



Effects of roads on the behaviour of the largest South American artiodactyl (*Lama guanicoe*) in an Argentine reserve



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ARTICLE INFO

Article history:

Received 5 January 2017

Initial acceptance 20 February 2017

Final acceptance 16 June 2017

MS. number: A17-00028R2

Keywords:

disturbance stimuli
guanaco
human–animal interaction
predation risk
roads

Animals may divert time and energy in similar ways in the presence of predators, humans or landscape infrastructures. Roads have facilitated the economic and social development of human populations. Nevertheless their presence and human use cause environmental changes, such as clearing, which increase perception of predation risk. Among the responses to this are changes in animal behaviours. In the present study, we sought to assess whether roads in an Argentine reserve affect perception of predation risk by guanacos, *Lama guanicoe*, through behaviour changes. We analysed the effects of two types of roads (unpaved track and paved route) and their surrounding environment (e.g. vegetation structure) on group size variation and on three behaviours: vigilance, foraging and movement. We also used the group structure of guanacos, such as the number of calves, to explain these behaviours. Roads in the protected area had no impact on the size of guanaco groups. However, individuals in larger groups were less vigilant and foraged more closely to roads, indicating that closeness to roads is less risky for these animals. Although guanacos' time spent moving was not affected by roads, nearness to the unpaved track and high plant cover showed the highest proportions of animals moving in the area, and individuals moved more when in small groups and in areas with medium-height vegetation. The number of individuals displaying vigilance or foraging behaviours was not affected by any of the explanatory variables. Based on these findings, we conclude that guanacos perceive the roadside environment as safer, possibly because open areas adjacent to roads facilitate detection of predators. Knowing the effects of roads on wildlife in protected areas is necessary to find ways to reach a balance between the economic development of a region and conservation of its biodiversity.

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Nonlethal human disturbances can be considered analogous to nonconsumptive effects of predation (Frid & Dill, 2002; Lykkja et al., 2009). Some studies suggest that animals invest time and energy similarly when in the presence of predators, humans or landscape infrastructures (Proffitt, Grigg, Hamlin, & Garrott, 2009; Walther, 1969). To remain in a place, animals must trade-off their energy needs so as to survive, taking into account the limitations imposed by the environment and predation (Searle, Stokes, & Gordon, 2008; Wolff & Van Horn, 2003). The human activities

that condition these energy needs and produce behaviour changes have been defined as disturbance stimuli (Frid & Dill, 2002). When the energy cost involved in antipredator behaviour is high, individuals may move to other environments. When this is not possible, individuals may be compelled to stay in environments where the costs of antipredator behaviour are high (Gill, Norris, & Sutherland, 2001). Animal responses to humans would be the cause of the ancestral predator–prey relationship, and those elicited by human infrastructures would be the result of the environmental changes they bring about, all of which affect the animal's perception of predation risk (Beauchamp, 2010; Cappa et al., 2014; Taraborelli et al., 2014).

Among human infrastructures, roads (tracks and routes) facilitate the economic and social development of human populations. Nevertheless their presence and their human uses cause

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environmental changes (Forman et al., 2003). These changes, due to clearing, substrate compaction, introduction of materials foreign to the system and noise, among others (Casella & Paranhos Filho, 2013; Forman et al., 2003), along with human presence, may affect animals negatively or positively (Berger & Cunningham, 1988; Forman et al., 2003; Lacy & Martins, 2003). In species such as guanaco, *Lama guanicoe*, and other ungulates, in which sight is the most used sense for detecting predators, clearing could be beneficial because the cover and height of vegetation act as a visual barrier to early detection of predators (Mitchell & Skinner, 2003; Sarno, Grigione, & Arvidson, 2008).

Moreover, vegetation provides predators with hiding spots, increasing their likelihood of hunting success (Baldi, Campagna, & Saba, 1997; Frid & Dill, 2002; Périquet et al., 2010).

