



RESEARCH PAPER

Costs and Benefits of Sociality Differ Between Female Guanacos Living in Contrasting Ecological Conditions

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Abstract

According to current theory, anti-predator benefits promote group formation in open-dwelling ungulates. An inverse relationship between vigilance effort and group size has been documented frequently and thought to reflect the consequent decrease in perceived predation risk as group size increases. In contrast, competition costs are supposed to set the upper limit to the number of individuals that can forage together. As anti-predator behavior is no longer functional in the absence of predation and competition costs might be affected by resource distribution, the net benefit of aggregation will depend on the particular combination of predation risk and habitat structure experienced by the individual. To test this hypothesis, group-size effects on female time allocation and within-group aggression rate were compared between two guanaco populations exposed to contrasting levels of puma predation. Habitat structure within both sites consisted of mosaics of shrublands and grasslands, and group-size effects were also compared between these habitat types. Females under predation risk showed a strong reduction in vigilance as the number of adults in the group increased, whereas females from the predator-free population showed overall low levels of vigilance, regardless of group size. These results emphasize the anti-predator significance of the group-size effect on female vigilance, as well as guanaco plasticity to adjust time allocation to local conditions. On the other hand, within-group aggression rate increased with the number of adults in the group. Aggression rate was almost null within groups located in grasslands but was significantly higher in shrublands, regardless of predation risk, suggesting that the more heterogeneous distribution of shrubs increases the interference competition level. These results strengthen the notion of predation pressure and habitat structure as major determinants of the balance between costs and benefits of group living, and highlight the potential of individual behavioral patterns to make qualitative predictions about group-size variation within territorial ungulates.

During the last four decades, behavioral ecologists have conducted numerous studies on the ecological correlates of group-size variation between and within species (Jarman 1974; Lagory 1986; Shankar Raman 1997; Borkowski 2000; Gerard et al. 2002; Creel & Winnie 2005; Isvaran 2007), as well as on

group-size effects on individual behavior (Pulliam & Caraco 1984; Elgar 1989; Lima 1995; Roberts 1996; Beauchamp 2008). Differences in individual behavior may serve to make testable predictions about group-size variation among contrasting ecological conditions. So far, however, there is a lack of

empirical studies relating the individual behavioral patterns found within a species to the corresponding variation in group size. Regarding ungulates, the occurrence of larger groups in open grasslands in contrast to other habitat types has been documented extensively (Jarman 1974; Shankar Raman 1997; Isvaran 2007; Pays et al. 2007; Cappozzo et al. 2008), but the proximal factors promoting this pattern remain unclear (Gerard et al. 2002; Isvaran 2007). Within ungulate species that form relative stable groups, a costs/benefits approach at the individual level can be particularly useful to identify the processes shaping group-size variation between populations inhabiting different ecological scenarios.

It is generally accepted that herbivores living in groups experience a trade-off between predation-related benefits and feeding-competition costs (Jarman 1974; Kie 1999), and the nature of this trade-off is likely influenced by habitat structure (Isvaran 2005). Regarding anti-predator benefits, living in a larger group may reduce individual predation risk through earlier detection of predators, dilution and confusion effects, and in some cases, cooperative defense (Pulliam & Caraco 1984). A decrease in individual vigilance as group size increases is often observed in birds and mammals and thought to reflect this reduction in perceived predation risk (Pulliam & Caraco 1984; Lima & Dill 1990). However, as other processes would also predict a decrease in individual vigilance with group size (Roberts 1996; Lung & Childress 2007; Rieucou & Giraldeau 2008), this effect might not be necessarily caused by predation risk variation. As an alternative to the 'predation hypothesis', the 'competition hypothesis' states that group-size effect on vigilance reflects scramble competition (i.e. collective depletion of limited resources) (Lima et al. 1999; Fortin et al. 2004; Beauchamp 2008; Rieucou & Giraldeau 2008). Thus, as group size increases, each individual has to invest more time in foraging activities to maintain its intake rate, leaving less time available to spend in anti-predator vigilance. As larger groups consume food patches more quickly and they must travel farther to find sufficient food, the consequent reduction in foraging efficiency is often reflected in increased travel time. The energetic costs associated with this increase in searching effort have been suggested as a mechanism by which scramble limits group size (Janson 1988; Chapman & Chapman 2000; Snaith & Chapman 2008). Therefore, the reduction in vigilance effort as group size increases could be the consequence of a perceived benefit or an indicator of the cost of group living. Sociality-

