



# Vigilance behaviour of the year-round territorial vicuña (*Vicugna vicugna*) outside the breeding season: Influence of group size, social factors and distance to a water source

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## ABSTRACT

We conducted focal observations of vicuña, a year-around territorial mammal, to compare vigilance behaviour between territorial and bachelor males outside the reproductive season. We hypothesized that the time spent vigilant would depend on male social status, considering the potential effects of several variables: sampling year, group size, distances to the nearest neighbour and to a *vega* (mountain wetland). We fit GLM models to assess how these variables, and their interactions, affected time allocation of territorial and bachelor males. We found non significant differences between territorial and bachelor males in the time devoted to vigilance behaviour. Vigilance of territorial males was influenced by the sampling year and the distance to the *vega*. In turn, vigilance in bachelor males was influenced mainly by the sampling year, the group size and the distance to the *vega*. Our results suggest that sampling year and distance to the *vega* are more important than social factors in conditioning the behaviour of male vicuñas, during the non-reproductive season. Future studies of behaviour in water-dependant ungulates, should consider the influence of water and forage availabilities, and the interactions between group size and other variables.

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## 1. Introduction

Vigilance behaviour has been historically considered as an antipredator defence (Pulliam, 1973), but is also associated with protection against competitors, which are usually conspecifics (Elgar, 1989; Alberts, 1994; Yáber and Herrera, 1994; Artiss and Martin, 1995; Slotow and Rothstein, 1995). Other factors such as social status might influence the level of vigilance (Bertram, 1980; Cameron and Du Toit, 2005). In particular, in some ungulate species, territorial males are more vigilant than non-territorial males, because leader males compete for females and must avoid same-sex aggression from conspecifics (Roberts, 1988; Artiss and Martin, 1995).

In addition to social status, group size may influence the level of vigilance of gregarious mammals. Specifically, an inverse relationship between vigilance and group size in ungulates has been reported in several studies. Many of those studies documented that larger groups detect a predator sooner and that individual vigilance rates are lower for animals living in large groups (Underwood, 1982; Elgar, 1989; Illius and Fitzgibbon, 1994; Beauchamp, 2003). However, these effects of group size are not universal, as it depends on species identity, season, local environment conditions and social factors (Elgar, 1989; Bednekoff and Ritter, 1994; Burger and Gochfield, 1994; Shorrocks and Cockayne, 2005; Périquet et al., 2010). Indeed, some studies found that individuals responded more to the proximity of neighbours (social factors) than to group size, suggesting a negative influence of nearest neighbours on the amount of time devoted to vigilance (Treves, 1998; Hirsch, 2002; Cameron and du Toit, 2005).

Overall, it is assumed that vigilance behaviour is not mutually exclusive with processing food but that it usually is with food searching and handling (Frid, 1997). Therefore, being vigilant is costly in terms of energy gain and rate of food intake (Caraco,

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1979; Underwood, 1982). During the dry season, when resource availability is low, the trade-off between vigilance and food search is specially strong (Illus and Fitzgibbon, 1994). In this context of resources scarcity, animals living in groups would tend to be spaced from each other to reduce foraging interference, taking greater risks as hunger levels increase (Thouless, 1990). In water-dependant species living in dry environments, foraging near a waterhole can be detrimental in terms of an increased intra-specific interactions. On the other hand, the presence of other individuals near a water source may decrease the perceived risk of predation, allowing an animal to reduce the time it spends vigilant for potential predators (Fitzgibbon, 1990).

The vicuña is a polygynous ungulate with a stable social structure: familial groups with a territorial male and several females with their offspring, bachelor groups composed of non-territorial males and, solo individuals with or without an established territory (Koford, 1957; Franklin, 1983). Territorial males defend a high quality territory all year round from the intrusion of other males and tend to remain distant from their group (Vilá, 1995). They are also more aggressive than any other individual of this species and display a strong intolerance towards bachelors (Vilá, 1992, 1995). In contrast, bachelor males, usually occupy marginal areas with low-quality forage and perform different activities synchronously (Franklin, 1983; Cajal 1985; Vilá and Cassini, 1993; Mosca Torres and Puig, 2010).

Even though vicuñas are adapted to desert conditions, they drink water almost every day (Koford, 1957; Franklin, 1983), specially during drought conditions (Vilá and Cassini, 1993; Mosca Torres and Puig, 2012). In our study site water availability was scarce and only one *vega* (mountain wetland) was used by all social groups simultaneously (Mosca Torres and Puig, 2012).

During the reproductive season (wet season), the vigilance behaviour of territorial males increased and grazing decreased with the number of females in the families, suggesting that males increased their mating success through vigilance activities and incurred a high cost of decreased time to feed (Vilá and Cassini, 1994). Moreover, during the reproductive season is probably to observe bachelors initiating aggressions towards territorial males and becoming in the new territorial male (Vilá, 1992). However, little is known about the vigilance behaviour of vicuñas outside the breeding season (dry season), although several authors observed agonistic interactions between territorial and bachelor males in different vicuña populations in this season (Cassini et al., 2009).

