

Vigilance Patterns of Territorial Guanacos (*Lama guanicoe*): The Role of Reproductive Interests and Predation Risk

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Abstract

We conducted focal observations of territorial guanacos, a highly polygynous and social mammal, to compare time budgets between sexes and test the hypothesis that the differences in reproductive interests are associated with differential group size effects on male and female time allocation patterns. In addition, we used group instantaneous sampling to test the hypothesis that grouping improves detection capacity through increased collective vigilance. We fit GLM to assess how group size and group composition (i.e., presence or absence of calves) affected individual time allocation of males and females, and collective vigilance. As expected from differences in reproductive interests, males in family groups devoted more time to scan the surroundings and less to feeding activities compared to females. Both sexes benefited from grouping by reducing the time invested in vigilance and increased foraging effort, according to predation risk theory, but the factors affecting time allocation differed between males and females. Group size effects were significant when females were at less than five body-lengths from their nearest neighbour, suggesting that grouping benefits arise when females are close to each other. Female time budgets were also affected by season, topography and vegetation structure. In contrast to our expectation, males reduced the time invested in vigilance as the number of females in the group increased, supporting the predation risk theory rather than the intrasexual competition hypothesis. The presence of calves was associated with an increase in male individual vigilance; and vegetation type also affected the intensity of the group size effect over male time allocation. In closed habitats, collective vigilance increased with the number of adults but decreased with the number of calves present. Although male and female guanacos differed in their time allocation patterns, our results support the hypothesis that both sexes perceive significant anti-predator benefits of group living.

Introduction

In many species, vigilance (i.e. state of alertness where an individual is usually standing and watching with its head raised) can enhance survival through improved predator detection and escaping ability. However, if vigilance is mutually exclusive

with food searching and handling, individuals must reduce their feeding effort to scan for predators (Pulliam & Caraco 1984; Fortin et al. 2004). Living in groups is a well-known mechanism to reduce time invested in vigilance without increasing predation risk (Blumstein et al. 1999; Fernández et al. 2003). Grouped prey may detect an approaching predator

sooner than solitary individuals, as proposed by the collective detection hypothesis (Pulliam 1973; Lima 1995) and benefit with reduced probability of death per encounter with a predator, according to the individual risk hypothesis or dilution effect (Hamilton 1971; Bertram 1978; Fairbanks & Dobson 2007). Decreased individual vigilance in larger groups, as observed in many species of birds and mammals, is understood to reflect this reduction in the perceived predation risk (Lima & Dill 1990). However, most studies have focused in individual vigilance and few have assessed whether collective vigilance varies with group size (Fernández et al. 2003).

Besides group-size effects, some studies have shown that the time spent vigilant by an individual can also be affected by visual or spatial separation between the members of the group (Lima & Zollner 1996); distance to obstructive cover and distance to refuge (Elgar 1989). All these factors are likely to interact with group size to determine individual's predation risk perception (Frid 1997). In addition, vigilance may serve other functions such as territorial defence or mate guarding. For example, group size effects on time allocation of male vicuñas (*Vicugna vicugna*) were found opposed to expectations from the antipredator hypothesis. Vilá & Cassini (1994) found that vicuña males in Northwestern Argentina spent more time in vigilant behaviour and less time grazing when the number of females in their harems increased, and concluded that this was an indicator of the additional time-cost associated with territorial and female defence. Thus, the optimal time allocation to feeding and scanning for each individual may depend also on intrinsic factors, such as sex, age, nutritional and reproductive status (Dehn 1990; Childress & Lung 2003). These factors may interact with predation risk to shape the observed patterns of time allocation, and potentially mask group size effects, but they are not usually measured or controlled for in vigilance studies (Robinette & Ha 2001).

The aim of this study was to analyse guanaco (*Lama guanicoe*) vigilant behaviour under risk of predation by pumas (*Puma concolor*), accounting for sex and social-context effects. Guanacos, as well as vicuñas, the only South American wild camelids, are sexually monomorphic ungulates. Adults weigh 80–120 kg and their breeding system is a resource defence polygyny. An adult male defends a territory where a group of females and their offspring (chulengos) feed, from the intrusion of other males, although female herding has been occasionally observed as well (Marino pers. obs.). Females usu-

ally form highly cohesive and synchronised units in terms of behaviour while the territorial male tends to remain distant from the group. Territorial displays, and eventually male fights, are triggered when a peripheral male trespasses the territory borders, and these interactions are more common during the mating season (Puig & Videla 1995). Although the intensity of territorial behaviour can vary between seasons and populations (Puig & Videla 1995), male vigilant behaviour is expected to be a conspicuous component of intrasexual competition.

Guanacos are a good model to test predation risk hypotheses because their only natural predator hunts by stalking and stealth, relying on vegetation cover and terrain features to approach close enough to their prey before attacking (Hornocker 1970; Wilson 1984; Bank & Franklin 1998). As pumas do not chase their prey through long distances, early detection by guanacos can be especially advantageous to increase their likelihood to escape. In addition, as group size and habitat openness (in terms of vegetation and topography) are likely to affect predation risk, we expect these factors to have interactive effects on vigilance patterns (Frid 1997).