related costs can arise also in the form of interference competition, which can include brief contests over a single unit of resource, the guarding of ephemeral resource patches and dominance hierarchies (Archer 1998; Goldberg et al. 2001). Agonistic interactions may not only result in a reduced intake rate for one or both members (Goss-Custard 1980) but also may be very costly in terms of time, energy and risk of injury or death (Huntingford & Turner 1987). This type of competition can be noticeably affected by resource distribution (Isbell 1991; Vahl et al. 2005). The occurrence of food clumps increases the level of agonistic interactions in various species (Archer 1998; Goldberg et al. 2001; Vahl et al. 2005) but this effect has not been studied among ungulates. Although he did not consider aggressive interactions, Jarman (1974) proposed that the more homogeneous distribution of food items when comparing grasses with woody plants would have great influence on competition processes within antelope species, giving grazers a greater potential to form large groups than browsers. Under Jarman's theory, individual food items in shrubs are clumped in space (i.e. leaves, flowers of the same plant), whereas food items in grasses (i.e. the entire plant) are homogeneously distributed in space. Thus, shrubs could be considered as small food clumps within a foraging patch and are likely to increase interference competition when compared to homogeneous grasslands.

Comparative studies of the same species in contrasting ecological scenarios may help us to understand how natural selection has driven individual decisions that resulted in observed social patterns (Lott 1991; Caro 1998). The aim of this study was to evaluate how predation risk and habitat structure affect costs and benefits of group living in female guanacos (*Lama guanicoe*) to predict group-size differences between populations exposed to different conditions. First, both hypotheses on group-size effect on vigilance were tested against each other. Under the predation hypothesis, anti-predator advantages are the main promoters of group-size effect. The first prediction derived from it is that individual vigilance decreases as group size increases in a population exposed to high predation risk. But, if anti-predator vigilance is costly, it should be selected against in absence of predators (Blumstein & Daniel 2002). Therefore, the second prediction under the predation hypothesis is the occurrence of low levels of individual vigilance and moderate or null group-size effects in a predator-free population. The alternative hypothesis is that group-size effect on vigilance is the result of scramble competition; thus, individual

vigilance is expected to decrease as group size increases where resources are scarce, regardless of predation pressure. A second prediction derived from this hypothesis is that vigilance reduction should be accompanied by a higher investment in food searching as group size increases. These effects on vigilance and searching effort are expected to be slighter where food resources are relatively more abundant. Finally, a third hypothesis was tested: if the more heterogeneous distribution of shrubs compared with grasses increases interference competition among members of the group, aggression rate should increase more rapidly as group size rises in shrublands than in grasslands.

Methods

Guanaco Life History

Guanacos are one of the two species of South American wild camelids, and their breeding system is based on a resource-defense polygyny. Their mating season, which overlaps with the birthing season, occurs during late spring and early summer (Oct.–Feb.). The main social units in this system are family groups and non-territorial groups (which can be male only or mixed sex) (Franklin 1983). Family groups are composed of an adult male and one or more adult females with their offspring from the year, and usually form highly cohesive and behaviorally synchronized units. Guanacos have a wide distribution across South American deserts and semi-deserts and are found in different types of habitats, such as grasslands, shrublands and even austral woodlands (Franklin 1982). Their feeding habits are highly flexible, with variable proportions of forbs, grasses and shrubs in their diets (Puig et al. 1997). Therefore, guanacos are a good model to test costs/benefits hypotheses because their flexible behavior and wide distribution allow for comparisons between contrasting ecological scenarios.

