

Are there different vigilance strategies between types of social units in *Lama guanicoe*?



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ABSTRACT

Group vigilance is a cooperative behaviour in social species that reduces individual risk of predation. *Lama guanicoe* is a social species of camelid performing cooperative vigilance, but little is known about the vigilance behaviour of different social units. We analysed the vigilance behaviour in different types of social units of *L. guanicoe*, to better understand the complexity of this behaviour. The best supported models for both the frequency of vigilance and the proportion of time vigilant included the type and size of social units as the most important predictors that affect the vigilance behaviour. Solitary males devoted proportionally more time in vigilance behaviour than family, mixed or bachelor groups, whereas females in female groups spent more time vigilant than guanacos in mixed groups. Frequency of vigilance was higher in family individuals and solitary males than in bachelor or mixed groups. It is likely that that in family and females groups, the presence of offspring would increase the vigilance behaviour to detect possible predators. Topography and habitat characteristics that determine the predation risk, affected vigilance behaviour of mixed groups and solitary males. Our results suggest that vigilance behaviour should not be generalized for this species, since there are differences between the types of social units, probably related to intrinsic characteristics of each one and the perception of risk.

1. Introduction

Vigilance plays a role enhancing the probability of a successful escape when a predator is detected. Triggered by predation threats, vigilance can be considered as a pre-emptive measure to reduce the risk of attack because a detected predator is less likely to pursue the attack (Caro, 2005). Vigilance can also be aimed at conspecifics. For instance, mating competition is strong in males of polygynous mammals, so vigilance also serves a pre-emptive role by preventing or avoiding encounters with competing individuals (Li et al., 2009; Ferretti et al., 2014; Pecorella et al., 2018). This complex behavior can differ between males and females, but in territorial males like *Aepyceros melampus* (impalas) and *Vicugna vicugna* (vicuñas) levels displayed are higher, indicating the costs related with territorial and female defense (Vilá and Cassini, 1994; Shorrocks and Aimee Cokayne, 2005; Marino and Baldi, 2008; Li et al., 2012).

Amongst other group living advantages, social species benefit from group vigilance, can reduce per capita vigilance time and increases per capita foraging time and other activities (Lima, 1995; Vasquez, 1997;

Ebensperger et al., 2006). These species could experience reduced risk of predation through several mechanisms, including (a) many-eyes effect: individuals benefit from group vigilance, which reduces per capita vigilance time and increases per capita foraging time (Hoogland, 1981; Lima, 1995; Vasquez, 1997; Beauchamp, 2015); (b) cooperative vigilance: implies the shared monitoring by emitting alert calls and adopting alarm postures that trigger responses in the other individuals (Hoogland, 1981; Beauchamp, 2015); (c) simple dilution of per capita risk: when the number of individuals per group is larger, the probability of being caught by a predator decreases (Devenport, 1989; Beauchamp, 2015); (d) the selfish herd effect: individuals locating themselves such that other group members become more vulnerable to attacks (Hoogland, 1981; Romey, 1997; Beauchamp, 2015); and (e) active group defence: when grouped individuals repel predators more efficiently than solitary-living animals (Pulliam and Caraco, 1984; Manning et al., 1995; Beauchamp, 2015). Several studies showed that the level of vigilance is influenced by the group size. In this sense, an inverse relationship between vigilance and group size has been reported in several gregarious ungulates (Underwood, 1982; Illius and

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Fitzgibbon, 1994; Mosca Torres et al., 2015) as well as in many species of birds (Beauchamp, 2008).