Nevertheless, a greater presence of humans is also associated with roads, and this may increase perception of predation risk by ungulates (Lykkja et al., 2009; Manor & Saltz, 2003). Avoidance of near-road areas has been reported for mule deer, *Odocoileus hemionus*, and wapitis, *Cervus canadensis*, in Roosevelt National Forest (Canada; Rost & Bailey, 1979). In guanacos, individuals occupying a protected area of Argentina's Patagonia were found to exhibit longer flight distances in areas with denser vehicle traffic and in areas used by poachers (Taraborelli et al., 2014). Conversely, pregnant moose, *Alces alces*, use areas near roads (Berger & Cunningham, 1988), and although wapitis avoid nearness to roads, they have been recorded more frequently using areas within 200–400 m of roads in Banff, Kookenay and Yoho National Parks (Canada), because these areas are avoided by predators (Rogala et al., 2011), which are very sensitive to human presence (Woodroffe & Ginsberg, 2000).

Variation in group size is another behavioural strategy related to perception of predation risk (Elgar, 1989; Mooring, Fitzpatrick, Nishihira, & Reisig, 2004; Taraborelli et al., 2014). For example, bison, *Bison bison*, and guanacos form larger groups in environments perceived as riskier (Cappa et al., 2014; Fortin, Boyce, Merrill, & Fryxell, 2004; Marino & Baldi, 2008), whereas red deer, *Cervus elaphus*, disaggregate themselves in areas with higher predation risk (Creel, Schuette, & Christianson, 2014). Group size variation is not species specific and may depend on the environment and predators (density and kind of hunting). Because of this, group size alone cannot be used to evaluate predation risk, raising the need to address complementary behavioural aspects such as time spent on different behaviours.

Variation in vigilance can also be used as a measure of perceived predation risk (Ciuti et al., 2012; Marino & Baldi, 2008; Robinson & Merrill, 2013). Kudus, *Tragelaphus strepsiceros*, and giraffes, *Giraffa camelopardalis*, increase their vigilance time in the presence of lions, *Panthera leo* (Périquet et al., 2010). Guanacos also show variation in vigilance time in risky habitats, regardless of whether there are predators present (Cappa et al., 2014; Marino & Baldi, 2008). In deer, Proffitt et al. (2009) observed a decline in movement rate in places with low risk of predation from wolves or humans. An increase in time invested in vigilance and movement may compromise energy acquisition due to reduced time invested in foraging and other behaviours (Berger & Cunningham, 1998; Fortin et al., 2004; Frid & Dill, 2002).

In the present study, we hypothesized that the presence of roads and their use by humans cause environmental changes that increase guanacos' perception of predation risk. It is for this reason that we aim to assess whether roads in a protected area (Ischigualasto Provincial Park) affect perception of predation risk by guanacos. To achieve this, we studied the effects of the distance to two types of roads (unpaved track and paved route) on (1) group size and (2) time spent on different behaviours (vigilance, movement and foraging).

METHODS

Study Area

Ischigualasto Provincial Park (29°55'S, 68°05'W), declared a World Heritage Site by UNESCO (United Nations Educational, Scientific and Cultural Organisation) in 2000, together with Talampaya National Park, is located in the northeast section of San Juan province, Argentina. It stretches over 62 369 ha, with an average elevation of 1300 m above sea level.

The park includes the northern Monte, which is dominated by mountains and closed basins (Monte de Sierras y Bolsones; Pol, Camín, & Astié, 2005) and a small portion of Chaco Serrano (Burkart, Bárbaro, Sánchez, & Gómez, 1999; Torrella & Adámoli, 2005). It has a desert climate, with mean annual temperature below 18 °C and a mean annual rainfall of 100 mm, mainly concentrated in the summer season (Cortéz, Borghi, & Giannoni, 2005).

Vegetation cover is, overall, lower than 50%, and the dominant physiognomy is shrubland (Márquez, 1999). The wildlife occurring in the area is typical of the Monte ecoregion, with the puma, *Puma concolor* (Cortéz et al., 2005; Márquez, 1999) as apex predator.

