

Different factors that modify anti-predator behaviour in guanacos (Lama guanicoe)

P. Taraborelli, R. Ovejero, M. E. Mosca Torres, N. M. Schroeder, P. Moreno, P. Gregorio, E. Marcotti, A. Marozzi & P. Carmanchahi

Acta Theriologica

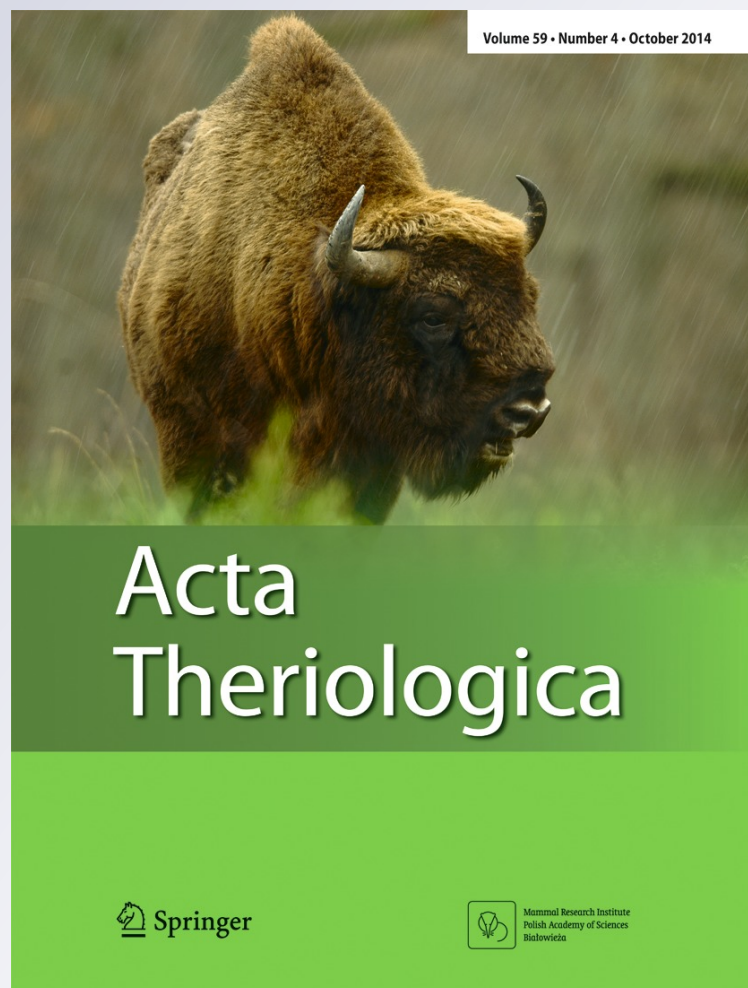
ISSN 0001-7051

Volume 59

Number 4

Acta Theriol (2014) 59:529-539

DOI 10.1007/s13364-014-0186-9



Your article is protected by copyright and all rights are held exclusively by Mammal Research Institute, Polish Academy of Sciences, Bia#owie#a, Poland. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Different factors that modify anti-predator behaviour in guanacos (*Lama guanicoe*)

P. Taraborelli · R. Ovejero · M. E. Mosca Torres ·
N. M. Schroeder · P. Moreno · P. Gregorio · E. Marcotti ·
A. Marozzi · P. Carmanchahi

Received: 9 April 2013 / Accepted: 3 April 2014 / Published online: 16 April 2014
© Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland 2014

Abstract Animals optimize the trade-off between the cost of not fleeing and the benefits of staying because the factors that influence flight decisions and the disturbance level of a particular stimulus can vary both spatially and temporally. Different factors (human impact and habitat characteristics) likely to modify anti-predator behaviour in different types of guanaco social groups were analysed. We found that group size was conditioned by high poaching, vehicle traffic,

predation risk and vegetation density. Solitary adult males showed shorter alert and flight initiation distances than bachelor and mixed groups. Alert distance was greater during the summer season, and assessment times were shorter when young were present in the groups. In high-predation-risk environments, guanacos detected threats at greater distances and flight initiation distance was longer. Alert distances were shorter on steeper sloped hills and assessment times were shorter in areas with irregular topography than on flat sites. In high traffic areas, flight initiation distance was longer and assessment times were shorter. And in areas with low poaching intensity, assessment times were greater than in those with high poaching levels. Therefore, guanacos may be able to evaluate a true threat. Social group and anti-predator responses were conditioned by habitat characteristics and human impact. We consider that plasticity of responses could be key to the survival of guanacos.

Communicated by: Rafał Kowalczyk

P. Taraborelli (✉)
Laboratorio de Desertificación y Ordenamiento Territorial
(LaDyOT), IADIZA, CCT-Mendoza, CONICET, Av. Ruiz Leal s/n,
Parque General San Martín, Mendoza ciudad, CC 507 5500,
Argentina
e-mail: ptarabor@mendoza-conicet.gob.ar

P. Taraborelli
e-mail: paulataraborelli@gmail.com

P. Taraborelli · R. Ovejero · N. M. Schroeder · P. Moreno ·
P. Gregorio · A. Marozzi · P. Carmanchahi
Grupo de Investigación en Ecofisiología de Fauna Silvestre
(GIEFAS), AUSMA–INIBIOMA–CONICET–UNCo, San Martín
de los Andes, Neuquén, Argentina

M. E. Mosca Torres
Grupo de Investigaciones de la Biodiversidad (GIB), IADIZA,
CCT-Mendoza, CONICET, Mendoza, Argentina

N. M. Schroeder
Lab. de Interacciones Ecológicas, IADIZA, CCT-Mendoza,
CONICET, Mendoza, Argentina

P. Moreno
Lab. de Ecología de Enfermedades, Fac. Cs. Veterinarias,
Universidad Nacional del Litoral, Esperanza, Santa Fe, Argentina

E. Marcotti
Unidad de Dendrocronología, IANIGLA, CCT-Mendoza,
CONICET, Mendoza, Argentina

Keywords Behavioural reactions · Human disturbance ·
Predation risk · Social group · Ungulate

Introduction

Animals optimize the trade-off between the cost of not fleeing and the benefits of staying because the factors that influence flight decisions and the disturbance level of a particular stimulus can vary both spatially (with population and human density differences) and temporally (with life history and seasonal differences in vulnerability; Frid and Dill 2002; Cooper and Frederick 2007; Stankowich 2008). High levels of inter- or intra-species variation in the effect of these factors suggest that animals pay attention to multiple factors and their responses likely depend on the interaction of many factors (Frid 1997). The decision to use a certain strategy (stay, fight or flee) affects many aspects of a prey animal's lifestyle,

including the habitats they select and the groups they form (Lima and Dill 1990; Lingle and Pellis 2002). Flight initiation distance (FID), which is the distance between predator and prey when the prey first flees, as well as other distance metrics are accurate indices of fear in animals (Blumstein 2003; Miller et al. 2006) and prove useful to the assessment of an animal's welfare (Dwyer 2004). Ungulates are morphologically and behaviourally adapted to react quickly to the presence of predators and to escape capture using effective flight strategies (Stankowich and Coss 2007). For example, escape responses of Columbian black-tailed deer (*Odocoileus hemionus columbianus*) were deeply dependent on variation in approach behaviour, environmental characteristics and proximity to an approaching human (Stankowich and Coss 2006a).

