



Original article

Low habitat overlap at landscape scale between wild camelids and feral donkeys in the Chilean desert



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ABSTRACT

Feral domestic ungulates may compete with the populations of wild herbivores with which they coexist, particularly so in arid regions. The potential competition between wild camelids and feral donkeys at the eastern sector of the Atacama Desert is evaluated in terms of their coincidence or segregation in habitat use and complemented with a comparison of reproductive output (yearling/adult ratio) of vicuña family groups in the proximity vs. distant from donkey observations. Habitat use of wild camelids and donkeys was sampled driving some 1250 km of roads and tracks at the dry and wet seasons. There were 221 vicuñas (*Vicugna vicugna*) sightings, 77 for donkeys (*Equus asinus*), 25 for guanacos (*Lama guanicoe*) and 8 for hybrids between guanacos and domestic llamas (*Lama glama*), as well as 174 randomly selected control locations. By means of Generalised Discriminant Analysis and Analysis of Variance we show that all ungulates actively select their habitat, with significant differences between use and availability in the area. Donkeys are relatively abundant in comparison with camelids and coincide broadly with both of them across the altitudinal gradient, but they fall between them in local scale habitat selection and do not seem to force their displacement from their preferred habitats. Thus donkeys occur preferentially on slopes with a high cover of tall shrubs, whereas vicuñas use valley bottoms with grass and guanacos the upper slope zones with grass. The potential for competition between donkeys and wild camelids is thus limited and it does not affect the reproductive output of vicuña in this region. Therefore, with the present knowledge we suggest that population control is not currently merited for feral donkeys.

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1. Introduction

The spread of alien species as an outcome of human activities and their naturalisation in ecosystems is regarded as one of the greatest threats to biodiversity. Such introduced species may alter the ecosystems through such processes as competition, predation, the spread of disease or the alteration of the physical environment (Meffe and Carroll, 1997; Primack, 1998). As a result, some native species may decline, sometimes to the extent of local or global extinction. The first species to disappear are frequently specialists and those that occur at low population densities (Davies et al., 2004). A cascade of effects is frequently set in train afterwards via

networks of interspecific interactions, with a variety of often poorly predictable collateral consequences (Traveset and Richardson, 2006). By this means diverse ecosystems see the replacement of indigenous species by those that are more tolerant of human activities, leading towards the biotic homogeneity that is currently one of the principal concerns of conservation biology (Olden et al., 2004; Olden, 2006).

The raising of grazing livestock is among the human-led processes that most modify ecosystems, on account of its extent and the variety of the effects generated. In the first instance, the primary objective of livestock introduction is to channel primary productivity towards human consumption, which invariably involves the occupation of the habitats of wild herbivores and a reduction of the resources available to the latter (Bagchi et al., 2004; Suryawanshi et al., 2010). Furthermore, there are deliberate human influences on livestock-grazed ecosystems that may modify

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vegetation to facilitate grazing (e.g. use of fire) and that may involve predator control or the forced displacement of wild herbivores from their preferred habitats in order to minimize competition (Michalski et al., 2006; Kissui, 2008).

Arid and semi-arid zones represent an extreme case of the use of ecosystems for extensive livestock raising and of potential for competition between native and exotic ungulates. Given the lack of water, such ecosystems are only exploitable for agriculture or intensive livestock raising in the vicinity of the few rivers and they are most frequently exploited for low-density grazing over extensive areas. However, the scarcity of resources also has an impact on wild herbivore populations, increasing the likelihood of adverse effects of competition with domestic herbivores (du Toit and Cumming, 1999, see however Homewood et al., 2001). This circumstance is exacerbated by the interannual variability of rainfall and availability of forage, given that herders will do their best to feed and water their animals when resources are scarce. As a result, the wild herbivore populations of arid zones may suffer greater deprivation during scarcity periods and may display fluctuations in abundance that are greater than those characteristic of their natural population dynamics (Marshall et al., 2008). The establishment of feral populations of livestock species is another collateral effect of extensive grazing in arid zones, arising from the minimal management of livestock and because such feral populations may represent a supplementary resource to humans during periods of scarcity.

The donkey is a paradigmatic animal in this context within the ecosystems of arid zones, but little is known about its effects on wild herbivores and their shared ecosystem. The donkey is a native of arid regions from Africa that has successfully colonised the American and Australian deserts following its introduction there by humans as a pack animal. It was introduced to the Americas in the 16th century and seems to have become established in the wild during the 19th century (McKnight, 1958; Grinder et al., 2006). From the human perspective, the donkey is indispensable as a pack animal in many arid regions and it is often the preferred choice given its resistance to adversity, its low forage requirements and its tolerance of water shortage (Smith and Pearson, 2005). In addition, its feral populations are often exploited by local people, both as a source of pack animals and for food in times of need (Attum and Mahmoud, 2012). The ecological effects of these donkeys are not well known but they may compete with other herbivores for food, water and shade (Choquenot, 1991; Marshall et al., 2008; Suryawanshi et al., 2010; Attum and Mahmoud, 2012), transmit parasites (Ferede et al., 2010) or damage vegetation (Abella, 2008; Malo et al., 2011). However, in some cases the donkeys show sufficient habitat segregation from native herbivores for the possibility of interspecific competition to be discarded (Marshall et al., 2012).

