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Livestock and the functional habitat of vicuñas in Ecuador: a new puzzle

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Abstract. Whether interactions between wildlife and livestock are competitive or facilitative is context dependent. Intermediary factors that explain how context (seasonal or regional characteristics of the ecological community) affects these interactions are rarely reported. We compared activity time and density in vicuñas (*Vicugna vicugna*) introduced into the Chimborazo Faunal Production Reserve (CFPR), Ecuador, to describe how they interact with livestock. We compared vicuña density in wetlands and uplands (two landscape structures) with and without livestock (two conditions) using an *isodar* approach. We measured, over two seasons, vicuña forage abundance, composition, preference and accessibility, time vicuñas spent vigilant, and their flight distances on approach. We tested optimal foraging theory relating to the hypothesis that time mediates behavior, and found that vicuñas were no less frequently vigilant, nor were flight distances greater, during a wet season or in habitats of greater forage abundance and accessibility. We also found no evidence that vicuña behavior was density dependent; instead, we found that more time was spent vigilant by vicuñas when they foraged near livestock in rainy regions during the dry season. Although forage abundance was similar throughout CFPR during a dry season, better forage quality in areas occupied by livestock may constitute an effect of their facilitating vicuñas. A puzzling finding, because it was not explained by any of the other variables we measured, was that at low densities vicuñas selected habitat irrespective of livestock, and where their density was higher, it was doubly so adjacent to livestock. We conclude that in the CFPR, spatial heterogeneity in habitat quality determines the interactions between livestock and vicuñas. To support recommendations that minimize competition between wildlife and livestock, and to expand on descriptions of the contexts that determine the direction of species interactions, future study may require a wider sampling of the densities of sympatric large herbivores in general, and, in the CFPR, a closer resolution of spatial heterogeneity in forage plant quality.

Key words: competition; context; habitat; isodar theory; livestock management; vicuña (*Vicugna vicugna*).

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INTRODUCTION

How animal behavior varies both with resource availability and with other, often human-induced changes to habitat is information critical to conservation. Van Dyck (2012) describes these two axes as consumables and condition, and the response of animals to a condition is accounted for by his concept of functional habitat, where animal behavior is a defining feature. The definition arises from Dennis et al.'s (2003) presentation of the concept of functional habitat with the butterfly as an example: Habitat can be mapped separately emphasizing different resources required for each of several behaviors, including egg laying, mate location, resting, roosting, feeding, and predator escape. Functional habitat defined this way is distinct from structural habitat, as the latter refers only generally to the physical attributes of habitat (Dennis et al. 2006). By mapping functional habitats, it can be revealed how changes to an animal's behavior can lead to changes in its interspecific interactions, and how these changes manifest is context dependent (Chamberlain et al. 2014, Ford et al. 2015). Van Dyck's (2012) example is the endangered desert lizard, for which a landscape restoration project including planting of trees in the Negev desert, Israel, led to further declines, because increased structural complexity in planted patches favoured avian predation (Hawlena et al. 2010); here, the avoidance of predator perch sites was not a behavior adopted by the lizard when the condition of the desert was changed. A general example is in pinpointing the net effects of competition (negative interactions) and facilitation (positive interactions) between sympatric herbivores, described as a critical issue in theoretical ecology and in wildlife management (Arsenault and Owen-Smith 2002). Context, how the plant and herbivore community varies by region, season, or scale, determines whether interactions are net negative or net positive.

The effect of the condition of range sharing by livestock on wildlife populations is generally described as net negative, due to the transformation of habitat to pasture, increased competition for resources, and increased likelihood of disease transmission (Fleischner 1994, Schulz and Skonhoft 1996, Lamprey and Reid 2004). As the beneficiaries of pastoralists, large livestock are often easily able to outcompete native herbivores, and widespread declines in wildlife populations have been linked to the expansion of human populations and their livestock (Ottichilo et al. 2000, Prins 2000, Laliberté and Ripple 2004, Mishra et al. 2004, Gordon 2009). Nevertheless, instances of net positive effects, such as feeding facilitation or release from predation, have been documented for native herbivores and sympatric livestock. Published evidence, still sparse and largely empirical, suggests that net facilitation occurs variably with season (Odadi et al. 2011, Augustine and Springer 2014), spatiotemporal scale (Arsenault and Owen-Smith 2002, Dave and Jhala 2011, Schuette et al. 2016), vegetation type or site productivity (Augustine et al. 2011, Augustine and Springer 2014), and with group size and relative densities of the herbivores (De Gabriel et al. 2011, Vijayan et al. 2012*a*, Arzamendia and Vilá 2015). Better recognition and understanding of the contexts leading to net positive or negative effects on sympatric herbivores can be critical to best management practices for livestock and conservation of biodiversity (Arsenault and Owen-Smith 2002, Franklin and Lindenmayer 2009).

Here, we describe vicuñas (*Vicugna vicugna* Molina, 1782), free-ranging camelids increasing in number in Ecuador, where we predict that their behavior varies with the presence of livestock. They were introduced to the Chimborazo Faunal Production Reserve (CFPR) in 1988 and 1993 into the traditional territory of indigenous pastoralists, who have kept other camelids since the arrival of the Incas (alpacas, *Vicugna pacos*, and llamas, *Lama glama*; Stahl 1988, 2003), and after arrival of the Spanish, cattle (*Bos taurus*), horses (*Equus ferus*), donkeys (*Equus asinus*), and sheep (*Ovis aries*). Livestock/wildlife conflicts exist or are perceived to exist to this day in the Andes (Lichtenstein 2009, Arzamendia and Vilá 2015). In Patagonia, guanaco (*Lama guanicoe*, another free-ranging camelid) declines in areas of coexistence with livestock, particularly sheep, have been assumed due to dietary overlap and potential competition (Baldi et al. 2004). Many authors describe similar net negative effects of livestock on camelids, but the effect vanishes at low livestock densities, perhaps due to habitat segregation or the ability of native camelids to persist in habitats that are suboptimal for livestock (Borgnia et al. 2008, Iranzo et al. 2013, Wurstten et al. 2014, Arzamendia and Vilá 2015). Our case is of a vicuña population that continues to grow exponentially into habitat that is restricted in extent, occupying foothills rather than altiplano, and where space sharing with livestock is common (Figs. 1, 2). Thus, we can provide insight that other studies based on observations of vicuñas at carrying capacity in altiplano cannot (Shaw et al. 2012, Arzamendia and Vilá 2015), as habitat selection and other behavioral changes in sympatric ungulates are density dependent (Iranzo et al. 2013, van Beest et al. 2014). We explore the idea that by observing the same system in different contexts—over a dry and a rainy season and over three regions that vary in forage abundance and in vicuña density—we might uncover and explain cases of feeding facilitation or apparent mutualism as net positive interactions.

Vicuñas, easily visible in their grassland habitats, offer a useful test case for predictions on

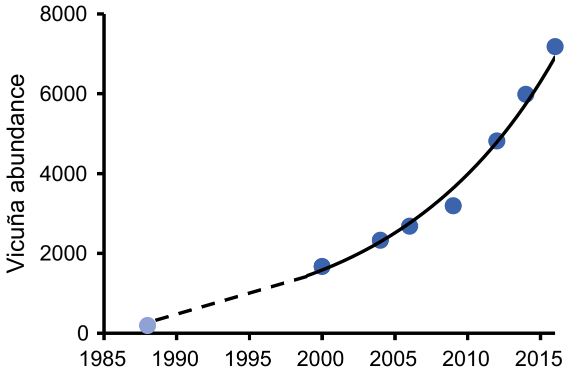

Fig. 1. Vicuña abundance in the Chimborazo Faunal Production Reserve, Ecuador, since introduction in 1988. The solid line is an exponential curve fit to the data from census years spanning 2000–2016 and approximates an annual rate of increase of 0.0896 ($\lambda = 1.094$, $F_{1,5} = 357$, $P < 0.001$, $R^2 = 0.98$). Source: Ecuador's Ministry of Environment.

their behavior and distribution on the landscape, as illustrated for similar, free-ranging large herbivores such as spotted deer (*Axis axis*, Vijayan et al. 2012*b*) and Thomson's gazelles (*Eudorcas thomsonii*, Bradbury et al. 2015). The CFPR study area offers a complex of structural habitats surrounding the Chimborazo volcano. Forage diversity and abundance vary with rainfall, and within each of three regions, topographic variation allows for both upland and wetland areas. Human settlements largely determine how portions of any of these areas serve as pasture for livestock. Wetlands, known locally as *bofedales*, or in some literature as *vegas*, are critical habitats for vicuñas (Koford 1957, Renaudeau d'Arc et al. 2000, Mosca Torres and Puig 2012, Cappa et al. 2014, Mosca Torres et al. 2015) and are locally shared with livestock (Wurstten et al. 2014, Andrade 2016). We investigated when interactions between vicuñas and livestock in the CFPR were net positive, net negative, or neutral, and how these interactions might be mediated by habitat. To do so, we assessed differences in parameters related to energetic costs: forage abundance and accessibility, vicuña activity budgets, and their flight distances on approach. We aimed to determine in which contexts and conditions we can associate higher costs (lower forage abundance and accessibility, higher rates of vigilance at the cost of foraging, and longer flight distances): wetland or upland habitats shared with livestock, upland habitats with and without livestock, wet or dry season, and which of three regions in the CFPR.