Firstly, we hypothesized that male and female guanacos differ in their time budgets as a result of differences in their reproductive interests. As males can enhance their fitness by monopolizing access to breeding females, intrasexual competition is expected to be intense and to affect male time allocation. In contrast, female reproductive success will depend mainly on the ability to acquire and transfer nutritional resources to the offspring. For most herbivores, this ability is likely to be related to the rate and efficiency of food collection and processing (Clutton-Brock et al. 1982). We predict that because of territorial defence, males spend more time than females in vigilant behaviour at expenses of foraging time. Secondly, we hypothesized that females perceive an antipredatory benefit from group living. Thus, as group size increases we expect that females devote less time to individual vigilance and more time to food searching and handling. In contrast, males with more females in their groups are exposed to increased intrasexual competition and should invest more time in territorial defence. We predict that males invest more time in vigilance and less in food searching and handling as the number of females in the group increases. Finally, we hypothesized that grouped guanacos benefit by increased collective detection, therefore, we predict that group vigilance should also increase with the number of animals.

Methods

Study Area

The work was conducted between January and April 2004 at La Esperanza Wildlife Refuge, a privately owned 6700 ha protected area located in the coast of the San Matías Gulf, in Chubut Province, Argentina (42°7' 43.92''S; -64°57' 40.99''W). Guanaco density is around 5 animals.km⁻², and puma predation was the main cause of mortality between 2002 and 2004 accounting for up to 40% of the dead guanacos (Baldi, unpubl. data). Average annual rainfall across the area is 200 mm. The vegetation is characteristic of the Southern Monte, tall shrubland covering 40–60% of the soil surface, but sharing plant species with the Patagonian Province in the coastal area (León et al., 1998). The creosote bushes *Larrea nitida* and *L. Divaricata* dominates the western side of the ranch where the Monte prevails across the higher plains, whereas the quilibay *Chuquiraga avellanadae* (up to 1 m height) dominates the cliffs and canyons towards the coastal steppe. The most abundant grasses are *Stipa tenuis* and *Poa ligularis* (Beeskov et al., 1995).

Behavioural Observations

Data were collected from 9:00 to 19:30 from seven different observation points located in elevated places. Simultaneous telemetry data available from a complementary project on nine radiocollared animals in six different groups showed that both group size and territory location were stable during the sampling period. The number of animals per group remained usually constant during weeks, changes were exceptional and resulted from either an adult moving between groups or a chulengo predated by pumas. Average annual territory size was around 4 km² (range 2–9 km²), while spatial overlap between neighbouring territories varied between 0 and 17%. However, animals from neighbouring territories were never recorded in the overlap area simultaneously (Burgi 2005). As the number of marked guanacos was low, we selected a different observation point in subsequent days to minimize repeated measures on the same individual. Thus, if repeated observations of the same animal occurred because it was unmarked, a period of at least 1 wk elapsed between two consecutive watches. Considering radiocollared and naturally marked individuals, and group location during each sampling day, we estimate that at least 70% of

our focal observations in each season corresponded to different individuals, in at least 12 different family groups.

We observed guanacos either in family groups or as solitary males. Defining a group in the field was straightforward because guanacos in sedentary populations are territorial, females form relatively stable and cohesive associations while the harem male is usually at 50–100 m away from the group. During the mating season, when an individual or a group come close to another group there are obvious aggressive interactions between territorial males (field observation). 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. For all occasions, this was confirmed by the subsequent displacement of the animals during the observations (i.e. the members of the group moved together in the same direction, while the other individual/s stayed in the same place or moved in another direction). However, ambiguous situations were unlikely as group density in this area is low. Therefore, we define a group as an association among an adult male and one or more females, with or without calves, which move together, behave relatively synchronized when within 300 m of each other, and show no obvious signs of territorial conflict among associated individuals. Observations in non-defendable patches (for example, around water sources) where several groups congregate and group definition is not clear were not considered in analyses.

Focal Observations

Observations were made using 8.5 × 44 binoculars and 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 genital organs (Franklin 1983). Accordingly, focal observations were carried out only when we were close enough to distinguish males from females accurately. For each group, the adult male and one of the females were continuously observed (Altmann 1974; Martin & Bateson 1993) during 15 min or less if they went out of sight, laid down or moved to another habitat type. Thus, we can refer our observations to the total time in activity and avoid data dependence because of the use of successive watches to compare habitat type effects. We discarded all the observations that lasted <3 min. We classified all the

individuals older than 1 year of age as adults and as chulengos those younger than 1 year, as only chulengos are obviously smaller than adults from distances greater than 300 m. Although juveniles (>1 < 2-years old) were included within the adult age-class they are often expelled from family groups before the ensuing reproductive season. We observed solo adult males, and groups of one adult male and up to 12 adult females, with or without chulengos. Therefore, 'number of adults in the group' refers to the adult male plus the adult females of his group.