Populations of feral donkeys are relatively frequent in the deserts and semi-deserts of South America, from lowlands up to altitudes of nearly 4000 m (Iriarte, 2007), although they have received little attention. They coexist with wild camelids: the guanaco *Lama guanicoe* and the vicuña *Vicugna vicugna*, with which they may compete for food (Borgnia et al., 2008; Reus et al. 2014; Wursten et al., 2014). The principal guanaco populations are on the steppes of Patagonia and Tierra del Fuego, and there are only small and fluctuating populations in desert areas (Baldi et al., 2008). Some of these latter occur at such low densities as to promote hybridisation with their domestic congener, the llama *Lama glama* (Kadwell et al., 2001). The vicuña, in contrast, inhabits semi-desert regions above 3700 m where it depends on montane meadows and swampy habitats -vegas (Franklin, 2011). The vicuña was in danger of extinction in the 1960s but its populations on the northern Chilean altiplano have increased and now they fluctuate in relation to plant productivity and other local environmental

conditions (Lichtenstein et al., 2008; Shaw et al., 2012). Poaching and competition with livestock are regarded as significant threats to both species despite they are listed as of Least Concern by IUCN (Baldi et al., 2008; Lichtenstein et al., 2008). There are few studies offering parallel data on feral donkeys and camelids and all of them have been from areas where donkeys are scarce. Such studies note that donkeys may compete with camelids for food but that they show some degree of difference in habitat selection at the landscape scale (Ovejero et al., 2011; Acebes et al., 2012).

In this context our principal objective is to evaluate potential competition between feral donkeys and wild camelids in desert and semi-desert areas of the Atacama Desert by examining their overlap or segregation in habitat use at the landscape scale. It is expected that both donkeys and wild herbivores will coincide within the most productive habitats, given the low productivity of the region, and in the areas of coincidence it is expected that wild herbivores will shift towards less preferred habitats where their fitness could be reduced. Conversely, if habitat selection by donkeys and wild camelids was very different, competition for resources due to habitat overlap could not arise and negative effects on fitness would not be expected. As secondary objectives of the paper we present data on abundance and habitat selection by donkeys and guanaco/llama hybrids in a South American desert, given the existing lack of such information.

2. Methods

2.1. Study area

The study area embraces all land above 2500 m a.s.l. in the Tarapacá region, Chile, an area of approximately 1,680,790 ha. Tarapacá is in the heart of the Atacama Desert, with areas in which precipitation is virtually absent and too unpredictable to allow the establishment of ungulate populations. Nevertheless, the altiplano and pre-cordillera areas here receive annual rains of 10–200 mm derived from humid tropical air that crosses the Andes during the Austral summer (Moreira-Muñoz, 2011). As a result there are herb and shrub formations on the hillsides and also plant communities dependent on humidity in the valley bottoms (Luebert and Pliscoff, 2006). Endangered populations of vicuñas and guanacos inhabit these ecosystems (Baldi et al., 2008; Lichtenstein et al., 2008).

2.2. Sampling

Roads and tracks accessible by vehicle were surveyed at the end of the wet season (April) and of the dry season (November) in 2012. The distance driven was approximately 1250 km each season (Fig. 1) spatially organized to minimise the risk of double-counting animals. Drives were at less than 30 km/h with two experienced wildlife observers in the vehicle who scanned the terrain for ungulates constantly.

The vehicle stopped wherever there was a sighting of ungulates and the location noted using GPS (Garmin Csx60). The distance and bearing of the animals relative to the vehicle were noted respectively using a digital rangefinder (Leica 1200RF) and a precision compass. The species and total number of animals was noted for each sighting, as well as the number of females and yearlings in family groups detected in April sampling. Alongside the animal data, the habitat within 50 m radius of the central point of each sighting was described in terms of two topographical variables at small scale (position on hillside and surface roughness), the mean and maximum vegetation heights and the percentage plant cover, estimated visually for distinct vegetal formations (see Iranzo et al. 2013 for a similar approach). The altitude and gradient of each sighting was later added using the ASTER Global Digital Elevation