Study Locations

This study was conducted in two protected areas in Patagonia (Argentina): Cabo Dos Bahías Provincial Reserve and Monte León National Park. Cabo Dos Bahías (C2B) is a small wildlife reserve (1700 hectares) located in southeastern Chubut (44°55'S; 65°31'W). The vegetation in this area is characteristic of the Patagonian Province and composed of shrublands and grasslands. Shrublands are characterized by *Chuquiraga avellanadae* and *Lycium chilense*

and grasslands by *Stipa tenuis* and *Poa ligularis* (Beeskov et al. 1987). Average annual precipitation is 250 mm (Beeskov et al. 1987). During this study, guanaco densities were 55–60 individuals/km². The stable population densities during a 4-yr period (2006–2009), the evidence of strong grazing pressure (Victoria Rodriguez, pers. comm.) in addition to information from previous studies on population dynamics in the area (Cévoli 2005), all suggest that C2B population was at carrying capacity. Because of high guanaco densities reached in C2B as well as the occurrence of the dry season during the sampling period, the level of intraspecific competition was expected to be at the maximum. Regarding predation risk, there have been no guanaco predators reported in the area for more than 20 yr. As tourists frequently visit the reserve, guanacos are habituated to human presence and can be observed from short distances without altering their behavior.

Monte León National Park (ML) is located on the Patagonian coast, in Santa Cruz Province (50°06'S; 68°54'W). It comprises 60 000 hectares of grasslands and shrublands. Shrublands are characterized by *Junellia tridens* and *Lepidophyllum cupressiforme* whereas grasslands are characterized by *Festuca pallenscens*, *Puccinellia* sp., *Agrostis* sp. and *Poa atropidiformis* (Oliva et al. 2006). Average annual precipitation is 240 mm. Guanaco densities during this study varied from 12 to 21 individuals/km², with evidence of seasonal movements between altitudinal strata. Recent studies indicate that ML guanaco population is near carrying capacity and that there are no evident overgrazing signs in the plant community (Suárez et al. 2009). Enhanced Vegetation Index assessed from MODIS satellite images indicates that annual production of vegetation (Pettorelli et al. 2005) at ML was twice that at C2B during 2007–2008 period, plus the fact that the greening period extends to late summer (Marino, unpublished data), lower guanaco densities and absence of overgrazing signs suggest that the level of intraspecific competition at ML during the sampling period was considerably lower than that corresponding to C2B. Pumas (*Puma concolor*), guanacos' natural predators, are common at ML and puma predation was the main cause of guanaco mortality during 2007 and 2008 (Marino 2009). To minimize the disturbance attributed to the presence of the observer, observations were conducted from Road 63, which is frequently used by tourists and where guanacos are habituated to human presence. Study sites description is summarized in Table 1.

Table 1: Summary of relevant environmental features at each site

| Site | Predation level | Local density (guanacos/km ²) | Relative forage availability | Habitat type | Season | Sample sizes | | Mean number of adults in family groups \pm SD |
|------|-----------------|---|------------------------------|-----------------------|-----------------------------------|--------------|--------|---|
| | | | | | | Individuals | Groups | |
| C2B | Null | 55–60 | Low | Grasslands/Shrublands | Reproductive Post-reproductive | 65 | 31 | 6.06 \pm 2.5 |
| ML | High | 12–21 | High | Grasslands/Shrublands | Reproductive Post-reproductive | 73 | 32 | 7.98 \pm 4.7 |

Behavioral Observations

Males' individual vigilance and aggressiveness should be affected by the level of intrasexual competition (Clutton-Brock et al. 1982). In contrast, as female behavior is expected to be affected mostly by intra-specific competition over key resources and predation pressure (Jarman 1974), which are the main factors involved in previous hypotheses, this analysis is restricted to adult females. Continuous focal watches (Altmann 1974) were conducted by three observers, during Jan. and Mar. 2008 at ML, and by one observer at C2B during Dec. 2007 and Apr. 2008. Observations were conducted between 7:00 AM and 9:00 PM. We observed guanacos in family groups, which are composed of an adult male and one or more females, with or without 'chulengos' (offspring younger than 1-yr old). Besides sex composition, behavioral aspects were considered to assign groups to this category: harem males usually stay some meters away from the entire group, often showing some degree of aggressiveness and/or territorial displays toward and neighboring groups, such as chasing and defecating. Females in family groups tend to be highly cohesive, with a high degree of synchronization in their activities. In contrast, bachelor or mixed groups are composed exclusively of juvenile and adult males, or all sex and age categories, respectively. These groups lack cohesion or clear hierarchies and look like loose aggregations where animals enter and leave continuously. Even though distance between individuals can be used as accessory data to define group size, harem males tend to chase intruders for long distances and territorial tolerance vary between populations, thus it is useful to complement distance with other behavioral aspects. Females of the same family group often stay within short distances from each other (C2B: 10 ± 23 ; ML: 15 ± 51 , measured as body lengths) whereas when there are neighboring groups present, they remain farther away (average distance between neighboring groups C2B: 325 ± 103 ; ML: 260 ± 154 m). Operational group size was defined as the number of