Predator–prey interactions involving large mammalian carnivores and their ungulate prey can play an important role in structuring terrestrial communities (Steneck 2005). In North America, puma (*Puma concolor*), brown bear (*Ursus arctos*) and wolf (*Canis lupus*) predation on a variety of ungulate species is considered to affect several important community-level functions, including altering prey densities and behaviours, or even habitat associations, with implications for a wide range of community members (Beyer et al. 2007; Ripple and Beschta 2008). In Argentina, data collected by Donadio et al. (2010) on puma diet and predation patterns suggest that, similar to North American pumas, South American pumas (1) heavily prey on large native ungulate species (including guanaco) and (2) display predatory and dietary patterns largely dictated by the availability of large mammalian prey. Guanacos and other ungulates rely extensively upon their vision to detect predators, which would be especially favoured in open habitats with low vegetation (Sarno et al. 2008) and where cooperative vigilance is displayed as an anti-predator mechanism (Taraborelli et al. 2012). In Torres del Paine National Park (Chile), 74 % of guanaco carcasses encountered were of animals killed by pumas (Bank et al. 2002). The puma hunts by stalking and stealth, relying on vegetation cover and terrain features to approach its prey close enough before attacking (Wilson 1984; Cajal and Lopez 1987; Bank and Franklin 1998; Donadio et al. 2010). The observed increase in collective vigilance in large groups of guanacos suggests improved detection ability in risky habitats (Marino and Baldi 2008; Taraborelli et al. 2012).

Human activities such as urbanization, poaching, ecotourism and off-road recreation have a negative impact on wild animals (Pomerantz et al. 1988), including changes in short-term behavioural patterns (e.g. likelihood of a flight response, Stankowich and Blumstein 2005; foraging and maternal behaviour, Fitzgibbon 1998), long-term behavioural patterns (e.g. distribution, patterns of mother–young behaviour,

activity patterns, habituation; Jeppesen 1987; Kufeld et al. 1988; Kilgo et al. 1998) and species biology (e.g. physiology, reproduction, physical health; Gabrielsen and Smith 1995). An increase in human recreational activities in natural areas can also increase the potential for disturbance to wildlife (Stankowich 2008). Stankowich (2008) found evidence that ungulates pay attention to the behaviour of the approaching human, having greater perceptions of risk when disturbed in open habitats, and that females or groups with young show greater flight responses than adult groups. Oil and gas exploitations cause environmental changes, such as building of roads and vehicle traffic, and these activities may directly interfere with the movement, habitat selection and behaviour of wildlife (Fiori and Zalba 2003; Sawyer et al. 2006, 2009). The direct effects of fragmentation by seismic lines (temporary roads for oil prospecting), disturbances originating from noise and movements of people, and vehicles associated with oil extraction activities can also modify behaviour of wildlife with broad distribution ranges (Fiori and Zalba 2003). The resulting increased access to an area can benefit hunters and poachers, and also favours activities such as cattle ranching due to the provision of access routes. Poaching of wild South American camelids remains widespread in Argentina, even inside protected areas (IUCN and EP Forum, 1991; Maki 1992). Our research is important because human impacts on *Lama guanicoe* are poorly known and managers are often left wondering whether information about disturbance effects on one species or population is relevant or useful to make management decisions for another species or population.

In this study, we put the spotlight on behavioural responses in different types of social groups of guanacos related to human impact and habitat characteristics. We measured anti-predator responses to a potential threat (human subject) at La Payunia Reserve (Mendoza Province, Central-west of Argentina). Our hypothesis is that guanacos living in more threatening scenarios (areas with higher predation risk, lower visual perception due to vegetation obstruction or irregular topography and higher human impact) respond more quickly with anti-predator behaviours, and that guanacos form social groups with larger number of individuals in order to reduce threat. We expect that (1) guanacos in mixed groups will detect and respond to threats earlier and will have greater flight initiation distances than solitary adult males, (2) alert and flight initiation distances by guanacos will be greater in areas with higher predation risk (predation by puma, areas with irregular topography and with dense vegetation) than in areas with lower risk and (3) guanacos in areas with poaching activity and high vehicle traffic will demonstrate higher alert and flight initiation distances, and shorter assessment time. Our research is one of the first attempts to add the effect of human impact and habitat characteristics on guanaco behavioural response.

Material and methods

Study area

This study was carried out at La Payunia Provincial Reserve in the south of Mendoza Province in central-west Argentina (36° 00' and 36° 36' S, and between 68° 34' and 69° 23' W, 1,300–2,000 m a.s.l.; Candia et al. 1993; Puig et al. 2003). La Payunia Reserve (665,000 ha) is dominated by a gently undulating relief and vast flatlands in combination with areas of steeper hills and volcanic outcrops (González Díaz 1972; Puig et al. 2001). The climate is semi-arid (Martínez Carretero 2004), mean temperatures in the study area range between 6 °C in winter and 20 °C in summer, with a mean annual precipitation of 198 mm (Candia et al. 1993; Puig et al. 2001). Vegetation is xerophytic, with 58 % of plant cover, and corresponds to La Payunia phytogeographic province (Martínez Carretero 2004). Sandy plains present herbaceous communities, while slopes and basaltic scoria are covered with shrub communities (Martínez and Dalmaso 1993; Puig et al. 1996, 1997). We selected different habitats used by guanacos, including sandy soils dominated by grasses, sites with more sloping topography and a higher proportion of phanerophytic shrubs, as well as basaltic steps co-dominated by grasses and shrubs. This Reserve holds the largest population of *L. guanicoe* of the central-west region of Argentina, which could reach to about 26,000 animals in spring (Schroeder 2013). The guanaco is a social species, and its populations are structured into family groups, bachelor groups, mixed groups and solitary adult males (Franklin 1983). Family groups are composed of one adult male and one or more adult females with their offspring from the current year. Family members usually form highly cohesive and behaviourally synchronized units (Franklin 1983; Taraborelli et al. 2012). Bachelor groups are composed mostly of adult males and yearlings, and mixed groups are composed of both sexes and all age classes (Franklin 1983). Mixed groups show low group cohesion, in other words the distances among members are greater than in bachelor and family groups (Taraborelli et al. 2012). The main predator of guanacos is the puma (*P. concolor*). At La Payunia, Bolgeri and Novaro (2010) found that 25 % of guanaco carcasses encountered presented signs of predation by pumas and that these attacks took place in the NE sector of La Payunia Reserve (32 % of guanaco carcasses) more than in the NW sector (13 % of guanaco carcasses). Furthermore, pumas were observed chasing mostly adult guanacos (78 %) and predation was related to the relative availability of guanacos (Bolgeri and Novaro 2010).

Current trends in land use at La Payunia include a sharp increase in oil exploitation and mining operations with a concomitant increase in the density of oil- and mining-related roadways, which in turn facilitates access to poachers.

In this reserve, tourism activity is very limited and tourist access is restricted and controlled by park rangers (Aros L., personal communication). In this region, human populations are scarce and goat breeding is the base of the subsistence economy (Candia et al. 1993; Carmanchahi et al. 2011). Although poaching of guanacos is currently forbidden at La Payunia, poaching pressure was intense during the 1960s and 1970s (Puig et al. 2003). Nowadays, hunters use vehicles and a network of dirt roadways from which they shoot the animals. If guanacos are too far from a road, poachers usually drive off road and chase them (Aros and Quiroga 2012; Dirección de Recursos Naturales Renovables 2012).