We compared vicuña densities with and without livestock using isodars (Morris 1987, 1988) to assist with insight on the contexts where net positive interactions can occur between livestock and sympatric herbivores. Predictions about the context dependence of the effect of livestock followed two hypotheses. First, behaviors in vicuñas have been shown to conform to predictions in optimal foraging theory (OFT, Mosca Torres and Puig 2010, 2012). An OFT-based hypothesis for the CFPR is that time modulates vicuña behavior, so that higher encounter rates of forage plants (more live leaves) or accessibility of forage (fewer dead leaves) during the wet season and in wetlands should lead to more of the vicuña activity budget spent vigilant (and less time spent foraging) during the wet season relative to the dry season, and in wetlands relative to uplands (Cappa et al. 2014, Mosca Torres et al. 2015). Second, the suggestion that group size or density modulates prey behavior (Vijayan et al. 2012*a*) leads to a second hypothesis, which was tested once for vicuñas in the absence of livestock and showed less time spent vigilant where intergroup distances were shorter (Mosca Torres et al. 2015). From other empirical evidence, we predict lower densities of vicuñas near livestock (Borgnia et al. 2008, Arzamendia and Vilá 2015), higher density in wetlands (Cappa et al. 2014), and temporal variations in local density, all of which make the group size/density and time hypotheses difficult to disentangle. For example, a density effect on vigilance may be compounded by temporal differences in food availability or distance of vicuña groups to wetlands (Mosca Torres et al. 2015). Coexistence with livestock, implying greater human encroachment on vicuña habitat, should result in flight of vicuña family groups at longer approach distances (Donadio and Buskirk 2006, Arzamendia and Vilá 2015). In contrast, prediction of a net positive effect of livestock, for example, that lower vigilance occurs in areas with livestock, especially in areas of lower vicuña density, is inferred from study of spotted deer (Vijayan et al. 2012*a*). Finally, a potential positive effect of livestock via feeding facilitation (greater removal of dead

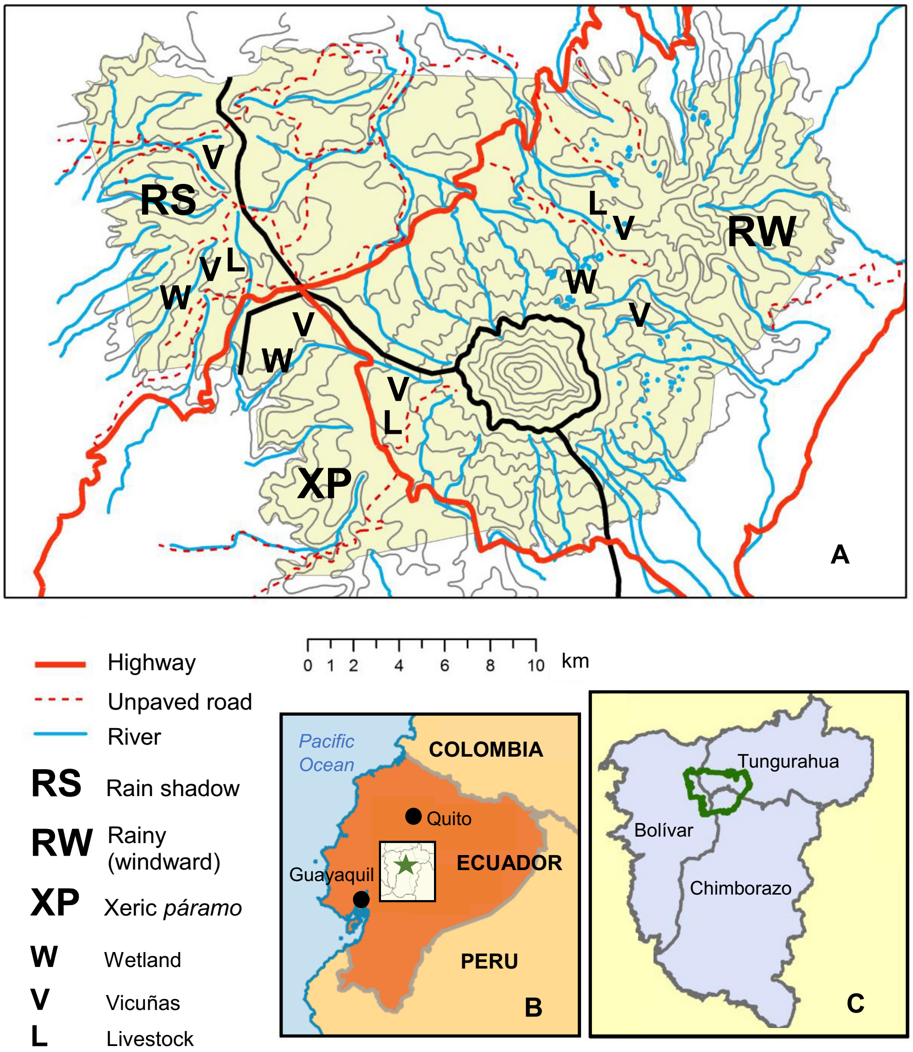

Fig. 2. Geographic distribution of the study sites in the Chimborazo Faunal Production Reserve (CFPR; shaded area; A), CFPR's location in central Ecuador (B) and relative to three provincial boundaries (C). Vicuñas (at study locations marked by V) were introduced near the communities of Sinche and Mechahuasca in 1988 and 1993; near these and other communities, vicuñas coexist with livestock (at study locations marked by L).

plant tissues) that results in higher vicuña density or lower vigilance, or both, may be limited to the wet season (Odadi et al. 2011).

METHODS

Study area

The CFPR, near Riobamba, Ecuador (Fig. 2), has an Andean climate with steady easterly winds, often associated with warmer temperatures during a wet season in the first half of the calendar year and a cooler, dry season over much of the second half of the year. Generally, the climate is characterized by high ultraviolet radiation and a high frequency of low-intensity rainfall events (Sarmiento 1986). The CFPR protects 58,560 ha encompassing the foothills and peaks of the Chimborazo volcano, 6268 m above sea level, the highest elevation in Ecuador. An arrangement in 1984 by which Ecuador was to accept vicuñas into formerly occupied territory as an effort to extend the range of the species was followed by creation of the CFPR in 1986 to protect habitat for vicuñas. The CFPR received 100 individuals each from Chile and Peru in 1988 and 77 from Bolivia in 1993. The initial population of 200 grew to a recent census estimate of 7185 (Ecuador's Ministry of Environment, *unpublished data*; Fig. 1). In Ecuador, management of the vicuña is discussed more frequently since the XVI meeting of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in March 2013, when its status changed from Appendix I to Appendix II.

Local predators of the vicuña are few, including the Andean fox (*Pseudalopex culpaeus*), feral dog (*Canis lupus familiaris*), and black-chested buzzard-eagle (*Geranoaetus melanoleucus*), all likely limited to preying on calves. The exponential rate of growth of the vicuña population suggests that neither predation nor carrying capacity is currently regulating it. Vicuñas are, however, poached and chased by dogs, leading in some cases to exclusion from richer areas of the CFPR also used by livestock, as reported for Argentina by Arzamendia and Vilá (2015).

The CFPR has been divided for purposes of vicuña management by Ecuador's Ministry of Environment into three sectors, associated with the introduction history of the vicuña, and varying in soil cover, geomorphology, and rainfall. The climatic classification ranges from dry to humid *páramo*, a high elevation, mostly treeless vegetation type, described generally by Podwojewski et al. (2002). In this paper, we refer to three regions (Fig. 2). Xeric *páramo* (XP) ranges 3960–4850 m above sea level and receives only 500–1000 mm rainfall per year. The rainy or windward (RW) region occurs at 4120–5480 m above sea level, receives 1500–2000 mm rainfall per year, and is a hyper wet zone east of the volcano peak (Navarro and Maldonado 2002). A rain shadow (RS) region occurs on the west side, from 4250 to 4860 m above sea level, and receives 1000–1500 mm rainfall per year. Vicuñas were introduced using a soft release with a 40-d quarantine period, in 1988 near Mechahuasca, in the RW region, and Sinche, in the RS region (Fig. 2). In 1993, the second soft release occurred in Sinche. Vicuñas later migrated into XP from these introduction sites. Today, RW and RS regions have a higher density of vicuñas than the XP region, probably due to the richer, denser vegetation and more extensive wetlands, and the earlier establishment of vicuñas compared to XP (Ecuador's Ministry of Environment, *unpublished data*).

Vicuña density mapping

We estimated the distribution of vicuña groups within sight along eight transects throughout the CFPR (three in XP, four in RS, and one in RW) in December 2015. We recorded the position of vicuña groups by measuring the perpendicular distance from each transect using a HALO model XRT6 Rangefinder and Garmin GPS model 60CSX. We chose transect locations such that a straight line could be followed over 2–3 km, crossing areas with livestock (cattle, sheep, horses, alpacas, and llamas) and areas where vicuñas were not in a sight line with livestock. Transects were also positioned to cross wetlands. We recorded group size, and we classified each vicuña group as occupying a wetland or in an upland territory. We considered vicuña groups to coexist with livestock if the nearest vicuña occurred <30 m from a domestic animal. We used the program DISTANCE (Buckland et al. 2015) to estimate density of vicuñas for each transect twice, first with a separate estimate for wetland and upland areas, and second with a separate estimate for groups with and without livestock. In each case, the paired estimates were plotted on a pair of axes and type II regressions were used to estimate *isodars* (Morris 1987). The theory behind *isodars* includes the possibility of comparison of quality in two habitat types by comparing density of individuals in them and using the assumption that individuals in the higher-quality habitat equilibrate at a higher density to maintain equal fitness and avoid competition with other species. Here, the *isodars* are used to compare habitat quality both by structure (wetland and upland areas) and condition (with and without livestock).