Overall, we completed 34 focal observations on females and 38 on males. During the focal watches, we registered in a tape recorder the time when the focal animal switched between successive behavioural states. These states were classified into five categories: scanning (standing with the head in an upright position), foraging (standing or walking slowly with the head below the shoulder height, usually handling food), walking, grooming and socializing. We did not include resting individuals in our sample in order to refer our observations to the time spent active. Also, as guanacos usually lay down to ruminate they can chose hills or open places where they can be both vigilant and process food simultaneously, therefore, no trade-off between predation risk and energy gain is possible in these conditions. To test our hypotheses, we focused on foraging and scanning behavior which together account for up to 90% of the time in activity for both guanaco females and males. We assumed that scanning was the best estimate of individual vigilance because, as in most ungulates, (1) the head-up posture brings all the sensory organs to a position that should increase the detection range, (2) it involves a cost in terms of a time loss that could be used in other activities and (3) it is the observed state of alertness when a predator is detected (Childress & Lung 2003). We subsequently used a digital audio editor to calculate the proportions of the observation time that the observed individual spent at each state.

Scan Samples

Collective vigilance was considered an indirect measure of group detection ability. Instantaneous samples were taken every 2 min during 20 min, by registering the behavioural state of each adult in the group (Martin & Bateson 1993). We defined collective vigilance as the proportion of 10 scans samples with at least one adult vigilant. We took 46 scan

samples, observing nine solo males and 37 family groups.

Independent Variables

At the beginning of each observation, we recorded the number of adults and chulengos in the group. In order to accurately evaluate our hypotheses, we also noted other variables that could affect time allocation. We registered the distance of the focal female to its nearest neighbour (in body-lengths) as a measure of group cohesion and subsequently grouped the distances into intervals (<2 body-lengths, 2–5 body-lengths and >5 body-lengths) for analysis. These intervals seemed to reflect three frequently observed situations: (1) tightly grouped females with obvious signs of stress, scanning the surroundings and usually moving out abruptly all together; (2) intermediate state with high level of synchronisation among females, and (3) highly spread and apparently relaxed groups. We did not consider this variable for male models, because in most of the observations, they were far apart from the rest of the group without any sign of synchronization or cohesion as observed in females.

Vegetation height relative to an adult guanaco was categorized into three classes: low vegetation, composed mainly by grasses and forbs; tall-sparse vegetation, and tall-dense vegetation, with low and high shrub cover, respectively; considering a patch of approximately 20–30 m around the group, consistent with the distance observed for a puma to perform a successful attack (Bank & Franklin 1998). We assumed that vegetation structure is an important factor affecting guanaco time allocation because (1) tall vegetation could be perceived as obstructive cover by guanacos as pumas can hide and approach the prey closely without being detected; and (2) feeding effort could differ between vegetation types due to potential differences in forage availability. Topography was classified either as irregular or flat according to the presence of canyons or hills, considering the same scale as vegetation types. The presence of canyons or hills could also improve puma hunting strategy through concealment. Finally, seasons were defined as reproductive (January and February) and post-reproductive (March and April) because most births occurred during November–December through the end of January. As females are expected to be sexually receptive approximately 10 d after parturition, the birthing and mating seasons overlap, therefore, we assumed that the categories described above are

appropriate to account for changes in intrasexual competition.

Statistical Analysis

To compare time devoted to vigilance and feeding between the sexes and across the different groups we considered successive or simultaneous focal samples of the adult male and one female in the same group, to avoid additional variation due to differences in habitat or social-context. From the total focal observations (34 females and 38 males), we observed 26 female–male pairs (i.e. 26 groups where a male and female were observed simultaneously). As the observations of a male and a female in the same group were not independent, we used paired t-tests to test the hypothesis that the mean difference of the response variable between males and females in the same group (i.e. each pair) was zero, without the independence assumptions required for between-means comparisons (Sokal & Rohlf 1997). We compared the proportion of time spent in each state (vigilant and feeding) by males and females using a paired t-test, previous arcsine-square root transformation to normalize the data (Shapiro-Wilk's W-test; $W = 0.96$ $p = 0.7502$ for vigilance and $W = 0.95$, $p = 0.5620$ for feeding).

To assess whether group size affected individual vigilance and feeding time of females, we fitted two independent generalized linear models to the 34 focal observations of females (GLM) (McCullagh & Nelder 1983). We tested the following explanatory variables: group size, distance to nearest neighbour, presence or absence of chulengos, vegetation type, topography and season; as well as their interactions with group size. We also fitted two independent GLM to assess how the number of females affected individual vigilance and feeding time of males, using the 38 focal observations conducted on males. The explanatory variables tested were number of females, vegetation type, topography and season, as well as their interactions with the number of females, and the presence or absence of chulengos. Finally, to assess how group size and composition affected collective vigilance (proportion of scan observations with at least one adult alert, $n = 46$ groups), we fitted a GLM including the number of adults, the number of chulengos, vegetation type, topography and season, as well as their interactions with the number of adults.