We investigated vigilance behaviour in territorial and bachelor male vicuñas outside the reproductive season that co-occur with the decrease of resource availability. First, we hypothesized that the time spent vigilant will be different according to the type of male (territorial and bachelor males), taking into account the differences in social status and reproductive interests. Therefore, and related to territorial defence, we predict that territorial males will spend more time vigilant than bachelors and as number of females in the group increase, at the expense of time devoted to other activities. Second, we hypothesized that bachelor males will benefit from the anti-predatory advantages of living in group. Thus, as group size increases we expect that bachelors will devote less time to being vigilant and more time to other activities such as eating and walking in search of food. Third, because social interactions may influence vicuñas' behaviour, we investigated whether the time invested by bachelor vicuñas in vigilance is affected by distance to the nearest neighbour. Given the decrease in forage availability during the dry season in the study site, we predicted that an individual would devote more time to foraging as it moves away from its nearest neighbour to reduce foraging interference, taking greater risks as hunger levels increase. Thus, the time spent vigilant would decrease as inter-individual distance amongst vicuñas increases, in contrast to the time devoted to foraging. We did not consider this

variable for territorial male models, because they were generally far apart from the rest of the group without any sign of cohesion as observed in bachelor groups. Finally, we tested whether the presence of many conspecific competitors in the *vega* influences the amount of time devoted to vigilance by both, territorial and bachelor males. We expected that territorial males would spend more time in vigilance in the *vega* than away from it due to the presence of potential conspecific competitors, while bachelors would spend less time in vigilance in the *vega* because of the presence of many individuals that may decrease the perceived risk of predation.

## 2. Material and methods

The study was carried out in Los Andes Reserve (14,400 km<sup>2</sup>), a protected area in the West of Salta province (Argentina), within the Puna biogeographic province (Cabrera and Willink, 1980). The climate is cool and dry, with broad daily and seasonal temperature ranges (−2 °C to 18 °C in summer, −12 °C to 16 °C in winter), low rainfall (130 mm/yr) occurring only in summer (December–March) and intense frosts. Food availability is extremely limited during the dry season (winter), when forage is too mature and of low quality (San Martín and Bryant, 1989; Van Saun, 2006).

The selected sampling site is located in a place called “Unquillal” located at 24°27'S and 67°12'W, with an approximate area of 11.6 km<sup>2</sup>. Density of vicuñas in the study area is 22.2 indiv./km<sup>2</sup>, comparatively much higher than the surrounding areas (0.75 indiv./km<sup>2</sup>, Baigún et al., 2008). The vegetation is dominated by a low shrub layer, complemented by several grasses of the Poaceae family (*Stipa*, *Poa* and *Festuca*). A *vega* (permanent mountain wetland) was present on a steep slope (>30°) with a dense layer of species of Cyperaceae and Juncaceae families, accompanied by some grasses. The *vega* was the only water source available for vicuñas of different social categories. During the winters of 2006 and 2007, plant cover was scarce (28%), whereas plant diversity and forage availability decreased compared to the reproductive season (Mosca Torres, 2010).

Territorial and bachelor male vicuñas were randomly selected using focal animal sampling (Altmann, 1974; Martin and Bateson, 1991). Territorial males were distinguished from bachelor males because they tend to be some metres away from females and calves of the group, often showing territorial displays towards other vicuñas, as chases and defecating (Franklin, 1983; Marino and Baldi, 2014). In contrast, bachelor groups are composed mostly by juvenile and adult males who perform different activities synchronously and are often aggregated (Vilá and Cassini, 1993; Marino and Baldi, 2014). Group size was recorded as the number of individuals in the group at the beginning of a sampling. The distance between individuals was used to determine the group size only for bachelor groups because territorial males tend to be away from the rest of the group as was mentioned before. We considered an individual as part of a bachelor group if it was less as 100 m away from the rest. Familial individuals were classified by sex; although females and calves were not sampled in this study, the number of both was recorded. We measured the distance to the nearest neighbour in vicuña units (VU), each unit corresponding to the length of an adult vicuña, approximately 1 m. Finally, we categorized the distance to the *vega* as: in the *vega* (0–5 m), close (5–50 m), medium (50–150 m) and away (>150 m) from it.

The time devoted to different activities by both types of males was recorded during 15 min. We observed an average of five territorial and bachelor males per day and no individual of the same group was sampled twice a day. Vicuñas at the study site were not marked, therefore repeated sampling of the same individual was actively avoided by selecting subsequent territorial males foraging away from the previous male. To reduce the probability that the

same individual was observed more than once in bachelor groups, only one to three individuals were observed in each group.

We considered an animal as being vigilant when it stood still and raised its head up, scanning its surroundings, and feeding when vicuñas were stationary (or moving along slowly) with their heads down, ingesting vegetation. Other categories recorded were: walking, when individuals moved slowly over three steps, with the head up, and “other” which generally includes rare or short-term activities, such as running, alarm vocalizations, grooming, and defecation. To test our hypotheses, we concentrated on vigilance, foraging and walking behaviours, which together account for up to 95% of time in activity for both territorial and bachelor males.

