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Roads have no effect on guanaco habitat selection at a Patagonian site with limited poaching

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ABSTRACT

Roads affect flora and fauna across the world. Large mammals are particularly vulnerable to road effects because their large home ranges lead to a higher probability of contact with road networks. Disturbance associated with roads can alter the probability of habitat use by making suitable habitat near roads inaccessible or underused. Many studies and monitoring programs for large mammals such as guanaco (*Lama guanicoe*) in South America, however, rely on counts made from roads to estimate population abundance and distribution. These counts implicitly assume that animal responses to roads are negligible, an assumption almost universally unstudied. We used density surface models with aerial survey data to evaluate the effects of unpaved roads on guanaco habitat selection, at the scale of the species' home range, in a Patagonian site with limited poaching. Contrary to expectations and regardless of disturbance level associated with roads, guanacos did not avoid roads at site (0.36 km²) or patch (2.4 km²) scales during any season. We posit two non-exclusive hypotheses to explain our results: (1) disturbance levels of roads are below thresholds of guanaco response, and (2) guanacos in our study area tolerated motorized vehicles due to limited harassment by poachers from roads. Our results, considered with opposite findings of strong road effects on guanaco at a landscape and regional scales, highlight the need to assess whether road surveys lead to biased estimates of ungulate abundance and distribution under different environmental conditions, human activities and scales of interest. Where long-term monitoring of large mammal populations relies on road surveys, aerial or other non-road surveys could be strategically conducted to determine whether counts from roads provide reliable estimates.

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1. Introduction

Road ecology, the study of ecological effects of roads and traffic, has grown remarkably as a sub-discipline over the past 20 years (Trombulak and Frissell, 2000; Forman et al., 2003; van der Ree et al., 2015). Documented impacts of roads in wildlife populations can be either negative, positive or neutral (i.e. no effect) depending on the taxa, ecological context, spatial scale and type of animal response considered. Slow-moving animals, less successful than fast ones at avoiding vehicles, generally are negatively affected by roads, as is the case for amphibians and reptiles (Steen et al., 2006; Stevens et al., 2006). Roads have positive effects on some species by increasing habitat quality, for example by providing novel food resources for scavengers that also are adept at avoiding vehicles (Lambertucci et al., 2009). Neutral road effects have been observed in small mammals, such as red squirrels (*Sciurus vulgaris*), which do not avoid roads and cross them during exploration and dispersal movements (Fey et al., 2016).

Large mammals are often negatively affected by roads (Rytwinski and Fahrig, 2012). Direct effects include mortality from collisions, increased vulnerability to hunters and poachers, increased movement rates and stress levels, and avoidance of areas near roads (Hayes et al., 2002; Gagnon et al., 2007; Beyer et al., 2013; Wilson et al., 2016). Indirect effects include habitat loss and fragmentation as well as loss of habitat quality, for example through increased abundance of exotic plants in verges (Fahrig and Rytwinski, 2009; D'amico et al., 2016). Disturbance associated with roads can alter the probability of habitat use by making suitable habitat near roads inaccessible or underused (Whittington et al., 2004). This response leads to a "road-effect zone", defined as the distance from the edge of the road over which significant ecological effects can be detected (Forman and Alexander, 1998). Not all roads open to traffic, however, elicit avoidance by large mammals. Characteristics such as road material, removal of vegetation along roadsides, traffic flow, traffic volume and vehicle speed are important disturbance factors that can influence the magnitude and extent of road avoidance (Forman et al., 2003). Additionally, long-lived animals with learning capacity, such as large mammals, are able to make spatio-temporal adjustments to the presence of roads, e.g., by using habitats close to roads or crossing roads during hours of reduced human activity (Laurian et al., 2008; Neumann et al., 2013; Thurfjell et al., 2015), or they are able to habituate to roads when they learn that the stimulus is not lethal (Haskell et al., 2006; Marino and Johnson, 2012).

Habitat selection in relation to roads is a hierarchical process acting at different spatial scales (Johnson, 1980). At coarse scales, roads and associated disturbances can alter home range selection and distributional ranges of species and ultimately affect population persistence. Caribou *Rangifer tarandus caribou*, for example, excluded a Canadian highway from their home ranges as the intensity of the highway disturbance increased (Leblond et al., 2013), and sizes of home ranges of moose *Alces alces* containing roads were larger than those without roads (Laurian et al., 2008). Once the home range is selected, the presence of roads and associated disturbances can affect local habitat quality, triggering behavioral processes like shifts in habitat patch or foraging site selection. Within their home range, for example, caribou used road-buffer zones less frequently and avoided habitat types that were selected elsewhere in their home range (Leblond et al., 2013), and elk *Cervus canadensis* crossed highways less frequently as traffic volume increased (Gagnon et al., 2007).