GLMs are a generalization of the traditional regression and ANOVA analysis. These models are linear in the parameters and random variables, but do

not necessarily involve a linear relationship between the response and explanatory variables (Crawley 1993). The linear predictor, composed by the parameters and random variables, is the systematic component of the model, and the shape of its relationship with the response variable is defined by the link function. We assumed a normal distribution of the error structure for all the models that was then confirmed by graphical methods (McCullagh & Nelder 1983). This error distribution can be adequate for these types of data which are proportions derived from ratios of times instead of ratios from counts of the binomial type (McCullagh & Nelder 1983). We used logit and complementary log–log link functions because they asymptote at 0 and 1 so that negative proportions, and responses of above 1, cannot be predicted (Crawley 1993). In each case, we selected the final model using stepwise backward elimination methods, beginning with the saturated model and subsequently discarding the terms when the p-value associated with the F-ratio was >0.05 . This method for selecting the terms of the model is straightforward to work with many terms and interactions. As backwards procedures compare each variable contribution once it has been excluded from the model, the variables that explain more variation are kept in (McCullagh & Nelder 1983; Crawley 1993; Fahrmeir & Tutz 1997). Non-significant terms were considered only when they were part of significant first-order interactions.

Factor parameters – Unlike the traditional ANOVA where factor levels depart from an overall mean, the GLM approach considers as the intercept of the linear model the mean for the first treatment, setting this mean as the reference level. The rest of the parameters are the difference between the reference level and the other levels of a given factor. Then estimated standard errors are used to test if the difference between the reference level and the other levels are significantly different from zero, and need to be retained in the model, using t-tests (see Crawley 1993; for detailed explanation and discussion). The standard error of the difference between two means is computed from the pooled estimate of variance from the model and sample sizes for each mean. Whenever response variables showed non-significant differences between two levels of the same factor, observations were grouped as for a single level to minimize model complexity (Crawley 1993).

Covariate parameters – To fit explanatory variables, GLM approach considers a common slope for each level of the factor/s, unless it can be demonstrated that the slopes are significantly different in each treat-

ment. A comparison of the treatments is then based on a comparison of the intercepts of the various parallel lines (Crawley 1993). Model fitting was performed using Genstat 7.1 software (Lawes Agricultural Trust-VSN International Ltd., Rothamstead, UK).

Results

Difference in Time Budgeting Between Females and Males

On average, females spent over two thirds of their time foraging ($72 \pm 21\%$) and only 18% (± 16) scanning. Whereas, males spent half of their time foraging ($49 \pm 21\%$) and 36% (± 20) scanning. Males invested 23% more time in vigilance ($t = 4.53$, $n = 26$, $p = 0.0001$) and 26% less in foraging activity than females ($t = -4.36$, $n = 26$, $p = 0.0002$). These differences persisted after we analysed the data for reproductive and post-reproductive seasons separately (rep.-scanning: $d = 20$, $t = 3.92$, $n = 13$, $p = 0.0021$; foraging: $d = 18$, $t = -2.92$, $n = 13$, $p = 0.0129$; post-rep.- scanning: $d = 26$, $t = 2.95$, $n = 13$, $p = 0.0122$; foraging: $d = 35$, $t = -3.47$, $n = 13$, $p = 0.005$).

Group Size Effect and Social Variables

The time that females spent vigilant was best explained by a model including season, topography, and the main effects and interaction between group size and distance to the nearest neighbour (DNN) (Table 1). This model accounted for 80.3% of the observed variation in individual vigilance

Table 1: Female model selection (v.r.: variance ratio, F pr.: Fisher probability)^a

Terms	Individual vigilance		Foraging time	
	v.r.	F pr.	v.r.	F pr.
Season (S)	26.76	<0.001	32.21	<0.001
Group size (GS)	60.58	<0.001	36.09	<0.001
Topography (T)	21.00	<0.001	0.260	0.614
DNN	18.24	<0.001	7.530	0.011
Vegetation (V)	0.760	0.391	10.82	0.003
Presence of chulengos (CH)	0.980	0.331	1.490	0.233
GS.DNN	12.86	0.001	11.41	0.002
GS.T	0.400	0.532	0.680	0.416
GS.V	0.020	0.894	4.300	0.048
GS.S	0.000	0.950	0.370	0.549

Selected models: Individual vigilance = S+GS+DNN+T+ GS.DNN.

Foraging time = S+GS+DNN+V+ GS.DNN+GS.V.

^aGeneral model: GS + S+T+DNN+V+ GS.S+GS.T+GS.DNN+GS.V.