Observations were carried out from a hill using binoculars (8 × 42) or a telescope (12–36 × 50), and a tape recorder to record the time spent by males at different behavioural activities. We recorded observations only during the activity time of the vicuñas, excluding resting animals. Winter sampling was from 8 am to 5 pm for 10 days of 2006 and 8 days of 2007. These differences in the number of sampling days between years were due to the worse weather conditions in 2007.

2.1. Statistical analyses

To conduct the comparative analysis of the proportion of time spent vigilant, feeding and walking between territorial (n = 51) and bachelor males (n = 50) we fitted generalised linear models (GLM) (McCullagh and Nelder, 1989) with a Binomial error distribution. Then, we fitted separated models for territorial and bachelor males to test the rest of our predictions. The response variables of each model were the proportion of time spent vigilant, foraging and walking during the sample period. We tested five independent factors: sampling year, group size, distance to the nearest neighbour (bachelor models only) and distance to the vega. Sampling year was included in the models because forage availability was higher in 2006 than in 2007 (Mosca Torres, 2010). Therefore, behaviour of vicuñas could be affected by the detrimental of food resources. Indeed, interactions between group size and sampling year; group size and distance to the vega; and group size and distance to the nearest neighbour, were also added to the models. In the GLMs performed for territorial males, we added the number of females as independent factor. We assumed a binomial distribution of the error structure for all models, which was confirmed by graphical methods.

We performed the GLMs using R statistical software version 3.1.0 (package “MASS”) (Development Core Team, 2012). Model selection was based on the Akaike information criterion (AIC) (Akaike, 1974) with function “stepAIC” (package “bbmle”). This

function performs a stepwise model selection by AIC values, selecting the best one (with the lowest AIC value).

3. Results

3.1. Differences in time allocation between territorial and bachelor males

Behavioural data were not normally distributed (Shapiro test for normality, p < 0.001, and Barlett–Box F test for homoscedasticity, p < 0.05), and therefore medians and inter-quartiles ranges are used. Of the 101 individuals observed during the study, 51 were territorial males and 50 bachelor males. The median size of family groups was 4 individuals (range 3–10), typically composed of one male, two females and one offspring (abbreviated formula: 1-2-1). Bachelor groups varied in number from 3 to 50 animals, with a median of 8 individuals.

Territorial and bachelor males devoted a median 60.0% (6.6–100; 0.0–100, respectively) of their time foraging. The median time vigilant by territorial males was 20.0% (0.0–80) and they only spent 6.6% of their time walking (0.0–66.6), whereas bachelors devoted a median 13.3% (0.0–86.7) of their time vigilant, and 6.7% (0.0–86.7) walking.

Models that compared vigilant, foraging and walking behaviours between territorial and bachelor males did not show any differences between males (Table 1), except that bachelors devoted more time to walk than territorial males in 2007 than in 2006 (Table 1 and Fig. 1). Two models of vigilance received a total 76% of the model weight (Appendix A), with very similar structures, differing only by the inclusion of the no significant interaction term “Year\*Group size” in the second best-supported model (Appendix C). Male type factor was a weak predictor and was excluded from the three first best-supported models. In general, individuals spent more time vigilant in 2006 than in 2007 and with increasing distance to the nearest neighbour (Table 1), whereas time devoted to vigilance decrease when vicuñas were at more than 50 m from the vega (Fig. 1 and Table 1).

The best-supported model of foraging behaviour received 55% of the model-selection weight, with an ΔAIC score 1.9 units better than the second best-supported model (21% of weight; Appendix A). Foraging was strongly affected by the year of sampling, since during 2007 vicuñas foraged proportionally more time than in 2006 (Table 1).

Two models of walking received similar support from the data, with weights of 80% and ΔAIC scores 2.7 with similar structures (Appendix A). Proportion of time walking was related to several factors as group size, distance to the vega and the interaction between

Table 1

Generalised linear models comparing the proportion of time spent vigilant, foraging and walking between territorial and bachelor vicuña males. The presented models are the most parsimonious of a general model (Appendix A). The response variables are the proportion of time vigilant, foraging and walking with a binomial distribution.

	Vigilant time		Foraging time		Walking time	
	ζ	p-value	ζ	p-value	ζ	p-value
Variables: level						
Male type: Bachelor <sup>a</sup>	–	–	0.029	0.933	0.508	0.085
Year: 2007 <sup>b</sup>	–0.402	0.010	0.572	<0.001	–0.454	0.238
Group size	–0.025	0.116	–	–	–0.088	0.015
Distance to the nearest neighbour	0.186	0.028	–0.149	0.155	–	–
Distance to the vega: 10–50 m <sup>c</sup>	–0.263	0.159	–0.347	0.274	1.303	0.003
Distance to the vega: 50–150 m <sup>c</sup>	–0.550	0.005	–0.307	0.324	1.167	0.010
Distance to the vega: >150 m <sup>c</sup>	–1.438	<0.001	–0.426	0.384	0.948	0.052
Male type: Bachelor × Year: 2007	–	–	–	–	1.206	0.018
Male type: Bachelor × Distance to the vega: 10–50 m <sup>c</sup>	–	–	–0.590	0.188	–	–
Male type: Bachelor × Distance to the vega: 50–150 m <sup>c</sup>	–	–	–0.052	0.909	–	–
Male type: Bachelor × Distance to the vega: >150 m <sup>c</sup>	–	–	0.673	0.252	–	–

<sup>a</sup> Male type reference level is territorial male.