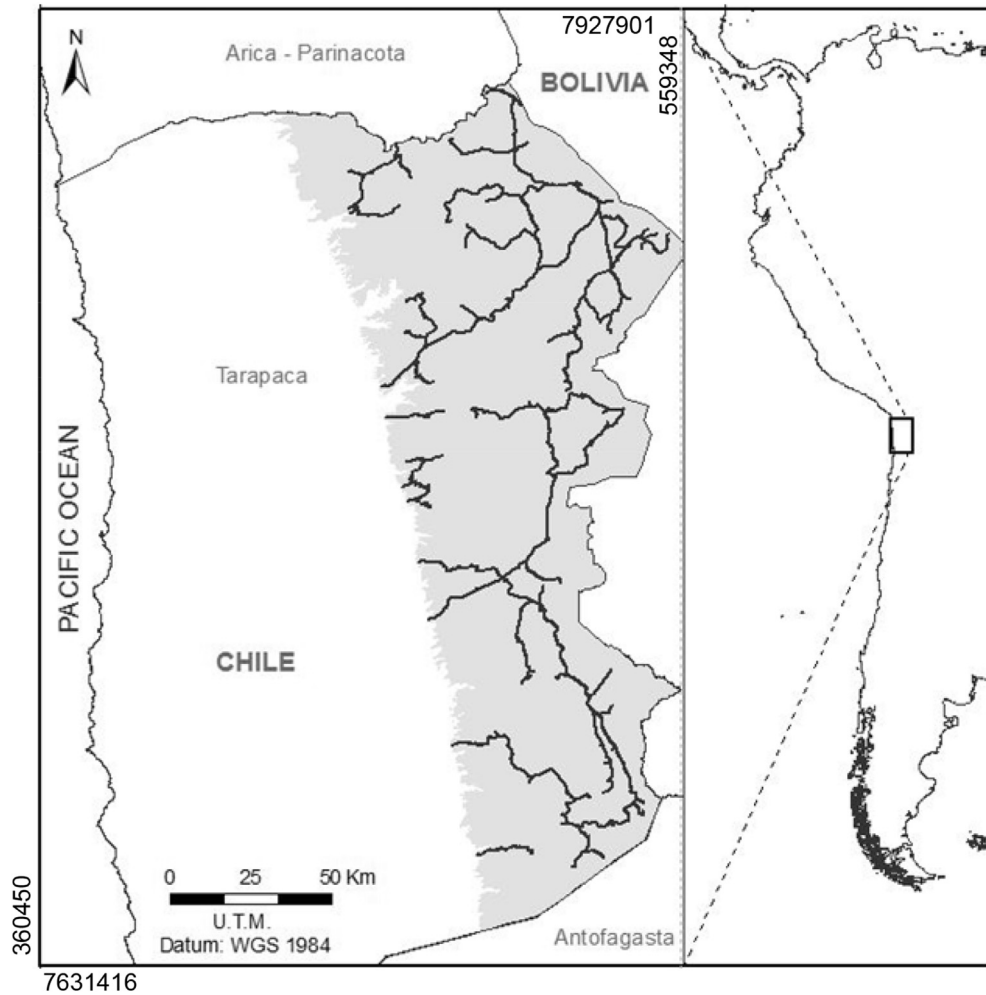


Fig. 1. Location of the study area in the context of South America and surveyed tracks within it. The grey area in the left panel represents lands above 2500 m a.s.l. in Tarapacá Region (Chile) with surveyed tracks in solid lines. The UTM coordinates within grid zone 19S are included in left-down and right-upper corners of the left panel.

Table 1
Variables used for the analysis of habitat selection by wild camelids and feral donkey in Tarapacá.

Variable	Definition	Variable type
<i>Topographic and physiognomic characteristics of the site</i>		
Altitude (m)	Altitude in metres above sea level obtained from the 30 m precision ASTER global digital elevation Model	Continuous
Gradient (°)	Terrain steepness computed in a 3x3 window of ASTER GEDDEM	Continuous
Position (1–2–3–4)	Topographical position: valley bottom (1), lower half of hillside (2), upper half of hillside (3) and summit (4)	Categorical
Roughness (1–2–3)	Small-scale unevenness of terrain potentially allowing predators to hide: low (1), medium (2) and high (3)	Categorical
Mean vegetation height (cm)	Visually estimated mean height of plants	Continuous
Maximum vegetation height (cm)	Visually estimated height of tallest plants	Continuous
<i>Ground cover of the site (adding up 100%)</i>		
Bare (%)	Cover of bare ground or loose pebbles	Continuous
Rockiness (%)	Rock cover	Continuous
Water (%)	Cover of flooded area	Continuous
Salt flat (%)	Cover of salt flat or salt-encrusted ground	Continuous
Moist herbaceous (%)	Cover of vegas and other flood-dependent herbaceous plant communities	Continuous
Dry herbaceous (%)	Cover of non flood-dependent herbaceous plant communities	Continuous
Grass steppe (%)	Cover of <i>Stipa</i> -dominated formations	Continuous
Mixed grass steppe-Tola scrub (%)	Cover of mixed <i>Stipa</i> and shrub formations	Continuous
Mixed Tola scrub-meadow (%)	Cover of medium-stature shrubs with dense herbaceous understorey	Continuous
Tola scrub (%)	Cover of 'tola' (<i>Parastrephia</i>) and other medium-stature shrubs	Continuous
Other scrub types (%)	Cover of scrub with a presence of columnar cacti, 'Llaretá' (<i>Azorella compacta</i>) and/or 'queñoña' (<i>Polylepis tarapacana</i>).	Continuous
Roads (%)	Area (%) occupied by roads and drivable tracks	Continuous
Other infrastructures (%)	Area (%) occupied by settlements or other human constructions	Continuous

Model accurate to 30 m (see variable definitions in Table 1).

The routes to be followed were selected prior to the field sampling and 174 randomly-chosen control points were established along them, in order to be able to analyse habitat selection relative to habitat availability. The location of sampling points followed the same logic as animal sightings though randomized by: i) previously deciding the location at which the vehicle would stop on the route, and randomly assigning ii) the bearing and iii) distance from the vehicle of the hypothetical ungulate group sampled. Thus, control stop points were chosen *a priori* on a map and were located more or less uniformly along the roads at a minimum straight-line separation of 3–5 km. Control bearings were chosen at random within the 0–360° range relative to North and distances were also chosen at random within a range of 0–800 m. The range of distances was based on previous experience showing that it covers over 90% of ungulate sightings from the vehicle.

2.3. Statistical analysis

The overall analysis of habitat selection by the different herbivore species employed a Generalised Discriminant Analysis (GDA) of the available habitat variables at each sighting location and control point (StatSoft, 2007; Zuur et al., 2007). This multivariate analysis generates a limited number of orthogonal axes based on observed variables that maximise the likelihood of detecting differences between groups of observations. The discriminatory capacity of the generated model, and of the different individual axes, may be evaluated using Wilks's $1-\lambda$ statistic which provides a measure of it on a scale of 0–1, in which 0 signifies that it is impossible to discriminate between groups and 1 indicates perfect discrimination. The significance of differences between groups of observations introduced into the analysis is afterwards evaluated using Mahalanobis distances (StatSoft, 2007).