($F_{5,28} = 27.89$, $p < 0.001$, $n = 34$). Females scanned significantly more during the reproductive season ($n = 18$) than thereafter ($n = 16$) ($t_{28} = -6.55$, $p < 0.001$) and spent more time alert in habitats with canyons or hills ($n = 11$) than in plain terrain ($n = 23$) ($t_{28} = -3.64$, $p = 0.001$). The time spent vigilant decreased with increasing group size but only when individual females were closer than five body-lengths from their nearest neighbour ($t_{28} = -4.85$, $p < .001$, $n = 24$). When they were farther apart, the group size effect was not significant ($t_{28} = 0.54$, $p = 0.595$, $n = 10$). Moreover, when females were over five body-lengths away from their neighbours, they showed relatively low levels of vigilance irrespective of group size ($t_{28} = -6.34$, $p < 0.001$, $n_1 = 24$, $n_2 = 10$) (Fig. 1).

Similarly, the selected model to explain the time females spent foraging included season, group size, DNN and vegetation type as factors, plus the group size DNN and group size – vegetation type interactions (Table 1). This model accounted for 74.5% of the observed variation in time spent foraging ($F_{6,27} = 17.06$, $p < 0.001$, $n = 34$). Foraging time increased with group size when females were closer than five body-lengths from their neighbors ($t_{27} = 3.36$, $p = 0.002$, $n = 24$), but when they were farther, foraging time was significantly higher ($t_{27} = 4.64$, $p < .001$, $n_1 = 10$, $n_2 = 24$) and independent of group size ($t_{27} = 1.74$, $p = 0.094$, $n = 10$) (Fig. 1). In addition, the increase in time that females spent foraging with group size was steeper when they were found in closed habitats (tall-dense vegetation, $t_{27} = -2.06$, $p = 0.049$, $n_1 = 16$, $n_2 = 18$) and the intercept, which indicates feeding time of females in small groups, was very low compared with open habitats (low or tall-sparse vegetation) ($t_{27} = -2.70$, $p = 0.012$, $n_1 = 16$, $n_2 = 18$). After the reproductive season, females showed a significant increase in foraging time ($t_{27} = 4.86$, $p < .001$, $n_1 = 18$, $n_2 = 16$).

The variation observed in time spent vigilant by males was best explained by the number of adults in the group, its interaction with vegetation type, and the presence of chulengos in the group (Table 2). The model explained 56% of the observed variation ($F_{4,33} = 12.76$, $p < .001$, $n = 38$). Male individual vigilance decreased with increasing number of adult females in the group ($t_{33} = -3.49$, $p = 0.001$, $n = 27$) and this decrease was steeper in habitats with low vegetation than in habitats with tall vegetation ($t_{33} = -3.50$, $p = 0.001$, $n_1 = 11$, $n_2 = 27$) as the intercept for the number of adults (group size = 1, i.e. solo male) was significantly higher in the former ($t_{33} = 3.34$, $p = 0.002$, $n_1 = 11$, $n_2 = 27$). Males

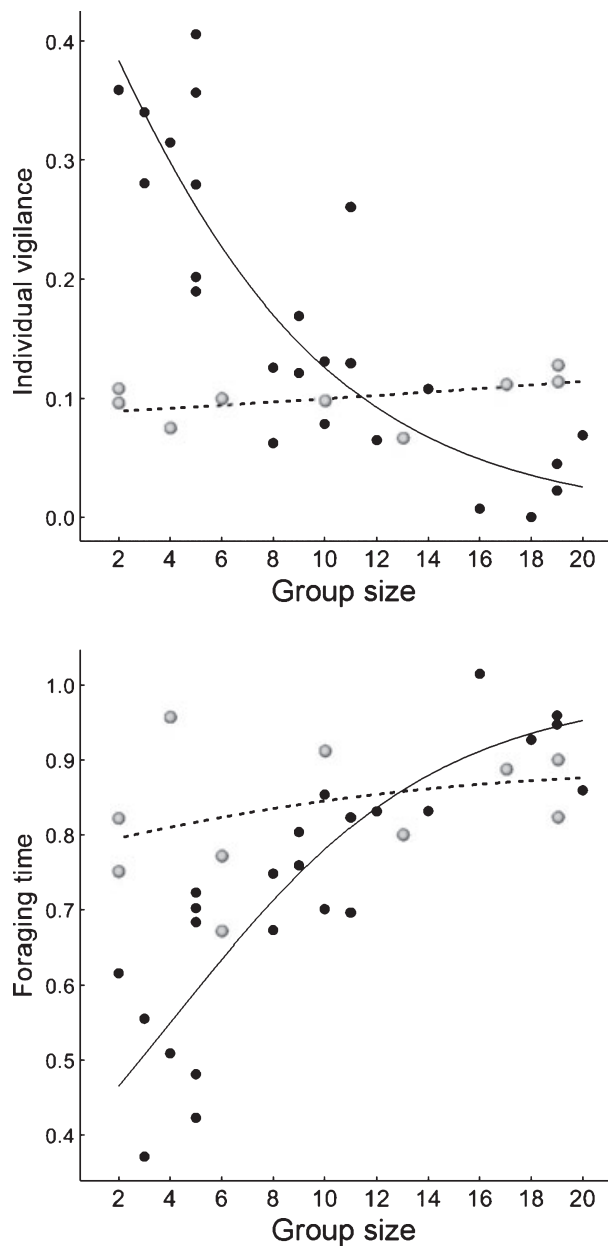


Fig. 1: Female foraging and vigilance response to group size, when being more than five body-lengths apart from their nearest neighbor (dashed line, empty circles) or closer to each other (solid line, filled circles), all data considered.

spent more time vigilant in groups with chulengos than in groups without chulengos ($t_{33} = 3.08$, $p = 0.004$, $n_1 = 15$, $n_2 = 23$) (Fig. 2).