Guanacos (*Lama guanicoe*, Camelidae) are one of the wild dominant herbivores in the steppe and grassland ecosystems of the Andes and Patagonia regions of South America (Franklin, 1982a, 1983). The guanaco is a social species with different types of social units: family groups, bachelor groups, mixed groups, female groups and solitary males. Families are composed of a territorial male and one or more females with their offspring from that current year. Family members usually form highly cohesive and behaviourally synchronized units (Franklin, 1983; Taraborelli et al., 2012). Bachelors groups are composed mostly of adult males and yearlings, whereas in mixed groups there are individuals of both sexes from different age classes (Franklin, 1983). Mixed groups show low group cohesion, with distances among members greater than in bachelor and family groups (Franklin and Fritz, 1991; Marchetti et al., 1992; Ortega and Franklin, 1995; Marino, 2010; Taraborelli et al., 2012). Female groups include adult females, yearlings and offspring of both sexes without an adult male. Finally, solitary males are adult individuals seeking or defending a territory without females (Franklin, 1982a, 1983).

Taraborelli et al. (2012) suggested that the benefit of social grouping in guanacos, through their increased probability of avoiding predator, results from cooperative vigilance. This means that a predator could be detected earlier when approaching a group than when approaching solitary individuals and could, therefore, be avoided faster. Considering antipredator responses in family groups of this species, Iranzo et al. (2018) suggested that the group size was influenced by the occurrence of predators and by the perceived predation risk associated with habitat structure. On the other hand, Marino and Baldi (2008) found that male guanacos in these sorts of groups devoted more time scanning the surroundings and less time in feeding activities compared to females. Moreover, these authors stated that both sexes benefited from grouping by reducing the time invested in vigilance increasing foraging effort according to predation risk theory, but the factors affecting the time allocated differed between males and females. Despite much work on vigilance behaviour in guanacos, there is still very scarce information about vigilance among different social units.

The objective of this study was to analyse the vigilance in different types of social units of *L. guanicoe* (family groups, bachelor males, mixed groups, female groups and solitary males). We hypothesized that the different social units would differ in vigilance behaviour as a result of differences in group size and composition. We predicted that solitary males, family and female groups would devote more time to individual vigilance than bachelor or mixed groups. The most time spent in vigilance would be for looking after the breeding, considering that offspring are more likely to be predated.

2. Materials and methods

This study was carried out in La Payunia Provincial Reserve, in the south of Mendoza Province. La Payunia is located in central-west Argentina (36° 00' and 36° 36' S, and between 68° 34' and 69° 23' W, 1300–2000 masl (Candia et al., 1993; Puig et al., 2003). It has an area of 665,000-hectares 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 semiarid (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 corresponding to La Payunia phytogeographic province (Martínez Carretero, 2004). This Reserve holds the largest population of *L. guanicoe* of the central-west region of Argentina, which could reach about 26,000 animals in spring (Schroeder, 2013).

For this study we observed different social units in two sectors of the reserve, one at the Northeast (NE) and other at the Northwest (NW).

Both areas differ in the risk of predation, being greater in the NE area (Bolgeri and Novaro, 2010), in human activities performed (presence of an oil company in NW sector, and high traffic roads) and in topography (NE steep area). Mean size of families was 8 guanacos/group, and ranges from 3 to 19 adults with 1 to 3 offspring. The average number of individuals in bachelors groups was 9, 3 to 26 individuals with 1 to 6 yearlings. Females groups ranged from 4 to 23 animals with an average of 16 individuals. We could found 1 to 17 yearlings and 1 to 2 offspring within this social unit. Finally, the average size of mixed groups (including adult females and males) was 27 guanacos, and ranged from 11 to 40 adults.

The main predator of guanacos in La Payunia reserve is the puma (*Puma concolor*). Pumas were observed chasing mostly adult guanacos (78%) and predation was related to the relative availability of guanacos (Bolgeri and Novaro, 2010).