<sup>b</sup> Year reference level is 2006.

<sup>c</sup> Distance to the vega reference level is 0 m.

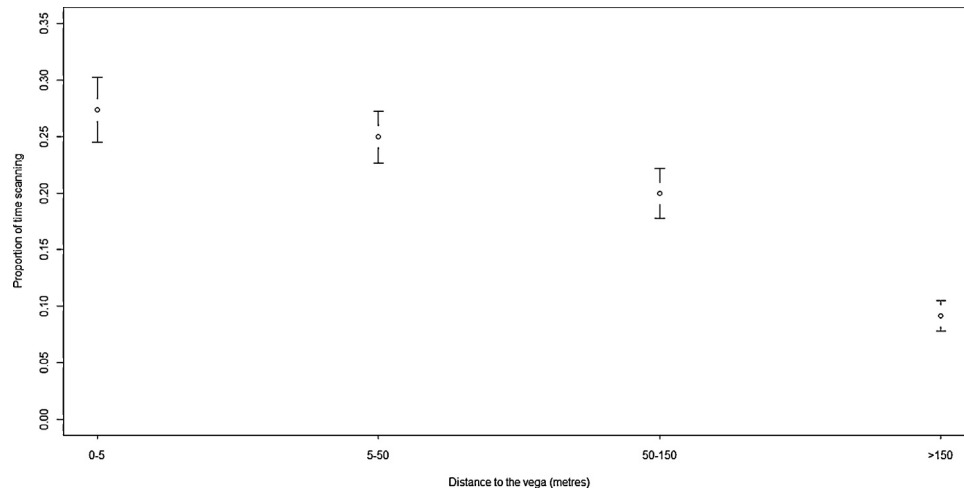


Fig. 1. Proportion of time spent vigilant by vicuña males when (a) the distance to the nearest neighbor got large and, (b) they move away from the Vega.

male type and year of sampling (Table 1 and Fig. 2). As group size increased, vicuñas spent less time walking, whereas the proportion of time increased as they move away from the vega (Table 1).

### 3.2. Effects of sampling year, group size and distance to the nearest neighbour and to the vega

#### 3.2.1. Territorial males

Two models of vigilance performed for territorial males received a total 78% of the model weight (Appendix B). These models had similar structures, differing only in the exclusion of the number of females in the group in the most parsimonious model (Table 2 and Appendix B). Sampling year and distance to the vega were the only two variables that better explained the vigilance behaviour of territorial males (Table 2). They spent more time vigilant in 2006 than in 2007 and also when they were close to the vega than away from it (Table 2).

The best-supported model of foraging for territorial males received a 61% of the model weight, with an AIC difference of 1.9 units with the second most parsimonious model (Appendix B). The foraging time was affected by the distance to the vega, and the interactions between sampling year and distance to the vega,

and between the number of females in the group and distance to the vega (Table 2 and Appendix B). The time allocated to foraging was higher closer to the vega than at more of 150 m away from it (Table 2). However, time devoted to foraging increased as number of females increased in groups placed away from the vega (Table 2). Indeed, territorial males spent more time foraging during 2007 than in 2006 in groups that were away from the vega (Table 2).

Time spent walking was dependant on a board set of variables. Only two models received a total of 100% of the model weights (Table 2 and Appendix B). These models were very complex and had similar structures, differing only in the exclusion of the interaction between the sampling year and the distance to the vega in the best-supported model (Appendix B). Despite the complexity of the models, only two variables had significant effects on the time spent walking by territorial males: the year of sampling and the interaction between this variable and the number of females in the group (Table 2). Territorial males allocated lower time to walking in 2007 than in 2006, whereas in 2007 as number of females in the group increased, the time spent walking also increased (Year\*Number of females in the group, interaction; Table 2).

**Table 2**  
Generalised linear models of vigilance, foraging and walking behaviours of territorial vicuña males. The presented models are the most parsimonious of a general model (Appendix B). The response variables are the proportion of time vigilant, foraging and walking with a binomial distribution.