Trial of anti-predator behaviours

Several studies on ungulates have analysed the anti-predator behaviours in response to an approaching human to investigate the relationships between pre-flight risk factors (i.e. distance to first detection, flight initiation distance, assessment time, predator behaviour, environmental factors) and escape behaviour (e.g. distance moved, escape angle, escape style; Fortin and Andruskiw 2003; Caro et al. 2004; Stankowich and Coss 2006b). Human subjects elicit similar anti-predator behaviour in prey species to those triggered by real predators (Frid and Dill 2002; de Boer et al. 2004; Stankowich and Coss 2006a; Birke et al. 2011). The appearance of a human on foot is more frequently associated with targeted harassment (e.g. poaching) than humans in vehicles; therefore, they are perceived as more threatening (Stankowich and Coss 2006a; Stankowich 2008). At La Payunia Reserve, due to a history of poaching, humans are likely perceived as potential threats by guanacos, as suggested by alarm calls uttered when humans approached during the study.

In our study, the human subject (hereafter HS) was always the same 1.6-m tall woman wearing the same outfit (green coat and green pants) for each trial. As the HS identified a social guanaco group from the roadside, she positioned herself in a straight line of sight to the guanacos and opposite to the wind (Taraborelli et al. 2012). The HS chased the identified guanaco groups at a constant speed of 1 m s⁻¹. The HS used a stopwatch, binoculars (Hokenn 10×50), a digital voice recorder (Olympus VN4000) and a Laser Rangefinder (Bushnell 1000) to record alert and flight initiation distances. When an alert response occurred, the HS threw a green flag on the ground for subsequent distance measurements and recorded the time of the event in seconds while keeping the same direction towards the guanacos and completely stopping the approach when a group member began to run or walk (Taraborelli et al. 2012). Two other observers used a Spotting Scope (Bushnell 2.6 in./65 mm) to record (1) group size, number of guanacos per group; (2) relative age and (3)

sex of group members to determine type of social group (solitary adult males, family, bachelor or mixed groups; Franklin 1982, 1983). We also recorded (4) relative height of vegetation (compared with an adult guanaco), and plant structure (sparse vegetation, dense vegetation), by measuring the vegetation where the group was situated and a patch located approximately 20–30 m from the group, considering the distance needed by a puma to perform a successful attack (Bank and Franklin 1998); (5) topography, classified as flat or irregular terrain depending on the presence of hills; (6) we used IDRISI Taiga 16.05 software to calculate the slope of every GPS trail point from a digital elevation model at 90-m spatial resolution obtained from the Global Land Cover Facility of University of Maryland (<http://glcfapp.glcf.umd.edu:8080/esdi/index.jsp>); and (7) predation risk was considered “low” in the NW sector and “high” in the NE of the reserve (Bolgeri and Novaro 2010). The before-mentioned observers were farther away from the roadside so as to not affect the behaviour of focal guanacos (Taraborelli et al. 2012).

We considered that the focal guanaco noticed the approaching HS whenever it interrupted foraging, walking or resting and remained motionless with its head raised and pointing directly towards the HS (Taraborelli et al. 2012). At the beginning of each trial, we excluded groups with individuals more than 300 m away from their neighbours (Marino and Baldi 2008; Taraborelli et al. 2012). At the end of each approach by the HS, we recorded (1) alert distance, distance between the dropped flag and one or more guanacos when it/they became alert to the threat (Lingle and Pellis 2002; Taylor and Knight 2003; Stankowich and Coss 2006a; Stankowich 2008; Colman et al. 2012); and (2) FID, distance between the HS and the first group member to take flight, either running or walking quickly (Donadio and Buskirk 2006; Stankowich and Coss 2006a; Stankowich 2008; Colman et al. 2012). We also estimated (3) assessment time as the time elapsed between the first detection and the start of flight by the first group member to take flight (Donadio and Buskirk 2006; Stankowich and Coss 2006a, b; Stankowich 2008).

All trials were conducted between 0830 and 2000 hours, during the southern hemisphere late spring (November and December 2010) when young less than 1 year old were not present and summer (February and March 2012) when young were present in the groups. In order to prevent habituation of guanacos to humans, we drove along existing roads at the reserve (a total of 786 km in 2010, 880 km in 2012) to prevent repeating the same focal group on the same day and conducted each trial in different areas of La Payunia. We carried out 69 trials in 2010 and 64 trials in 2012. All trial locations were recorded with GPS. Trials were discarded if there was any doubt about the distances and times measured or if guanacos were alarmed by a passing vehicle or other disturbing situations (Taraborelli et al. 2012).

Human impact assessment

Poaching Index In 2009, park rangers at La Payunia started a Natural Resource Protection Program using historical records of procedures and road controls dating from 1996 to 2008 (324 records) and also obtained from task controls from 2009 to 2011 (2,244 records). Conservation criteria and values were identified; threats associated with each value were categorized according to scope, duration and intensity, and related legal framework. After analyses, a map was created which identified critical areas at La Payunia Reserve with values ranging from 1 to 3 (Aros and Quiroga 2012; Dirección de Recursos Naturales Renovables 2012).

We used IDRISI Software (Taiga version) to assign the corresponding poaching index value (1, low; 2, medium; and 3, high) to each site used for anti-predator trials.

Traffic Vehicles seen at the area were recorded for 3 days in each season in the NW and NE sectors of La Payunia reserve. Traffic was categorized as low (0–1 vehicle/day), medium (2–19 vehicles/day) or high (>20 vehicles/day).

Statistical analysis

We fitted generalized linear mixed models (GLMM) to evaluate anti-predator behaviour in different social groups of guanacos using R package *lme4* (Bates et al. 2011; www.r-project.org). The response variables were the following: alert and flight initiation distances, assessment time and group size. Each variable was evaluated as a function of several fixed factors: season, poaching index, vehicle traffic, predation risk, topography, vegetation type, slope and group type. Individual observation was the random effect assumed to impact the variability of the data. We assumed a Poisson distribution of the error structure for the models which was then confirmed by graphical methods.

The best models were selected using Akaike's information criterion (AIC; Akaike 1974). We began with the full model and successively removed the variables/factors which decreased the AIC value. We considered that models differing in AIC value by more than one were significantly different (Ims and Yoccoz 1997; Appendix Table 5). Model selection was carried out using the AICtab function from the *bbmle* package (Bolker 2012).

Results

Group size related to different variables

In La Payunia's population, the average size of family groups was 4 ± 1 guanacos/group ($N=19$) and ranged from two to seven adults (including females and one male) and one to

three young. The average number of guanacos per bachelor group was 9 ± 2 guanacos/group ($N=38$) and ranged from 2 to 36 adult males and with one to six yearlings. And the average size of mixed groups (including females and males) was 53 ± 12 guanacos/group ($N=28$) and ranged from 7 to 290 adult guanacos. Mixed groups contained 1–25 females and 1–46 males, and ranged from 1 to 25 young and yearlings. In this study, we observed 48 solitary adult males.