2.1. Behavioural records

Data were collected from 8:00 to 20:30 during the springs and summers of 2009, 2010 and 2012. Observations were made using a 60 mm spotting scope at 150–1000 m away from the animals to minimize disturbance. As there is no obvious sexual dimorphism, guanaco sex can be assessed only after observing the testes (Franklin, 1983). According to the presence/absence of males we were able to determine the type of social unit. In order to define our study groups, at the beginning of each observation session, we excluded from a group all individuals that were more than 300 m away from their neighbours (Marino and Baldi, 2008). Sampling was carried out along different paths across the Reserve to ensure the same social group was not sampled more than once on a given day. The observations and social unit categorisation were only made about individuals that were accurately identified as female or male. Individuals were randomly chosen within the social unit, and only one individual was observed per group.

Guanaco's behaviour was categorized as vigilance when an individual was standing, watching with its head raised and erect ears looking towards the stimulus or threat (Lingle and Pellis, 2002; Young and Franklin, 2004; Stankowich and Coss, 2006; Taraborelli et al., 2011). This behaviour can also include alarm calls like sharp shouts (Franklin, 1982b; Taraborelli et al., 2011).

We performed focal sampling (focal-continuous sampling, Altmann, 1974; Martin and Bateson, 1993; Lehner, 1996) to record in a digital recorder the time devoted in vigilance behaviour by a focal individual during 12 min. Frequency is the total number of occurrences of vigilance behaviour (Martin and Bateson, 1993) during a focal sampling. The proportion is the duration of all vigilance bouts expressed as a percentage of total sampling time (Martin and Bateson, 1993). We observed individuals of 9 family groups, 18 bachelor groups, 28 female groups, 21 mixed groups and 64 solitary males distributed between NE and NW sectors during the 3-year study period. To reduce the probability that the same individual was observed more than once, only one individual was observed per group. We completed a total of 140 focal observations.

2.2. Statistical analysis

All statistical analyses were performed in R 3.4.2 (R Development Core Team, 2017). We used generalized linear mixed-effects models (GLMM), fit by the function glmer (package lme4; Bates and Maechler, 2009) with logit link function and binomial error distribution for analysing the proportion of time in vigilance behaviour by guanacos, and GLMM with log link function and Poisson error distribution for analysing the frequency of time an individual raised his head to look out. As fixed factors, we included social unit size, social unit type and sector of the Reserve (NE and NW). We also included the interaction between social unit size and sector of the Reserve; non-significant interactions were then removed from the models. Season of the year (summer and

spring) nested in year of sampling was included as random factor. We performed a post hoc test, using the `glht` function (“multcomp” package: Hothorn et al., 2008) to compare each social unit with every other social unit in a pairwise manner. Due to the potential effect of group size on vigilance behaviour, we first measured the effect of group size on the proportion of time vigilant and then with the standardized residuals as the response variable, we tested the effects of social units and sector of the Reserve in a 2-way ANOVA with the interaction between both predictors.

Finally, different GLMMs for each social unit were used to detect variations in the proportion and frequency of vigilance, related to unit size and sector of the Reserve. In models performed for mixed groups, we included the variable “sex” as fixed factor to detect possible differences between females and males in vigilance behaviour. The random effect was the nested effect of seasons within year of sampling.

Homogeneity of variance and normality of error were checked using plots and applying normality tests to the residuals of the models. Overdispersion was tested with the `overdisp_fun` function (Bolker, 2018). To select the best model we first built a set of possible models using the `drop1` and ANOVA functions (STATS package in R) to implement sequential Chi-tests using analysis of deviance. Then, with the `model.avg` function (“MuMIn” package: Barton, 2018) we averaged our set of GLMMs identified a priori to calculate the relative importance for each variable included in the model (Burnham and Anderson, 2002). Therefore, applying model averaging we obtained the weighted value for each predictor, the standard error, and its *z* and *p*-values to identify significant effects that best explains the behaviour of the response variable, given our data and the set of possible models. (Akaike, 1974; Burnham and Anderson, 2002).