Habitat selection responses in relation to roads have been extensively studied for some North American and European ungulates (see for example Rowland et al., 2000, 2004; Wisdom et al., 2005; Laurian et al., 2008; Leblond et al., 2013). Analyses of road impacts in other regions, however, are scarce. A South American endemic camelid, the guanaco *Lama guanicoe*, is the most widely distributed wild herbivore in South America and the main prey of the native carnivore, the cougar *Felis concolor* (Franklin et al., 1999; Zánón Martínez et al., 2012). Guanacos suffered a drastic population decline during the twentieth century, mainly caused by competition from livestock and poaching (Baldi et al., 2010). Although the road network has grown throughout the species' range along with the expansion of cities and livestock raising, the response of guanacos to roads has received little attention. The available evidence at broad scales suggests that guanacos are negatively affected by the density of roads mainly due to high poaching pressure spread through the road network (Radovani et al., 2014; Rivas et al., 2015), which possibly alters home range selection of this species. Disturbance of guanacos related to roads within the scale of the home range has not been assessed and could be potentially confounded with the impact of continuous harassment of poachers that use roads (Donadio and Buskirk, 2006). Evaluating the effect of roads in areas sustaining relatively low poaching levels can provide an appropriate context for understanding guanaco responses to roads across the spectrum of different road-associated disturbances, and help disentangle impacts of poaching from effects of regular vehicle traffic and speed.

Most studies of guanaco population density, age ratios, and social structure have been based on ground transect surveys from roads (Baldi et al., 2001; Travaini et al., 2015, 2007; Pedrana et al., 2010; Acebes et al., 2013; Nabte et al., 2013; Iranzo et al., 2013; Schroeder et al., 2013, 2014; Wursten et al., 2014; Radovani et al., 2014; Moraga et al., 2014). Wildlife researchers and resource managers extensively use road surveys as a cost-effective method because they are replicable and consistent for monitoring species like guanaco and for other large-bodied species (e.g. Grunewald et al., 2016; Arbieu et al., 2017; Yirga et al., 2017). For example, monitoring of population parameters (e.g. density and population structure) through road surveys provides key indicators used by the enforcement authority to approve the annual permits for live-shearing guanacos in southern Mendoza province, Argentina (Carmanchahi et al., 2014). Surveying from roads, however, implicitly assumes that wildlife responses to roads are neutral or negligible, which typically has not been evaluated. In summary, understanding road effects on guanaco and other species is important because: (1) roads can alter habitat selection patterns and ultimately, affect population persistence (Rytwinski and Fahrig, 2012), and (2) biases that may result from using roads in ground surveys for wildlife monitoring are poorly understood (Marques et al., 2013).

In this study, we evaluated the effect of roads associated with different disturbance levels on guanaco habitat selection at the scale of a home range, in a protected area of northern Patagonia with low poaching pressure. We estimated spatial and seasonal variation in guanaco local abundance using the density surface model approach (hereafter, dsm) (Miller et al., 2013), which combines the fundamentals of distance sampling based on the probability of detection with the flexibility of Generalized Additive Models (GAM) (Wood, 2006). Unpaved roads are typical of rural environments and protected natural areas where wild species, even the most threatened, mostly occur. In turn, this type of road is used commonly for wildlife sampling worldwide and in different biomes, so the study of the effects of unpaved roads is especially relevant. Animals moving through a landscape may avoid roads due to 1) the removal of vegetation that otherwise may have served as cover from predators (gap avoidance, Chen and Koprowski, 2016), 2) disturbances associated with traffic such as noise, lights, vibrations, and dust in suspension (traffic-emission avoidance, Forman and Alexander, 1998), or 3) vehicles themselves, in the case of those species that have the cognitive ability to do so such as long-lived animals (vehicle avoidance, Fahrig and Rytwinski, 2009). Our study area, like the rest of the Patagonian steppe, includes expansive open areas dominated by pastures, with patches of low-statured shrub vegetation (<1 m) and relatively flat topography. Thus, constructing roads in our area does not likely produce a noticeable change in the vegetation (gaps) as may happen in forested areas. Previous studies have found that guanacos may perceive traffic disturbance as a threat (similar to predation risk, Taraborelli et al., 2014), thus, they are expected to change habitat use accordingly. Therefore, the underlying hypothesis is that the disturbance associated with roads alters guanaco habitat selection within the home range. Specifically, we expected lower local abundance of guanacos close to primary roads, which have higher levels of disturbance associated with higher traffic rates and speed of the vehicles.