Group sizes were conditioned by poaching, vehicle traffic, plant structure and slope. Group sizes were larger in areas with high poaching index values (16 ± 3 guanacos/group and 12 ± 2 guanacos/group in areas with low poaching levels), high vehicle traffic (15 ± 3 guanacos/group, 11 ± 1 guanacos/group in areas with low vehicle traffic), dense vegetation (17 ± 4 guanacos/group, 4 ± 1 guanacos/group in areas with sparse vegetation) and on hills with lower slope ($<4^\circ$: 16 ± 3 guanacos/group, $N=121$; $\geq 4^\circ$: 3 ± 1 guanacos/group, $N=10$; Table 1). As regard to high predation risk, we found a marginally significant effect on group size (18 ± 5 guanacos/group, 10 ± 2 guanacos/group in areas with low predation risk; Table 1) but the predation–group size relationship was significant in the second generalized linear mixed-effects model (estimate = -1.143 ; $z=2.131$; $p(z)=0.033$).

Alert distance in guanacos

Alert distance in guanacos was related to season, predation risk, slope and group type. Alert distance was shorter during the spring season (344.3 ± 18.5 m, 373.8 ± 16.5 m in the

Table 1 Generalized linear mixed models for group sizes related to different environmental, anthropic and social variables. The model presented is the most parsimonious of several models with lowest AIC value (Appendix Table 5). The response variable is group size (number of guanacos by group) with a Poisson distribution. Fixed factors are vehicle traffic, predation risk, plant structure and group type. Individual identity was considered a random effect

Fixed effects	Estimate	SD	<i>z</i>	<i>p</i>
Intercept	0.820	0.581	1.412	0.158
Season_spring	-0.640	0.352	-1.821	0.069
Poaching_high	2.912	1.325	2.243	0.025
Vehicle traffic_medium	0.000	0.444	0.000	0.999
Vehicle traffic_high	1.499	0.747	2.008	0.044
Predation risk_high	0.995	0.528	1.883	0.059
Plant structure_dense	0.873	0.295	2.962	0.003
Slope	-0.229	0.097	-2.374	0.018
Random effects				
Groups	Name	Variance	SD	
Observations	Intercept	1.630	1.277	

Italic indicate significant differences

No. of observations, 133; groups: observations, 133

summer season). In high predation risk environments, guanacos detected the threat at greater distances (375.3 ± 18 m, 340.6 ± 17 m in areas with low predation risk). Alert distances were shorter in steeper sloped hills ($\geq 4^\circ$: 293.6 ± 40.8 m, $<4^\circ$: 364.5 ± 13.2 m). Solitary adult males showed shorter alert distance (309.4 ± 19.5 m) than bachelor (383.6 ± 23.8 m) and mixed groups (406.2 ± 31.3 m; Table 2, Fig. 1).

Flight initiation distance in guanacos

In areas with high vehicle traffic and high predation risk, flight initiation distance was longer (209.1 ± 14.6 and 213.7 ± 13.5 m, respectively) than in areas with low traffic and low predation risk (199.8 ± 15.9 and 202.8 ± 11.4 m, respectively). Solitary adult males (152.2 ± 9.5 m) took flight at shorter distances than mixed and bachelor groups (290 ± 22.4 and 226.6 ± 17.8 m, respectively). And mixed groups did so at greater distances to the threat than solitary adult males and bachelor groups (Table 3, Fig. 2).

Assessment times in guanacos

Assessment times were affected by poaching, vehicle traffic, topography and season. Assessment times were shorter in medium traffic areas (77 ± 14 s) compared to low traffic areas (132 ± 13 s), and in areas with irregular topography (103 ± 10 s) than in flat sites (130 ± 10 s). Assessment times were greater in

Table 2 Generalized linear mixed models for alert distance in different guanaco groups related to environmental, anthropic and social variables. The model presented is the most parsimonious of several models with lowest AIC value (Appendix Table 5). The response variable is alert distance (in metres) with a Poisson distribution. Fixed factors are predation risk, topography, slope and group type. Individual observation was considered a random effect

Fixed effects	Estimate	SD	<i>z</i>	<i>p</i>
Intercept	5.855	0.169	34.59	<0.001
Season_spring	-0.243	0.104	-2.33	0.019
Vehicle traffic_medium	0.097	0.122	0.80	0.423
Vehicle traffic_high	0.368	0.214	1.72	0.086
Predation_high	0.387	0.154	2.51	0.012
Topography_irregular	-0.135	0.074	-1.84	0.066
Group type_mixed	-0.031	0.126	-0.25	0.803
Group type_solitary	-0.247	0.119	-2.08	0.037
Group type_bachelors	0.047	0.126	0.38	0.707
Slope	-0.053	0.027	-2.0	0.046
Random effects				
Groups	Name	Variance	SD	
Observations	Intercept	0.162	0.403	

Italic indicate significant differences

No. of observations, 133; groups: observations, 133

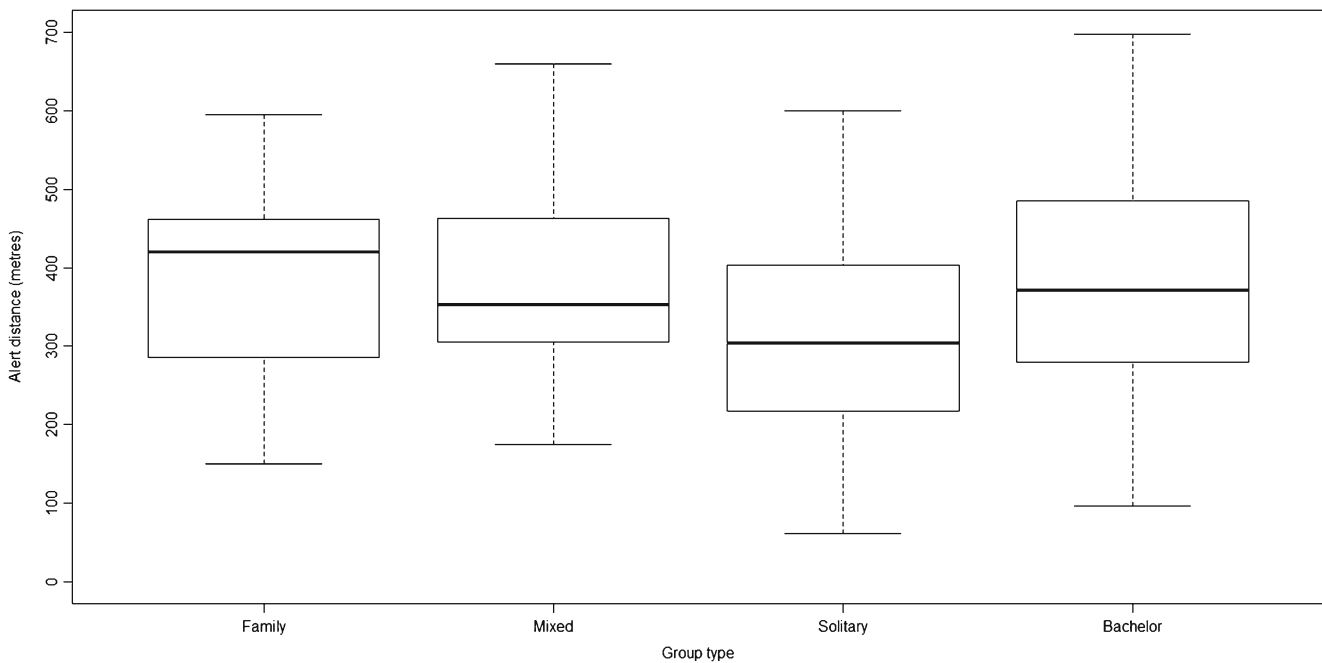


Fig. 1 Box plots showing alert distance (metres) in different social group types of guanacos (family, mixed, solitary and bachelor groups). Box plots depict the median (**bold bar**), 25–75 % quartiles (**box**), 10–90 % quantiles (**whiskers**) and outliers (**points**)

areas with low poaching index value (122 ± 10 s and 107 ± 15 s in areas with high poaching levels). Assessment times were shorter during the summer season than in spring (79 ± 10 , 160 ± 11 s, respectively), when young were present in the groups (Table 4).

