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Habitat selection by reintroduced guanacos (*Lama guanicoe*) in a heterogeneous mountain rangeland of central Argentina

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Abstract. Quebrada del Condorito National Park is located in the upper belt of the mountains of central Argentina and preserves a heterogeneous rangeland area. After the creation of the National Park, in 1996, domestic livestock were gradually removed to avoid soil loss and degradation due to overgrazing in this fragile ecosystem. Lack of large-scale herbivory allowed the expansion of tussock grasslands over grazing lawns. In 2007 a guanaco (*Lama guanicoe*) population was reintroduced; this large native herbivore, that had become extinct in the region was selected, because it is a low-impact grazer. Habitat selection by the guanaco population reintroduced to the National Park was studied. Seven habitat types previously defined for the region were considered, each one exhibiting a particular dominant plant growth form and different per cent cover of plant species. Guanacos made a positive selection of moist and dry grazing lawns, and avoided tussock grasslands and forests. The reintroduced guanacos selected landscapes with short plants and a high percentage of perennial graminoids and forbs, which are guanacos' preferred food items. The results indicate that availability of forage of a nutritive value and dominant plant growth form largely explain habitat selection by guanaco in the National Park; this information can be useful for both the ongoing guanaco reintroduction project and the design of management strategies aimed at ecological restoration of this important rangeland region of central Argentina.

Additional keywords: grazed patches, large herbivore, mountains of central Argentina, reintroduction.

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Introduction

The upper belt of the mountains in central Argentina is a fragile rangeland area that comprises the higher sectors of the principal water basins in the region (Cingolani *et al*. 2004). Livestock rearing has been the main productive activity since the Spanish conquest, more than 400 years ago (Díaz *et al*. 1994). Overgrazing and the frequent use of fire to induce grass regrowth have produced a widespread process of soil erosion and replacement of the vegetated surface by rock pavements (Cingolani *et al*. 2008).

In 1996, Quebrada del Condorito National Park was created with the aims of protecting part of these basins from degradation and preserving the rich biodiversity and endemic species of the area (Díaz *et al*. 1994). To meet those aims, domestic livestock were removed from a large area of the National Park (Tavarone *et al*. 2007). However, as the region has a long evolutionary history of herbivory (Cingolani *et al*. 2005), livestock exclusion caused a disproportionate expansion of *Poa stuckertii*, a thick-leaved tussock grass (hereafter 'thick tussock grass'), at the expense of grazing lawns (Cingolani *et al*. 2003). As a consequence, vegetation diversity and spatial heterogeneity were reduced, which in turn reduced avifaunal biodiversity (García *et al*. 2008; Cingolani *et al*. 2010). In an attempt to address this problem, livestock were reintroduced in some portions of the National Park; however, even at low stocking rates, erosion processes were resumed (A. M. Cingolani and D. Renison, unpubl. data).

With the aim of controlling landscape homogenisation and at the same time avoiding soil erosion processes induced by livestock, in 2007 the National Parks Administration reintroduced a population of guanacos (*Lama guanicoe*), a large native herbivore that historically inhabited the region but became extinct early in the 19th century (Berberián and Roldán 2001). This herbivore was selected because it is a low-impact grazer. Unlike domestic livestock, it has footpads instead of hooves, and feeds by cutting the plants with the teeth without uprooting them. Both factors help to ameliorate soil compaction and degradation (Erlich 1984).

The reintroduction of guanacos was performed following IUCN protocols (IUCN 1998). This project was a milestone in the history of the reintroduction of wild species in the national system of protected areas in Argentina. However, reintroductions are complex and costly processes that may fail due to the lack of knowledge on the ecology of the species at the reintroduction site

(Armstrong and Seddon 2008). Habitat selection studies during the post-release stage play a particularly important role in understanding the relationship between the reintroduced population and the environment and, therefore, are useful for management decision-making (Wakefield *et al*. 2002).

Numerous studies on large herbivores have indicated that habitat selection is strongly associated with dominant plant growth form (Bellis *et al*. 2004; Kaczensky *et al*. 2008; Godvik *et al*. 2009). In wild guanacos and vicuñas (*Vicugna vicugna*), the sites selected are characterised by short and open growth forms because they provide these species with forage of high nutritive value, and also facilitate early detection of predators (Puig *et al*. 1997; Sosa and Sarasola 2005; Arzamendia *et al*. 2006; Borgnia *et al*. 2008; Acebes *et al*. 2010). Habitats with these characteristics are very important for the reproductive ecology of guanacos, a species in which dominant males maintain their group of females by defending sites of high resource availability and low risk of predation against other males (Bank *et al*. 2003; Young and Franklin 2004).