Vicuña foraging opportunities and behavior

We collected forage plant data and observed vicuña behavior twice with the same methodology, once during a dry season (October and November 2012) and a second time during a rainy season (February and March 2013). In each region (XP, RS, and RW), we classified vicuña family groups encountered in upland habitats as either sympatric with livestock or distant from communal livestock grazing areas (Fig. 2). We classified vicuñas encountered in wetlands separately, and nearly all wetlands in the CFPR are used by livestock and their herders. A difference among vicuñas occurring in wetlands is their shared intraspecific (i.e., non-territorial) use of these habitats, while in upland habitats, a male vicuña guards a number of females and calves that are kept separate from adjacent family groups (Koford 1957).

During each season, we sampled forage abundance, accessibility, and forage plant selection along fifteen transects in upland areas of two regions, RS and RW. We located each transect in a distinct, non-overlapping vicuña territory, five with livestock near the territory and five without livestock. In upland areas of XP, where forage was sparsest, we increased replication to ten transects with livestock and ten transects without livestock. We located five additional transects during each season in each of five distinct wetland areas in each of the three regions. We defined forage abundance as the frequency of live leaves at 1-m intervals along four compass directions per transects to a total of 100 contact points, at which we also identified forage plant species (Appendix S1: Table S1). Vicuñas are catholic in their diet and consume most plant species occurring in the study area (Borgnia et al. 2010, Mosca Torres and Puig 2010); we excluded a few plant species that are never consumed by vicuñas. We compared selection by vicuñas of the forage plants we encountered using Ivlev's selection index, or the number of bites relative to the total frequency of each plant species (Ivlev 1961). We distinguished vicuña bites from those of larger livestock by their small size. Values for Ivlev's selection index range from −1 (total avoidance) through 0 (no selection) to 1 (total selection). Forage accessibility was measured as the frequency of dead leaves along the same transects on which forage abundance was measured; relative accessibility is the reciprocal of the number of dead leaves; that is, we assumed that fewer dead leaves equated to greater accessibility to live leaves.

For each experimental unit or focal family group of vicuñas (for each of two seasons and near each transect across the three regions: XP, $n = 25$; RW, $n = 15$; RS, $n = 15$), we monitored the male and one female vicuña with a spotting scope for a period of 10 min, using scans every 30 s, to determine the time allocated to foraging, vigilance, or other behaviors, such as movement. We recorded group size and flight distance in meter when the vicuña group was approached. Approaching and observing the vicuña groups conformed to an approved protocol (AUP 12 05-06) reviewed by the Lakehead University Animal Care Committee.

We used non-metric multidimensional scaling (NMDS) to categorize the forage communities, and we chose five forage plant species that were common in all communities and had high selection indices for individual comparisons of abundance and fraction consumed (see Appendix S1: Table S1). We first used multivariate analysis of variance (MANOVA) to compare forage abundance and accessibility between regions and seasons (fixed factors representing context), nesting within regions the conditions with and without livestock and the two structural habitat types, wetlands and uplands with livestock. It was possible to represent structures and conditions with a single fixed factor representing the three cases, since wetlands always occurred with livestock. We applied an arcsine transformation to the fraction of forage plants consumed. For all significant factors in the MANOVA, we used generalized linear models (GLMs) to compare condition and structure in the habitat within each region. Regions and seasons were compared as separate, fixed factors. We also used MANOVA and then GLMs to detect differences in vicuña group size, time allocated to vigilance (separately for males and females), and flight distance between seasons and regions. For these measures, we used separate models to compare the conditions with and without livestock and the two structural habitat types, wetlands and uplands with livestock. In all post hoc comparisons, we used a modified Wald method with a Bonferroni correction.

RESULTS

Vicuña density

Vicuñas at relatively low densities appear to select areas irrespective of the presence of livestock (*isodar y*-intercept = 2.29 [−1.20, +0.36 SE]), but their density increases at double the rate in areas adjacent to livestock compared to areas of the same transects where livestock are absent (Fig. 3, slope = 2.3 [1.6, 3.0 SE], $R^2 = 0.28$, $F_{1,6} = 9.63$, $P = 0.02$). Although forage abundance in wetlands was higher in two of the three regions (XP and RS; Table 1), there was no evidence for density-dependent selection of wetlands (Fig. 3).

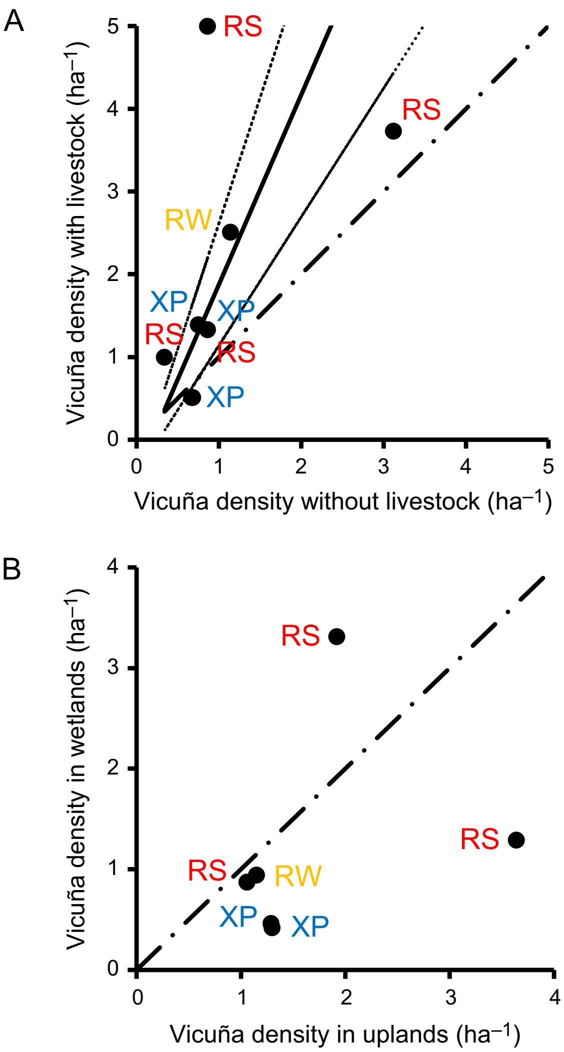

Fig. 3. *Isodars* of vicuñas in territorial groups encountered along transects estimating vicuña density with and without livestock (A), and in wetlands and uplands (B). Density was estimated in xeric *páramo* (XP), rain shadow (RS), and rainy or windward (RW) regions of the Chimborazo Faunal Production Reserve. The heavy solid line in A is a type II linear regression with the lighter lines showing mean ± SEM for the slope and intercept of vicuña density with livestock against vicuña density without livestock. In both A and B, the dashed line is for a slope of 1, equivalent to a case where habitat selection is not occurring.

Forage abundance and accessibility

Plots with NMDS showed that forage plant communities in areas with and without livestock were generally indistinguishable in terms of composition, with the exception of three transects sampled in the dry season, where forage plant communities in areas with livestock more resembled those of wetlands during this season (Fig. 4). Wetlands supported a different plant community composition, also one that was generally more diverse than that of uplands (Appendix S1). In total, we identified 25 forage species in the CFPR, of which five (*Bidens humilis*, *Calamagrostis intermedia*, *Paepalanthus ensifolius*, *Poa annua*, and *Stipa ichu*) had high scores in Ivlev's selection index and were common to all regions; these five plants are listed hereafter as preferred forage. Low stress values (<0.2 for both seasons) for the NMDS indicated that community composition including all forage plants was almost fully explained by two dimensions that corresponded with gradients in precipitation and elevation (Fig. 4). The three regions were dispersed along both dimensions, with XP and RS regions supporting similar communities with more distance from the forage plant communities in the RW region.

The MANOVA conducted on forage abundance and accessibility showed that these measures varied with context (season and region), habitat structure (upland or wetland), and habitat condition (the presence of livestock). As expected, both forage abundance and accessibility were greater during the wet season. The seasonal difference in abundance was largest for the RS region, and the seasonal difference in accessibility was largest for the RW region (Fig. 5). Forage abundance was greater in the RW than in the RS region, and greater in the RS region than in XP, a sequence generally followed by the five preferred forage plants (Table 1). The arrival of the wet season changed this pattern somewhat, as forage abundance and accessibility increased most substantially in the RS region. In the RW region, forage accessibility was lower than in the other two regions, a difference that was not significant during the wet season, due to increased accessibility of forage in wetlands (Fig. 5). During both seasons, in the RW region, areas with livestock had higher forage abundance than areas without livestock, a pattern also evident in four of the five preferred forage plants (Table 1). In the RS region, forage abundance was similarly higher in the presence of livestock, but only in the wet season, whereas in XP and RS, forage

Table 1. Summary of effects from generalized linear models comparing vicuña foraging opportunity and behavior over two seasons (dry and wet) and in three regions: xeric *páramo* (XP), rain shadow (RS), and rainy or windward (RW) areas of the Chimborazo Faunal Production Reserve.