The functions generated by the GDA may be interpreted as niche axes characterised by the variables measured in the field and they can be used individually or in combination to assess the degree of overlap between groups of observations (Iranzo et al., 2013). To assist interpretation of the results, the correlations of the original variables with the functions are presented individually, noting those instances in which the correlation $|r| > 0.20$ indicating $p < 0.001$ corrected for multiple testing. In addition, the means of the different types of observations (herbivores and controls) are shown on the graphical representations of the GDA together with the explicative variables in the form of arrows, whose length represents the combined correlation between that variable and the axes (Zuur et al., 2007). A comparative MANOVA between species was performed in order to better understand which habitat variables explain the differences between herbivores, using the positions on the GDA axes as independent variables.

To improve habitat use descriptions, the habitat selection of herbivores in relation to habitat availability was addressed by means of direct comparisons between the observational and control data. The comparisons were performed using ANOVAs followed by *a posteriori* Tukey's HSD tests for continuous variables (Quinn and Keough, 2002). The altitude and vegetation height data were log-transformed, and the percentage cover data arcsine transformed, for these analyses. Categorical variables, such as position on hillside, were analysed using non-parametric Kruskal–Wallis tests followed by pairwise comparisons with Bonferroni corrections for multiple testing. All analyses employed STATISTICA 8.0 (StatSoft, 2007).

Finally, to test the presence of changes in habitat selection, herd size or reproductive output of camelids in the presence of donkey, observations of the former within the altitudinal range shared with the donkey were categorized as in the proximity (less than 5 km,

see Saltz et al., 2000) or distant from donkey observations (otherwise). The potential habitat displacement generated by donkey was then explored as above through MANOVA tests on GDA positions of observations from each camelid species in the proximity vs. distant from donkeys. Due to the key role exerted by altitude in habitat selection (see below) and the potential to bias this analysis of a dataset unbalanced in altitude, the absence of differences in altitude between observations of both camelid species in the proximity vs. distant from donkeys was checked with ANOVA ($p > 0.1$ for both cases). Changes in herd size and reproductive output were tested by comparing group size (log-transformed) and yearling/female ratios in camelid families observed in the proximity vs. distant from donkey observations through ANOVA. Exploratory analyses including altitude showed that this variable does not affect the results presented here.

3. Results

3.1. Habitat selection by ungulates

In total, 331 animal groups were detected during the course of the two sampling periods with very similar features in both seasons. In all, they comprised 221 sightings of vicuñas (average of 515 individuals by season), 77 of donkeys (161.5 individuals by season), 25 of guanacos (28 individuals by season) and 8 of guanaco x llama hybrids (20 individuals by season).

The multivariate GDA analysis permitted differentiation between the two types of observation (ungulate species and controls) effectively (canonical $r = 0.488$; $p < 0.0001$), showing that the first three discriminant functions were of interest (aggregated Wilk's $1-\lambda = 0.463$ Fig. 2). The three significant axes produced by the analysis contained some 93.6% of the capacity to differentiate observations in terms of habitat variables, showing a quite similar explanatory capacity among themselves ($1-\lambda$ change range 0.13–0.17).

The structure of the discriminant functions (Table 2) shows that axis 1 is negatively correlated with altitude and two physiognomic variables, indicating that the observations at its negative extreme correspond to high altitude locations, relatively smooth and within valley bottoms or on lower slopes (levels 1 and 2 of variable Position). This part of the axis also shows a tendency to encompass flood-dependent herbaceous formations (chiefly *vegas* and wet meadows) or mixed grass steppe-shrub formations. Against these, within the positive part of the first axis, are observations characterised by lower altitude, of opposite physiognomy to that earlier described and with greater cover of medium-height to tall shrubs and/or scrubs with a presence of columnar cacti, *queñoa* (*Polylepis tarapacana*) or *llareta* (*Azorella compacta*) grouped as 'other shrub'.

The negative sector of the second axis differentiates observations of relatively smooth surfaces with greater bare ground cover and mixed scrub-meadow formations or other shrubs from observations in level areas with rocks, and steppe-like, dry- or flood-dependent grasslands, located in the positive sector of the axis. Finally, axis 3 is characterised at its negative extreme by grass steppe and in its positive extreme by formations of *tola* (*Parastrephia* spp.) or other shrubs of medium stature, of relatively large mean and maximum height and located in level and relatively smooth parts of valley bottoms. The analysis of overall similarity between observation types (Table 3) shows that there are significant differences in the characteristics of all ungulates between each other and relative to the controls, with the exception of those corresponding to the guanaco x llama hybrids. The observations from such hybrids were only differentiated from those of the guanaco. The general results of this analysis coincide with those of the MANOVA ($F_{12,1283} = 28.74$; $p < 0.001$), which furthermore permits the testing of the between-group differences on the different axes.