3. Results

Detected variations in the proportion of time vigilant were explained by a model that included the social unit size and type, whereas sector of the reserve and its interaction with the social unit had a marginally significant effect (Table 1). Vigilance decreased as social unit size increased. Solitary males spent proportionally more time vigilant than guanacos in families, bachelor and mixed groups (Table 1), whereas females in female groups devoted more time in vigilance than individuals in mixed groups ($Z = -2.21, p = 0.035$) (Fig. 1). Residual vigilance (vigilance after remove the group-size effect) was affected only by social unit type (2-way ANOVA: $F = 2.83, p = 0.049$), particularly due to solitary males who spent more time

vigilant than guanacos belonging to mixed groups (Table 2).

Frequency of vigilance was only affected by social unit type, where solitary males raised their head to look around more frequently than guanacos of mixed and bachelor groups (Table 1). Moreover, results of comparisons among social unit type shown that frequency of vigilance of guanacos from family groups was higher than frequencies observed in mixed and bachelor individuals ($Z = -2.39, p = 0.017$ and $Z = -2.14, p = 0.032$, respectively) (Fig. 2). Residual vigilance was not affected neither by the sector of the Reserve nor by social unit type, except that the frequency of vigilance of solitary males was higher than in bachelor guanacos (Table 2).

In relation to the vigilance behaviour observed in different social units types, we detected that family individuals spent proportionally more time vigilant as group size increased (Table 3). Individuals of mixed groups devoted proportionally more time vigilant at the NW than at NE sector of the Reserve, whereas solitary males were less vigilant at the NW than at NE sector (Table 3). Frequency of vigilance was not affected by group size, sector and sex predictors (the last predictor was only included in mixed groups model). In the other social units the proportion and frequency of vigilance were not affected by any of the predictors considered in this study (Table 3).

4. Discussion and conclusions

Our results suggest that the vigilance response cannot be generalized for *Lama guanicoe*, since the best supported models for both the proportion of time vigilant and the frequency of vigilance, included the type of social unit as the most important predictor that affects the vigilance behaviour. As expected, solitary males showed the highest proportion of time devoted to vigilance, which could be explained because solitary guanacos need to defend a territory from competitors to attract females and perhaps but they are also alone to defend themselves from predators. This level of individual vigilance is contrary to that observed in bachelors and mixed groups, where the time allocated to vigilance per capita was lower than that in solitaries. This is expected since these groups are not territorial. But it is also advantageous to have multiple eyes scanning the surroundings as well as creating a dilution effect to protect individuals from being chased by a predator (Hoogland, 1981). Taraborelli et al. (2012) found that larger groups were more likely to spot a predator than smaller groups and hence they were more likely to flee. We found that groups with more members responded earlier and at a greater distance from the predator, due to an earlier detection of terrestrial predators. Additionally, these groups

Table 1
Explanatory variables (average) influencing the proportion of time in vigilance behaviour and frequency of vigilance.

	Proportion of vigilance ^a			Frequency of vigilance ^b		
	Estimate	Adjusted SE	<i>p</i> -value	Estimate	Adjusted SE	<i>p</i> -value
Intercept	-0.883	0.278	0.002	2.177	0.094	< 0.001
Social unit size	-0.025	0.012	0.043	-0.007	0.005	0.221
Social unit: Family group ¹	-1.062	0.538	0.048	0.065	0.240	0.786
Social unit: Female group ¹	-0.634	0.499	0.204	-0.195	0.170	0.252
Social unit: Mixed group ¹	-2.164	1.012	0.032	-0.593	0.295	0.044
Social unit: Bachelor group ¹	-1.533	0.510	0.003	-0.590	0.237	0.013
Sector: NW ²	-0.556	0.297	0.062	-0.018	0.147	0.905
Social unit size * NW ³	-0.012	0.023	0.592	-0.008	0.013	0.528
Family group * NW ⁴	-0.684	2.111	0.745	-0.938	1.072	0.382
Female group * NW ⁴	0.264	0.589	0.654	0.275	0.406	0.499
Mixed group * NW ⁴	1.977	1.061	0.063	0.109	0.584	0.852
Bachelor group * NW ⁴	0.770	0.820	0.347	-0.269	0.560	0.631

^a Random factor of GLMM with Binomial distribution: Season of the year nested in year of sampling.