In the upper belt of the mountains in central Argentina, the combined effect of livestock and topography has created a very heterogeneous vegetation mosaic, which includes forest thickets, tussock grasslands and short grazing lawns, combined with patches of rocky surfaces (Cingolani *et al*. 2004, 2008). Previous studies in the area have shown that grazing lawns are dominated by short graminoids (i.e. short grasses, sedges and rushes) and forbs, which according to diet studies, are the most commonly consumed forage items because of their soft leaves of high nutritive value compared with leaves of tall tussock grasses or woody species (Pucheta *et al*. 1998; Falczuk 2002; Cingolani *et al*. 2007; Vaieretti *et al*. 2010). In turn, tussock grasslands and woodlands have relatively low abundance of short graminoids and forbs.

For large herbivores, the selection of plant communities within a landscape is a function of the relative abundance of preferred plant species (Senft *et al*. 1987). Based on habitat use patterns of wild camelids in other areas, and considering the high nutrient content of short graminoids and forbs and their short size, it is predicted that individuals of the reintroduced guanaco population will select grazing lawns over other habitat types. Therefore, the aim of the present work was to investigate habitat selection by guanacos reintroduced to Quebrada del Condorito National Park. The specific objectives were (1) to calculate a selectivity index for each habitat type present in the area, and (2) to analyse the relationships between selectivity index values and the average abundances of different types of forage species and topographical characteristics across the habitat types. The results may be useful to make management decisions that promote the effective recovery of the species in the National Park, as well as to understand the role of this large herbivore in the restoration of the fragile ecosystem in the high mountains of central Argentina.

Materials and methods

Study area

Quebrada del Condorito National Park is located in the upper portion of the Córdoba mountains (1700–2800 m a.s.l., 31°34′S, 64°50′W) in central Argentina, covering an area of 24 774 ha. Mean annual temperature in the region is 8°C, with an absolute minimum of −15°C and mean precipitation ranging between 800 and 900 mm, concentrated between October and April. Three types of physiographic units can be distinguished: very steep escarpments, rocky hills, and slopes and plateaus with variable degree of dissection (Cingolani *et al*. 2008). Although the area belongs to the Chaco Serrano Phytogeographic District, almost 50% of the flora is of Andean Patagonian lineage (Cabido *et al*. 1998). Moreover, this high plateau is isolated from surrounding regions; hence, it is considered a true biogeographic island, which also harbours a high number of endemic taxa (Díaz *et al*. 1994).

Based on descriptions made by Cingolani *et al*. (2004) and von Müller (2011), there are seven habitat types dominated by different plant growth forms and species: forest, thick tussock grassland, thin tussock grassland (i.e. grassland dominated by thin-leaved tussocks), dry lawn, moist lawn, rock outcrops and erosion pavement. Each habitat type was also characterised by different cover types in variable percentages, which include all forage items plus bare rock and bare soil (Tables 1 and 2). The

Table 1. Habitat types and their total plant cover, dominant species and vegetation height (range in cm) in Quebrada del Condorito National Park, central Argentina (adapted from Cingolani *et al*. 2003, 2004; and unpubl. data)

Habitat type	Total plant cover (%)	Dominant plant species	Vegetation height (cm)
Forest	90–100	*Polylepis australis*, as trees or shrubs, associated with the tree *Maytenus boaria* and the shrub *Berberis hieronymi*	200–600
Thick tussock grassland	90–95	The tussock grass *Poa stuckertii*, with the forb *Alchemilla pinnata* and other short species in the intertussock space	50–150
Thin tussock grassland	90–100	The tussocks *Deyeuxia hieronymi* and/or *Festuca tucumanica*, sometimes with *F. hieronymi*	30–130
Dry lawn	85–100	*A. pinnata* and the sedge *Carex fuscula*, sometimes with the presence of the grasses *Muhlenbergia peruviana* (annual) and *Sorghasatrum pellitum* (perennial) or small tussocks of *F. tucumanica* or *D. hieronymi*	2–20
Moist lawn	99–100	*A. pinnata* and the sedge *Eleocharis albibracteata*	2–20
Erosion pavement	0–20	Few individuals of the grass *Stipa juncoides*, and the forbs *Hypochaeris caespitosa*, *Plantago brasiliesnsis* var. *cordobensis* and *Noticastrum argenteum*	0–10
Rock outcrop	5–40	The shrubs *Berberis hieronymi*, *Satureja odora*, *Heterothalamus alienus* and/or *Croton argentines*. Often also small tussocks and the fern *Blechnum penna-marina*	0–100