2. Material and methods

2.1. Study area

The study area was in northern Patagonia, in the west-central part of Argentina (36°36'S, 68°34'W), a volcanic landscape of scrub and grassland steppes (Martínez Carretero, 2004). The area encompassed 3800 km² of the northeastern part of La Payunia Provincial Reserve (Fig. 1) with a combination of private and public lands. The road-network density in the study area was 0.16 km km⁻², composed of primary and minor roads. Primary roads were 6–7 m wide, unpaved provincial routes connecting Mendoza, La Pampa and Neuquén provinces with an estimated mean traffic of 27 vehicles per day (Taraborelli et al., 2014), and vehicle speeds up to 80–100 km/h. Minor roads were narrow (~2 m) unpaved tracks used occasionally by rural people, park rangers, and researchers, with an estimated mean traffic of 4 vehicles per day (Taraborelli et al., 2014), and

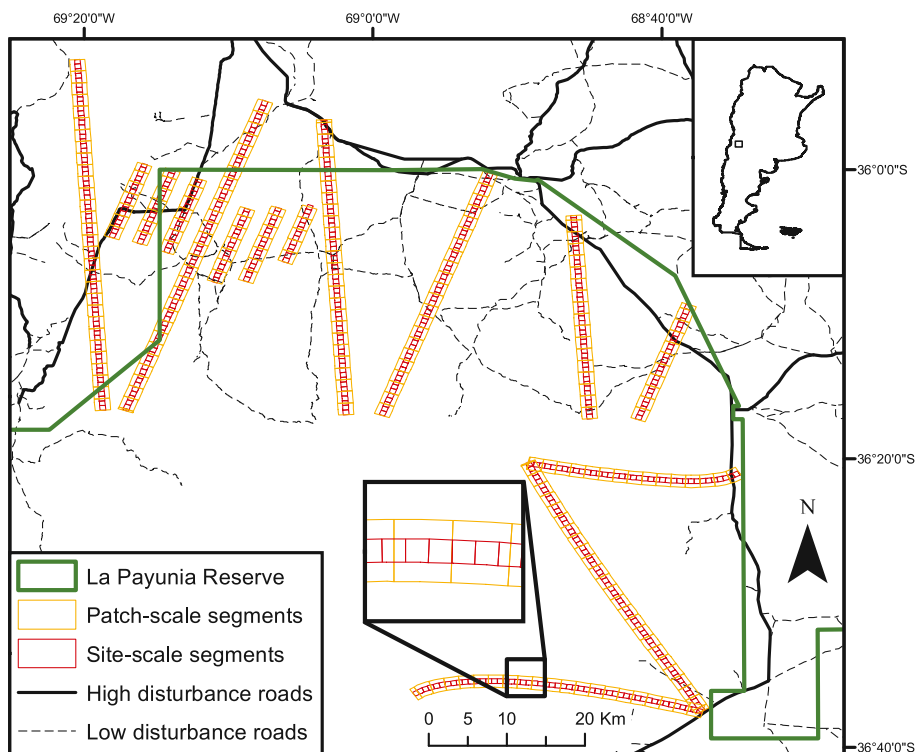


Fig. 1. Study area in La Payunia Reserve and surroundings, located in northern Patagonia (central west of Argentina).

vehicle speeds up to 30 km/h (Fig. 1). We used primary and minor roads as proxies of high and low disturbance levels, respectively.

At La Payunia, poaching was continuously monitored by reserve rangers. Based on a 9-year study of guanaco survival, annual poaching mortality in Payunia was low (<1%; Bolgeri and Novaro, 2015). Few humans inhabited the study area. The dominant land use was livestock grazing, primarily by goats. Oil exploration, extraction, and mining activities surrounded the reserve area, and contributed to the daily traffic on primary roads near these operations.