Parameter	df	*F*	*P*	Direction of effects (see *Notes*)
1. Forage abundance (live leaves encountered per 100 pins)				
Season	1, 72	115.7	<0.001	Dry < Wet
Region	2, 72	55.5	<0.001	XP < RS < RW
Condition/Structure	6, 72	35.5	<0.001	XP, RS: L = NL < W RW: L > NL
Season × Region	2, 72	11.4	<0.001	Dry: XP = RS < RW Wet: XP < RS = RW
Season × Condition/Structure	6, 72	3.9	0.001	
2. Abundance of *Bidens humiles* (live leaves encountered per 100 pins)				
Dry: Condition/Structure	4, 41	7.3	<0.001	L: RS > XP = RW NL: XP = RS = RW, XP < RW RW: L > NL
Wet: Condition/Structure	4, 41	8.0	<0.001	L: XP < RS = RWNL: XP = RS = RW, XP < RW
3. Abundance of *Calamagrostis intermedia* (live leaves encountered per 100 pins)				
Dry: Condition/Structure	4, 41	5.0	0.003	L: XP = RS < RW NL: XP = RS = RW, XP < RW
Wet: Condition/Structure	4, 41	4.9	0.003	NL: XP = RS = RW, XP < RW
4. Abundance of *Paepalanthus ensifolius* (live leaves encountered per 100 pins)				
Dry: Condition/Structure	4, 41	23.8	<0.001	L: XP < RS < RW NL: XP < RW RW: L > NL
Wet: Condition/Structure	4, 41	10.0	<0.001	L: XP = RS < RW NL: XP < RW
5. Abundance of *Poa annua* (live leaves encountered per 100 pins)				
Dry: Condition/Structure	4, 41	30.5	<0.001	L: XP < RS = RW NL: XP = RS < RW RW: L > NL
Wet: Condition/Structure	4, 41	7.3	<0.001	XP < RW
6. Abundance of *Stipa ichu* (live leaves encountered per 100 pins)				
Dry: Condition/Structure	4, 41	8.6	<0.001	L: XP < RS = RW NL: RS > XP = RW RW: L > NL
Wet: Condition/Structure	4, 41	7.0	<0.001	L: XP < RS = RW RW: L > NL
7. Forage accessibility (inverse of dead leaves encountered per 100 pins)				
Season	1, 72	11.1	<0.001	Dry < Wet
Region	2, 72	30.0	<0.001	XP = RS > RW
Condition/Structure	6, 72	79.6	<0.001	XP, RS: L = NL < W RW: L = NL = W
Season × Region	2, 72	10.7	<0.001	Dry: XP = RS > RW Wet: XP = RS = RW
Season × Condition/Structure	6, 72	10.5	<0.001	

(Table 1. *Continued*)

Parameter	df	*F*	*P*	Direction of effects (see *Notes*)
8. Fraction of *Bidens humiles* consumed (% of live leaves encountered with bites)				
Dry: Condition/Structure	4, 41	10.2	<0.001	NL XP < RS = RW XP: L > NL
Wet: Condition/Structure	4, 41	4.0	0.008	L: XP = RS < RW
9. Fraction of *C. intermedia* consumed (% of live leaves encountered with bites)				
Dry: Condition/Structure	4, 41	12.8	<0.001	NL: XP < RS = RW XP: L > NL
Wet: Condition/Structure	4, 41	3.5	0.015	XP = RS < RW
10. Fraction of *Pa. ensifolius* consumed (% of live leaves encountered with bites)				
Dry: Condition/Structure	4, 41	14.4	<0.001	NL: XP < RS = RW XP: L > NL
Wet: Condition/Structure	4, 41	9.3	<0.001	L: XP = RS < RW
11. Fraction of *Po. annua* consumed (% of live leaves encountered with bites)				
Dry: Condition/Structure	4, 41	4.1	0.007	NL: XP < RS = RW XP: L > NL
Wet: Condition/Structure	4, 41	2.83	0.036	XP = RS < RW
12. Fraction of *S. ichu* consumed (% of live leaves encountered with bites)				
Dry: Condition/Structure	4, 41	4.1	0.007	NL: XP < RS = RW XP: L > NL
Wet: Condition/Structure	4, 41	2.8	0.036	L: XP = RS < RW NL: XP < RS = RW RS: L < NL
13. Vigilance in male vicuñas (% of scan; two models are shown)†				
Season	**1, 68**	**56.7**, **54.6**	**<0.001**	Dry > Wet
Region	**2, 68**	**8.6**, **14.1**	**<0.001**	XP = RS < RW
Condition/Structure	**1, 68**	**4.8**, 0.5	**0.03**, 0.48	L > NL
Season × Region	**2, 68**	**10.8**, 1.4	**<0.001**, 0.25	XP: L = NL
Region × Condition/Structure	**2, 68**	**4.5**, 0.2	**0.01**, 0.80	RS: Dry = Wet Wet: XP = RS = RW
Condition/Structure × Season	**2, 68**	**6.8**, 1.9	**0.01**, 0.17	Wet: L = NL
Three-way interaction	2, 68	1.5, **7.4**	0.23, **0.001**	
14. Vigilance in female vicuñas (% of scan; two models are shown)†				
Season	**1, 68**	**18.3**, **15.0**	**<0.001**	Dry > Wet
Region	**2,** 68	2.7, **3.0**	0.07, **0.05**	XP = RS < RW
Condition/Structure	1, 68	0.6, 0.6	0.44, 0.45	
Season × Region	**2,** 68	1.4, **3.0**	0.25, **0.05**	Dry: RS < XP = RW
Region × Condition/Structure	2, 68	1.2, 2.5	0.29, 0.08	
Condition/Structure × Season	2, 68	0.4, 1.7	0.50, 0.20	
Three-way interaction	2, 68	1.2, 2.4	0.30, 0.09	
15. Vicuña group size (excluding calves)‡				
Season	1, 58	1.2	0.28	
Region	2, 58	1.8	0.17	
Structure	**1, 58**	**5.2**	**0.02**	L < W
Season × Region	2, 58	1.6	0.20	
Region × Structure	2, 58	2.3	0.10	
Structure × Season	**1, 58**	**4.7**	**0.03**	Wet: L < W
Three-way interaction	2, 58	1.9	0.16	

(Table 1. *Continued*)

Parameter	df	*F*	*P*	Direction of effects (see *Notes*)
16. Flight distance for approached vicuña groups (two models are shown; see *Notes*)†				
Season	**1, 68**	**20.0, 17.5**	**<0.001**	Dry > Wet
Region	**2, 68**	**6.3**, **6.3**	**0.002**	XP = RS < RW = XP
Condition/Structure	1, 68	1.2, 2.6	0.27, 0.11	
Season × Region	**2, 68**	**7.4**, **6.7**	**0.001**	Dry: RS < XP = RW
Region × Condition/Structure	2, 68	2.7, 1.4	0.07, 0.24	
Condition/Structure × Season	2, 68	**3.8**, 3.6	**0.05**, 0.06	Dry: L > NL
Three-way interaction	**2, 68**	**3.3**, 2.7	**0.04**, 0.07	

Notes: Nested within each region are comparisons of uplands with livestock (L) and without livestock (NL), and of wetlands (W) and uplands with livestock (L). Forage comparisons are in a single model, while vicuña behavior comparisons use two models, one comparing L to NL (two habitat conditions), the second comparing L to W (two structural habitat types related to topography). Significant differences were calculated using a modified Wald method with a Bonferroni correction. Significant effects in three-way interactions that are not listed here can be interpreted from Figs. 3–5. Encounter rates with preferred forage plants were smaller, so simplified tests for differences with and without livestock were conducted separately for each season.

† Models comparing vicuña behavior show two calculated *F* and *P* values for the separate comparisons of condition (presence of livestock, L to NL) and habitat structure (uplands, L, to wetlands, W), shown in this order, with significant effect(s) in boldface. Error degrees of freedom are reduced from 68 to 58 in the second model.

‡ Statistics presented for vicuña group size are limited to the comparison of uplands, L, to wetlands, W (habitat structure), as the condition (L to NL) comparison produced a model not significantly different from the null model ($F_{11,\ 68} = 1.4$, $P = 0.16$).

accessibility was always similar with and without livestock (Fig. 5).

There were regional differences in the consumption of preferred forage plants by vicuñas, usually with larger fractions consumed in the RS and RW regions than in the XP region. These differences were consistent with vicuña density differences, but evident only in the dry season (Table 1). A consistent change for the wet season across nearly all habitats and in all five preferred forage plants was greater fractional consumption in the RW region than the RS region, likely an effect of the greater seasonal increase in forage abundance in RS over RW. Consumption was greater where livestock occurred only in the dry season and only in XP. In one case, in the RS region during the wet season, *S. ichu* was less consumed in areas of coexistence with livestock, although the abundance of this plant was similar in areas with and without livestock.

Predictions for vicuña behavior

Based on the most consistent differences among forage abundance and accessibility, the clearest predictions from the *time modulation hypothesis* are that (1) vigilance should occur more often in the wet season than in the dry season, and (2) for the XP and RS regions, vigilance should occur more often in wetlands, assuming that lower forage accessibility in wetlands is less important than higher forage abundance. For the first prediction, based on differences in forage abundance, the largest seasonal difference should be detected in the RS region, and if forage accessibility is a stronger determinant of foraging time, it might be detected in the RW region (Fig. 5). Outcomes with livestock can be compared to the situations where vicuñas were observed without livestock. For the second prediction, based on differences in forage abundance, larger differences in vigilance between uplands and wetlands should occur in XP and during the wet season.