The terms in the model to describe the foraging time of males were the same obtained for individual vigilance (Table 2), and accounted for 30% of the variance in time spent foraging ($F_{4,33} = 4.94$, $p = 0.003$, $n = 38$). Males allocated more time to foraging activities as the number of

Table 2: Males model selection (v.r.: variance ratio, F pr.: Fisher probability)^a

Terms	Individual vigilance		Foraging time	
	v.r.	F pr.	v.r.	F pr.
N° Adults (N°AD)	18.88	<0.001	7.660	0.009
Vegetation (V)	2.470	0.126	0.340	0.564
Presence of chulengos (CH)	5.130	0.030	5.690	0.023
Season (S)	0.240	0.630	0.000	0.954
Topography (T)	3.150	0.086	1.180	0.287
N°AD.V	24.58	<0.001	6.060	0.019
N°AD.S	1.470	0.235	0.280	0.599
N°AD.T	0.000	0.974	0.000	0.969

Selected models: individual vigilance = $N^{\circ}AD+V+CH+N^{\circ}AD.V$.

Foraging time = $N^{\circ}AD+V+CH+N^{\circ}AD.V$.

^aGeneral model: $N^{\circ}AD+V+S+T+CH+N^{\circ}AD.V+N^{\circ}AD.S+N^{\circ}AD.T$

adult females increased ($t_{33} = 3.68$, $p < 0.001$, $n = 27$) and this relationship was stronger in habitats with low vegetation ($t_{33} = 2.51$, $p = 0.017$, $n_1 = 11$, $n_2 = 27$). Also, males in groups with chulengos spent less time searching and handling food compared with males in groups without them ($t_{33} = -3.24$, $p = 0.003$, $n_1 = 15$, $n_2 = 23$) (Fig. 2).

Collective Vigilance

The variation in collective vigilance (proportion of time with at least one adult alert) was best explained by a model including the number of adults and the interaction between number of adults and vegetation type, the number of chulengos and topography (Table 3). It accounted for 39.3% of the observed variation ($F_{7,38} = 5.16$, $p < 0.001$, $n = 46$). Collective vigilance increased with the number of adults (females) in the group in habitats with tall-dense vegetation ($t_{38} = 3.98$, $p < 0.001$, $n = 22$), but this effect was not significant in the other habitat types (low vegetation ($t_{38} = 0.90$, $p = 0.371$, $n = 13$), tall-sparse vegetation ($t_{38} = 1.23$, $p = 0.227$, $n = 11$)) (Fig. 3). The intercept for the relationship between collective vigilance and number of adults in habitats with tall-dense vegetation was significantly lower than in habitats with tall-sparse vegetation ($t_{38} = 2.22$, $p = 0.032$, $n_1 = 22$, $n_2 = 11$) or low vegetation ($t_{38} = 2.72$, $p = 0.01$, $n_1 = 22$, $n_2 = 13$). While the difference between the intercepts of habitats with low and tall-sparse vegetation was not significant ($t_{38} = 1.13$, $p = 0.264$, $n_1 = 13$, $n_2 = 11$). The increase in the number of chulengos was accompanied by a decrease in collective vigilance ($t_{38} = -2.98$, $p = 0.005$, $n = 46$). Finally, collective vigilance was lower in groups situated in irregular