2.2. Data collection

We evaluated the potential effects of roads on guanaco local abundance and distribution using aerial surveys. Two datasets from a previous study designed to estimate guanaco abundance in this area were used. The first dataset was obtained from a large-scale design with nine 16–45 km line transects arranged in a zig-zag pattern (Buckland et al., 2001). The second came from a simultaneous smaller-scale design with six 10-km parallel line transects, 3 km apart (Fig. 1), intended to calibrate aerial vs. terrestrial surveys of guanacos. The smaller area was specifically chosen as representative of the whole area (similar environmental features) to extrapolate the calibrated measures to the larger area, so substantial biases from pooling these two datasets for this study were not expected. Moreover, segments (and not lines) were our sampling units (section 2.4 Data analysis below), so the (shorter) transects arranged in this smaller area have a reduced relative weight. Surveys were conducted in December 2007 (austral spring) and repeated using the same designs, plane and observer team in February 2008 (summer) and June 2008 (autumn) to account for temporal variation in guanaco distribution.

A Cessna 182 fixed-wing aircraft was used, flying at a mean speed of 150 km/h. Mean flying altitudes were 167 m above ground level (magl) in December 2007, 470 magl in February 2008, and 450 magl in June 2008. This variation in flight height was due to safety concerns and weather conditions (i.e., wind). The characteristic volcanic landscape of our study area (i.e., dark soil and scarce vegetation) provided a good background to detect and count guanacos without difficulty so detectability was assumed not affected by flight altitude. Guanaco detection occurred 500–100 m forward from the plane to fix their initial positions, previous to any potential movement induced by the plane. However, the distance between their (original) positions and each transect was measured once they were under the plane to avoid angular distortions. In general, guanacos ignored the plane or fled short distances in random directions (probably the direction of the perceived noise depended on local topography). Furthermore, guanaco movements were brief and much slower than the plane so the chance of double counting them (in adjacent lines) was very small. Once guanacos were observed, group size, perpendicular distance to flight path and geographic location of the observer were recorded. Perpendicular distances were obtained from five distance intervals projected to the ground, by adhering tape to wing mounts and windows (Rudran et al., 1996), and from flight altitude at the moment each group was observed. Sampling effort of each survey covered 368 km of transects. Actual position of each guanaco observation was obtained with observer locations and perpendicular distances.

2.3. Data analysis

Prescribed distance intervals during aerial surveys were adjusted according to mean flight height of each survey. Following standard distance sampling methodology (Buckland et al., 2001), we first adjusted a detection function $g(y)$ from perpendicular distances of each observation to account for the probability of detecting guanacos during the three surveys. Truncation distance (w) was defined by the farthest interval: 201–335 m (December), 564–939 m (February), 486–810 m (June), which in turn was defined by flight height. Since probability of detecting animals may be high for large groups, we compared detection models with and without group size as covariate (Marques and Buckland, 2004). We used Akaike's Information Criteria (AIC) (Burnham and Anderson, 2002) and chi-square goodness-of-fit tests to select the best detection function model (Buckland et al., 2001). Analyses were performed using the *Distance* package for R (<https://www.r-project.org/>).

2.4. Density surface model (dsm)

We divided each transect into segments of length l , defined by approximately twice the truncation distance w . Differences in w between the three survey periods defined two spatial resolutions of survey units (segment sizes): a “patch scale” $l = 1500$ m (2.4 km^2) applied to February and June data, and a “site scale” $l = 600$ m (0.36 km^2) applied to the three surveys (Fig. 1). Estimated seasonal home-range sizes of guanacos in our study area were $63\text{--}632 \text{ km}^2$ for sedentary guanacos and $62\text{--}712 \text{ km}^2$ for migratory guanacos (M.J. Bolgeri and A. Novaro, unpublished data); therefore, patch and site scales defined are within guanaco home ranges. We recorded the number of animals within each segment as n_i , $i = 1, \dots, T$, totaling 239 segments (patch scale), and 586 segments (site scale). We used GAM (Wood, 2006), with a negative binomial error distribution and logarithmic link function to relate the animal count n_i in each segment j with spatial covariates. For December, we modeled “estimated abundance” instead of “counts”, using a Horvitz-Thompson-like estimator (Hedley and Buckland, 2004) because the detection function included an observation-level covariate other than distance (i.e., group size, Supplementary material S1):

$$\hat{N} = \sum_{r=1}^{R_j} \frac{S_{jr}}{\hat{p}(z_{rj})}$$

where R_j was the number of animals in segment j , S_{jr} was the size of the r th cluster in segment j , and p_{ij} was the estimated probability of observing an animal i in a segment j as a function of covariate z , obtained from the detection function.