females and young foraging together, in the same vegetation patch, moving slowly in the same direction, plus the adult male that remains closest to these females and shows no territorial displays toward them but does toward neighboring groups. Only three observations from a total of 75 groups had to be excluded from this analysis because group size could not be determined precisely because of the ambiguous interactions among group members. As there were no marked individuals, we used scars, natural spots or molting wool patterns to identify individuals and avoid observing the same female twice. Regarding group stability, family groups seem to be relatively stable in the number of adults and membership throughout the mating season. In more than 180 h of observations (average of 110 min per group), group-size changes in family groups were never witnessed whereas bachelor groups often fuse and split up during focal watches. In addition, successive sightings of two or more naturally marked adults in the same family group suggest that group membership was stable during the study; however, these observations are anecdotic because of the low number of permanently marked individuals. Family groups are highly territorial, and group location is predictable between successive days. This fact was confirmed by observing permanently marked individuals (scars and spots), temporary marked individuals (molting wool patterns), group size and group composition in terms of age categories, in the same location during different days. In addition, observation points at ML, where not all family groups were seen every day as in C2B, were at least 5 km apart from each other and never used twice within the same season. Thus, all observations at C2B corresponded to different groups and at least 70% ($n = 26$) of all groups observed at ML can be considered different based on the presence of marked individuals, group size and location. The remaining 30% had a low probability of pseudoreplication based on group size and location. Females in mixed groups were not considered in this analysis because these social units are significantly larger than family

groups, frequently numbering hundreds of individuals. Anti-predator benefits at the individual level probably have reached an asymptote at group sizes as large as these and probably other factors are involved in the costs/benefits balance of group living than those stated in the former hypotheses. In addition, as mixed groups are unstable and non-territorial, minimizing pseudoreplication of observing the same individual/group more than once is more difficult than with family groups. Observations were made using 8.5 × 44 binoculars and a 60-mm spotting scope (at 30–500 m away from the animals). When possible, two active (i.e. not resting) females from each group were continuously observed during 15 min or less until they went out of sight, laid down or moved to another habitat type. Observations that lasted less than 3 min were discarded.

During the focal watches, the observers registered in a voice digital recorder the moment when the focal animal switched between successive behavioral states. These states were defined as Scanning (standing with the head in an upright position but without handling or chewing vegetation), Handling food (masticating while standing with the head in an upright position), Walking (moving among adjacent vegetation patches with the head in an upright position), Head-down walking (walking slowly with the head below shoulder height often searching for preferred forage) and Cropping vegetation (either grazing or browsing). Other behavioral states that were less frequent were combined into the category Others and included the proportion of time grooming, defecating/urinating and wallowing in the dust. However, as this category represented less than 1% of the activity budget, it was considered negligible. Observation time was completely divided into the previous categories thus resulting in complementary proportions. Aggression events were defined as agonistic interactions between two individuals of the same group that led one or both of them to interrupt its feeding bout. These interactions included threatening displays, such as ear down movements and head-up postures, and direct aggressions such as spits, bites and chases, and were registered either if the focal individual was the perpetrator or the victim. All aggressive interactions observed within groups lasted less than 3–4 s so they were considered as short events instead of behavioral states (Altmann 1974). The software Etholog 2.2 (Ottoni 2000) was used to calculate the proportions of the observation time that the individual spent at each state, vigilance rate (vigilance bouts per minute) and mean length of vigilance bouts (expressed in seconds). The pro-