^b Random factor of GLMM with Poisson distribution: Season of the year nested in year of sampling.

¹ Reference level of social unit type: Solitary male.

² Reference level of sector of the Reserve: NE.

³ Reference level of the interaction social unit size * sector of the Reserve: social unit size * NE.

⁴ Reference level of the interaction social unit type * sector of the Reserve: solitary male * NE.

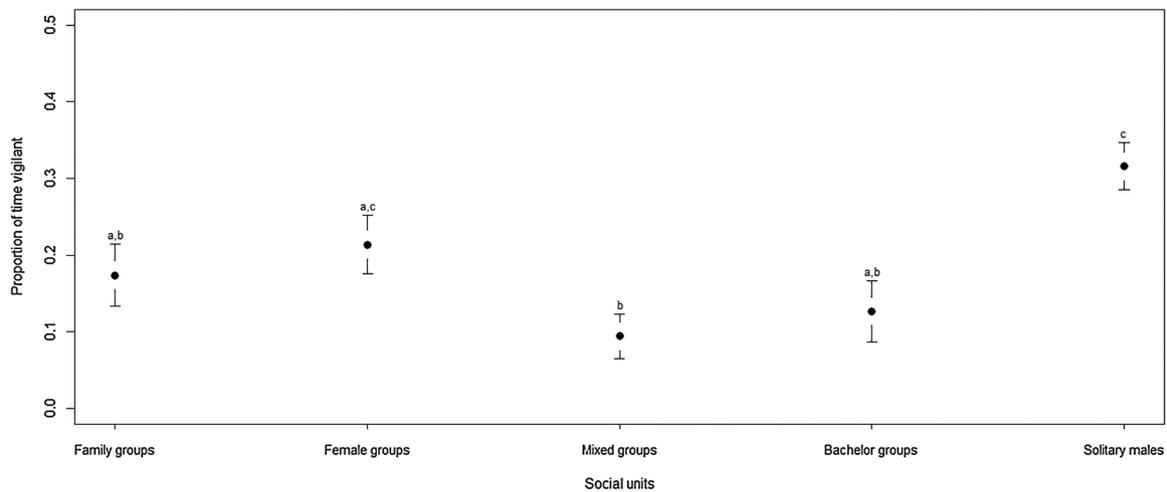


Fig. 1. Proportion of time vigilant between different social units. Social units that differ significantly ($p \leq 0.05$) are denoted with different letters.

Table 2

Explanatory variables (average) influencing the residual vigilance of proportion of time vigilant and frequency of vigilance of guanacos.

	Proportion of vigilance			Frequency of vigilance		
	Estimate	Adjusted SE	p-value	Estimate	Adjusted SE	p-value
Intercept	0.172	0.205	0.402	-0.076	0.147	0.604
Social unit: Family group ¹	-0.611	0.375	0.103	0.207	0.354	0.559
Social unit: Female group ¹	-0.321	0.245	0.190	-0.101	0.225	0.653
Social unit: Mixed group ¹	-0.218	0.284	0.442	-0.093	0.249	0.711
Social unit: Bachelor group ¹	-0.783	0.291	0.007	-0.560	0.266	0.035
Sector: NW ²	-0.185	0.239	0.438	0.008	0.176	0.962
Family group * NW ³	-0.160	1.091	0.883	-1.051	1.084	0.332
Female group * NW ³	0.379	0.517	0.463	0.366	0.513	0.476
Mixed group * NW ³	1.017	0.528	0.054	-0.033	0.524	0.950
Bachelor group * NW ³	0.678	0.594	0.253	-0.292	0.590	0.620

¹ Reference level of social unit type: Solitary male.

² Reference level of sector of the Reserve: NE.