We carried out work in two areas, each of which contained a different type of road: an unpaved track and a paved route. The unpaved track (a tourist circuit) was 40 km long and 5–7 m wide, with adjacent areas not cleared of vegetation. The paved route included a section of National Route No. 150, ~7 km long and ~80 m wide (10 m paved, with 5 m of roadside berm and 30 m of cleared area on each side), that leads to the park entrance. This route is part of the Central Bi-Ocean Corridor, aimed to link Porto Alegre (Brazil) with Coquimbo (Chile; Borghi et al., 2012). Traffic on the track is controlled, since vehicles are only driven in caravans guided by park rangers at agreed times (between 0900 and 1700 hours) and at controlled speeds (<40 km/h). On the route, all types of vehicles can be driven with no strict speed limit enforced, reaching speeds of up to 80–120 km/h (F. M. Cappa, personal observation).

Study Species

The guanaco is the largest-bodied wild camelid in America. It reaches 1.8 m in total height (1.2 m at wither) and weighs between 100 and 120 kg (Campos, 1996). It is a species with resource defence polygamy. Family groups constitute harems, formed by females and offspring, controlled by an adult territorial male (Franklin, 1982). Although the species is considered of minor concern by the IUCN (International Union for Conservation of Nature, <http://www.iucnredlist.org/details/11186/0>), the population inhabiting Ischigualasto Provincial Park is of particular importance because of its low density (<0.4 individuals/km²; Acebes, Ovejero, Traba, Malo, & Borghi, 2010; Baigún, Bolkovic, Aved, Li Puma, & Scandalo, 2008), as well as for being one of the few populations under protection in the hyper-arid zone.

Roads have a greater effect on large animals and on those with greater mobility (greater likelihood of crossing roads; Carr & Fahrig, 2001), low reproduction rates and density, as well as those who are less able to rebound from low numbers and/or to persist with few individuals (Fahrig & Rytwinski, 2009; Gibbs & Shriver, 2002; Rytwinski & Fahrig, 2011). The guanaco meets all these features, which makes it an ideal model to answer our questions.

Ethical Note

This work was approved by the Bioethics Commission, Biology Department, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, Argentina (FCEFYn-UNSJ, File No. 02-2962-C-14).

Experimental Design

Behavioural data were recorded on off-road trips no further than 2000 m from roads (0900–1700 hours) during the dry and wet seasons over 4 years (2011–2014). For all groups observed, we recorded the number of animals, classified into three categories: calf (<1 year old), juvenile (1–3 years old) and adult (>3 years old; Franklin, 1982).

Behavioural data were recorded using continuous focal sampling and instantaneous scan sampling. We randomly selected two adults from each group as focal animals, because adults perform vigilance behaviour (Marino & Baldi, 2014). Focal records were performed for 5 min; those lasting less than 3 min were ruled out (Marino, 2010). Instantaneous scan sampling was done when all individuals of the group were observable. This sampling was done with a Sony DCR-SR68 video camera. When animals directed vigilance behaviour towards the observer, sampling was delayed until this behaviour stopped (Young & Franklin, 2004). The behaviours analysed were vigilance (animal with head higher than wither height), foraging (animal with head lower than wither height) and movement (animal walking, trotting or galloping with head higher than wither height). To assess the time spent on each of these behaviours, we only used data from focal animals that displayed the behaviours analysed (Robinson & Merrill, 2013): vigilance ($N = 172$), foraging ($N = 182$) and movement ($N = 177$), as the absence of these behaviours in a focal animal is not absolute and may be due to insufficient sampling time. Results of continuous focal sampling are expressed as percentages of time spent engaged in each behaviour, and results of instantaneous scan sampling are expressed in proportions of individuals.

We estimated the distance of the groups from the nearest roads using the geographical location of the observer (GPS, Garmin Vista HCx), distance from the observer to each group ($\bar{x} \pm SE = 243.9 \pm 12.45$ m; laser distance meters, 7 × 26 Bushnell ELITE 1500) and the angle respect to north (GPS).