The MANOVA conducted on vicuña vigilance, group size, and flight distance showed that all three measures varied with context (season and region), habitat structure (upland or wetland), and habitat condition (the presence of livestock). Vigilance in both male and female vicuñas was more frequent overall during the dry season, opposite to the prediction given the *time modulation hypothesis* (Table 1). In the RS region only, this counterintuitive seasonal difference was not significant for males, but likely for lack of differences only in wetlands (i.e., the three-way interaction was also significant; Fig. 6, Table 1). Our second set of predictions was also not met by our observations: Vicuñas were not more frequently

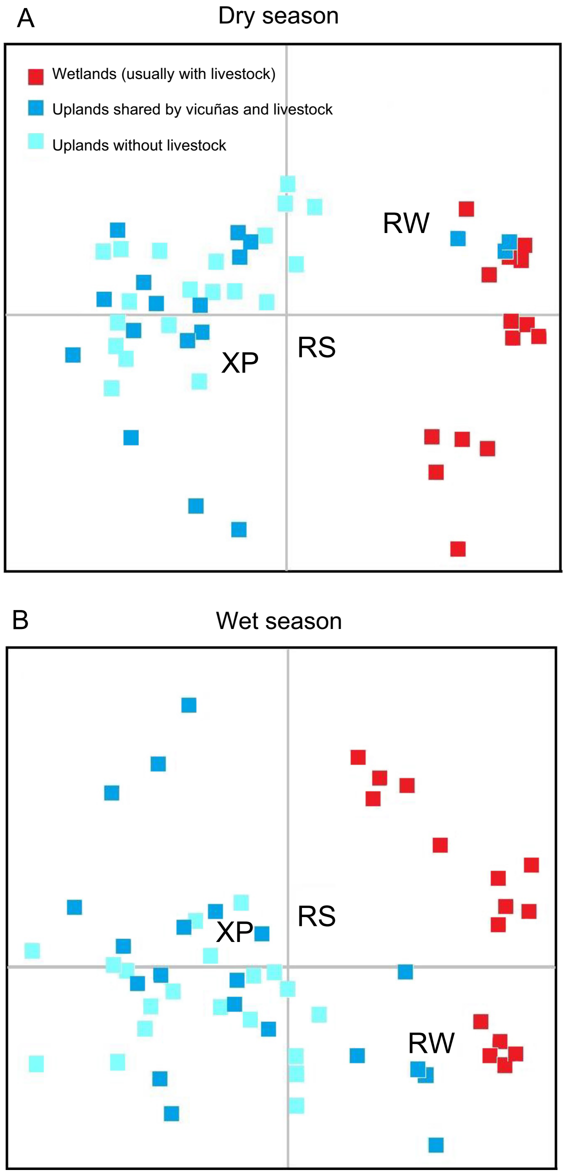

Fig. 4. Plots illustrating forage plant community composition using non-metric multidimensional scaling (NMDS) on plant frequency counts collected during a dry (A) and wet seasons (B). Counts were conducted in wetlands (red symbols), uplands shared by vicuñas and livestock (blue symbols), and uplands without livestock (turquoise symbols) in xeric *páramo* (XP), rain shadow (RS), and rainy or windward (RW) regions of the Chimborazo Faunal Production Reserve. The *x*-axes approximate gradients of increasing precipitation and the *y*-axes gradients in elevation.

vigilant in wetlands in any region for either sex, and season did not influence comparisons of vigilance in uplands and wetlands (Table 1). Results associated with the presence of livestock were mixed or counterintuitive: For males only, vigilance was more frequent with livestock, a difference that occurred during the dry but not the wet season (when forage accessibility is higher), and was the result of a difference only in the RW region (Fig. 6). More frequent vigilance was recorded in both male and female vicuñas in the RW region relative to the other two regions, but this difference varied considerably by season and by habitat and inconsistently for males and females. The difference was also not among our predictions, because it is inconsistent with lower accessibility of forage in RW, particularly in the dry season. Moreover, we predicted that the difference in forage abundance (XP < RS) in uplands during the wet season would be associated with a similar difference in vigilance, which it did not.

Testing instead the predictions for the *group size or density modulation hypothesis*, we are confronted with an absence of theory, but trends reported by other studies suggest that (3) where vicuña density is higher in the RS and RW regions, vigilance should be less frequent and flight distances shorter compared to XP, (4) when forage abundance and accessibility are similar, as in RS and XP during the dry season, higher density in RS should be associated with less frequent vigilance, and (5) group sizes or density should be lower, vigilance less frequent, and flight distances shorter with livestock and in wetlands. With respect to the fourth prediction, differences are tests of positive or negative effects of livestock. With respect to the fifth prediction, generally no positive effect of livestock on forage accessibility in upland habitats was recorded (Fig. 5, Table 1). However, during the wet season in the RW region, when forage abundance is greater and forage accessibility is similar with livestock, density of vicuñas may be higher, consistent with the outcome reported in the *isodar*.

Group size in vicuñas was on average larger in wetlands than in uplands (Fig. 7, Table 1). This difference, expected from studies throughout the Andean altiplano, was not significant in the CFPR during the dry season. No significant patterns emerged for time spent vigilant or flight

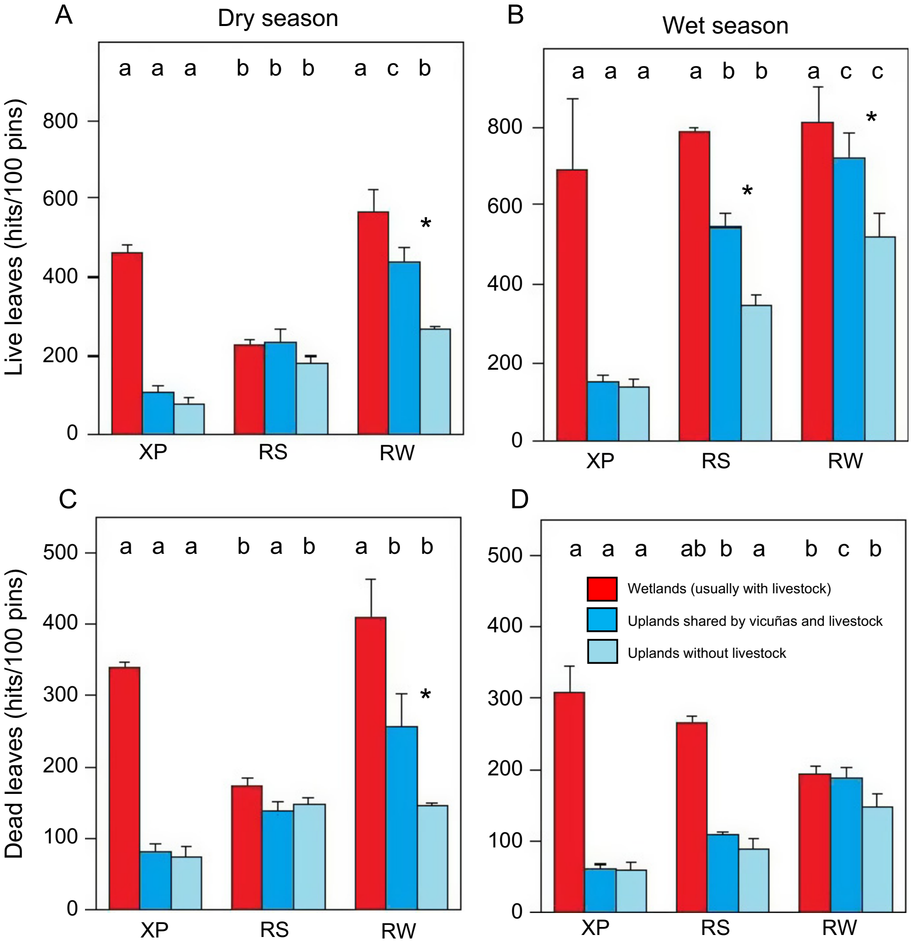

Fig. 5. Forage abundance as encounter rates (mean ± SEM) of live leaves (A, B) and an inverse of forage accessibility as encounter rates of dead leaves (C, D) of all forage plants along transects in vicuña territories sampled during a dry (A, C) and wet seasons (B, D). Forage counts were along transects in wetlands (red bars), uplands shared by vicuñas and livestock (blue bars), and uplands without livestock (turquoise bars) in xeric *páramo* (XP), rain shadow (RS), and rainy or windward (RW) regions of the Chimborazo Faunal Production Reserve. Significant differences across these regions are indicated with dissimilar letters for the same habitat structure and condition (wetlands, uplands with livestock, and uplands without livestock), and asterisks indicate cases of significantly higher encounter rates in areas with livestock. Forage abundance is significantly higher, and accessibility significantly lower (more dead leaves) in wetlands, except in RS during the dry season and RW during the wet season. Other significant differences in forage abundance and accessibility are listed in Table 1.

distances and group size, and the relationship with group size was not a correlation in the MANOVA. The only pattern, not significant, consistent with the literature involved with the *group size or density modulates prey behavior* hypothesis, was smaller group sizes in RW with livestock, where significantly lower vigilance occurred compared to areas without livestock (Figs. 6, 7). Vigilance was not less frequent, and flight distances were not shorter in the RS and RW regions relative to XP, offering no support for the third prediction (Figs. 6, 8, Table 1). Time spent vigilant was not different with livestock presence during the dry season, comparing RS and XP regions, offering no support for the fourth prediction (Fig. 6). The only significant differences