For modeling, we followed three steps. First, we fit a road-effect density surface model (dsm) using distance to low and high disturbance roads as covariates. Considering that animals may respond to roads only within a certain distance threshold (Rowland et al., 2000; Forman and Deblinger, 2000; Frair et al., 2008), we also considered *distance to* variables at 4, 5, 7.5 and 10 km thresholds (Table 1). Second, we fit environmental-effect models, using combinations of different variables related to plant productivity, topography and human impact (Table 1) shown to influence guanaco distribution and resource selection (Pedrana et al., 2010; Schroeder et al., 2013; Rivas et al., 2015). Finally, we combined the best road-dsm with the best environmental-dsm into a full model, and compared it with the environmental-dsm (without road effect), to identify the final model. We tested for multicollinearity between variables using Pearson's pairwise correlation analysis and concavity analysis (Miller et al., 2013), before and after fitting models, respectively.

To fit the GAM we used an extra penalty and the (approximate) p -values to remove smoothing terms (Wood, 2006). We performed smoothness selection using Maximum Likelihood methods (ML) (Wood, 2006). Best-fit models were selected based on the lowest AIC values, but also by taking into account parsimony, residual diagnostic plots, and the deviance explained (Miller et al., 2013). Modeling was done with the *dsm* package for R, and GIS analysis was conducted using QGIS 2.12.3 <http://www.qgis.org/es/site/>. We tested for autocorrelation of final model residuals using the function *dsm.cor* in the R package *dsm*, and the function *correlog* in the R package *ncf*; the latter is a function to estimate spatial correlograms based on Moran's I test. We conducted these analyses separately for February (at both scales) and December (only site scale). We withheld June data for model validation.

Table 1

Description of the predictor variables used in density surface models of guanaco distribution in relation to roads in La Payunia Reserve, Patagonia, Argentina.

Model type	Variable	Code	Description	Source	
Road model	Roads ^a	distR	Euclidean distance to any road	National Geographic Institute database (IGN), own records	
	High disturbance roads ^a	distHi	Euclidean distance to high disturbance roads without threshold, and up to 4, 5, 7.5, 10 km.		
		distHi4			
		distHi5			
		distHi7.5			
		distHi10			
	Low disturbance roads ^a	distLo	Euclidean distance to low disturbance roads without threshold, and up to 4, 5, 7.5, 10 km.		
		distLo4			
		distLo5			
		distLo7.5			
distLo10					
Environmental model	Plant productivity ^b	evimax_mean	Maximum and mean value in 11 years (2001–2011) and in time of survey of the enhanced vegetation index (EVI), at 250-m spatial resolution.	MODIS satellite imagery seasonal database (https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table)	
		evimean_mean			
		decMea_evi			
		febMea_evi			
	Topography ^b	DEM_mean	Elevation of 30-m grid in meters	GDEM2 elevation model from NASA Earth Database (https://reverb.echo.nasa.gov/reverb)	
		slope_mean			
		TRI_mean			Terrain ruggedness index (TRI) is the sum of changes in elevation within an area. Vector ruggedness measure (VRM) quantifies ruggedness by measuring the dispersion of vectors orthogonal to the terrain surface (Sappington et al., 2005). We used radius = 4 (9 × 9 cell) = 270 m (scale), (1 cell = 30 m) for both indexes.
		VRM_mean			
	Human impact ^a	distHS	Euclidean distance to any human settlement	Own records and information from park rangers	
		distPerm	Euclidean distance to permanent human settlements		
		distTemp	Euclidean distance to temporary human settlements: seasonal settlements built as shelters with indigenous materials and mostly located in areas with poor accessibility.		
	Spatial location	x,y	Latitude (y) and longitude (x) of the center of each segment		

^a The values were estimated to the segment centroid.

^b The values were averaged by segments.

2.5. Model validation

We evaluated the predictive capacity of our final models for each month (February and December) and scale using data from surveys conducted along the same transects in June 2008. We applied a validation process based on [Johnson et al. \(2006\)](#) and [Nielson et al. \(2016\)](#), as follows:

1. Predict intensity of use across sampling units. Specifically, use June data to predict the abundance of guanacos by segment using the final models (per months and scale). Then, reclassify the units into 20 equal-area bins, e.g., bin 20 contained the highest 5% predicted use of the study area.
2. Determine the median prediction $w(x_i)$ for each bin i .
3. Determine the utilization $U(x_i)$ value for each bin i using the formula:

$$U(x_i) = w(x_i) / \sum_{k=1}^{20} w(x_k)$$

4. Sum the count of guanacos observed in June, adjusted for probability of detection, that fall within each bin (N_{Obs}).
5. Estimate the expected sum of guanacos observed, adjusted for probability of detection, within each bin, using

$$N_{Exp.} = N \times U(x_i)$$

where N is the total number of guanacos observed, adjusted for probabilities of detection (total N_{Obs}).