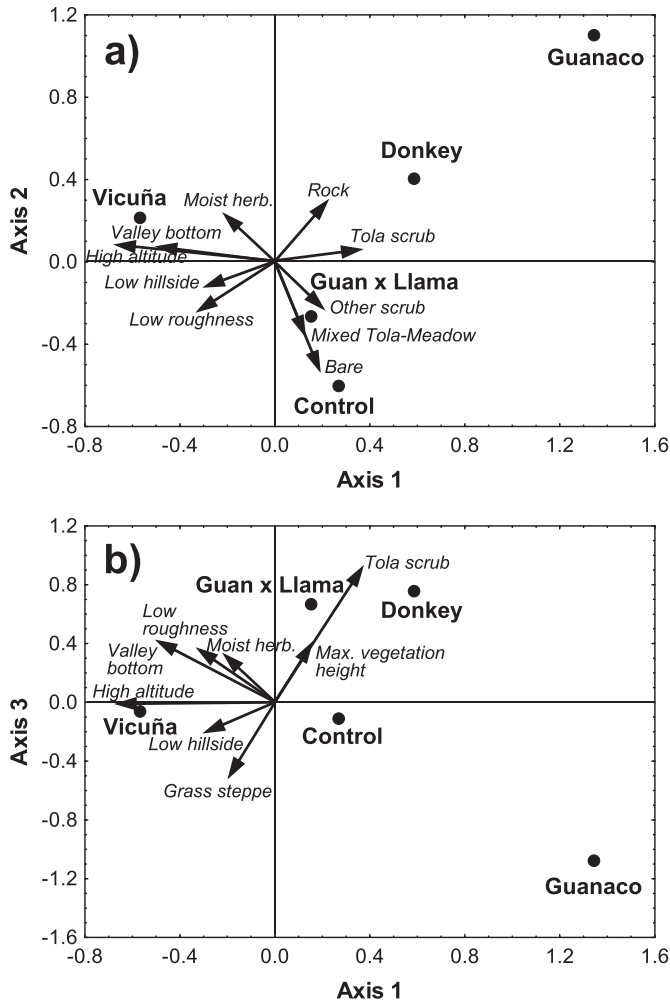


Fig. 2. Results of the generalised discriminant analysis (GDA) of the observations of available habitat (control) and that used by wild camelids and feral donkeys in the Atacama Desert. Hybrids between guanaco and llama are labelled as Guan x Llama. Panel a) representation of axes 1 vs. 2 of the GDA; panel b) representation of axes 1 vs. 3 of the GDA. Dots mark the locations of the centroid from each observation type and arrows show the correlation of the habitat variables with the axes for cases in which the joint value for the two axes was $|r| > 0.30$.

Hence, the donkey observations are differentiated (Tukey HSD test, $p < 0.05$) from those of the vicuñas and guanacos in GDA axes 1 and 3, and of the controls in axes 2 and 3. The donkey shows something of an intermediate character in its habitat selection relative to the two camelids (Fig. 2). With respect to habitat availability in the region the donkey significantly selects shrublands of medium stature, such as those dominated by *tola*, and it avoids areas with much bare ground (Table 4). The data show that the donkey occupies a broad altitudinal range and a great variety of situations, generally making use of areas between the valley bottoms and medium slopes, seeking out productive areas: scrub taller than 30–40 cm or herbaceous communities, whether dry or near water, although often near water sources, such as streams and freshwater pools. Conversely, it avoids salt flats.

The vicuña observations are differentiated in GDA axis 1 from all the others except for those of the guanaco x llama hybrids; from the controls and guanacos in axis 2, and from the guanacos and donkeys in axis 3. In summary (Fig. 2, Table 4), the vicuña selects valley bottoms or lower levels of hillsides with high cover of *vegas* or grass steppe within very high altitude locations. This species avoids areas

Table 2

Structural coefficients of the first three axes of the generalised discriminant model built to differentiate the groups of observations of ungulates and controls. Each value represents the correlation of the variable with the respective axis, indicating the respective factor level for the qualitative variables. Values of $|r| > 0.20$ are in bold type.

	Axis 1	Axis 2	Axis 3
<i>Topographic and physiognomic characteristics of the site</i>			
Altitude	−0.680	0.077	0.004
Gradient	0.088	−0.050	−0.205
Position (1)	−0.509	0.070	0.308
Position (2)	−0.305	−0.130	0.153
Position (3)	−0.102	−0.119	0.040
Roughness(1)	−0.334	−0.253	0.266
Roughness(2)	−0.055	−0.088	0.245
Mean vegetation height	0.056	−0.042	0.237
Maximum vegetation height	0.161	0.046	0.302
<i>Ground cover of the site</i>			
Bare	0.192	−0.550	−0.056
Rockiness	0.227	0.308	−0.025
Water	−0.145	0.096	0.062
Saltflat	−0.167	−0.042	−0.093
Moist herbaceous	−0.223	0.243	0.243
Dry herbaceous	0.007	0.250	−0.112
Grass steppe	−0.199	0.210	−0.378
Mixed grass steppe-Tola scrub	−0.235	−0.083	−0.077
Mixed Tola scrub-Meadow	0.135	−0.370	−0.058
Tola scrub	0.378	0.060	0.668
Other scrub types	0.216	−0.243	−0.150
Roads	−0.029	−0.010	−0.122
Other infrastructures	0.002	−0.094	−0.040

Table 3

Results of the significance test of the squared Mahalanobis distances between the groups of observations included in the generalised discriminant analysis. The *F* values, which directly indicate the distance (mathematical difference) between types, and the probability associated with them (degrees of freedom: 23, 465), are given for each comparison between types of observation.

	Vicuña	Guanaco	Donkey	Guan x Llama hybrid
Guanaco	5.32	<0.001		
Donkey	4.86	3.59	<0.001	
Guan x Llama hybrid	1.12	2.12	0.93	0.323
Control	5.67	4.72	4.16	0.95
	<0.001	<0.001	<0.001	0.527

of high cover of *tola* scrub mixed with pastures as well as scrub with columnar cacti, *queñoa* or *llareta*.