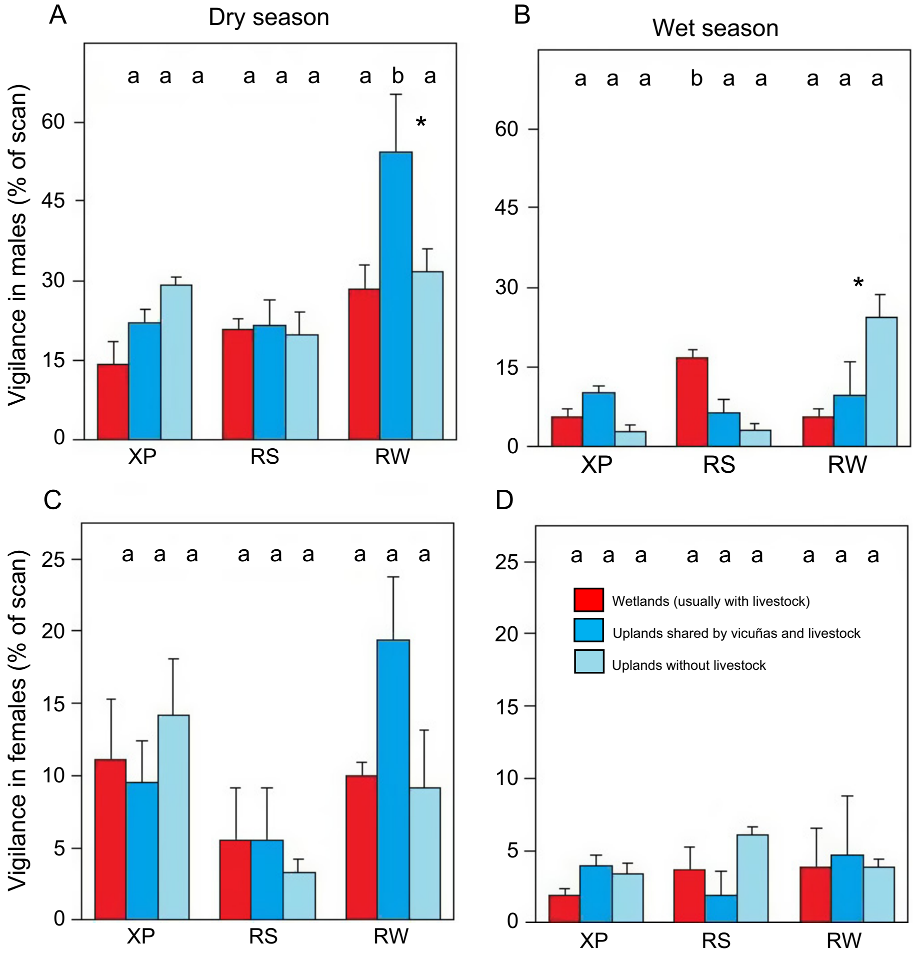

Fig. 6. Vigilance as a percent of a 10-min scan (mean ± SEM) in male (A, B) and female (C, D) vicuñas in territorial groups encountered along transects sampled during a dry (A, C) and wet seasons (B, D) in wetlands (red bars), uplands shared by vicuñas and livestock (blue bars), and uplands without livestock (turquoise bars) in xeric *páramo* (XP), rain shadow (RS), and rainy or windward (RW) regions of the Chimborazo Faunal Production Reserve. Significant differences across regions are indicated with dissimilar letters, and for condition (with livestock) with asterisks, as in Fig. 5. Other significant differences are listed in Table 1 for two models accounting for differences in vigilance for each sex, one comparing areas with and without livestock (condition), and the second comparing wetland and upland areas (structure). The significant three-way interaction in the model comparing males in wetland and upland areas is due to higher vigilance in uplands in RW during the dry season only, and to a lack of difference in vigilance between RS and RW in wetlands during the dry season.

involving vigilance and flight distance were opposite to the fifth prediction: Not only was more frequent vigilance recorded, but also longer flight distance, where livestock occurred during the dry season in XP (Figs. 6, 8, Table 1). The difference would also have been significant and in the same direction during the dry season in RW, except for one outlier group (Fig. 8). However, with the arrival of the wet season, neither of these differences was significant. Such a change would be predicted if some very local differences in forage abundance, higher in areas of livestock especially in the dry season, are the cause for variation in vicuña behavior.

Discussion

Presence of livestock did not reduce the time vicuñas spent vigilant at any density, unlike the conclusion of Vijayan et al. (2012*b*) for spotted deer. In fact, in the RW region of the CFPR,

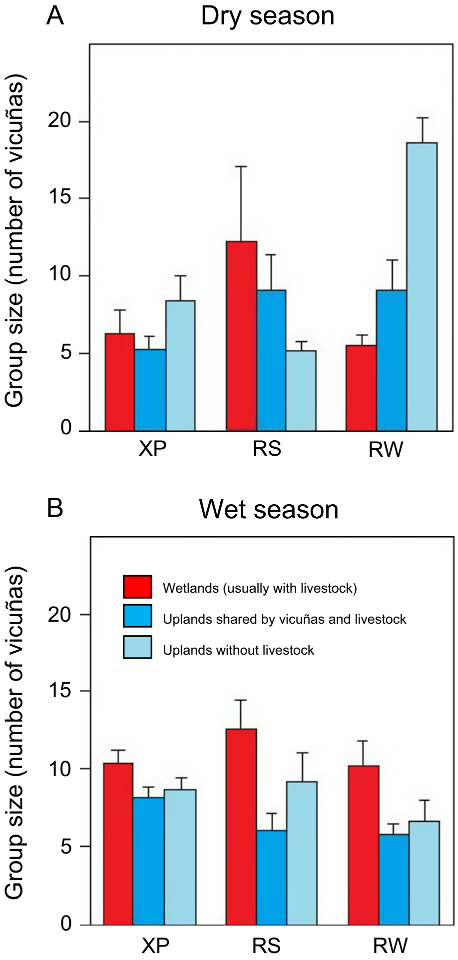

Fig. 7. Group size as number of adult vicuñas (mean ± SEM) in territorial groups encountered along transects sampled during a dry (A) and wet seasons (B) in wetlands (red bars), uplands shared by vicuñas and livestock (blue bars), and uplands without livestock (turquoise bars) in xeric *páramo* (XP), rain shadow (RS), and rainy or windward (RW) regions of the Chimborazo Faunal Production Reserve. Significant differences only occur in a model comparing group size in wetland and upland habitats; vicuñas occur in larger groups in uplands, with a significant effect limited to the wet season (Table 1).

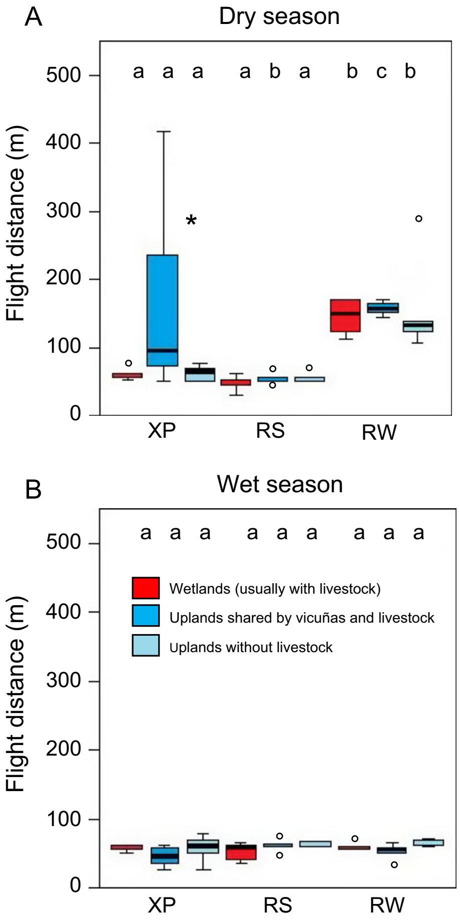

Fig. 8. Flight distance (m) for approached vicuña groups encountered along transects sampled during a dry (A) and wet seasons (B) in wetlands (red bars), uplands shared by vicuñas and livestock (blue bars), and uplands without livestock (turquoise bars) in xeric *páramo* (XP), rain shadow (RS), and rainy or windward (RW) regions of the Chimborazo Faunal Production Reserve. Box-and-whisker plots show median, quartiles, and outliers (small circles). Significant differences across regions are indicated with dissimilar letters, and for condition (with livestock) with asterisks, as in Fig. 5. Other significant differences are listed in Table 1 for two models explaining differences in flight distance, one comparing areas with and without livestock (condition), and the second comparing wetland and upland areas (structure). The significant three-way interaction in the model comparing condition is due to the lack of seasonal differences in flight distance in RS and RW in areas without livestock.

vigilance was more frequent and flight occurred with longer approach distances where livestock were present. This difference, like so many of our observations, did not easily conform to OFT, as it occurred only during a dry season, when foraging should have occupied more time, leaving less for vigilance. In the wet season, the difference in vigilance and flight distance with livestock vanished, inconsistent with the greater forage abundance with livestock that arrived with the wet season. Perhaps one reason OFT predictions are complicated is that, while our measures showed structural differences in the forage plant communities of uplands and wetlands in the CFPR, such differences were only very seldom encountered comparing upland areas with and without livestock. That structural differences are less important than the functional difference in habitat created by the presence of livestock is a reminder of the study of the response of bighorn sheep (*Ovis canadensis*) in Sheep River Provincial Park, Alberta, to cattle occupying the protected area (Brown et al. 2010): Lower rates of foraging and higher rates of vigilance occur for bighorn sheep with cattle nearby, and aggregation occurs between the free-ranging and the domestic herbivores, despite this presumably negative interaction between them.

In the CFPR, differences in forage abundance matched our expectations for regional and seasonal variation, and forage abundance was higher in wetlands, but none of these differences determined vicuña behavior in a way that OFT predicts, and neither did vicuña density respond to higher forage abundance in wetlands. Indeed, this latter effect elsewhere was limited to bad years in a more seasonal environment (Mosca Torres and Puig 2012, Shaw et al. 2012). Wetlands are also habitats temporarily visited for reasons other than finding forage, for example, for consuming water during a dry season (Koford 1957). These are some of the contextual differences that the empirical literature needs to build and that we need in order to have confidence in the results of our tests of density-dependent habitat selection.