6. Compare expected (from step 5, N_{Exp}) to observed (from step 4, N_{Obs}) values, using linear regression and Spearman's rank correlation analysis.

Finally, to more fully evaluate potential road effects, we plotted raw data of an indicator of social structure (group size) in relation to distance to high and low disturbance roads up to 5 and 2 km. Additionally, we plotted group size, number of groups, and guanaco local abundance in relation to density (calculated by segment, in QGIS software) of high and low disturbance roads, at both scales of segment size.

3. Results

Guanaco observations recorded in the aerial transects are summarized in [Table 2](#). The selected detection function for guanaco observations in all surveys was half-normal, with group size as a covariate for December only (Supplementary material S1). As a result of the multicollinearity analysis, mean and maximum enhanced vegetation index (EVI; evi_mean_mean , $evimax_mean$, respectively), mean elevation (DEM_mean), ruggedness indexes (TRI_mean, VRM_mean), distance to any human settlements (distHS) and to any road type (distR) were excluded from analysis (Pearson's pairwise correlation, $|r| > 0.6$).

We did not find consistent effects of either high or low disturbance roads on estimated guanaco abundance in any months or scales analyzed ([Table 3](#), [Supplementary material S2](#), [Tables S2.A–C](#)). In all cases, the best-fitting models were environmental models without road effects, with a deviance explained of 23.56% for February (patch scale), 50.41% for February (site scale), and 45.75% for December (site scale, [Table 3](#)). At the site scale, estimated guanaco abundance was explained solely by spatial covariates of latitude and longitude, while at the patch scale, guanaco were more abundant at higher values of mean EVI at the time of survey, at longer distances to permanent human settlements, closer distances to temporary human settlements, and at intermediate values of slope, although this effect was not significant ([Table S2.D](#), [Figures S2.A–C](#)). We did not find problems with spatial correlation in the residuals of any of the final models (Supplementary material S3). Model validation results indicated that February models can be used to reliably predict guanaco abundance for June (Patch scale: $r^2 = 0.8$, $p < 0.0001$, and $\rho = 0.49$; Site scale: $r^2 = 0.28$, $p < 0.01$ and $\rho = 0.61$, [Figure S3.D](#)). On the contrary, the December model did not predict June abundance well ($r^2 = -0.033$, $p = 0.53$, and $\rho = 0.32$, [Figure S3.D](#)). Finally, we did not find any patterns between group size, number of groups and guanaco abundance plotted against distance/density of roads

Table 2

Guanaco data by survey period obtained from aerial line transects in La Payunia Reserve, Argentina.

	December 2007	February 2008	June 2008
Number of guanacos	792	866	1073
Number of groups	188	135	54
Mean group size	4.21	6.41	19.9
Min/Max group size	1/32	1/80	1/150

Table 3

Density surface model results by month and scale in La Payunia Reserve, Argentina, including the best selected model with smooth terms by each step (section 2.4 in the text), Akaike Information Criterion (AIC), adjusted R square (Rsqr), maximum likelihood score (ML), and deviance explained (DevExpl). The number after the covariate name in the selected model column is the effective degrees of freedom which indicates the complexity of the smooth function. Final models are in bold. References for covariates are in Table 1.

Month/scale	Model step	Selected model	AIC	Rsqr	ML	DevExpl
February/patch-scale (2.4 km ²)	Road model	s (distHi4, 1)	492.5	0.0009	243.2	3.02%
	Environmental model	s(febMea_evi, 0.82), s(slope_mean, 0.91), s(distPerm, 1.78), s(distTemp, 1.83)	481.8	0.040	239.2	23.56%
	Environmental model + road model	s (febMea_evi, 0.83), s (slope_mean, 0.79), s (distPerm, 1.72), s (distTemp, 1.85), s (distHi4, 0.93)	482.1	0.030	239.1	25.24%
February/site-scale (0.36 km ²)	Road model	s (distHi, 0.93), s (distLo, 4.11)	1143.6	0.00192	573.6	11.42%
	Environmental model	s(x,y, 19.03)	1040.3	0.04316	533.8	50.41%
	Environmental model + road model	s (x,y, 18.75), s (distHi, 0.30), s (distLo, 0.80)	1045.7	0.02594	533.7	50.91%
December/site-scale (0.36 km ²)	Road model	s (distLo5, 1.94)	1374.3	0.02822	686.0	3.6%
	Environmental model	s(x,y, 19.64)	1263.5	-0.00321	645.6	45.75%
	Environmental model + road model	s (x,y, 19.62), s (distLo5, 0.18)	1268.8	-0.01410	645.6	45.83%