For its part, the guanaco is differentiated from all the others as well as from controls in all three GDA axes (Fig. 2, Table 4). In short, the most noteworthy elements of habitat selection by the guanaco are its use of upper parts of slopes and summits with much rocky terrain and bare ground. Furthermore, mean values point to a tendency for guanacos to appear at lower geographical elevations, as detected in axis 1, and to use the grass steppe of the altiplano (Table 4). Nevertheless, the broad altitudinal range occupied by this species (2745–4315 m) prevents these tendencies being significant relative to habitat availability. The observations from guanaco x llama hybrids could only be differentiated with respect to habitat (in all the three axes $p < 0.05$) relative to the guanaco, and in no individual variable with respect to habitat availability. In this case, it is important to note that the small sample size makes it hard to detect significant differences. In short, our results point to guanaco x llama hybrids selecting in comparison with guanaco points with denser and taller scrubs within valley bottoms or lower part of hillsides.

Table 4
Means (\pm standard deviations in continuous variables) of the habitat variables measured within an area of 50 m radius around the locations of herbivore sightings in the Atacama Desert. Hybrids between guanaco and llama are denoted as Guan x Llama. Significant differences (** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$) for each observation type are relative to availability in the study area (at control sites), obtained by a *a posteriori* comparison of ANOVAs and Kruskal–Wallis tests. The ranges of values of altitude and mean and maximum plant height are shown in brackets.

	Control N = 174	Donkey N = 77	Vicuña N = 221	Guanaco N = 25	Guan x Llama N = 8
Altitude (m)	3908 \pm 448 (2509–4834)	3848 \pm 288 (3043–4393)	4130 \pm 239*** (3736–4834)	3697 \pm 505 (2745–4316)	3825 \pm 232 (3382–4207)
Gradient (°)	15.93 \pm 13.76	14.89 \pm 10.73	14.16 \pm 10.43	18.38 \pm 14.49	16.90 \pm 9.23
Position (1–2–3–4)	2.18	2.03	1.64***	3.00***	1.50
Roughness(1–2–3)	1.24	1.31	1.19	1.76	1.00
Mean vegetation height (cm)	23.29 \pm 13.60 (0–60)	25.62 \pm 15.81 (1–60)	20.03 \pm 12.51 (0–60)	18.60 \pm 12.32 (0–50)	26.88 \pm 11.63 (0–40)
Maximum vegetation height (cm)	48.65 \pm 43.56 (0–300)	53.63 \pm 31.95 (5–250)	40.68 \pm 50.75 (0–150)	42.60 \pm 25.62 (0–110)	54.37 \pm 42.71 (0–150)
Bare (%)	16.31 \pm 31.62	4.27 \pm 10.64**	3.63 \pm 14.13***	2.60 \pm 12.00	12.50 \pm 35.36
Rockiness (%)	2.38 \pm 13.76	5.73 \pm 12.16	3.28 \pm 15.25	12.12 \pm 26.37*	0.25 \pm 0.71
Water (%)	0.37 \pm 4.56	0.64 \pm 3.75	1.32 \pm 6.99	0.00 \pm 0.00	0.00 \pm 0.00
Saltflat (%)	2.36 \pm 14.25	0.00 \pm 0.00	3.74 \pm 16.83	0.00 \pm 0.00	0.00 \pm 0.00
Moist herbaceous (%)	2.11 \pm 11.56	11.13 \pm 28.27	10.33 \pm 26.91**	0.00 \pm 0.00	0.00 \pm 0.00
Dry herbaceous (%)	4.59 \pm 18.60	9.13 \pm 28.19	9.31 \pm 28.19	17.88 \pm 34.85	0.00 \pm 0.00
Grass steppe(%)	16.92 \pm 34.24	10.17 \pm 25.44	29.17 \pm 41.70*	36.80 \pm 45.27	12.50 \pm 35.36
Mixed grass steppe-Tola scrub (%)	19.24 \pm 38.17	10.33 \pm 29.65	24.64 \pm 42.01	8.00 \pm 27.69	25.00 \pm 46.29
Mixed Tola scrub-Meadow (%)	7.90 \pm 26.61	1.33 \pm 11.55	0.46 \pm 6.77***	0.00 \pm 0.00	0.00 \pm 0.00
Tola scrub (%)	20.66 \pm 36.68	44.72 \pm 41.39***	12.15 \pm 28.34	16.00 \pm 28.90	49.75 \pm 53.19
Other scrub ^a (%)	4.98 \pm 20.28	1.33 \pm 11.54	0.05 \pm 0.68**	4.60 \pm 19.25	0.00 \pm 0.00
Roads (%)	1.54 \pm 5.46	1.07 \pm 4.37	1.72 \pm 6.92	2.20 \pm 8.18	0.00 \pm 0.00
Other infrastructures (%)	0.58 \pm 7.58	0.00 \pm 0.00	0.21 \pm 3.05	0.00 \pm 0.00	0.00 \pm 0.00

^a Scrub with columnar cacti, Llaretta (*Azorella compacta*) and/or Queñoa (*Polylepis tarapacana*).