Variables: level	Vigilant time		Foraging time		Walking time	
	$\zeta$	<i>p</i> -value	$\zeta$	<i>p</i> -value	$\zeta$	<i>p</i> -value
Year: 2007 <sup>a</sup>	-2.020	0.043	1.602	0.109	-2.029	0.042
Group size	-	-	-	-	-0.251	0.802
Number of females in the group	-	-	-0.063	0.950	-0.303	0.762
Distance to the vega: 10–50 m <sup>b</sup>	-0.060	0.952	-0.475	0.634	-0.781	0.435
Distance to the vega: 50–150 m <sup>b</sup>	-0.994	0.320	-0.935	0.349	-1.107	0.268
Distance to the vega: >150 m <sup>b</sup>	-2.206	0.027	-2.638	0.008	-1.039	0.299
Year: 2007 × Group size	-	-	-	-	-1.945	0.052
Year: 2007 × Number of females in the group	-	-	-	-	2.354	0.019
Year: 2007 × Distance to the vega: 10–50 m	-	-	-0.712	0.476	-	-
Year: 2007 × Distance to the vega: 50–150 m	-	-	-0.361	0.718	-	-
Year: 2007 × Distance to the vega: >150 m	-	-	2.300	0.021	-	-
Group size × Distance to the vega: 10–50 m	-	-	-	-	-0.332	0.740
Group size × Distance to the vega: 50–150 m	-	-	-	-	1.276	0.202
Group size × Distance to the vega: >150 m	-	-	-	-	0.811	0.417
Number of females in the group × Distance to the vega: 10–50 m	-	-	0.149	0.881	0.736	0.462
Number of females in the group × Distance to the vega: 50–150 m	-	-	0.635	0.526	-0.834	0.404
Number of females in the group × Distance to the vega: >150 m	-	-	2.344	0.019	-0.414	0.679

<sup>a</sup> Year reference level is 2006.

<sup>b</sup> Distance to the vega reference level is 0 m.

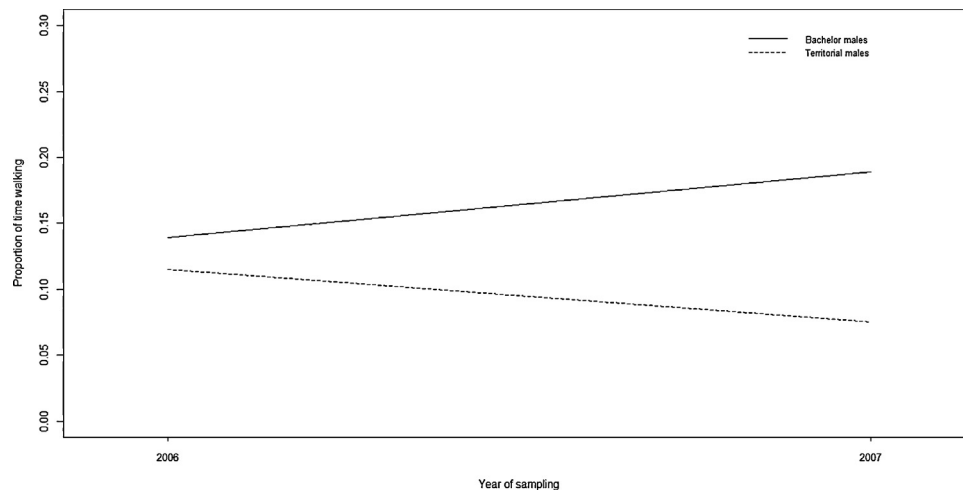


Fig. 2. Difference in the proportion of time spent walking by territorial and bachelor vicuña males during 2007.

3.2.2. Bachelor males

The most parsimonious models of vigilance, foraging and walking performed for bachelor males included the same set of variables: the sampling year, the group size, the distance to the vega and the interaction between the sampling year and group size (Table 3 and Appendix C). Time allocated to vigilance decreased during 2007, as well as group size increased and when the individuals were away from the vega (Table 3). Bachelors also devoted less time to foraging closer to the vega than when they were in it (Table 3). Finally, time spent walking was higher in 2007 than in 2006, and when the individuals moved away from the vega (Table 3).

4. Discussion

In general and in contrast to our predictions, there were no differences between territorial and bachelor males in the time devoted to vigilance, foraging and walking. One possible explanation of this result could be the scarcity of vegetation available during the sampling period, particularly in 2007 (Mosca Torres and Puig, 2010), so vicuñas might optimise their behaviour to solving the trade-off between foraging and vigilance (territorial males) and between foraging and walking to searching for food (bachelors). In this sense, both type of males must mitigate limitations in nutritional requirements devoting higher proportions of their time foraging when food density became scarce.

During the winter of 2007, the low proportion of time that vicuña males engaged in vigilance declined in comparison to 2006, and this could be offset by an increase in the proportion of time feeding. Therefore, it seems that vicuña males responded to a reduction of food resources availability by modify both, foraging and vigilance time investments, indicating that vicuñas may exhibit some plasticity in their social behaviour in response to forage

declining as was observed in other ungulates species (Tallion and Côté, 2007). However, we have to take these results with caution because when considering males types separately this correlation was absent.

Foraging by territorial males is restricted to the territory that they defend (Koford, 1957), so territorial males would expand their territories during the dry season to compensate for the low availability of food (Franklin, 1983; Mosca Torres, 2010), devoting a large amount of time in food patches at the expense of time spent vigilant and searching for food. Rebores and Fernández (1997) observed a similar behaviour in greater rhea males (*Rhea americana*) during the non-breeding season which co-occurs with the dry season. Rheas were more vigilant in the breeding season when food were more abundant and therefore they devoted less time foraging to fulfil their energetic requirements.