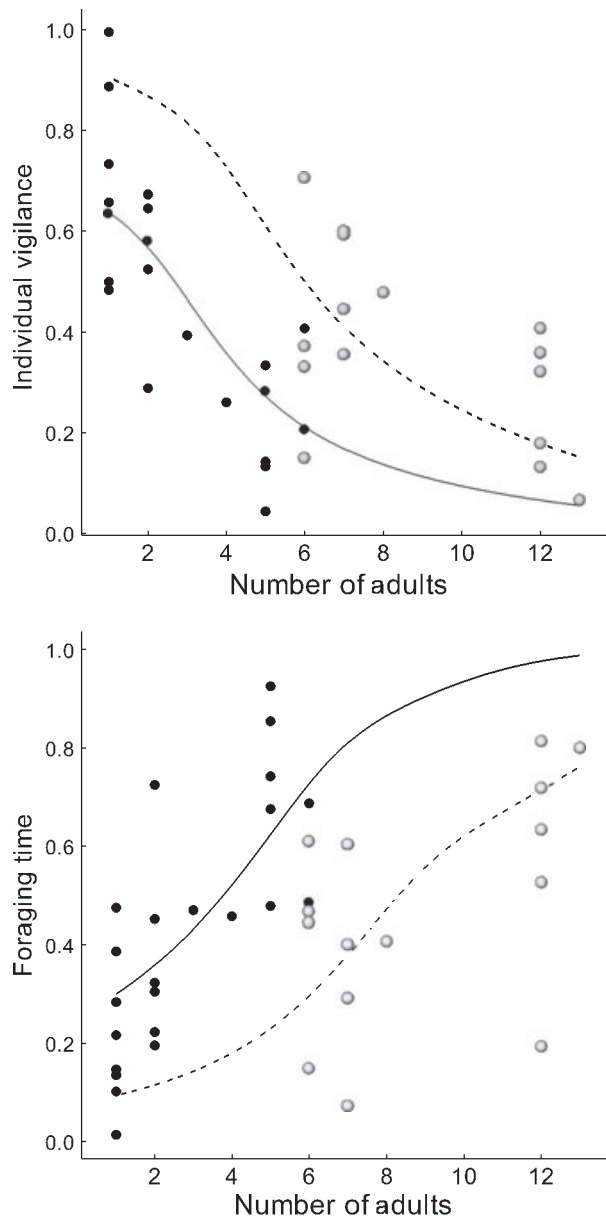


Fig. 2: Male foraging and vigilance response to the number of adults (solo males or males with one or more adult females) in groups with chulengos present (dashed line, empty circles) and groups without chulengos (solid line, filled circles), all data considered.

terrain than those in flat terrain ($t_{38} = 2.57$, $p = 0.014$, $n_1 = 16$, $n_2 = 30$).

Discussion

Sex Differences

Altogether, vigilance and foraging accounted for almost 90% of the diurnal time budget of territorial

Table 3: Collective vigilance model selection (v.r.:variance ratio, Fpr.: Fisher probability)³

	v.r.	F pr.
N° Adults (N°AD)	0.040	0.837
N°Chulengos (N°CH)	6.800	0.013
Vegetation (V)	2.640	0.086
Topography (T)	7.130	0.011
Season (S)	0.590	0.448
N°AD.T	0.010	0.929
N°AD.S	0.270	0.609
N°AD.V	7.300	0.002

Selected model: collective vigilance = N°AD+V+N°CH+T+ N°AD.V.

³General model: N°AD+V+S+T+N°CH+ N°AD.V+ N°AD.S+ N°AD.T

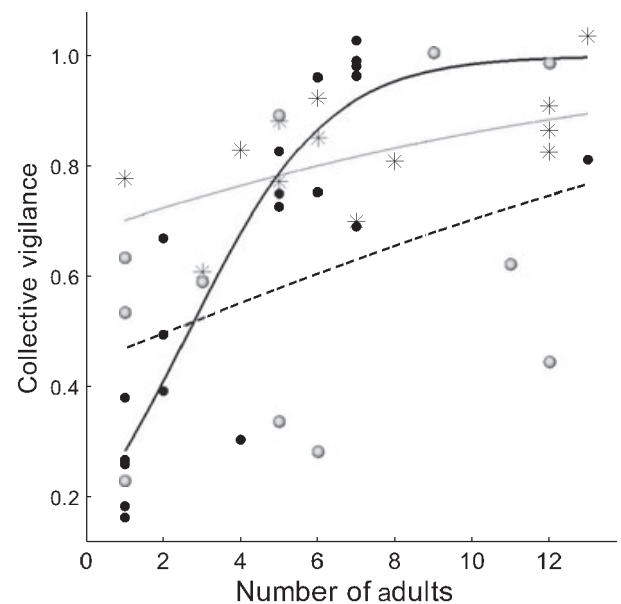


Fig. 3: Collective vigilance as a function of the number of adults in the group, in habitats with tall-dense vegetation (solid line, filled circles), tall-sparse vegetation (dashed line, empty circles) and low vegetation habitats (grey dotted line, asterisks), all data considered.

male and female guanacos. As predicted, territorial males spent more time scanning and less time foraging than females, even after the mating season. This result is compatible with the year-round territoriality observed in this population (Burgi 2005). Vicuñas showed a similar pattern which has been related to the higher energetic demands of females because of gestation and lactation (Vilá & Cassini 1994). Other species show the opposite trend, with females scanning more than males. This is the case of the sexually dimorphic elk (*Cervus elaphus*), which are non-territorial and form groups segregated by sex and age classes. Time budget variation is attributed to body

mass differences resulting in higher vulnerability of females to predation and higher energetic demands of males because of larger body size (Childress & Lung 2003). In contrast, as guanacos are monomorphic, the observed differences in time allocation can be associated to differences in reproductive interests between sexes. The consequent behavioural differences can result in increased vulnerability of the less vigilant individuals and even promote prey selection by predators (FitzGibbon 1989).