3.2. Potential effects of donkeys on wild camelids

The hypotheses of camelid displacement from preferred habitats by donkeys or a reduction in herd size and reproductive output were not supported by the data. In the case of vicuña, 63 observations within the altitudinal range shared with donkey were done closer than 5 km from a donkey observation and classified as 'in the proximity', while 130 observations were classified as 'distant'. MANOVA tests detected significant differences between the habitats (GDA axes) of both types of vicuña observation (Wilks $F_{3,186} = 11.05$, $p < 0.0001$) but also between the subset of vicuña and donkey observations done in the proximity of the other species (Wilks $F_{3,104} = 8.06$, $p < 0.0001$). Thus, observations of vicuñas carried out in the proximity of donkeys are located in the habitat space depicted in Fig. 2 closer than the average to those of donkey (univariate tests $p < 0.0001$ for Axes 1 and 3), but still significantly separated from them (univariate tests $p < 0.0001$ for Axis 1, and $p < 0.01$ for Axis 3). Regarding the group size and reproductive output of vicuña, no difference was detected between the herd size (ANOVA test, $F_{1,76} = 0.83$, $p = 0.3658$) or the yearling/adult female ratio (ANOVA test, $F_{1,76} = 1.47$, $p = 0.2295$) of April groups found in the proximity (Mean \pm SE herd size 5.93 ± 0.46 individuals; yearling/adult female ratio 0.44 ± 0.07 , $n = 30$) or distant from donkey observations (5.25 ± 0.61 individuals; ratio 0.33 ± 0.06 , $n = 48$).

In the case of guanaco, 9 observations were made in the proximity of donkeys and 11 distant from them, and no habitat differences (Wilks $F_{3,17} = 0.35$, $p = 0.7914$) measured through GDA axes were detected between the two subsets of data. The scarcity of family groups detected in April sampling ($n = 4$) precluded any testing of changes in either the group size or the reproductive output of the species.

4. Discussion

The results show that habitat selection by camelids differs from that of wild donkeys and support the absence of both habitat displacement away from preferred sites and a decrease in herd size or reproductive output in camelid groups living close to donkeys. These results point to a low potential level of competition of donkey with both camelid species although local negative impacts

on camelid populations cannot be ruled out. The value of this finding is reinforced by the large extent of the prospected region in which donkeys and camelids coincide relative to that covered by previous studies (Borgnia et al., 2008; Mosca Torres and Puig, 2010; Rojo et al., 2012; Reus et al., 2014; Wursten et al., 2014), the threat status of the camelid populations involved (Baldi et al., 2008; Lichtenstein et al., 2008) and the abundance of donkeys relative to camelids there.

In the first instance, the results demonstrate that feral donkeys are relatively abundant in the area (see below) and so they could offer a not negligible level of competition for forage with the wild camelids. Assuming equal detectability of the three species, the number of sighted animals (Table 2) indicates that density of donkeys (c. 0.13 donkeys/km surveyed) is five or six times greater than that of guanacos and a third of that of the vicuñas. Nevertheless, bearing in mind that the donkey (c. 250 kg, Iriarte, 2007) is much heavier than the guanaco or the vicuña (110 kg and 60 kg respectively, Franklin, 2011), and that its digestive system is less efficient than that of the camelids (Illius and Gordon, 1992; Van Soest, P.J. 1996), it becomes evident that the total forage consumption by the donkeys exceeds that of the wild species. It is thus possible to estimate that the daily dry mass intake of a donkey is equivalent to that of 3.4 guanacos or 5.2 vicuñas, on the basis of parameters provided by Illius and Gordon (1992). Against this background, the total intake of all the donkeys in the study area would represent 19.3 times that of guanacos and 1.6 times that of vicuñas. There may thus possibly be competition for food between donkeys and wild camelids within the study area as a whole, a pattern that other more local studies have found in some South American desert areas (Borgnia et al., 2008; Rojo et al., 2012), although it is not the a general rule (Mosca Torres and Puig, 2010; Wursten et al., 2014).

Despite the high degree of overlap between donkeys and the two wild camelids on a large geographical scale there is a degree of habitat segregation between them at the landscape scale. Wild donkeys were found to be very dispersed within the study area and occurred approximately between 3000 and 4400 m above sea level, showing broad altitudinal overlap both with the guanaco (2700–4300 m) and the vicuña (3700–4900 m). Given the altitudinal ranges described for the two wild species (Iriarte, 2007;

Franklin, 2011), the donkey overlaps with both of them almost completely except at the highest elevations used by vicuñas and perhaps also in the most arid sectors of the lowest levels used by the guanaco (Saltz et al., 2006; Ovejero et al., 2011).

With respect to habitat selection at the landscape scale, the donkey fits into the native herbivore community by occupying an intermediate situation among them in terms of physiographic features. The wild camelids show in our study area a niche segregation that is generally interpreted as a consequence of adaptive divergence established during their shared evolutionary history (Cajal et al., 2010; Wurstten et al., 2014, see however, Lucherini et al., 2000), and this seems to be unaffected by the presence of donkey in the region. Thus, the vicuñas strongly selected sites in very level valley bottoms, as previously described for this species (Lichtenstein et al., 2008; Franklin, 2011). Their diet there principally comprises grasses from the grass steppes or wet meadows (Borgnia et al., 2008; Mosca Torres and Puig, 2010; see however Reus et al., 2014). In contrast, guanacos strongly selected sites on upper slopes and peaks, with a more sloping and more rocky surface. This finding is similar to that described by other studies of guanaco habitat selection in diverse parts of its area of distribution (Puig et al., 2008; Iranzo et al., 2013) and it has been interpreted as part of an antipredator strategy that shapes the behaviour of this species (Marino and Baldi, 2008; Taraborelli et al., 2012; Acebes et al., 2013). Accordingly, the guanaco is known to select short herbaceous communities for feeding (Baldi et al., 2004; Burgi et al., 2012; Flores et al., 2012).