Density of vicuñas did not determine their behavior; instead, local density appeared to be a function of the presence of livestock, a functional habitat difference that we did not expect. Facilitation would occur between the sympatric herbivores if forage plants were kept in a more productive or accessible state, or if the plants were higher in quality as a result of livestock grazing. This grazing lawn hypothesis, used in the past to explain gregariousness in herbivores (McNaughton 1976, 1984, reviewed by Arsenault and Owen-Smith 2002), fits the trend of higher forage abundance with livestock in several contexts in the CFPR, but should also be tested with comparisons of forage plant quality, because forage abundance and accessibility were not consistently different. For example, the trend of higher forage abundance in areas of livestock occurred only in RS during the wet season, and forage accessibility was not higher with livestock. Odadi et al. (2011) described a net positive interaction between free-ranging herbivores and livestock by confirming that differences in forage accessibility conformed to the grazing lawn hypothesis. We might explain the case of higher density of vicuñas with livestock by suggesting that livestock simply graze where forage is more abundant, a statement not requiring the grazing lawn hypothesis. Sympatry of livestock and vicuñas in the CFPR, as shown by our isodar, occurs at scales of <30 m that we did not investigate in terms of variation in forage abundance or accessibility. Fuhlendorf and Engle (2001) previously suggested that medium-scale spatial heterogeneity in rangelands leads to more diversity in sympatric wildlife. Brown et al. (2010) also explained apparent attraction of free-ranging bighorn sheep to cattle using the grazing lawn hypothesis.

Perhaps more puzzling is that our results are so different from other studies of vicuñas. Coexistence with livestock, let alone evidence of preference for areas with livestock, is in stark contrast to the more frequently reported selective use of habitat to avoid livestock reported elsewhere for vicuñas (Borgnia et al. 2008). One explanation is that vicuñas were introduced to areas with livestock and the soft introduction into the CFPR implied a 40-d quarantine period, during which vicuñas were kept close to livestock and grew tolerant of them. This explanation is consistent with the continued higher densities of vicuñas at their points of introduction, where livestock herding is still more frequent compared to other areas of the CFPR. Another explanation is that levels of livestock grazing, poaching of vicuñas, and activity of feral dogs have been mitigated by the level of protection Ecuador's Ministry of Environment affords the CFPR. Indeed, Arzamendia and Vilá (2015) report that intermediate levels of livestock allow mixed herds with vicuñas, concluding that only at higher densities should segregation occur. Nevertheless, densities of livestock in the CFPR are almost certainly higher than those reported by Borgnia et al. (2008; 1.0 and 4.4 km^{-2} for donkeys and other livestock, respectively), so differences in density or grazing intensity of livestock will not offer a full explanation for cases of coexistence relative to segregation, but these differences should nevertheless be explored. Elsewhere, variation in vicuña flight behavior was mediated by the presence of poachers (Donadio and Buskirk 2006) or pumas (Donadio and Buskirk 2016), which likely both occur in the CFPR, but rarely. On the other hand, observations in nearby Cotopaxi National Park, Ecuador, support a considerable effect of feral dogs just by their presence in the Andean ecosystem (Zapata-Ríos and Branch 2016).

Most likely, it is moderate grazing by livestock in the CFPR that allows vicuñas to coexist with them without negative effects of competition, and we present considerable evidence for positive effects of livestock conveyed to vicuñas. Vicuñas are less selective when habitat quality deteriorates (Arzamendia et al. 2006), and a switch to a more generalist diet during the dry season is a documented effect elsewhere (Mosca Torres and Puig 2010) that could explain the variation from OFT predictions in the CFPR. The fact that vicuñas themselves are apparently not at carrying capacity in the CFPR lends credence to different outcomes; for example, in northern Chile, where vicuñas exist at carrying capacity, rainfall is a better predictor of vicuña density and behavior than forage abundance or livestock density, and overall habitat productivity overrides the competitive effects of sympatric livestock (Shaw et al. 2012), the same effect that has been reported for spotted deer (Dave and Jhala 2011). Clark et al. (2017) report that elk (*Cervus elaphus*) and cattle graze differently, the free-ranging herbivore aiming to access areas of higher forage quality, and cattle aiming to conserve energy by limiting movement whenever forage quality is compromised; this study explains coexistence by niche differentiation that may be common to other cases of sympatry between free-ranging and domestic herbivores.

Interactions between animals are ubiquitous and are directly responsible for the shaping of ecosystems (Stachowicz 2001). In situations where livestock have been introduced to an environment, the most evident resultant interaction with other large herbivores is direct competition for forage (Bagchi et al. 2004, Madhusudan 2004, Young et al. 2005, Gordon 2009). Livestock and wild herbivores are also susceptible to apparent competition when a shared predator or parasite population is bolstered by an increase in density of either wildlife or livestock (Norman et al. 1999, Daszak et al. 2000, Bengis et al. 2002, Brook and McLachlan 2006, Kilpatrick et al. 2009). Odadi et al. (2011) found that wild ungulates compete with cattle during the dry season when forage was limited, but that wild ungulates facilitated cattle during the wet season via physiological differences between them that allow resource partitioning. We conclude from consistently higher vigilance and flight distances during the dry season that vicuñas were in a more alert situation when forage was more limited, in this case in a similar way to what has been concluded elsewhere (Arzamendia et al. 2006, Mosca Torres and Puig 2010). In areas or during seasons when vegetative productivity is low and likely constraining populations of herbivores, competition is more likely to occur (Himalayan cold desert, Bagchi et al. 2004, African savannah during the dry season, Odadi et al. 2011). Similarly, season and sheep density influence the detection of negative effects of livestock grazing on elk range in the western United States (Alpe et al. 1999, Clark et al. 2000). In the CFPR, especially during the wet season, spatial heterogeneity in forage plant quality may alleviate competition between livestock and vicuñas up to a higher threshold than might be expected in more homogenous landscapes.

To conclude, landscape heterogeneity may determine the degree to which positive or negative interactions between wildlife and sympatric livestock occur. So far, outcome of our study of vicuñas in the CFPR matches another disparate result from a study of guanaco and sheep coexistence in Patagonia, which the authors speculate owes to high habitat heterogeneity and very fine-scale niche segregation (Iranzo et al. 2013). To explore further how context affects ecological interactions, a wider and more precise sampling of densities of sympatric large herbivores may be required to specify thresholds for habitat homogeneity at which negative interactions disappear. Such study in general could inform mitigation efforts to reduce pastoralist/wildlife conflict by implementing maximum stocking densities. In multi-ungulate systems where facilitation has been detected, low dietary niche overlap has contributed to the effect of facilitation (Odadi et al. 2011). Dave and Jhala (2011) found that spotted deer benefit from sympatric livestock on short timescales, but that long-term sympatry with livestock caused deer populations to decline. The continued exponential growth of vicuñas so far makes this conclusion less of a possibility in the CFPR. In the Andes, mixed herds of sheep and domestic camelids have been common for centuries (Tichit and Genin 1997). The complexity of the camelid ecosystem provides an opportunity to expand on descriptions of the contexts that determine the direction of species interactions; our next step is to test forage plant quality differences in areas of coexistence of vicuñas and livestock.

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LITERATURE CITED

Alpe, M. J., J. L. Kingery, and J. C. Mosley. 1999. Effects of summer sheep grazing on browse nutritive quality in autumn and winter. Journal of Wildlife Management 63:346–354.

Andrade, J. M. 2016. Determinación del estado de conservación de los bofedales de la Reserva de Producción de Fauna Chimborazo. Thesis. Escuela Superior Politécnica de Chimborazo, Riobamba, Ecuador.

Arsenault, R., and N. Owen-Smith. 2002. Facilitation versus competition in grazing herbivore assemblages. Oikos 97:313–318.

Arzamendia, Y., M. H. Cassini, and B. Vilá. 2006. Habitat use by vicuña *Vicugna vicugna* in Laguna Pozuelos Reserve, Jujuy, Argentina. Oryx 40: 198–203.

Arzamendia, Y., and B. Vilá. 2015. Vicugna habitat use and interactions with domestic ungulates in Jujuy, Northwest Argentina. Mammalia 79:267–278.

Augustine, D. J., and T. L. Springer. 2014. Competition and facilitation between a native and a domestic herbivore: trade-offs between forage quantity and quality. Ecological Applications 23:850–863.

Augustine, D. J., K. E. Veblen, J. R. Goheen, C. Riginos, and T. P. Young. 2011. Pathways for positive cattle-wildlife interactions in semiarid rangelands. Smithsonian Contributions to Zoology 2011: 55–71.

Bagchi, S., C. Mishra, and Y. V. Bhatnagar. 2004. Conflicts between traditional pastoralism and conservation of Himalayan ibex (*Capra sibirica*) in the Trans-Himalayan Mountains. Animal Conservation 7:121–128.

Baldi, R., A. Pelliza-Sbriller, D. Elston, and S. Albon. 2004. High potential for competition between guanacos and sheep in Patagonia. Journal of Wildlife Management 68:924–938.

Bengis, R. G., R. A. Kock, and J. Fischer. 2002. Infectious animal diseases: the wildlife/livestock interface. Revue Scientifique et Technique de l'Office International des Épizooties 21:53–65.

Borgnia, M., B. L. Vilá, and M. H. Cassini. 2008. Interactions between wild camelids and livestock in an Andean semi-desert. Journal of Arid Environments 72:2150–2158.

Borgnia, M., B. L. Vilá, and M. H. Cassini. 2010. Foraging ecology of vicuna, *Vicugna vicugna*, in dry puna of Argentina. Small Ruminant Research 88: 44–53.

Bradbury, J. W., S. L. Vehrencamp, and K. E. Clifton. 2015. The ideal free antelope: foraging dispersions. Behavioral Ecology 26:1303–1313.

Brook, R. K., and S. M. McLachlan. 2006. Factors influencing farmers' concerns regarding bovine tuberculosis in wildlife and livestock around Riding Mountain National Park. Journal of Environmental Management 80:156–166.

Brown, N. A., K. E. Ruckstuhl, S. Donelon, and C. Corbett. 2010. Changes in vigilance, grazing behaviour and spatial distribution of bighorn sheep due to cattle presence in Sheep River Provincial Park, Alberta. Agriculture, Ecosystems and Environment 135:226–231.