Table 2. The mean percentage (%) of the different cover types (forage items, bare soil and bare rock) in the habitat types of the Quebrada del Condorito National Park, central Argentina (adapted from Cingolani *et al.* 2008; and von Müller 2011)

Cover types	Habitat type						
	Forest	Thick tussock	Thin tussock	Dry lawn	Moist lawn	Erosion pavement	Rock outcrops
Forage items							
Trees	81	0	0	0	0	0	1
Shrubs	1	1	0	0	0	0	1
Thin tussocks	5	15	68	20	2	2	3
Thick tussocks	0	70	5	4	6	0	0
Perennial graminoids[A]	2	5	11	31	59	5	2
Forbs	2	7	10	37	33	5	1
Annual graminoids	0	0	1	5	0	1	0
Ferns	4	1	0	0	0	0	1
Mosses	1	0	0	1	0	1	1
Other cover types							
Bare soil	0	1	1	1	0	5	1
Rock	4	1	2	1	0	90	88

[A]Short perennial grasses, sedges and rushes.

study area was highly heterogeneous, and the habitat types were distributed in an intricate mosaic, where an average of three habitat types could be found in a small area of 900 m^2 (Cingolani *et al*. 2004).

Data collection

Based on a feasibility study (Tavarone *et al*. 2007), the National Parks Administration reintroduced in 2007 more than 100 guanaco individuals from a wild population of Río Negro province, northern Patagonia (40°47′S, 66°45′W) to Quebrada del Condorito National Park. Guanacos were released with only a few days of acclimatisation ('hard release'). Each guanaco was marked with coloured and numbered plastic ear tags; nearly 25% of them were also radio-collared. Out of the total number of guanacos reintroduced in that year, nearly 80% died during the critical post-release stage (Barri *et al*. 2009). At the start of this study, 1 year after the reintroduction, only two reproductive groups survived and were effectively settled in the National Park: a family group composed of one male and nine females (three of them radio-collared), and another family group that included one male and four females (two of them radio-collared).

The area was visited at 2-week intervals between November 2008 and May 2009. Individuals were located using radio-telemetry, by surveying the study area on foot, on horse or by truck. The interval between visits was long enough to obtain independent samples of each reproductive group (Boyce *et al.* 2003). Because of the difficulties in locating both groups on the same day, each visit consisted of 2 consecutive days of field work, with observations being made between 10:00 and 18:00 hours. Twenty-three days (hereafter 'dates') of observation were completed (on one date it was not possible to locate the smallest guanaco group). On each date, using telescope and binoculars, the number of individuals present in each habitat type was counted from a distance of between 50 and 150 m. It was possible to distinguish the habitat used by each individual of a group due to both the proximity of the observation site to the location of the animals and the plant growth form characteristics of each habitat type, which facilitates visual observation (described in Tables 1 and 2). Moreover, once the number of individuals in each habitat type had been counted, the habitat types previously observed were confirmed by waiting until all individuals had moved from the site (average waiting time: 45 min). The coordinates of the central point where the guanaco group was located were also recorded with GPS (Garmin Etrex; Garmin, Kansas City, MO, USA), for *a posteriori* mapping of the territory.

Territory and habitat mapping

The habitat selection process of the guanacos was analysed at the home range hierarchical level (Johnson 1980) and at the plant community scale (Senft *et al*. 1987). Only the availability of the different habitat types within the specific territory occupied by the reintroduced guanaco population in the National Park was considered. This procedure was used taking into account the territorial behaviour of the species (Bank *et al*. 2003) and, because this study was conducted 1 year after the release of the individuals, once the territory of the reproductive groups had been established (Barri and Fernández 2011).