The donkeys, in contrast to the two wild camelids, were chiefly found on lower and mid-level slopes and they strongly selected dense scrublands such as those dominated by *Parastrephia* spp., *Fabiana* spp., *Junellia seriphioides* and *Lampaya medicinalis* (Teillier, 1998; Luebert and Plissock, 2006). In general, the locations in which the donkey occurs offer abundant vegetation, whether shrubby or herbaceous, of taller mean and maximum height than across the area as a whole and taller than that selected by the wild camelids. Habitat selection by feral donkeys has been little studied but it is commonly described using woodland or scrub formations and sloping areas (Woodward and Ohmart, 1976; Hamrick et al., 2005; Acebes et al., 2012), although it has also been found to feed in meadows and near water sources (Wurstten et al., 2014). The donkeys are generalists for whom shrubs predominate in the diet over grasses, graminoids and other herbaceous plants, especially during the dry season (Moehlman et al., 1998; Grinder et al., 2006; Abella, 2008; Marshal et al., 2012). Nevertheless, donkeys may concentrate on grasses and graminoids in humid areas where the supply is abundant (Abella, 2008; Borgnia et al., 2008; Reus et al., 2014; Wurstten et al., 2014).

Hence, although spatial overlap between the donkey and the vicuña may not be extensive, it is worth emphasising the particular case of the use of *vegas*. Some 15.7% of the 70 observations of donkeys above 3,700 m a.s.l., and 15.4% of the vicuña observations, were within these herbaceous communities that are associated with the presence of freshwater in the substrate, thus showing a similar tendency to use such humid areas. These observations did not show interspecific temporal segregation, with greater use of meadows by livestock during the mornings, as hypothesised by Borgnia et al. (2008), given that 45.5% of the observations of donkeys, and 38.2% of those of vicuñas, occurred before 13:00 h. The data thus show that despite the donkeys show habitat selection that differentiates them from the vicuñas, there is some degree of overlap between both species and they may compete for food locally in some *vegas*.

On the other hand, habitat selection by the donkey at the landscape scale differentiates it from the guanaco sufficiently for its effect on that species to be of lesser concern. In addition to their

separation in physiographic terms, the guanaco makes much more use of the grass steppe and avoids dense scrub (see also Cortes et al., 2003; Flores et al., 2012), its overlap with donkey being restricted to some use of other dry herbaceous communities. This finding may have some significance given the arid and hyper-arid character of much of the area that the two share, bearing in mind the low number of guanacos that inhabit this desert sector of their distribution (Baldi et al., 2008; González, 2010).

Nevertheless, the fact that on average 20 hybrids between guanaco and llama were recorded per sampling season, against 28 guanacos, is much more noteworthy from the perspective of guanaco conservation. It points to the risk of genetic intrusion by the domestic camelid being a significant problem for the guanaco populations of this desert area (Kadwell et al., 2001; Marín et al., 2013), probably posing a greater medium-term threat than potential competition with the donkey. Interestingly, the habitat selection of guanaco x llama hybrids is sharply different to that of guanaco and points to the use of locations more similar to those selected for llama herding in search of both flat areas and the combination of forage abundance with protein-rich shrubs (Tomka, 1992; Yacobaccio et al., 2009).

Finally, it must be noted that the small overlap in habitat use at the landscape scale does not rule out the possibility that feral donkeys have other negative impacts on wild camelids, even though our evidences from habitat selection, herd size and reproductive output do not support it. In the first instance, wild generalist herbivores could be displaced to suboptimal habitats by the presence of livestock and herders (Baldi et al., 2001; Bagchi et al., 2004; Borgnia et al., 2008), though our observations of habitat selection by camelid groups found close to donkeys do not point in that direction. Also, the expected reduction in herd size or the yearling/adult ratio in case of an increased limitation of access to plant resources (Shaw et al., 2012; Marino and Baldi, 2014) was not detected in vicuña families living close to donkeys (see also Choquenot, 1991), contrary to the case of reproductive limitation described in North American mountain sheep (Marshal et al., 2008). Anyhow, it is also possible that negative effects arise from other processes that pass undetected in our observational study, like competition with donkeys for other limiting resources such as water springs (Ostermann-Kelm et al., 2008; Attum and Mahmoud, 2012), the possibility that donkeys negatively affect the habitat of vicuñas trampling (Deluca et al., 1998), or that the feral animals act as vectors of parasites towards other herbivores (Beldomenico et al., 2003; Landaeta-Aquevque et al., 2014).

5. Conclusion

In conclusion, all the large herbivores of the area actively select their habitat and the donkey occupies an intermediate position in habitat selection within the camelid community that makes it unlikely that intense competition for food exists between them. Such competition could nevertheless occur locally and a definitive conclusion in such cases would depend on a comparative analysis of the herbivores' diet, and on a fuller understanding of the factors limiting local populations of the wild species. With the present knowledge on habitat selection the conservation of the wild camelids of the Atacama Desert does not support measures to be taken against feral donkey populations there.

Authors' contribution

JEM, BAG and CFE conceived and designed the study; JEM, BAG, AV, DSD and NF carried out fieldwork; JEM, BAG DSD and CME did the analysis and built up the GIS. All authors contributed to manuscript writing and correction.

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