Bachelor males that do not defend a territory, should spend more time searching for food with acceptable quality (Franklin, 1983; Cajal, 1985; Vilá and Roig 1992; Mosca Torres et al., 2006; Arzamendia, 2008), in detriment of the time spent in vigilance, specially during the bad weather conditions of 2007. Similar results were observed by Delerum et al. (2008) in blesbok (*Damalisca pygurus philipsi*), a gregarious African species. These authors observed that the main activity not related to vigilance or foraging was walking, allocated an average of 16% of their time on this activity. Therefore, it is possible that walking behaviour is the driving force that differently affected the time spent foraging and vigilant by both territorial and bachelor male vicuñas.

Our results did not support our prediction that group size and number of females in the group affect the time invested by territorial males in vigilance and foraging behaviour. These findings are opposite to the observations made by Vilá and Cassini (1993) in vicuñas of Jujuy. These authors found that territorial males devoted

Table 3

Generalised linear models of vigilance, foraging and walking behaviours of bachelor vicuña males. The presented models are the most parsimonious of a general model (Appendix C). The response variables are the proportion of time vigilant, foraging and walking with a Binomial distribution.

	Vigilant time		Foraging time		Walking time	
Variables: level	$\zeta$	p-value	$\zeta$	p-value	$\zeta$	p-value
Year: 2007 <sup>a</sup>	-2.345	0.019	-0.286	0.775	2.501	0.012
Group size	-2.062	0.039	-1.008	0.314	-0.685	0.493
Distance to the vega: 10–50 m <sup>b</sup>	-0.978	0.328	-2.340	0.019	2.435	0.015
Distance to the vega: 50–150 m <sup>b</sup>	-2.331	0.020	-0.624	0.532	2.945	0.003
Distance to the vega: >150 m <sup>b</sup>	-4.120	<0.001	0.711	0.477	2.198	0.028
Year: 2007 × Group size	1.801	0.072	1.403	0.161	-1.567	0.117

<sup>a</sup> Year reference level is 2006.

<sup>b</sup> Distance to the vega reference level is 0 m.

more time vigilant as number of females in the group increased. It is possible that out of the breeding season, territorial males decrease their vigilance level due to a lower strength of the agonistic interactions with other males of the population. Therefore, regardless of the number of females (and group size), territorial males would spend less time in vigilance and more time foraging due to the low resource availability. A similar lack of effect of group size was found in several other ungulate species, and the explanations of these findings are diverse (Beauchamp, 2014). However, family groups of vicuñas are a particular case because the territorial male stay with their females all year round, which is unusual amongst mammals. Furthermore, it is interesting to note that in our study site mean distance between territorial males and their nearest neighbour (female or calve) was about 11 m, which suggests that they should be more vulnerable to predators than bachelor males, who remain close to their nearest neighbour (1–5 m). Thus, vigilance behaviour in territorial males appears to be independant of the number of females in the group group size and distance to the nearest neighbour, at least during the non-breeding season.

During 2007, territorial males devoted more time walking as the number of females in the group increased compared to 2006. As was pointed out above, a plausible explanation of this finding is that territorial males increased their territory size when food availability decreased in 2007, forcing territorial males to increase the time patrolling the boundaries (Franklin, 1983; Mosca Torres and Puig, 2010). The increase in territory size could be a response to the need of pregnant females to meet basic nutritional needs (Vilá, 1995) thus as number of females in the group increase, the territory size would also increase.

Unlike territorial males, bachelors decreased their vigilance time as group size increased. These results agree with two anti-predator strategies proposed previously: the dilution effect (Hamilton, 1971) and the “many eyes” effect (Pulliam, 1973). However, in the context of the social organisation of the vicuña, vigilance behaviour by bachelor males could be related not only to predation avoidance but also to the assessment of patch quality (Templeton and Giraldeau, 1996; Beauchamp, 2004) and the location of food patches discovered by individuals of the same group (Bertram, 1980; Coolen et al., 2001). This behaviour would also explain the continuous displacement of bachelor groups searching for food of acceptable quality (Vilá, 1995; Arzamendia, 2008; Mosca Torres and Puig, 2010) away from the *vega*. During the dry season forage availability and quality declined, except in the *vega*, where forage maintained an acceptable nutritional value (Mosca Torres and Puig, 2010).

Our results support the prediction that territorial males would devoted more time vigilant when they were in the *vega* than away from it, because of the potential interactions with individuals of other groups who used simultaneously this micro-habitat (Mosca Torres and Puig, 2012). In contrast, we predicted that bachelors would spend less time vigilant in the *vega* due to the presence of many individuals that may decrease the perceived risk of predation. However, our results did not support this prediction, because bachelors increased their vigilance time in the *vega* than away from it. One possible explanation of this behaviour is that bachelors maintained a high level of vigilance in the *vega* because they were continuously threatened by territorial males. Vilá (1992) observed that bachelor vicuñas were the main recipients of aggression from territorial males, although the aggression level is lower (threats) during the non-breeding season than in the breeding season (fighting and harassment). Thus, low levels of aggression by the territorial males allow the simultaneous presence of bachelor groups in the *vega* who maintain a constant level of alert. In our study site, social status rather than predation risk could be the main factor affecting the vigilance behaviour by vicuña males in the *vega*.