(Supplementary material S4), supporting the absence of road effects on guanaco abundance and social structure under the conditions occurring in our study area.

4. Discussion

Contrary to our expectations and regardless of the level of road disturbance, roads had no measurable effect on guanaco local abundance, indicating that guanacos did not avoid roads at either spatial scale during any seasonal period analyzed. Guanaco group size and number of groups also did not appear to be affected by roads. Overall, we found no pattern of avoidance of roads, a finding different from the strong road avoidance often documented for other ungulates (Rowland et al., 2000; Whittington et al., 2004; Wisdom et al., 2005; D'Amico et al., 2016). Our results suggest that the effect of roads on guanaco local abundance and distribution was neutral at the level of traffic (up to 27 vehicles per day in average), vehicle speed (up to 80–100 km/h), and analysis scales (0.36–2.4 km²) of our study area, one with only low-intensity poaching.

This unexpected result of no road avoidance may have several explanations, which may serve as hypotheses for guiding future research. It is likely that the disturbance levels of La Payunia roads were below the threshold to which guanacos respond. Previous studies have demonstrated that animal responses to roads could be non-linear; i.e., a functional response. For example, the probability of elk occurrence was higher at road densities lower than 0.5 km km⁻² (Frair et al., 2008), and road-crossing frequencies of moose were lower than expected by chance above road densities of 0.2 km km⁻² (summer) or 0.4 km km⁻² (winter) (Beyer et al., 2013). Although clear differences in disturbance levels existed between routes and tracks considered in this study, the number of circulating vehicles on both types of roads was lower than those considered in most other studies, for example, vehicles on highways (Gagnon et al., 2007). This level of traffic, however, is typical for habitats within the species' range, for example in Argentina, where 80% of the guanacos of the world reside (Baldi et al., 2016). Because of relatively low level of disturbance on guanacos during our study, it is possible that open roads in Payunia are functionally equivalent to closed roads. More research is needed to elucidate the precise levels of traffic disturbance that elicit a response in guanacos, and the duration of that response.

An alternative, non-exclusive explanation is that guanacos tolerate the level of disturbance associated with the traffic and speed of vehicles in the study area because they do not experience negative consequences by staying instead of fleeing when they detect a vehicle. Marino and Johnson (2012) showed that guanacos can become rapidly habituated (in 4 years of study) to motorized vehicles if harassment ceases and subsequent traffic acts as a neutral stimulus for enough time. Habituation to human presence has also been observed in guanacos of Torres del Paine (Chile, Franklin and Johnson, 1984), of Ischigualasto Provincial Park (Argentina, Malo et al., 2011), and in other large mammals in protected areas usually exposed to tourism as a non-lethal human contact (Rogala et al., 2011; Goldberg et al., 2014). The road-network density in our study area has been stable in recent decades. Poaching of guanacos was common in the past, but declined since the creation of the protected area in 1982 (Puig et al., 2003). Although guanacos may be more attentive and vigilant close to high-disturbance roads (Taraborelli et al., 2014) as shown for other ungulates (Stankowich, 2008), it is possible that vigilance in response to traffic may not equate to road avoidance or altered habitat selection; this may be the case for our study, particularly under the low intensity of harassment by poachers.

Our results fit the low end of the spectrum of road use in contrast to previous guanaco studies at landscape scale in other study areas of northern Patagonia (Radovani et al., 2014; Rivas et al., 2015). These authors found a direct and negative

association between road density and probability of presence (Rivas et al., 2015), density, recruitment and social structure (Radovani et al., 2014) of guanacos, interpreted as a consequence of increased poaching pressure associated with the extensive network of roads. Radovani et al. (2014) found that densities of guanacos declined dramatically (up to 93–96%) and populations became fragmented over a 20-year period, likely in response to a substantial increase in road density (from 0.14 to 1.84 km km⁻²) associated with oil exploration. The low road density (0.16 km km⁻²) and the dispersed spatial distribution of roads in our study area in La Payunia, along with the frequent presence of rangers and low harassment of poachers, probably contributed to roads not being perceived as a threat. This protected area may serve as a refuge for the guanaco population, which is the largest in northwestern Patagonia and seems to have been growing during the last two decades (Schroeder et al., 2014). Consequently, it is likely that at the landscape scale, guanacos select home ranges with few roads, but within their home range they do not avoid roads locally (i.e. they readily cross and use areas close to roads).