We classified vegetation height into three categories: low (lower than the knee of an adult guanaco), medium (between knee and wither) and high (higher than wither height). To estimate vegetation cover, we used a straight-line equation using the relationship between field cover data and image data (90×90 m; $R^2 = 0.68$, $P < 0.0001$; Cappa, Giannoni, Perucca, & Borghi, 2016). Image data correspond to the mean of texture value for a 3×3 pixel moving window, obtained from the reflectance of band 4 (visible red, Landsat 8 OLI). Reflectance of band 4 and plant cover, especially shrub cover, is negative (Asner, Wessman, Bateson, & Privette, 2000; Maldonado et al., 2004; for details using this method, see; Hall-Beyer, 2007; Haralick, Shanmugam, & Dinstein, 1973). We used a Landsat 8 OLI image with 30 m resolution (23 May 2013, path 232, row 081), with the following set of references: datum WGS 84; UTM projection (Universal Transverse Mercator); zone: Argentina 19 South (United States Geological Survey, USGS, <http://earthexplorer.usgs.gov/>). Digital processing was done using the ENVI (Environment for Visualizing Images, Research Systems Inc., Broomfield, CO, U.S.A.) software version 4.3.

Statistical Analysis

We assessed the correlation among numerical explanatory variables using Spearman rank correlation, and in all cases $|r| < 0.7$, so no variable was eliminated (Wood, Pidgeon, Radeloff, & Keules, 2012). We then analysed the variance inflation factor (VIF) for the full models, and again, no variable was dropped (VIF < 10; Allison, 1999). We corroborated the spatial correlation among sampling points using correlograms with Pearson's residuals for each model (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). No evidence of spatial

dependence was found in the models (see Supplementary Figs S1, S2, S3).

Generalized linear mixed models (GLMMs) and generalized linear models (GLMs) were used. To assess group size and time spent in each behaviour, we fitted models with a negative binomial distribution due to overdispersion ($\hat{c} > 1$, Crawley, 2007). We used the following response variables: site, distance to roads, vegetation cover, vegetation height, number of calves, group size, year and season (Table 1).

To analyse the effect of roads on group size, we only used distance to roads as a fixed variable. To assess time spent on each behaviour and to control for the different focal times, we used the duration of each focal observation as an offset variable (Robinson & Merrill, 2013). We used site, distance to roads, vegetation cover, vegetation height, number of calves and group size as fixed variables. Year and season were considered random variables. In assessing their contribution using the information theory method (Asner et al., 2000), only year was considered a random factor for vigilance (GLMM).

We analysed variation in the proportion of guanacos per group displaying the three different behaviours using the above-mentioned explanatory variables. Models were fitted with a binomial distribution. To select all models, we used the information theory method (Burnham & Anderson, 2002) based on Akaike's information criterion corrected for small sample sizes (AICc). We considered Akaike weight (w_i) for each model, which determines the relative likelihood that the model/models selected is/are the best of the set of adjusted models. Among these candidates, we considered the model with the fewest parameters to be the most parsimonious one (Burnham & Anderson, 2002). We also calculated the estimates with their mean errors for all models, as well as the confidence interval limits (CL = 95%) for each of the estimated parameters.

RESULTS

We obtained 203 continuous focal samplings and 70 instantaneous scan samplings from 129 groups (group size, $\bar{x} \pm SD = 5.93 \pm 4.27$). Guanacos spent the greatest percentage of time foraging (51.2%), followed by vigilance (<25%) and movement (<14%).

Group size was not affected by distance to roads (GLM_{Neg.Binom}: $z = -0.52$, $P = 0.6$). Time spent on vigilance was explained by group size and distance to roads ($w_i = 0.15$; Table 2). Guanacos spent more time on vigilance when they were in smaller groups and as they moved away from the roads (Table 3). Foraging time was explained by distance to roads and group size ($w_i = 0.08$; Table 4). Guanacos foraged more as distance to roads decreased and group size increased (Table 5). Vegetation height and group size explained variation in movement behaviour ($w_i = 0.14$; Table 6). Time spent moving was highest in areas with medium vegetation height and diminished as group size increased (Table 7).

The proportion of guanacos engaged in vigilance, as well as in foraging, was not affected by any of the variables measured, in both cases, the best model was the null model ($w_i = 0.09$ and $w_i = 0.10$, respectively). The best model for the proportion of animals moving contained the variables site, plant cover and height, but only site and plant cover were significant ($w_i = 0.14$). The proportion of guanacos showing movement behaviour was lower in areas affected by the route (GLM_{Binom}: $t = -2.33$, $P = 0.02$; Fig. 1a) and where plant cover was low (GLM_{Binom}: $t = 2.42$, $P = 0.02$; Fig. 1b).