Table 3 Generalized linear mixed models for flight initiation distance in different guanaco groups related to environmental, anthropic and social variables. The model presented is the most parsimonious of several models with lowest AIC value (Appendix Table 5). The response variable is flight initiation distance (in metres) with a Poisson distribution. Fixed factors are vehicle traffic, predation risk, topography and group type. Individual observation was considered a random effect

Fixed effects	Estimate	SD	z	p
Intercept	4.959	0.160	30.974	<0.001
Vehicle traffic_medium	0.243	0.125	1.953	0.051
Vehicle traffic_high	0.385	0.182	2.120	0.034
Predation_high	0.352	0.140	2.518	0.012
Topography_irregular	-0.058	0.079	-0.736	0.462
Group type_mixed	0.304	0.135	2.247	0.025
Group type_solitary	-0.381	0.128	-2.983	0.003
Group type_bachelors	-0.011	0.135	-0.084	0.933
Random effects				
Groups	Name	Variance	SD	
Observations	Intercept	0.188	0.435	

Italic indicate significant differences

No. of observations, 133; groups: observations, 133

Discussion

According to our study, the anti-predator behaviour of *L. guanicoe* was conditioned by social group type, human impact and habitat characteristics. Solitary adult males were alert and took flight at shorter distances than bachelor and mixed groups. Also, guanaco group sizes were larger in areas with high vehicle traffic, high predation risk and dense vegetation. In other words, guanacos form social groups with greater number of individuals in risky areas. Also, Malo et al. (2011) found a group-size effect on the probability of flight response in guanacos. This result would be related to mechanisms of cooperative vigilance, and the many-eyes effect enhances the ability of individuals to detect threats and predators (Hoogland 1981). Studies on mule deer (*O. hemionus* spp.), white-tailed deer (LaGory 1987; Lingle and Wilson 2001), roe deer (*Capreolus capreolus*), fallow deer (de Boer et al. 2004), Columbian black-tailed deer (Stankowich and Coss 2006a, b), caribou (*Rangifer tarandus*: Aastrup 2000) and rocky mountain mule deer (Taylor and Knight 2003) have demonstrated that flight initiation distances due to the presence of a particularly wary animal are greater in a larger group, and that the movements of the wariest member of the group can have a contagious effect on the rest of the group. Therefore, guanacos in risky areas would form social groups with a large number of individuals because they are more likely to spot a threat than smaller groups, and thus, individuals are more likely to flee from it.

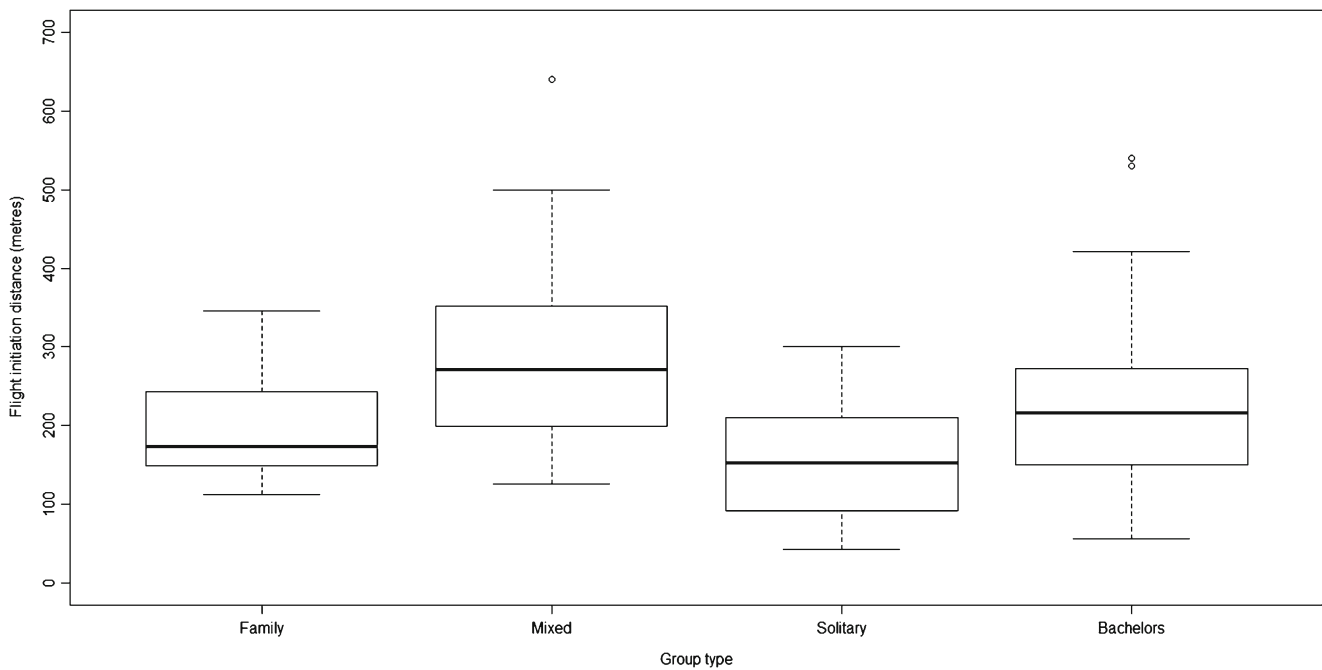


Fig. 2 Box plots of flight initiation distance (metres) in different social group types of guanacos (family, mixed, solitary and bachelor groups). Box plots depict the median (*bold bar*), 25–75 % quartiles (*box*), 10–90 % quartiles (*whiskers*) and outliers (*points*)

On the other hand, alert distance was greater and assessment times were shorter during the summer, when young were present in the groups. This response suggests that group

Table 4 Generalized linear mixed models for assessment time in different guanaco groups related to environmental, anthropic and social variables. The model presented is the most parsimonious of several models with lowest AIC value (Appendix Table 5). The response variable is assessment time (in seconds) with a Poisson distribution. Fixed factors are season, poaching index, vehicle traffic and topography. Individual observation was considered a random effect

Fixed effects	Estimate	SD	<i>z</i>	<i>p</i>
Intercept	5.097	0.306	16.669	<0.001
<i>Season_summer</i>	-1.316	0.192	-6.856	<0.001
<i>Poaching_low</i>	0.444	0.204	2.182	0.029
<i>Vehicle traffic_medium</i>	-0.541	0.199	-2.710	0.007
Vehicle traffic_high	-0.155	0.252	-0.615	0.538
<i>Topography_irregular</i>	-0.483	0.161	-2.994	0.003
Group type_mixed	-0.372	0.271	-1.373	0.169
Group type_solitary	0.241	0.254	0.948	0.343
Group type_bachelors	0.363	0.270	1.345	0.179
Slope	-0.037	0.058	-0.630	0.528
Random effects				
Groups	Name	Variance	SD	
Observations	Intercept	0.765	0.875	