Territorial and bachelor males devoted a higher proportion of time foraging (or drinking) inside than outside the *vega*. It is possible that the social pressure exerted during foraging by the simultaneous presence of several groups in the *vega*, could be such that animals even increase their harvest rate as competitor density increases (Shrader et al., 2007; Courant and Fortin, 2012). In contrast to the seasonal waterholes found in other arid environments where animals go only to drink (Crosmary et al., 2012), the *vegas* in the Puna environments receive a ground-water supply all year round. These conditions promote the formation of moist soils in which grass grows abundantly (Rabinovich et al., 1998), making *vegas* an excellent source of water and high quality forage for vicuñas (Renaudeau d'Arc et al., 2000; Mosca Torres and Puig, 2010).

Contrary to our expectations, distance to the nearest neighbour was unimportant in determining vigilance and foraging behaviours of bachelor males. Regardless of the environmental conditions and the type of activity performed by them, the distance to the nearest neighbour was always between 1 and 5 m. The strong cohesion observed in bachelor groups of our study site was also recorded in other vicuña populations of Argentina (Vilá, 1995) and Peru (Franklin, 1983). It is possible that the main advantages of maintaining group cohesion are not only the reduction of predation risk, but also the acquisition of information about the location of food sources (Beauchamp, 2009), particularly during the dry season when resource availability decrease.

## 5. Conclusions

Our results allow us to conclude that resource availability and the distance to a water source were more important than social factors in conditioning the vigilance and foraging behaviours of territorial and bachelor male vicuñas, at least during the non-reproductive dry season. The effects of group size were only evident in the vigilance behaviour of bachelor males, suggesting that in the context of the social organisation of the vicuña, bachelors would benefit of an increase in group size not only to avoid predation but also to locate food patches discovered by individuals of the same group. Finally, in light of our results, we believe that in vigilance studies is essential to consider the interactions between several independant variables to properly evaluate their effects on the behaviour of social animals.

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## Appendix A.

A priori generalised linear models of vigilance, foraging and walking behaviours of territorial and bachelor vicuña males. The most parsimonious model is presented first (i.e., models are ranked in descending order according to AIC value). Models with AIC weight <0.005 are not displayed. The response variables are the proportion of time vigilant, foraging and walking with a binomial distribution.

Models	AIC	ΔAIC	AIC weight
Vigilance ~ Year + GroupSize + Neighbour + DistanceVega	244.1	0.0	0.476
Vigilance ~ Year + GroupSize + Neighbour + DistanceVega + Year × GroupSize	245.1	1.0	0.288
Vigilance ~ Year + GroupSize + Neighbour + DistanceVega + Year × GroupSize + Year × Neighbour	246.6	2.4	0.14
Vigilance ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + Year × GroupSize + Year × Neighbour	248.3	4.2	0.059
Vigilance ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × GroupSize + Year × GroupSize + Year × Neighbour	250	5.9	0.024
Vigilance ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × Year + MaleType × GroupSize + Year × GroupSize + Year × Neighbour	251.9	7.8	0.009
Foraging ~ MaleType + Year + Neighbour + DistanceVega + MaleType × DistanceVega	364.3	0.0	0.535
Foraging ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × DistanceVega	366.2	1.9	0.205
Foraging ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × DistanceVega + Year × GroupSize	367.5	3.2	0.108
Foraging ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × Year + MaleType × DistanceVega + Year × GroupSize	368	3.8	0.081
Foraging ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × Year + MaleType × GroupSize + MaleType × DistanceVega + Year × GroupSize	369.2	4.9	0.045
Foraging ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × Year + MaleType:GroupSize + MaleType × DistanceVega + Year × GroupSize + Year × Neighbour	371.1	6.8	0.017
Foraging ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × Year + MaleType × GroupSize + MaleType × Neighbour + MaleType:DistanceVega + Year × Neighbour	373.1	8.8	0.006
Walking ~ MaleType + Year + GroupSize + DistanceVega + MaleType × Year	223.6	0.0	0.475
Walking ~ MaleType + Year + GroupSize + DistanceVega + MaleType × Year + Year × GroupSize	224.4	0.7	0.328
Walking ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × Year + Year × GroupSize	226.4	2.7	0.121
Walking ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × Year + Year × GroupSize + Year × Neighbour	228.2	4.6	0.048
Walking ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × Year + MaleType × GroupSize + Year × GroupSize + Year × Neighbour	230.1	6.5	0.019
Walking ~ MaleType + Year + GroupSize + Neighbour + DistanceVega + MaleType × Year + MaleType × GroupSize + MaleType × Neighbour + Year × GroupSize + Year × Neighbour + Year × DistanceVega	232.1	8.4	0.007

**Appendix B.**

A priori generalised linear models of vigilance, foraging and walking behaviours of territorial vicuña males. The most parsimonious model is presented first (i.e., models are ranked in descending order according to AIC value). Models with AIC weight <0.005 are not displayed. The response variables are the proportion of time vigilant, foraging and walking with a binomial distribution.