DISCUSSION

Roads in the protected area of Ischigualasto Provincial Park had no impact on variation in guanaco group size. However, individuals

Table 1
Variables used for analysing the effect of the environment created by roads on guanacos in Ischigualasto Provincial Park

Variable	Definition	Variable type
Site	Kind of road that effected this area (unpaved track and paved route)	Categorical
Distance to road	Minimum distance (in metres) of group from to the nearest road	Continuous
Vegetation cover	Estimated using the straight-line equation between the data from the field and from the images at the study	Continuous
Vegetation height	Visually estimated mean height of plants	Categorical
Calves	Number of calves per group	Discrete
Group size	Total number of individuals per group	Discrete
Year	Year of sampling	Categorical
Season	Season of sampling	Categorical
Focal time	Duration (in seconds) for each focal	Discrete

Table 2
Best five models and the null model, listed in decreasing order of importance according to the time guanacos spent on vigilance

Model	<i>k</i>	AICc	ΔAICc	<i>w_i</i>
Dist km+cov+group size	6	1910.58	0.00	0.20
Dist km+group size	5	1911.12	0.54	0.15
Dist km+cov+roads+group size	7	1912.59	2.01	0.07
Dist km+roads+group size	6	1912.66	2.08	0.07
Dist km+cov+calves+group size	7	1912.72	2.14	0.07
Null	3	1918.77	8.19	0.00

k is the number of estimated parameters; AICc: Akaike's information criterion corrected for small samples; *w_i*: Akaike weight; dist km: minimum distance to the closest road (in km); cov: vegetation cover (%); group size: number of animals per group; roads: route and track; calves: number of young <1 year old per group. The chosen model is in bold.

Table 3
Parameter likelihoods, estimates (±SE) and 95% confidence interval limits (CL) for explanatory variables describing the time guanacos spent on vigilance, considering the minimum distance to the closest road (dist km) and group size

Explanatory variable	Parameter likelihood	Parameter estimate±SE	CL	
			Lower	Upper
Intercept		−1.14±0.18	−1.49	−0.77
Dist km	0.83	0.34±0.13	0.08	0.59
Group size	1	−0.05±0.02	−0.09	−0.01

spent more time vigilant and less time foraging as they moved away from roads or when in smaller groups. Time spent on movement also increased in small groups and when animals were in areas with medium-height vegetation, irrespective of the distance from either type of road. On the other hand, the proportion of

Table 4
Best 10 models and the null model, listed in decreasing order of importance according to the time guanacos spent foraging

Model	<i>k</i>	AICc	ΔAICc	<i>w_i</i>
Dist km+cov+group size	5	2227.83	0.00	0.10
Dist km+cov+veg height+group size	7	2227.92	0.09	0.10
Dist km+group size	4	2228.20	0.37	0.08
Cov+veg height+group size	6	2228.44	0.61	0.08
Cov+group size	4	2228.64	0.81	0.07
Dist km+veg height+group size	6	2228.89	1.06	0.06
Dist km+roads+group size	5	2229.35	1.52	0.05
Dist km+cov+roads+group size	7	2229.79	1.96	0.04
Dist km+cov+calves+group size	6	2229.92	2.09	0.04
Dist km+cov+roads+group size	6	2239.95	2.12	0.04
Null	2	2235.53	7.70	0.00

k is the number of estimated parameters; AICc: Akaike's information criterion corrected for small samples; *w_i*: Akaike weight; dist km: minimum distance to the closest road (in km); cov: vegetation cover (%); group size: number of animals per group; veg height: vegetation height (in cm); roads: route and track; calves: number of young <1 year old per group. The chosen model is in bold.