Italic indicate significant differences

No. of observations, 133; groups: observations, 133

composition has an influence on behavioural responses, and that groups with young are more cautious than those without. Marino and Johnson (2012) found in a sedentary population (Argentine Patagonia) that groups with at least one young among their members had a significantly greater probability to flee than did groups with only adults. In another study, camelid groups with juveniles fled more frequently than adult-only groups in areas with poaching (Donadio and Buskirk 2006). And Malo et al. (2011), assessing the effect of tourists on guanaco behaviour, found that groups with young also had the highest likelihood of flight in response to a vehicle when compared with adult-only groups or solitary individuals. Caribou females are more wary when they are guarding newborns or young, which are more vulnerable to predation (Stankowich 2008). White-tailed deer and mule deer females may be more effective in protecting their fawns during the first few months of life, a period when most ungulates are too small and slow to outrun predators (Lingle and Pellis 2002). Also, Recarte et al. (1998) observed that park fallow deer female groups took flight more often than other group types, possibly due to differences in ecological strategy where protection of young is a high priority for females. The same responses could be occurring in guanaco females, suggesting an ecological strategy with a high adaptive value.

Guanacos showed greater alert and flight initiation distances in areas with high predation risk from pumas than in areas with low predation risk. We have to take into account other characteristics associated with predation risk such as

plant structure, topography and slope. We found that group sizes were larger in areas with high predation risk from pumas and dense vegetation, probably as a strategy of having more individuals to detect a threat due to lower visual perception caused by vegetation obstruction. Also, alert distances were shorter on steeper sloped hills and assessment times were shorter in areas with irregular topography than in flat sites, and the largest number of social groups was located in low-sloped areas. Therefore, guanacos respond more quickly with anti-predator responses in high risk habitats. Prey may flee as soon as they detect a threat, but reduced flight initiation distances in closed and steep areas may also be due to a limited ability to detect a threat at longer distances (Swenson 1982; Stankowich and Coss 2006b, 2007). In southern Argentina, individuals of different guanaco populations increased vigilance in closed habitats and remained constant in open habitats (Marino and Baldi 2008). Wirsing et al. (2010) argued that the nature of the defensive spatial response of a prey species with a particular escape strategy also depends on the hunting approach used by its predator and the setting of the predator–prey interaction (i.e. landscape features). Accordingly, an integrated approach that accounts for prey escape behaviour and the context provided by predator hunting mode and landscape features should lead to a better understanding of anti-predator spatial shifts and improve our ability to anticipate the consequences of changes in predator numbers for prey distributions and ecosystem dynamics.

The interaction with humans and their recreational activities has significant impacts on ungulate behaviour (Stankowich 2008; Benhaïem et al. 2008). We found that flight initiation distance was longer and assessment times were shorter in areas with high vehicle traffic. And assessment times were greater in areas with low poaching than with high poaching levels. At La Payunia Reserve, hunters use pick-up trucks to enter roads built for the oil company, and ecotourism is low within the reserve (Aros L., personal communication). Schroeder et al. (2013) found that guanacos selected areas with low poaching level during fall–winter at La Payunia Reserve. These authors suggested that human activity, whether expressed as hunting pressure or direct persecution, has a negative impact on *L. guanicoe*. And these analyses reflect the selection pattern exhibited by guanacos across a poaching intensity gradient associated with roads (Schroeder et al. 2013). In this regard, our results would indicate that guanacos may be able to evaluate the true threat and that they perceive human presence as threat (a dangerous stimulus). Donadio and Buskirk (2006) found that flight frequency of guanacos is higher within protected areas where poaching is common, than within reserves with effective protection. This lower tolerance level suggests that sensitisation to vehicle-related stimuli has occurred in heavily hunted populations. In

another study, Marino and Johnson (2012) assessed temporal variation in guanaco's tolerance of motorized vehicles at a new reserve in Argentine Patagonia (Refugio de Vida Silvestre San Pablo de Valdés) ever since management practices changed and harassment to wildlife ceased. Their results suggest that, if harassment ceases and negative stimuli are replaced by neutral stimuli, guanacos can rapidly adjust their tolerance level. Also, the apparent minor effects of tourists on guanacos at Ischigualasto Provincial Park (San Juan, Argentina) is probably the result of these individuals becoming accustomed to non-aggressive human presence, which leads to a reduction in their reaction to approaching vehicles and pedestrians (Malo et al. 2011). Then, if animals associate human presence with no threat, they will show reduced flight responses (Carranza 2000; Alcock 2005; Pearce 2008). But if they are hunted, stalked or subjected to repeated harassment, they will flee from humans (Dwyer 2004; Stankowich and Blumstein 2005; Picton 1999). Therefore, at La Payunia Reserve, where vehicle traffic is strongly related to poaching and is a negative stimulus for guanacos, we recommend continued application of the Natural Resource Protection Program made by La Payunia's rangers, and increasing the level of control at main entrances to the reserve, and in small roads into it, in order to decrease the levels of poaching. In addition, the closing of abandoned roads built by oil companies within the reserve will provide guanacos with undisturbed areas and secure refuges.

In summary, we have identified key factors that reliably affect anti-predator behaviour in guanacos via the examination of the results of empirical research on alert and flight responses, including social group type, habitat characteristics, predation risk and human impact (poaching and traffic). Furthermore, we found that social groups and anti-predator responses were conditioned by habitat characteristics and human impact. Response plasticity could be a key part of guanaco's survival. And alert and flight initiation distances, and assessment times would be an accepted methodology for measuring sensitivity to disturbance and are good indicators of the threats the species studied perceives. We agree with Donadio and Buskirk (2006) that monitoring flight initiation distances and assessment times of a species is an inexpensive and simple method which can be easily applied with little training.

Acknowledgments This study was partially financed by CONICET, PIP 11220100100386, Agencia-FONCYT, PICT-2010-1305 and PICT-2011-2304. Equipment was partially financed by IDEA WILD. The authors wish to express their thanks to the park rangers of the natural protected areas of the southern zone (Malargüe Department, Mendoza, Argentina) for information regarding poaching index. Thanks also to ME Periago and N Horak for the English version of the manuscript. Special thanks to MJ Bolgeri for information about predation risk at La Payunia Reserve.