Social Factors and Group Size Effect

Contrary to our expectations, not only females but also males benefited from group living with reduced individual vigilance and increased foraging effort, although the factors affecting their time budgets were different. Females obtained significant benefits as group size increased but only when they were close to their nearest neighbour. When close, individual females in groups of 10 individuals scanned almost 25% less and foraged 32% more time than females in groups of two individuals. This result supports the hypothesis of Lima & Zollner (1996), which states that the benefits of grouping against predators decrease as the distance between the members of the group increases. In contrast, group size effects on vigilance and foraging time were non-significant when the individuals were spaced over five body-lengths. Increased spacing between individuals may reduce interference competition for clumped resources such as shrub patches. Aggressive interactions among guanacos of the same group often ended up in the displacement of an individual from a forage patch by an apparently dominant adult, interrupting its feeding bout. We hypothesize that individual females will tend to increase the distance to their group neighbours when the balance between nutritional status and perceived predation risk results in the priority of maximizing energy intake. The low investment in individual vigilance and high level of foraging effort recorded for females in loose groups (>5 body-lengths of spacing), observed across all group sizes, and the fact that a female's first reaction to a threat is to reduce the distance between neighbours (field observation), supports this idea.

Among the additional factors selected for modeling female response, 'season' was one of the most consistent. Females scanned more and spent less time foraging during the breeding season than thereafter. As in other ungulates, the presence of young calves, highly vulnerable to predation, could rein-

force maternal vigilance and cost feeding time (Clutton-Brock et al. 1982). Although we were not able to accurately distinguish mothers from females without chulengos in this study, a high proportion of our observations in larger groups (> 6 adults) corresponded to females with dependent offspring. But mothers vigilance reinforcement alone could not account for the seasonal change in female vigilance in smaller groups where chulengos were few or absent. It is likely that other factors affected female time budgets. For example, forage availability decreases towards late summer and early autumn (Baldi et al. 2004) as well as air temperature. Therefore, after the breeding season, guanacos should spend more time searching for food to fulfil their energy requirements, resulting in less time available for antipredator vigilance. A similar increase in feeding activities during seasons when forage is poorer was observed in vicuñas (Vilá 1998). Finally, habitat characteristics also affected female time allocation. Individual vigilance was higher in irregular than in plain terrain, and foraging benefits of grouping also were enhanced in habitats with tall-dense vegetation. These results are consistent with the increase in predation risk perception according to the ambush hunting strategy of pumas. Even though accounting variation because of habitat characteristics has allowed us to better assess group size effects, additional studies with meticulous designs are needed to precisely detail the effect of habitat characteristics on guanaco time allocation.

Male guanacos also benefited from grouping but responded differentially to the number of adult females and the presence of chulengos. Solo males spent on average 40% more time scanning and more than 20% less time in foraging activities than males in groups of six adults (five females) (Fig. 2). Unexpectedly, males in groups with chulengos were more vigilant than males in groups without them, with the consequent decrease in foraging effort. Male parental care is uncommon in mammals (Clutton-Brock 1991) and as chulengos were conceived 1 year before we could not assess whether they were related to the observed males. Alternatively, increased male vigilance in groups with chulengos might be a secondary effect of group size. As chulengos are present only in relatively large groups, the apparent increase in vigilant effort could instead represent a slower decrease in vigilance compared to smaller groups, where chulengos are less likely to be present (Fig. 2).

Although we cannot discriminate whether guanacos are scanning for predators, intruders or both, the

observed patterns support the predation risk hypothesis rather the intrasexual competition hypothesis. The fact that males did not react to the number of females as we predicted according to intrasexual competition hypothesis (we expected that males would invest more time in vigilance as the number of females increased) may be related to this particular scenario, where predation pressure is relatively high. We can expect natural selection to favour some flexibility in the way that guanaco males respond to the number of females in their groups, enabling them to optimise time allocation.

Collective Vigilance

Even though males and females benefit from grouping by reducing vigilance effort, collective vigilance increased with the number of adults in the group in closed habitats, and remained constant in open habitats. However, collective vigilance decreased with the number of chulengos present. As we defined collective vigilance as the proportion of scan samples with at least one adult vigilant, and group composition in terms of adults consisted in one male and several females, the observed effect of chulengos might be related to females vigilance patterns. According to our results, females adjusted their behaviour to the total number of individuals in the group, regardless of group composition in terms of age classes. Thus, the increase in collective vigilance with group size should be slower in groups with a higher proportion of chulengos, essentially because they are non-vigilant.

Most of the guanacos killed by pumas during this study were found at sites with tall vegetation (>50 cm) (Fernández, pers. com.). Vegetation cover is crucial for pumas to approach guanacos close enough and succeed in the attack (Wilson 1984; Bank & Franklin 1998). Therefore, the observed increase in collective vigilance in larger groups suggests improved detection ability in risky habitats.

To conclude, despite that time allocation differ between sexes, our results suggest that female and male territorial guanacos benefit from grouping within a context of puma predation, as the observed vigilance patterns are consistent with hypotheses derived from antipredatory strategies. As behavioural responses and grouping patterns may affect prey selection (FitzGibbon 1989), predator encounter rates and functional responses (Hebblewhite & Pletscher 2002), further research is needed to identify the potential consequences of individual decisions on prey social structure, predator-prey interactions,

and ultimately population dynamics in guanaco-puma systems.

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