and another wild South American camelid, the vicuña spent a great amount of time in flat areas (Lucherini, 1996).

Group-size effect was found only in the shrub-steppe. In this habitat we found a negative relationship between group size and vigilance (percentage of vigilant individuals); this relationship is referred to as the group-size effect on vigilance and has been reported for many species (Lima and Dill, 1990; Taraborelli et al., 2012). This moderate group-size effect suggests that other factors not evaluated in the present study, such as sex, spatial position in the group, physiological state, and dominance level, might be also influenced by predation risk, as suggested for other species (Beauchamp, 2008). By contrast, in the vegas vigilance did not covary with group size, and the magnitude of the group-size effect on time devoted to vigilance was the same in large and small groups. Catteral et al. (1992) found that vigilance was not related to group size and suggested that this result might be due to a lack of predators. This is not the case of our study, because we found guanaco carcases in three of the five vegas evaluated, and all puma faeces were also recorded in the vegas (F. Cappa pers. obs.). In fact, one of us video-recorded a puma lying among the rocks in one vega (F. Cappa). We did not detect group-size effect in the vegas, which could be attributed to the ability of guanacos to perceive this habitat as highly risky. Indeed, the tall vegetation and rocks pose a visual obstacle and reduce the effectiveness of vigilance; hence, almost all members of the group monitored the environment. Other possible explanation for the lack of group-size effect may be that the vegas are narrow habitats in the study area and in a large herd the probability of collisions in the presence of predators is increased (Semeniuk and Dill, 2004). However, future studies are necessary to confirm the lack of relationship between group size and vigilance, and to explore if it is due to the characteristics of this habitat. In a review, Elgar (1989) suggests that several variables could confound the lack of negative relationship between vigilance and foraging, such as food density and quality, which generate competition among members of a group. Because the vegas have high food density and quality (Borgnia et al., 2008; Cajal, 1989; Puig et al., 2011), we consider that food is not a factor that can explain the lack of group-size effect in this habitat. Indeed, guanacos spent 5.2 more times foraging in the shrub-steppe that in the vegas; hence, risk of predation could be a more important factor than food. In the vegas, guanacos are in a head-down posture when drinking (the most common behaviour), which reduced predator detection, making them vulnerable to attacks by puma. In this risky situation, guanacos might use social information when they have their heads down; however, the complexity of this habitat reduces the effectiveness of social information transmission among members of the group (Li et al., 2012). In habitats with these characteristics, it is hardly likely that animals can find great advantages of group-size effect (such as dilution and detection), and therefore more guanacos than predicted by group-size effect model are vigilant in the vegas (Lima, 1995). On the other hand, in the shrub-steppe guanacos seem to take advantage of collective detection (Elgar, 1989; Lima, 1995). In contrast to our results, Puig et al. (2011) found that guanacos preferred to feed on vegetation from the wetland and avoided the shrubs; however, they studied a guanaco population present in a broad wetland, with greater possibility of escape and of early detection of predators.

Overall, complex and heterogeneous habitats, with tall plants, such as the vegas studied, are perceived as risky by guanacos compared to simple habitats with low plants, such as the shrub-steppe studied. Guanacos devoted more time to vigilance compared to foraging and increased the number of members per group that monitored the environment in the risky habitat. Although the vegas are a habitat with high risk of predation, they were used by guanacos to obtain mainly free water but not to forage, despite the high quality of food. Consequently, although the vegas are a very scarce habitat ($<1\%$ of the area), they represent a

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critical habitat for guanaco in the Desert Puna, requiring actions for the conservation of this species and biodiversity of this hyperarid environment.

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