Appendix

Table 5 A priori generalized linear mixed-effects models for group size, alert distance, flight initiation distance, and assessment time in guanacos. Only fixed effects are presented. The most parsimonious model is presented first (i.e. models are ranked in descending order after AIC value)

Models	AIC	ΔAIC	AICweight
Group sizes of guanacos related to different variables			
<i>Group size~season+ poaching index+ traffic index+ predation risk+ plant structure+ slope+ (1 observations), family=poisson</i>	441.8	0.0	0.361
<i>Group size~season+ poaching index+ traffic index+ predation risk+ height of vegetation+ plant structure+ slope+ (1 obs), family=poisson</i>	442.2	0.3	0.305
<i>Group size~poaching index+ traffic index+ predation risk+ plant structure+ slope+ (1 observations), family=poisson</i>	443.0	1.2	0.197
<i>Group size~season+ poaching index+ traffic index+ predation risk+ vegetation height+ plant structure+ topography+ slope+ (1 observations), family=poisson</i>	443.8	1.9	0.137
Alert distance by guanacos			
<i>Alert distance~season+ traffic index+ predation risk+ topography+ group type+ slope+ (1 observations), family=poisson</i>	687.7	0.0	0.561
<i>Alert distance~season+ traffic index+ predation risk+ plant structure+ topography+ group type+ slope+ (1 observations), family=poisson</i>	689.7	2.0	0.207
<i>Alert distance~season+ traffic index+ predation risk+ vegetation height+ plant structure+ topography+ group type+ slope+ (1 observations), family=poisson</i>	690.2	2.5	0.160
<i>Alert distance~season+ poaching index+ traffic index+ predation risk+ vegetation height+ plant structure+ topography+ group type+ slope+ (1 observations), family=poisson</i>	691.9	4.1	0.071
Flight initiation distance			
<i>Flight initiation distance~traffic index+ predation risk+ topography+ group type+ (1 observations), family=poisson</i>	629.0	0.0	0.724
<i>Flight initiation distance~season+ traffic index+ predation risk+ topography+ slope+ group type+ (1 observations), family=poisson</i>	631.4	2.4	0.220
<i>Flight initiation distance~season+ traffic index+ predation risk+ vegetation height+ plant structure+ topography+ slope+ group type+ (1 observations), family=poisson</i>	634.4	5.4	0.049
<i>Flight initiation distance~season+ poaching index+ traffic index+ predation risk+ vegetation height+ plant structure+ topography+ slope+ group type+ (1 observations), family=poisson</i>	638.2	9.2	0.007
Assessment time			
<i>Assessment time~season+ poaching index+ traffic index+ topography+ slope+ group type+ (1 observations), family=poisson</i>	709.8	0.0	0.564
<i>Assessment time~season+ poaching index+ traffic index+ topography+ (1 observations), family=poisson</i>	711.7	1.9	0.214
<i>Assessment time~season+ poaching index+ traffic index+ vegetation height+ plant structure+ topography+ slope+ group type+ (1 observations), family=poisson</i>	712.3	2.5	0.162
<i>Assessment time~season+ poaching index+ traffic index+ Predation risk+ vegetation height+ plant structure+ topography+ slope+ group type+ (1 observations), family=poisson</i>	714.3	4.5	0.059

References

- Aastrup P (2000) Responses of West Greenland caribou to the approach of humans on foot. *Polar Res* 19:83–90
- Akaike H (1974) A new look at statistical model identification. *IEEE Trans Autom Control* AU 19:716–722
- Alcock J (2005) Animal behavior. An evolutionary approach. Sinauer Associates, Inc. Arizona State University, Arizona
- Aros LA, Quiroga LE (2012) Protección integral de la fauna silvestre desde las Áreas protegidas, sistematización y análisis de la información, áreas naturales protegidas de zona sur de Mendoza, Argentina. X Congreso Internacional de Manejo de Fauna Silvestre en la Amazonia y América Latina. Ciudad de Salta, Salta, Argentina
- Bank MS, Franklin WL (1998) Puma (*Puma concolor patagonica*) feeding observations and attacks on guanacos (*Lama guanicoe*). *Mammalia* 62:599–605
- Bank MS, Sarno RJ, Campbell NK, Franklin WL (2002) Predation of guanacos (*Lama guanicoe*) by southernmost mountain lions (*Puma concolor*) during a historically severe winter in Torres del Paine National Park, Chile. *J Zool* 258:215–222
- Bates D, Maechler M, Bolker B (2011) lme4: linear mixed-effects models using S4 classes. R package version 0.999375-42
- Benhaïem S, Delon M, Lourtet B, Cargnelutti B, Aulagnier S, Hewison AJM, Morellet N, Verheyden H (2008) Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Anim Behav* 76:611–618
- Beyer HL, Merrill EH, Varley N, Boyce M (2007) Willow on Yellowstone's northern range: evidence for a trophic cascade? *Ecol Appl* 17:1563–1571
- Birke L, Hockenhull J, Creighton E, Pinno L, Mee J, Mills D (2011) Horses' responses to variation in human approach. *Appl Anim Behav Sci* 134:56–63
- Blumstein DT (2003) Flight-initiation distance in birds is dependent on intruder starting distance. *J Wildl Manag* 67:852–857