To estimate and map the territory used by the population, all the location points recorded for both family groups on the 23 sampling dates were employed. The method of minimum convex polygon was applied, considering a buffer area of 500 m around each point, which represented on average the area used by individuals during the observation time (Boyce *et al*. 2003; Kaczensky *et al*. 2008). The polygon was projected on a Quick Bird image obtained from Google Earth, and the different habitat types within it were mapped using Arc-View 3.1. The habitat types were distinguished by colour and texture based on field experience and following the criteria of von Müller (2011). The proportion of each habitat type available in the territory used by the guanaco population was calculated from the vegetation map, by dividing the available area of each habitat type by the entire territory area. Additionally, the topography associated with each habitat type was described by combining the habitat type map for the territory used by guanacos with topographic layers obtained from a digital elevation model (Cingolani *et al*. 2008). Based on Cingolani *et al*. (2008), the following parameters were used: average slope (%), topographic position (from 0% for sites at valley bottoms to 100% for sites at ridges), and landscape roughness (from 0% for very smooth landscapes to 100% for the roughest landscape found in the area).

Data analyses

For each sampling date, the proportion of guanacos observed in each habitat type was calculated by dividing the number of individuals observed in such habitat by the total of individuals recorded in all habitat types on that sampling date. Then all dates were averaged to obtain one value of proportional use for each habitat type. To determine habitat selection by the guanaco population reintroduced to the National Park, the Ivlev (1961) index for each habitat type was calculated by using the equation:

$$ISi = (Gi - Ai)/(Gi + Ai)$$

where ISi is the Ivlev selection index for the habitat type i, Gi is the average proportion of guanacos observed in type i, and Ai is the proportional area of type i.

The Ivlev's electivity index scales from –1 to 1, with negative values indicating avoidance of the habitat type, zero indicating random selection from the environment, and positive values indicating active selection. To analyse whether the Ivlev index value obtained for each habitat type differed significantly from zero, 100 random simulations were performed. Each simulation consisted in randomly distributing on the territory the number of individuals observed at each sampling date. As with values recorded in the field, the 23 simulated dates were averaged; thus, with these data a simulated Ivlev index was obtained for each habitat type. This procedure was performed 100 times to obtain a distribution of the error of zero values for the index, which would be expected for the random use of habitat types by guanacos. The minimum and maximum values obtained from the 100 simulations were used to determine a >99% confidence interval for each habitat type. The index values of each habitat type obtained in the field that fell outside that interval were considered significantly different from expected by chance ($P < 0.01$).

Finally, to determine a possible relationship between selectivity and habitat type characteristics, Spearman correlations between the Ivlev indices obtained for each habitat type and the mean values of the different cover types (Table 2) and topographic parameters (slope, topographic position and roughness) were performed by the InfoStat program (Di Rienzo *et al*. 2010).

Results

The territory used by guanacos reintroduced to the National Park was 49.1 km^2. Within that territory, thick tussock grasslands was the most commonly available habitat type, followed by erosion pavements, dry lawns, thin tussock grasslands, rock outcrops, forests and, finally, moist lawns (Table 3). According to previous studies, the association between topography and habitat type should be weak because past livestock pressure and fires had strongly modified the original vegetation patterns (Cingolani *et al*. 2008). Nevertheless, forests and rock outcrops tended to be at lower topographic positions, and in steeper and more rugged sites than the other habitat types. Conversely, moist grazing lawns and thick tussock grasslands tended to be at upper topographic positions in the flattest and smoothest sites (Table 4). Guanacos actively selected moist and dry grazing lawns, avoided forests and thick tussock grasslands, and used thin tussock grasslands, rock outcrops and erosion pavements at random (Table 3).

Table 3. Area of the different habitat types, percentage of the total area, habitat type used by guanacos as a percentage of total habitat types and Ivlev's electivity index for each habitat type in the territory occupied by the reintroduced guanaco population in the Quebrada del Condorito National Park, central Argentina

* Index values significantly different from zero ($P < 0.01$)

Habitat type	Area (km^2)	Percentage of area	Habitat type used as a percentage of total habitat types	Ivlev index
Forest	3.42	7.0	0	–1.00*
Thick tussock grassland	12.1	24.9	4.3	–0.70*
Thin tussock grassland	7.31	14.9	7.7	–0.32
Dry lawn	9.26	18.8	47.1	0.43*
Moist lawn	1.93	3.9	14.4	0.57*
Erosion pavement	9.6	19.5	16.5	–0.08
Rock outcrop	5.50	11.2	10.0	–0.06

Regarding cover types, perennial graminoids and forbs were positively correlated with the Ivlev index ($r_s = 0.779$, $P = 0.04$, $n = 7$ and $r_s = 0.783$, $P = 0.04$, $n = 7$; respectively), whereas percentage of ferns was negatively correlated ($r_s = –0.758$, $P = 0.05$, $n = 7$) (Fig. 1). The remaining cover types (trees, shrubs, thin tussocks, thick tussocks, annual graminoids, mosses, bare soil and bare rock) were not significantly correlated with Ivlev index values. Ivlev index values were not correlated with slope, topographic position or the roughness index ($r_s = –0.50$, $P = 0.22$, $n = 7$, $r_s = –0.39$, $P = 0.36$, $n = 7$ and $r_s = 0.07$, $P = 0.86$, $n = 7$; respectively).