Table 5
Parameter likelihoods, estimates (±SE) and 95% confidence interval limits (CL) for explanatory variables describing the time guanacos spent foraging, considering the minimum distance to the closest road (dist km) and group size

Explanatory variable	Parameter likelihood	Parameter estimate±SE	CL	
			Lower	Upper
Intercept		−0.71±0.11	−0.93	−0.48
Dist km	0.67	−0.20±0.09	−0.38	−0.02
Group size	1	0.04±0.01	0.01	0.06

Table 6
Best 10 models and the null model, listed in decreasing order of importance according to the time guanacos spent moving

Model	<i>k</i>	AICc	ΔAICc	<i>w_i</i>
Veg height+group size	5	1744.13	0.00	0.14
Cov+veg height+group size	6	1744.64	0.51	0.11
Veg height+calves+group size	6	1744.92	0.78	0.09
Cov+veg height+calves+group size	7	1745.08	0.94	0.09
Veg height+roads+group size	6	1745.91	1.77	0.06
Dist km+veg height+group size	6	1746.02	1.89	0.05
Dist km+roads+group size	5	1746.43	2.30	0.04
Cov+calves+group size	7	1746.57	2.44	0.04
Veg height+calves+roads+group size	7	1746.74	2.60	0.04
Veg height+calves+dist km+group size	7	1746.80	2.67	0.04
Null	2	1757.60	13.46	0.00

k is the number of estimated parameters; AICc: Akaike's information criterion corrected for small samples; *w_i*: Akaike weight; veg height: vegetation height (in cm); group size: number of animals per group; cov: vegetation cover (%); calves: number of young <1 year old per group; roads: route and track; dist km: minimum distance to the closest roads (in km). The chosen model is in bold.

animals per group devoted to vigilance or foraging was not affected by any of the variables considered. However, nearness to the unpaved road (tourist circuit), as well as low plant cover, generated the lowest proportions of animals moving in the area.

Roads are accompanied by physical changes (Forman et al., 2003), such as reduced (Casella & Paranhos Filho, 2013) or increased (Johnson, Vasek, & Yonkers, 1975) plant cover, resulting in environments that may be perceived by animals as less or more

Table 7
Parameter likelihoods, estimates (±SE) and 95% confidence interval limits (CL) for explanatory variables describing the time guanacos spent moving, considering vegetation height (veg height) and group size

Explanatory variable	Parameter likelihood	Parameter estimate±SE	CL	
			Lower	Upper
Intercept		−1.85±0.21	−2.23	−1.44
Veg height	0.8			
Medium		0.51±0.19	0.11	0.89
High		0.10±0.23	−0.35	0.57
Group size	1	−0.05±0.02	−0.08	−0.02

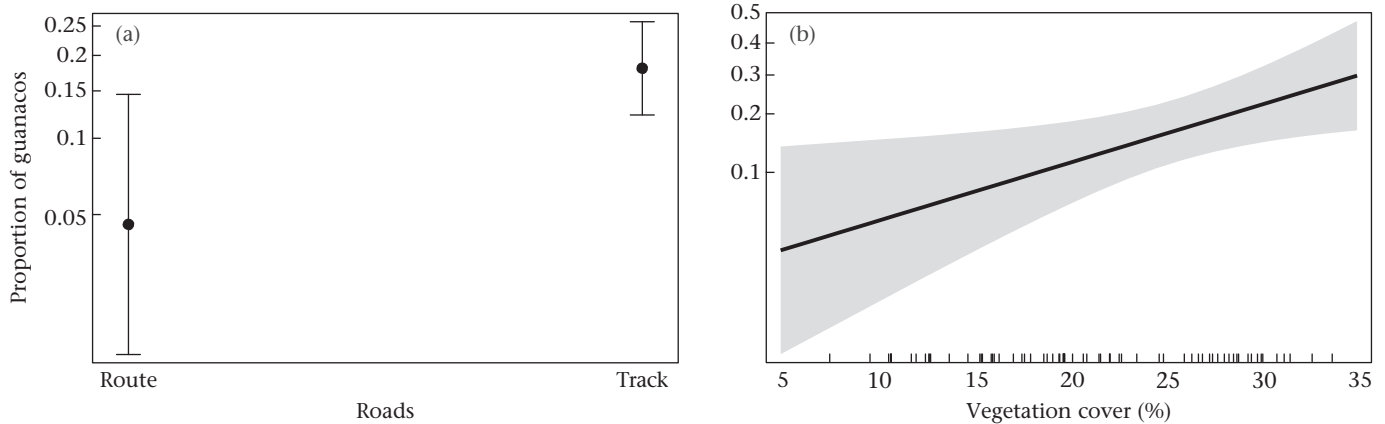


Figure 1. Proportion of guanacos moving in relation to (a) roads and (b) vegetation cover.