³ Reference level of the interaction social unit type * sector of the Reserve: solitary male * NE.

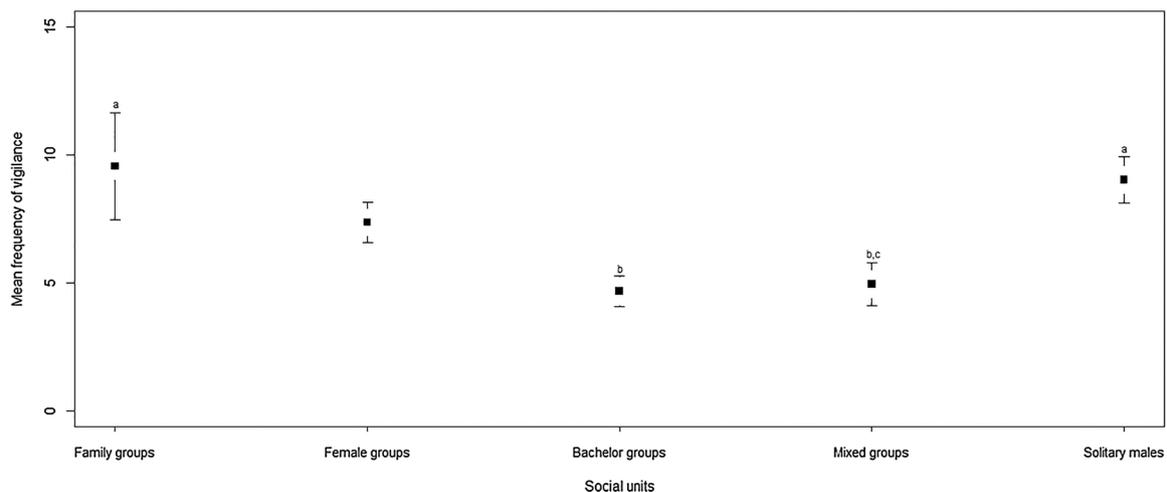


Fig. 2. Mean frequency of vigilance between different social units. Social units that differ significantly ($p \leq 0.05$) are denoted with different letters.

showed longer distances moved during their flight. Taraborelli et al. (2012) concluded that cooperative vigilance would be the dominant antipredator mechanism used by guanacos. Guanaco communication through alert posture and vocalizations, which are low cost alarm signals for other guanacos, benefits the individual by increasing the number of guanacos fleeing when a potential predator is sighted. And Iranzo et al. (2018) suggested that a mix of predator occurrence and

perceived predation risk influences guanaco grouping behaviour.

Family groups were the only social unit that showed a positive association between group size and the proportion of time of vigilance. Family groups are territorial hence, the time that individuals devote to vigilance is considerable giving the presence of offspring in the groups, which are the most prone to be predated. Taraborelli et al. (2012) studied the guanaco antipredator response considering all social units,

Table 3

Explanatory variables (average) influencing the proportion of time in vigilance behaviour and frequency of vigilance of different social unit types: family, female, mixed and bachelor groups or solitary males.