Discussion

The guanaco population reintroduced to Quebrada del Condorito National Park did not use the habitat types of their territory homogeneously. Availability of forage of high nutritive value and dominant plant growth form influenced habitat selectivity by guanacos. This was evident in the positive selection of grazing lawns and the avoidance of forests and thick tussock grasslands. Habitat selection determined in the reintroduced guanaco

Table 4. Slope, topographic position and roughness index (with s.e. of mean) for each habitat type in the territory occupied by the reintroduced guanaco population in the Quebrada del Condorito National Park, central Argentina

Habitat type	Slope (%)	Topographic position (%)	Roughness index (%)
Forest	13.3 ± 6.3	44.2 ± 21.9	24.8 ± 10.1
Thick tussock grassland	7.4 ± 5.6	44.8 ± 25.8	18.9 ± 9.1
Thin tussock grassland	8.0 ± 4.8	56.0 ± 24.6	20.0 ± 7.6
Dry lawn	7.9 ± 5.1	53.7 ± 25.6	20.2 ± 8.7
Moist lawn	6.3 ± 4.9	43.2 ± 24.5	16.8 ± 7.9
Erosion pavement	8.9 ± 5.6	54.8 ± 25.6	21.1 ± 9.0
Rock outcrop	10.2 ± 5.8	48.0 ± 24.6	22.5 ± 9.0

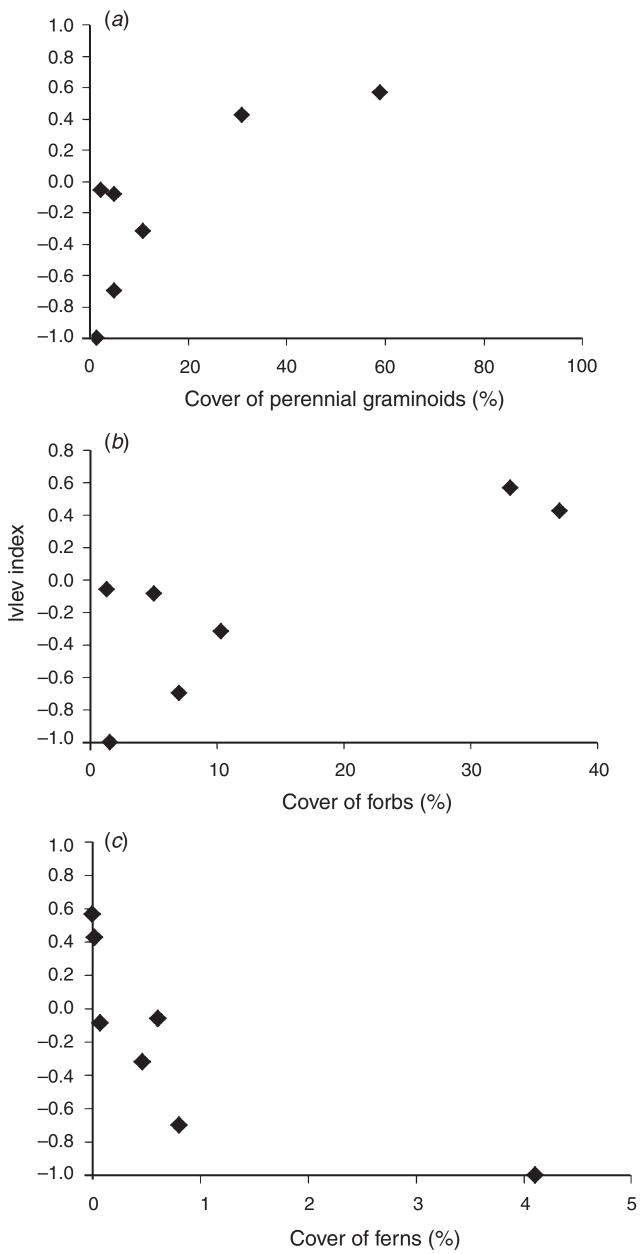

Fig. 1. Ivlev's electivity index values of the seven habitat types correlated with their mean cover of (*a*) perennial graminoids, (*b*) forbs and (*c*) ferns in the Quebrada del Condorito National Park, central Argentina.

population is consistent with observations reported for the same species in other regions within its distribution range (Lawrence 1990; Puig *et al*. 1997; Bank *et al*. 2003; Sosa and Sarasola 2005; Acebes *et al*. 2010). This pattern has also been observed in vicuña, another South American wild camelid, which exhibits a positive selection for open sites and dry grazing lawns, avoiding areas of dense vegetation or with abundance of trees and shrubs (Cassini *et al*. 2009).