risky (Fiori & Zalba, 2003; Sawyer, Kauffman, & Nielson, 2009). Vegetation cover and height may act as a visual barrier to early detection of predators in guanaco and other ungulates in which sight is the most used sense for detecting predators (Mitchell & Skinner, 2003; Sarno et al., 2008). Also, predation risk is modified by human disturbance, because animals may perceive humans as potential predators (Frid & Dill, 2002; Walther, 1969), so animals must be capable of adapting to these changes (Lima & Dill, 1990), since survival is a function of resource acquisition and predator avoidance (Wolff & Van Horn, 2003).

Grouping is a proactive behaviour that ungulates use in places they perceive to be risky (Creel, Christianson, Liley, & Winnie, 2007). Not finding an effect of distance to roads on group size may be indicative of these environments not being perceived as being risky per se.

Guanacos in Ischigualasto spent less time vigilant as they approached a road. This may be because predator detection is enhanced in these open environments (Acebes, Malo, & Traba, 2013; Sarno et al., 2008), which would diminish the animals' perception of risk (Cappa et al., 2014; Marino & Baldi, 2008). Time spent vigilant is context dependent and its variability does not always depend on the predator's presence (Cappa et al., 2014; Périquet et al., 2010). Being near roads could reduce predation risk from pumas since these predators are sensitive to anthropized environments (Rogala et al., 2011). This type of relationship has been observed between brown bears, *Ursus arctos*, and moose (Berger & Cunningham, 1988), and in deer and wolves, *Canis lupus* (Rogala et al., 2011).

At Ischigualasto Provincial Park, foraging time increased as guanacos approached the roads, suggesting that these environments are perceived as having lower predation risk. Guanacos also spent more time foraging in places with lower plant cover and predation risk as do other ungulates (Cappa et al., 2014; Frid & Dill, 2002). We also found, as did Marino and Baldi (2008), that foraging time increased with the number of individuals per group. In different social mammals, foraging time increases with group size (Lima & Dill, 1990).

When groups of guanacos were close to the tourist track and in areas with higher vegetation cover, the proportion of guanacos moving increased. Even though Proffitt et al. (2009) showed that movement rates for *C. elaphus* increased in areas with high predation risk, our results do not show a relationship between movement and distance to roads. This could be due to other factors (i.e. foraging, water needs and/or predation risk) affecting this behaviour.

While we found that guanacos perceived the environments near roads as safer, human activities may have negative or positive

impacts on wildlife (Forman et al., 2003; Frid & Dill, 2002; Pomerantz, Decker, Goff, & Purdy, 1988). Our results could be due to roads creating open areas. Further research is needed to assess other factors, such as spatial and temporal use of areas near roads by guanacos in relation to, for example, vehicle traffic and type. This would help test the absence of negative effects on these animals. This type of research is particularly important for developing and implementing management strategies for guanacos and other species in protected areas.

Conclusion

Roads are essential to the economic and social development of humans. The guanacos' perception of road areas as not risky in the reserve is indicative of a harmonious relation between road development and conservation goals in this area. Our study highlights the importance of future research into how roads affect wildlife and conservation practices in protected areas.

Acknowledgments

We thank the staff of Ischigualasto Province Park for providing all the necessary facilities during fieldwork. We also thank Nelida Horak for assisting us with the English version. This study will be a portion of the first author's doctoral thesis in the Postgraduate Program in Biology, National University of Cuyo, Mendoza, Argentina (PROBIOL). We thank the reviewers for providing constructive and useful comments that improved an earlier version of this article. This research was supported by 'The chica, the retamo and the algarrobo: umbrella species for the conservation of the Native Forest of the Ischigualasto Provincial Park and nearby zones. Biological interactions, effects of human activities and their mitigation', Plan for the Conservation of Native Forests—Forest Law 26.331.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2017.07.020>.

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