	Proportion of vigilance ^a			Frequency of vigilance ^b		
	Estimate	Adjusted SE	p-value	Estimate	Adjusted SE	p-value
Family groups						
Intercept	-2.296	0.635	< 0.001	2.108	0.547	< 0.001
Social unit size	0.023	0.012	0.044	0.018	0.055	0.734
Sector: NW ¹	-0.458	1.625	0.778	-0.900	1.601	0.574
Social unit size * NW ²	-	-	-	-	-	-
Female groups						
Intercept	-1.008	0.506	0.046	1.984	0.306	< 0.001
Social unit size	-0.030	0.058	0.608	-0.020	0.030	0.499
Sector: NW ¹	-0.327	0.583	0.575	0.270	0.314	0.391
Social unit size * NW ²	0.017	0.157	0.912	-0.039	0.078	0.618
Mixed group						
Intercept	-3.243	0.961	0.001	1.588	0.277	< 0.001
Social unit size	-0.012	0.018	0.508	-0.003	0.004	0.536
Sector: NW ¹	1.834	0.932	0.049	0.063	0.322	0.845
Sex: Male	1.053	2.488	0.672	0.082	0.287	0.790
Social unit size * NW ²	-0.012	0.026	0.640	-0.005	0.010	0.613
Male * NW ³	-2.587	2.943	0.379	-0.496	0.701	0.479
Bachelor groups						
Intercept	-1.956	0.528	< 0.001	1.716	0.236	< 0.001
Social unit size	-0.023	0.052	0.658	-0.014	0.019	0.476
Sector: NW ¹	0.153	0.522	0.769	-0.207	0.528	0.695
Social unit size * NW ²	-0.301	0.347	0.385	-0.181	0.126	0.150
Solitary males						
Intercept	-0.471	0.307	0.126	2.202	0.133	< 0.001
Sector: NW ¹	-0.607	0.311	0.050	-0.015	0.233	0.948

^a Random factor of GLMM with Binomial distribution: Season of the year nested in year of sampling.

^b Random factor of GLMM with Poisson distribution: Season of the year nested in year of sampling.

¹ Reference level of sector of the Reserve: NE.

² Reference level of the interaction social unit size * sector of the Reserve: social unit size * NE.

³ Reference level of guanaco sex: Female.

and evidenced that both detection of a surrogate predator and flight distances increased with a greater number of guanacos per group. Also, Malo et al. (2011) found a group-size effect on the probability of flight response in guanacos. In accordance to our results, it has been suggested that the benefit of group size arise in family groups when the females are at shorter distance between them within the group (Marino and Baldi, 2008). Moreover, Iranzo et al. (2018) evaluated vigilance through the number of guanacos displaying vigilance behaviour in family groups and concluded that this pattern is affected by group size during the breeding season. Family groups seem to behave in an intermediate way between the solitary and the other social units. Marino and Baldi (2008) observed that the presence of offspring increased the level of alertness to possible predators in family groups of guanacos in Patagonia. Moreover, Marino and Johnson (2012) found in a sedentary population that groups with at least one young among their members had a significantly greater probability to flee than groups with only adults. In the same sense, Taraborelli et al. (2014) found that the alert distance was greater and the assessment time was shorter when offspring were present in the groups. This suggests that guanacos are more alert when offspring are present in the group. This could be an ecological strategy with a high adaptive value, suggesting that group composition has an influence on behavioural responses, and that groups with young individuals are more cautious than those without them. Similar behaviour was registered in females of other ungulate species like the *Rangifer tarandus* (caribou, Stankowich, 2008), *Odocoileus virginianus* (white-tailed deer), *Odocoileus hemionus* (mule deer, Lingle and Pellis, 2002) and *Dama dama* (fallow deer, Recarte et al., 1998). Conversely, wild plains zebras males (*Equus quagga*) resulted more vigilant than females. This equid species, like *Lama guanicoe*, is polygynous, but in contrast males defend mating rights to small year-round harems, and the between-gender difference in vigilance is explained by the direct interference between males that requires them to allocate time in

monitoring rivals (Rubenstein and Hack, 2004; Barnier et al., 2016).

The ungulates respond to predation risk displaying proactive responses (aimed to respond to long-term variation in risk, i.e. grouping patterns) and reactive responses (directed to short-term variation in risk, i.e. intense vigilance) (Creel et al., 2014). Our results lead us to conclude that *Lama guanicoe* is a good model to test predation risk hypotheses because is a gregarious species with a flexible social organization. This particular feature allow to detect different intensities of the same behaviour or different behaviours showed among the social units to manage with the same stimulus, as for example being stalked by the same predator, the puma. Further research is needed to understand predator-prey interactions and the relationship between social units and antipredator behaviours in Artiodactyla with flexible social organization.

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