The positive selection of lawns by reintroduced guanacos is probably related to the higher nutritive value of the dominant perennial graminoids and, to a lesser extent, forbs than that of tussock grasses (Pucheta *et al*. 1998; Cingolani *et al*. 2004, 2007). Perennial graminoids (short grasses, sedges and rushes) have also been reported as the most important forage species in the diet of wild populations of guanacos (Puig *et al*. 1997). Further preliminary data on selection of forage species in the diet indicate that guanacos reintroduced to the National Park consume a high percentage of perennial graminoid species, such as *Sorgastrum pellitum*, *Briza subaristata* and *Carex fuscula* (F. R. Barri, V. Falczuk, A. M. Cingolani, S. Díaz, unpubl. data), all of which are most abundant in grazing lawns (Cingolani *et al*. 2004).

Although habitat types tended to differ in their topographic characteristics to some extent, the lack of relationships with the Ivlev index values indicates that topographic characteristics do not have a direct influence on individuals' choice. Guanacos avoided forests as well as thick tussock grasslands, two habitat types with opposite topographic characteristics. On the other hand, they positively selected lawns of topographic characteristics similar to those of thick tussock grasslands. This evidence reinforces the idea that the main driver of habitat selection by reintroduced guanacos in the National Park is the availability of forage of high nutritive value.

Another factor that might have influenced habitat selection by reintroduced guanacos is plant growth form. Individuals positively selected open flat landscapes and habitat types bearing short plants, avoiding habitat types with tall plants. In wild populations of guanacos in Patagonia, habitats with tall plant growth forms may be a barrier to early detection of predators, reducing the chances to escape (Lawrence 1990; Bank and Franklin 1998). Areas of dense vegetation are associated with a greater risk of predation by puma, the only natural predator of guanacos (Bank *et al*. 2003). Pumas take advantage of these areas, which they use to stalk the prey before attack (Bank and Franklin 1998). Since the guanaco population was reintroduced to the National Park, puma attacks have been recorded and guanaco remains were found in puma faeces in the area (Pía 2011). Likewise, guanaco behaviour in the National Park suggests that individuals would be under high predation risk by puma (Barri and Fernández 2011).

In the upper belt of the mountains of central Argentina, grazing lawns are also the habitat type positively selected by domestic livestock (von Müller 2011). This result should be taken into account when formulating management strategies for the project of guanaco reintroduction to the National Park, because sympatry with livestock would have a negative impact on guanaco movements and habitat selection. In 2012, new groups of guanacos were reintroduced; on this occasion, a 'soft release' was used (i.e. guanacos were allowed a long-term acclimatisation period), and thus survival rates during the critical post-release stage were significantly higher than in 2007 (F. R. Barri, unpubl. data). Hence, as has been observed in other wild populations of guanacos (Baldi *et al*. 2001), if livestock are not completely removed from the National Park, the reintroduced guanacos may be displaced towards areas of forage with a lower nutritive value. In turn, in other areas it has been observed that, when domestic livestock are excluded and guanacos are protected, population density of guanacos can increase considerably, without producing negative impacts on the vegetation, which has been found when livestock numbers increase (Burgi *et al*. 2012).

The present results suggest that plant growth form and availability of forage with a high nutritive value largely explain habitat selection by guanaco in the National Park. In addition, if the current stocking rates were increased, the guanaco population might contribute to the maintenance of grazing lawns, as indicated by the results of Burgi *et al*. (2012). This may because the consumption of tussock seedlings growing in the grazing lawns would prevent the expansion of tussock grasslands, as has been observed with domestic livestock (A. M. Cingolani, pers. obs.); however, this hypothesis requires to be tested further. The information on habitat selection, provided in the present study, can contribute both to the guanaco reintroduction project and to the design of management strategies aimed at ecological restoration of the Quebrada del Condorito National Park.

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