At the patch scale, our results indicate that suitable habitat consists of areas of higher productivity, greater distance to permanent human settlements (although close to temporary ones), and slightly steep slopes. Animals may perceive different levels of risk to different types of human disturbance. For example, humans on foot can be more disrupting for ungulates than in vehicles (Stankowich, 2008), and humans off trails can be perceived as more threatening than on trails (Miller et al., 2001; Taylor and Knight, 2003). The permanent human settlements in our study area are mostly on the flat zones of reserve's periphery with strong presence and abundance of livestock in its areas of influence (Schroeder et al., 2013, 2014). Settlers on horseback with dogs frequently herd livestock every night to avoid predation by cougars. On the contrary, temporary human settlements are a few settlements of seasonal use, located in areas of low accessibility (Ovando et al., 2011). Strong negative associations between guanaco and livestock, especially sheep and goats, have been extensively documented, providing evidence of a mechanism of competition for forage among these ecologically similar herbivores (Baldi et al., 2001; Pedrana et al., 2010; Schroeder et al., 2013; Radovani et al., 2014; Rivas et al., 2015). Therefore, although our study does not allow inference about the mechanisms underlying the patterns found, the higher presence of herders on horseback with dogs, combined with higher interspecific competition with livestock and lower availability of forage close to permanent human settlements, probably explain guanaco selection for inner habitats in the reserve (Schroeder et al., 2014).

At the site scale, habitat selection was related only to geographic coordinates. Guanacos are more abundant in the northern parts of the reserve in December, moving to central-southern zones in February (Supplementary material S2, Figures S2.B, C) and also in June, as shown by model validation. The guanaco is a social species that forms different social units more or less stable in time depending on the environmental conditions and the possibilities of dispersion (González et al., 2006). Migrating guanacos form large mixed herds in late summer-autumn to search for better weather and forage supply. Our June data reflected fewer but larger groups (Table 1), especially in comparison with December, when the animals are in reproductive stage forming family harems, non-reproductive male groups and solitary males. Thus, changes in the social structure and seasonal migratory movements could explain the similarities in habitat selection between February and June, as well as differences in December.

In conclusion, our results present an interesting and uncommon case of roads not posing the typical anthropogenic disturbance normally reported for large mammals, and may be unique to guanacos due to special circumstances in the study area. Additional research to evaluate guanaco responses to a wider range of traffic volumes and speeds, road densities and in response to different types of road use (e.g., for livestock management versus poaching/hunting, energy extraction, or tourism) and human harassment experience, is needed to elucidate the broader pattern of guanaco-road relationships across the species' range. The incorporation of experimental studies with a BACI design (before-after-control-impact) as much as possible is strongly recommended to maximize inferential strength and contribute to road planning decisions (Roedenbeck et al., 2007).

Finally, our results have methodological implications for research and management of guanaco and other large mammals. Most published research on abundance and distribution of guanaco across the species' range (e.g. Travaini et al., 2007, 2015; Schroeder et al., 2014; Moraga et al., 2014) but also of other large-bodied animal species in other landscapes (Grünewald et al., 2016; Arbieu et al., 2017; Yirga et al., 2017) has relied wholly or partially on counts from roads, without formally assessing the behavior of species that may be avoiding the roads. Our findings suggest that a low-poaching level landscape with <0.16 km km⁻² of unpaved road density and an average traffic disturbance of 27 vehicles per day does not affect guanaco local abundance and distribution. This means that it is possible to use road counts for this species in similar conditions. However, we suggest caution with generalizations to other landscapes and contexts since, as discussed previously, the conditions of our study could be the exception for most of the guanaco range. The differences between our findings and previous research show the risk of assuming beforehand that no road avoidance occurs when roads are used as transects to estimate guanaco density. On the contrary, these potential biases should be evaluated across different environmental conditions and scales of interest to allow effective research and management.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.gecco.2018.e00394>.

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