- Bolgeri MJ, Novaro A (2010) Patrones de depredación (*Puma concolor*) sobre una población de guanacos (*Lama guanicoe*) en Payunia, Mendoza. IV Reunión Binacional de Ecología. Buenos Aires, Argentina
- Bolker B (2012) Package “bbmle”. <http://cran.r-project.org/web/packages/bbmle/bbmle.pdf>
- Cajal JL, Lopez NE (1987) El puma como depredador de camélidos silvestres en la Reserva San Guillermo, San Juan, Argentina. Rev Chil Hist Nat 60:87–91
- Candia R, Puig S, Dalmaso A, Videla F, Martínez Carretero E (1993) Plan de Manejo de la Reserva La Payunia. Multequina 2:5–87
- Carmanchahi PDA, Ovejero RA, Marull CC, López GCD (2011) Physiological response of wild guanacos to capture for live shearing. Wildl Res 38:61–68
- Caro TM, Graham CM, Stoner CJ, Vargas JK (2004) Adaptive significance of antipredator behaviour in artiodactyls. Anim Behav 67: 205–228
- Carranza J (2000) Etología. Introducción a la Ciencia del Comportamiento. Universidad de Extremadura, Madrid
- Colman JE, Lilleeng MS, Tsegaye D, Vigeland MD, Reimers E (2012) Responses of wild reindeer (*Rangifer tarandus tarandus*) when provoked by a snow-kiter or skier: a model approach. Appl Anim Behav Sci 142:82–89
- Cooper WE, Frederick WG (2007) Optimal flight initiation distance. J Theor Biol 244:59–67
- de Boer HY, van Breukelen L, Hootsmans MJM, van Wieren SE (2004) Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. Wildl Biol 10:35–41
- Dirección de Recursos Naturales Renovables (2012) Informe Programa de Control y Vigilancia Zona Sur 2011-PCV. Secretaría de Ambiente y Desarrollo sustentable
- Donadio E, Buskirk SW (2006) Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. Biol Conserv 127:139–214
- Donadio E, Novaro AJ, Buskirk SW, Wursten A, Vitali MS, Monteverde MJ (2010) Evaluating a potentially strong trophic interaction: pumas and wild camelids in protected areas of Argentina. J Zool 280:33–40
- Dwyer CM (2004) How has the risk of predation shaped the behavioural responses of sheep to fear and distress? Anim Welf 13:269–281
- Fiori SM, Zalba SM (2003) Potential impacts of petroleum exploration and exploitation on biodiversity in a Patagonian Nature Reserve, Argentina. Biodivers Conserv 12:1261–1270
- Fortin D, Andruskiw M (2003) Behavioral response of free-ranging bison to human disturbance. Wildl Soc B 31:804–813
- Franklin WL (1982) Lama language. Modes of communication in the South American camelids. Llama World 1:5–11
- Franklin WL (1983) Contrasting socioecologies of South America's wild camelids: the vicuña and the guanaco. In: Eisenberger SF, Kleinman DG (eds) Advances in the study of mammalian behavior. American Society of Mammals, USA, N7, pp 573–629
- Frid A (1997) Vigilance by female Dall's sheep: interactions between predation risk factors. Anim Behav 53:799–808
- Frid A, Dill L (2002) Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology, 6, Online article #11: <http://www.consecol.org/vol16/iss11/art11>
- Gabrielsen GW, Smith EN (1995) Physiological responses of wildlife to disturbance. In: Gabrielsen GW, Smith EN (eds) Wildlife and recreationists: coexistence through management and research. Island Press, Washington, DC, pp 95–107
- González Díaz EF (1972) Descripción geológica de la Hoja 30-d, Payún Matru (Mendoza). Carta Geológica Económica de la República Argentina, Boletín 130. Dirección Nacional de Geología y Minería, Buenos Aires
- Hoogland JL (1981) The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). Ecology 62:252–272
- Ims RA, Yoccoz NG (1997) Ecological methodology: study design and statistical analysis. University of Oslo, Norway
- Jeppesen JL (1987) Impact of human disturbance on home range movements and activity of red deer *Cervus elaphus* in a Danish environment. Dan Rev Game Biol 13:1–38
- Kilgo JC, Labisky RF, Fritzen DE (1998) Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. Conserv Biol 12:1359–1364
- Kufeld RC, Bowden DC, Schrupp DL (1988) Influence of hunting on movements of female mule deer. J Range Manag 41:70–72
- LaGory KE (1987) The influence of habitat and group characteristics on the alarm and flight response of white-tailed deer. Anim Behav 35:20–25
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640
- Lingle S, Pellis SM (2002) Fight or flight? Antipredator behavior and the escalation of coyote encounters with deer. Oecologia 131:154–164
- Lingle S, Wilson WF (2001) Detection and avoidance of predators in white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*). Ethology 107:125–147
- Maki AW (1992) Of measured risk: the environmental impacts of the Prudhoe Bay, Alaska, oil field. Annu Rev Environ Toxicol Chem 11:1691–1707
- Malo JE, Acebes P, Traba J (2011) Measuring ungulate tolerance to human with flight distance: a reliable visitor management tool? Biodivers Conserv 20:3477–3488
- Marino A, Baldi R (2008) Vigilance patterns of territorial guanacos (*Lama guanicoe*): the role of reproductive interests and predation risk. Ethology 114:413–423
- Marino A, Johnson A (2012) Behavioural response of free-ranging guanacos (*Lama guanicoe*) to land-use change: habituation to motorised vehicles in a recently created reserve. Wildl Res 39:503–511
- Martínez Carretero E (2004) Provincia Fitogeográfica de la Payunia. Bol Soc Argent Bot 39:195–223
- Martínez E, Dalmaso A (1993) Flora y vegetación. Diseño del plan de manejo para la Reserva La Payunia (Mendoza, Argentina). Multequina 2:19–22
- Miller KA, Gamer JP, Mench JA (2006) Is fearfulness a trait that can be measured with behavioural tests? A validation of four fear tests for Japanese quail. Anim Behav 71:1323–1334
- Pearce JM (2008) Animal learning & cognition. An introduction, 3rd edn. Psychology Press, Hove
- Picton HD (1999) Energetic cost of wildlife displacement by winter recreationists. In: Olliff T, Legg K, Kaeding B (eds) Effects of winter recreation on wildlife of the Greater Area: a literature review and assessment. Report to the Greater Yellowstone Coordinating Committee. Yellowstone National Park, Wyoming, pp 135–144
- Pomerantz GA, Decker DJ, Goff GR, Purdy KG (1988) Assessing impact of recreation on wildlife: a classification scheme. Wildl Soc B 16:58–62
- Puig S, Videla F, Cona MI, Monge SA (1996) Use of food availability by guanaco (*Lama guanicoe*) and livestock in Northern Patagonia (Mendoza, Argentina). J Arid Environ 47:291–308
- Puig S, Videla F, Cona M (1997) Diet and abundance of the guanaco (*Lama guanicoe*) in four habitats of northern Patagonia, Argentina. J Arid Environ 36:343–357
- Puig S, Videla F, Cona MI, Monge SA (2001) Use of food availability by guanacos (*Lama guanicoe*) and livestock in Northern Patagonia (Mendoza, Argentina). J Arid Environ 47:291–308
- Puig S, Ferraris G, Superina M, Videla F (2003) Distribución de densidades de guanacos (*Lama guanicoe*) en el norte de la Reserva La Payunia y su área de influencia (Mendoza, Argentina). Multequina 12:37–48
- Recarte JM, Vincent JP, Hewison AJM (1998) Flight responses of park fallow deer to the human observer. Behav Process 14:65–72
- Ripple JW, Beschta RL (2008) Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. Biol Conserv 141: 1249–1256

- Sarno RJ, Grigione MM, Arvidson LD (2008) Lack of response of an open-habitat ungulate to the presence of predator urine. *Rev Chil Hist Nat* 81:179–183
- Sawyer H, Nielson R, Lindzey F, McDonald LL (2006) Winter habitat selection of mule deer before and during development of a natural gas field. *J Wildl Manag* 70:396–403
- Sawyer H, Kauffman M, Nielson RM (2009) Influence of well pad activity on winter habitat selection patterns of mule deer. *J Wildl Manag* 73:1052–1061
- Schroeder N (2013) Interacción entre el guanaco (*Lama guanicoe*) y herbívoros domésticos en el paisaje de La Payunia (sur de Mendoza, Argentina). PhD thesis, Universidad Nacional de Cuyo, Mendoza, Argentina
- Schroeder N, Ovejero R, Moreno P, Gregorio P, Taraborelli P, Matteucci S, Carmanchahi P (2013) Including species interactions in resource selection of guanacos and livestock in Northern Patagonia. *J Zool* 291:213–225
- Stankowich T (2008) Ungulate flight responses to human disturbance: a review and meta-analysis. *Biol Conserv* 141:2159–2173
- Stankowich T, Blumstein DT (2005) Fear in animals: a review and meta-analysis of risk assessment. *P Roy Soc B Biol Sci* 272:2627–2634
- Stankowich T, Coss RG (2006a) Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. *Behav Ecol* 17:246–254
- Stankowich T, Coss RG (2006b) Effects of risk assessment, predator behavior, and habitat on escape behavior in Columbian black-tailed deer. *Behav Ecol* 18:358–367
- Stankowich T, Coss RG (2007) The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. *P Roy Soc B Biol Sci* 274:175–182
- Steneck RS (2005) An ecological context for the role of large carnivores in conserving biodiversity. In: Ray JC, Redford KH, Steneck RS, Berger J (eds) Large carnivores and the conservation of biodiversity. Island Press, Washington, DC, pp 9–33
- Swenson JE (1982) Effects of hunting on habitat use by mule deer on mixed-grass prairie in Montana. *Wildl Soc B* 10:115–120
- Taraborelli P, Gregorio P, Moreno P, Novaro A, Carmanchahi P (2012) Cooperative vigilance: the guanaco's (*Lama guanicoe*) key anti-predator mechanism. *Behav Process* 91:82–89
- Taylor AR, Knight RL (2003) Wildlife responses to recreation and associated visitor perceptions. *Ecol Appl* 13:951–963
- Wilson P (1984) Puma predation on guanacos in Torres del Paine National Park, Chile. *Mammalia* 48:515–522
- Wirsing AJ, Cameron KE, Heithaus MR (2010) Spatial responses to predators vary with prey escape mode. *Anim Behav* 79: 531–537