Models	AIC	ΔAIC	AIC weight
Vigilance ~ Year + DistanceVega	236.5	0.0	0.547
Vigilance ~ Year + NumberFemales + DistanceVega	238.2	1.7	0.23
Vigilance ~ Year + GroupSize + NumberFemales + DistanceVega	239.4	3.0	0.123
Vigilance ~ Year + GroupSize + NumberFemales + DistanceVega + Year × NumberFemales	240.6	4.2	0.067
Vigilance ~ Year + GroupSize + NumberFemales + DistanceVega + Year × GroupSize + Year × NumberFemales	242.5	6.1	0.026
Vigilance ~ Year + GroupSize + NumberFemales + DistanceVega + Year × GroupSize + Year × NumberFemales + Year × DistanceVega	245.5	9.1	0.006
Foraging ~ Year + NumberFemales + DistanceVega + Year × DistanceVega + NumberFemales × DistanceVega	217.5	0.0	0.609
Foraging ~ Year + GroupSize + NumberFemales + DistanceVega + Year × DistanceVega + NumberFemales × DistanceVega	219.4	1.9	0.24
Foraging ~ Year + GroupSize + NumberFemales + DistanceVega + Year × GroupSize + Year × DistanceVega + NumberFemales × DistanceVega	221.2	3.7	0.095
Foraging ~ Year + GroupSize + NumberFemales + DistanceVega + Year × GroupSize + Year × NumberFemales + Year × DistanceVega + NumberFemales × DistanceVega	222.4	4.9	0.052
Walking ~ Year + GroupSize + NumberFemales + DistanceVega + Year × GroupSize + Year × NumberFemales + GroupSize × DistanceVega + NumberFemales × DistanceVega	216.2	0.0	0.68
Walking ~ Year + GroupSize + NumberFemales + DistanceVega + Year × GroupSize + Year × NumberFemales + Year × DistanceVega + GroupSize × DistanceVega + NumberFemales × DistanceVega	217.7	1.5	0.32

## Appendix C.

A priori generalised linear models of vigilance, foraging and walking behaviours of bachelor vicuña males. The most parsimonious model is presented first (i.e., models are ranked in descending order according to AIC value). Models with AIC weight <0.005 are not displayed. The response variables are the proportion of time vigilant, foraging and walking with a binomial distribution.

Models	AIC	$\Delta$ AIC	AIC weight
Vigilance ~ Year + GroupSize + + DistanceVega + Year $\times$ GroupSize	192.9	0.0	0.571
Vigilance ~ Year + GroupSize + DistanceNeighbour + DistanceVega + Year $\times$ GroupSize	194.4	1.4	0.281
Vigilance ~ Year + GroupSize + DistanceNeighbour + DistanceVega + Year $\times$ GroupSize + GroupSize $\times$ DistanceNeighbour	195.9	3.0	0.127
Vigilance ~ Year + GroupSize + DistanceNeighbour + DistanceVega + Year $\times$ GroupSize + Year $\times$ DistanceVega + GroupSize $\times$ DistanceNeighbour	199.8	6.8	0.019
Foraging ~ Year + GroupSize + DistanceVega + Year $\times$ GroupSize	166.1	0.0	0.613
Foraging ~ Year + GroupSize + DistanceNeighbour + DistanceVega + Year $\times$ GroupSize	167.7	1.6	0.269
Foraging ~ Year + GroupSize + DistanceNeighbour + DistanceVega + Year $\times$ GroupSize + GroupSize $\times$ DistanceNeighbour	169.7	3.6	0.099
Foraging ~ Year + GroupSize + DistanceNeighbour + DistanceVega + Year $\times$ GroupSize + GroupSize $\times$ DistanceNeighbour + GroupSize $\times$ DistanceVega	173.3	7.2	0.017
Walking ~ Year + GroupSize + DistanceVega + Year $\times$ GroupSize	175.8	0.0	0.499
Walking ~ Year + GroupSize + DistanceVega + Year $\times$ GroupSize + Year $\times$ DistanceVega	176.7	0.9	0.313
Walking ~ Year + GroupSize + DistanceNeighbour + DistanceVega + Year $\times$ GroupSize + Year $\times$ DistanceVega	178.6	2.9	0.118
Walking ~ Year + GroupSize + DistanceNeighbour + DistanceVega + Year $\times$ GroupSize + Year $\times$ DistanceVega + GroupSize $\times$ DistanceNeighbour	179.9	4.1	0.064
Walking ~ Year + GroupSize + DistanceNeighbour + DistanceVega + Year $\times$ GroupSize + Year $\times$ DistanceNeighbour + Year $\times$ DistanceVega + GroupSize $\times$ DistanceNeighbour + GroupSize $\times$ DistanceVega	184.6	8.9	0.006

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