Buckland, S. T., E. A. Rexstad, T. A. Marques, and C. S. Oedekoven. 2015. Distance sampling: methods and applications. Springer, New York, New York, USA.

Cappa, F. M., C. E. Borghi, V. E. Campos, N. Andino, M. L. Reus, and S. M. Giannoni. 2014. Guanacos in the Desert Puna: a trade-off between drinking and the risk of being predated. Journal of Arid Environments 107:34–40.

Chamberlain, S. A., J. L. Bronstein, and J. A. Rudgers. 2014. How context dependent are species interactions? Ecology Letters 17:881–890.

Clark, P. E., D. E. Johnson, D. C. Ganskopp, M. Varva, J. G. Cook, R. C. Cook, F. B. Pierson, and S. P. Hardegree. 2017. Contrasting daily and seasonal activity and movement of sympatric elk and cattle. Rangeland Ecology and Management 70:183–191.

Clark, P. E., W. C. Krueger, L. D. Bryant, and D. R. Thomas. 2000. Livestock grazing effects on forage quality of elk winter range. Journal of Range Management 53:97–105.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Wildlife ecology – Emerging infectious diseases of wildlife – Threats to biodiversity and human health. Science 287:443–449.

Dave, C., and Y. Jhala. 2011. Is competition with livestock detrimental for native wild ungulates? A case study chital (*Axis axis*) in Gir Forest, India. Journal of Tropical Ecology 27:239–247.

De Gabriel, J. L., S. D. Albon, D. A. Fielding, D. J. Riach, S. Westaway, and R. J. Irvine. 2011. The presence of sheep leads to increases in plant diversity and reductions in the impact of deer on heather. Journal of Applied Ecology 48:1269–1277.

Dennis, R. L. H., T. G. Shreeve, and H. van Dyck. 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102: 417–426.

Dennis, R. L. H., T. G. Shreeve, and H. van Dyck. 2006. Habitats and resources: the need for a resource-based definition to conserve butterflies. Biodiversity and Conservation 15:1943–1966.

Donadio, E., and S. W. Buskirk. 2006. Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. Biological Conservation 127:139–145.

Donadio, E., and S. W. Buskirk. 2016. Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes. Journal of Mammalogy 97:966–977.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8:629–644.

Ford, A. T., J. R. Goheen, D. J. Augustine, M. F. Kinnaird, T. G. O'Brien, T. M. Palmer, R. M. Pringle, and R. Woodroffe. 2015. Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade. Ecology 96:2705–2714.

Franklin, J. F., and D. B. Lindenmayer. 2009. Importance of matrix habitats in maintaining biological diversity. Proceedings of the National Academy of Sciences USA 106:349–350.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience 51:625–632.

Gordon, I. J. 2009. What is the future for wild, large herbivores in human-modified agricultural landscapes? Wildlife Biology 15:1–9.

Hawlena, D., D. Saltz, Z. Abramsky, and A. Bouskila. 2010. Ecological trap for desert lizards caused by anthropogenic changes in habitat structure that favor predator activity. Conservation Biology 24: 803–809.

Iranzo, E. C., J. Traba, P. Acebes, B. A. González, C. Mata, C. F. Estades, and J. E. Malo. 2013. Niche segregation between wild and domestic herbivores in Chilean Patagonia. PLoS ONE 8:e59326.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA.

Kilpatrick, A. M., C. M. Gillin, and P. Daszak. 2009. Wildlife-livestock conflict: the risk of pathogen transmission from bison to cattle outside Yellowstone National Park. Journal of Applied Ecology 46:476–485.

Koford, C. B. 1957. The vicuña and the puna. Ecological Monographs 27:143–219.

Laliberté, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience 54:123–138.

Lamprey, R. H., and R. S. Reid. 2004. Expansion of human settlement in Kenya's Maasai Mara: What future for pastoralism and wildlife? Journal of Biogeography 31:997–1032.

Lichtenstein, G. 2009. Vicuna conservation and poverty alleviation? Andean communities and international fibre markets. International Journal of the Commons 4:100–121.

Madhusudan, M. D. 2004. Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. Journal of Applied Ecology 41:858–869.

McNaughton, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191:92–94.

McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist 124:863–886.

Mishra, C. H., S. E. Van Wieren, P. Ketner, I. M. Heitkonig, and H. Prins. 2004. Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian trans-Himalaya. Ecology 41:344–354.

Morris, D. W. 1987. Tests of density-dependent habitat selection in a patchy environment. Ecological Monographs 57:269–281.

Morris, D. W. 1988. Habitat-dependent population regulation and community structure. Evolutionary Ecology 2:253–269.

Mosca Torres, M. E., and S. Puig. 2010. Seasonal diet of vicunas in the Los Andes protected area (Salta, Argentina): Are they optimal foragers? Journal of Arid Environments 74:450–457.

Mosca Torres, M. E., and S. Puig. 2012. Habitat use and selection by the vicuña (*Vicugna vicugna*, Camelidae) during summer and winter in the High Andean Puna of Argentina. Small Ruminant Research 104:17–27.

Mosca Torres, M. E., S. Puig, A. Novilloa, and R. Ovejero. 2015. Vigilance behavior of the year-round territorial vicuña (*Vicugna vicugna*) outside the breeding season: influence of group size, social factors and distance to a water source. Behavioural Processes 113:163–171.

Navarro, G., and M. Maldonado. 2002. Geografía ecológica de Bolivia. Vegetación y ambientes acuáticos. Centro de Ecología Simón I. Patiño, Departamento de Difusión, Cochabamba, Bolivia.

Norman, R., R. G. Bowers, M. Begon, and P. J. Hudson. 1999. Persistence of tick-borne virus in the presence of multiple host species: tick reservoirs and parasite mediated competition. Journal of Theoretical Biology 200:111–118.

Odadi, W. O., M. K. Karachi, S. A. Abdulrazak, and T. P. Young. 2011. African wild ungulates compete with or facilitate cattle depending on season. Science 333:1753–1755.

Ottichilo, W. K., J. De Leeuw, A. K. Skidmore, H. H. T. Prins, and M. Y. Said. 2000. Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. African Journal of Ecology 38:202–216.

Podwojewski, P., J. Poulenard, T. Zambrana, and R. Hofstede. 2002. Overgrazing effects on vegetation cover and properties of volcanic ash soil in the páramo of Llangahua and La Esperanza (Tungurahua, Ecuador). Soil Use and Management 18:45–55.

Prins, H. H. T. 2000. Competition between wildlife and livestock in Africa. Pages 51–80 *in* H. H. T. Prins, J. G. Grootenhuis, and T. T. Dolan, editors. Wildlife conservation by sustainable use. Kluwer Academic Press, Boston, Massachusetts, USA.

Renaudeau d'Arc, N., M. H. Cassini, and B. L. Vilá. 2000. Habitat use by vicuñas *Vicugna vicugna* in the Laguna Blanca Reserve (Catamarca, Argentina). Journal of Arid Environments 46:107–115.

Sarmiento, G. 1986. Ecological features of climate in high tropical mountains. Page 13–45 *in* F. Vuilleumier and M. Monasterio, editors. High altitude tropical biogeography. Oxford University Press, Oxford, UK.

Schuette, P., S. Creel, and D. Christianson. 2016. Ungulate distributions in a rangeland with competitors, predators and pastoralists. Journal of Applied Ecology 53:1066–1077.

Schulz, C.-E., and A. Skonhoft. 1996. Wildlife management, land-use and conflicts. Environment and Development Economics 1:265–280.

Shaw, A. K., J. L. Galaz, and P. A. Marquet. 2012. Population dynamics of the vicuña (*Vicugna vicugna*): density-dependence, rainfall, and spatial distribution. Journal of Mammalogy 93:658–666.

Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. BioScience 51:235–246.

Stahl, P. W. 1988. Prehistoric camelids in the lowlands of western Ecuador. Journal of Archaeological Science 15:355–365.

Stahl, P. W. 2003. The zooarchaeological record from Formative Ecuador. Pages 175–212 *in* J. S. Raymond and R. L. Burger, editors. Archaeology of formative Ecuador. Dumbarton Oaks Research Library and Collection, Washington, D.C., USA.

Tichit, M., and D. Genin. 1997. Factors affecting herd structure in a mixed camelid–sheep pastoral system in the arid Puna of Bolivia. Journal of Arid Environments 36:167–180.

van Beest, F. M., P. D. McLoughlin, E. Vander Wal, and R. K. Brook. 2014. Density-dependent habitat selection and partitioning between two sympatric ungulates. Oecologia 175:1155–1165.

Van Dyck, H. 2012. Changing organisms in rapidly changing anthropogenic landscapes: the significance of the '*Umwelt*'-concept and functional habitat for animal conservation: perception and habitat in anthropogenic landscapes. Evolutionary Applications 5:144–153.

Vijayan, S., B. E. McLaren, D. W. Morris, and S. P. Goyal. 2012*a*. Can rare positive interactions become common when large carnivores consume livestock? Ecology 93:272–280.

Vijayan, S., D. W. Morris, and B. E. McLaren. 2012*b*. Prey habitat selection under shared predation: Tradeoffs between risk and competition? Oikos 121:783–789.

Wurstten, A., A. J. Novaro, and R. S. Walker. 2014. Habitat use and preference by guanacos, vicuñas, and livestock in an altitudinal gradient in northwest Argentina. European Journal of Wildlife Research 60:35–43.

Young, T. P., T. M. Palmer, and M. E. Gadd. 2005. Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. Biological Conservation 122: 351–359.

Zapata-Ríos, G., and L. C. Branch. 2016. Altered activity patterns and reduced abundance of native mammals in sites with feral dogs in the high Andes. Biological Conservation 193:9–16.

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