portion of time spent in vigilance was defined as the proportion of time that each female spent with its head above shoulder height, either exclusively scanning, handling food (chewing vegetation) or walking. The proportion of time that each female spent chewing vegetation with its head above shoulder height out of the total time invested in individual vigilance was considered as the overlap between vigilance and food handling effort. Vigilance rate was defined as the number of events in which a female lifted its head per minute of observation. Total time spent on walking was defined as the proportion of time moving, either with the head above or below shoulder height and is expected to reflect differences in searching effort. Aggression rate was expressed as the total number of agonistic events per hour of observation in each group.

Independent Variables

At the beginning of each observation, we recorded the number of adults in the group. Group sizes ranged from 1 to 14 adults. Observations of single females with or without offspring were considered as group size of one. The number of adults was considered instead of group size because younger individuals, mostly dependent offspring younger than 5 mo old, do not watch for predators or display aggressive behavior. Furthermore, adult females and the adult male, which suffer relative lower mortality than younger individuals, are the stable core of the family group on a year-round basis in these populations. Vegetation fisonomy in a radius of approximately 50 m around the group was described and classified into two types: Open grasslands, composed mainly of grasses and forbs, and Shrublands, with variable proportions of shrub cover. To accurately evaluate the hypotheses of interest, potentially confounding factors as reproductive state (Lipetz & Bekoff 1982) and season were considered. Whenever possible, the focal female was classified as Mother, if a lactating young was observed, and Without dependent offspring if there were no young individuals, or if all the offspring could be assigned to other females in the group. From a total of 138 observed females, the reproductive state of 43 (31%) were classified as Undetermined. Seasons were defined as Reproductive (Dec.–Feb.), when most births occur, and Post-reproductive (Mar.–Apr.). Thus, both populations were observed during both seasons, and this factor was considered to account for possible seasonal variations in behavioral responses.

Statistical Analysis

Linear mixed models were fitted to the proportion of time spent in vigilance and walking by each female. These proportions were previously arcsine transformed to meet model assumptions (Sokal & Rohlf 1995). The fixed terms considered in these models were the number of adults, site (C2B vs. ML), reproductive state, vegetation type and season, and their corresponding interactions with the number of adults. Parameters for factors are expressed as differences compared with the reference level that is the first treatment considered. Then, estimated standard errors were used to test whether the difference between the reference level and the other levels is significantly different from zero using unpaired *t*-tests, considering an alpha level of 0.05 (Crawley 1993). To remove within-group data dependence and to account for individual variation, group identity was considered as a random factor. Once a minimum adequate fixed model was obtained by maximum likelihood methods, restricted maximum likelihood method was used to fit final models to the data (Crawley 2007).

Mean duration of vigilance bouts, expressed in seconds, and vigilance rate, expressed as number of vigilance bouts per minute, were calculated from each focal observation and log transformed to meet model assumptions (Sokal & Rohlf 1995). Linear mixed models were fitted to these variables. The fixed terms considered in these models were the number of adults, site (C2B vs. ML), reproductive state, vegetation type and season, and their corresponding interactions with the number of adults. Group identity was considered as a random term.

The total number of agonistic interactions recorded during the watches of individuals of the same group were pooled and referred to the total observation time on that group. Aggression rate was defined as the number of agonistic interactions per hour in each group, obtaining a sample of 63 groups. A set of generalized linear models (GLM) assuming a negative binomial distribution for the error term and a logarithmic link function were fitted to the aggression data. The negative binomial distribution, adequate for count data, was selected to account for the variation structure of the aggression data and the logarithmic link function to ensure that the fitted values are bounded below (Crawley 2007), preventing negative aggression rate which would have no biologic sense. Model fitting was performed using R 2.9.2 (The R Foundation for Statistical Computing, Vienna, Austria) software.

Results

Proportion of Time Spent in Vigilance, Vigilance Rate and Vigilance Bouts Length

Final model terms for time spent in vigilance were the number of adults, the site and their interaction. The proportion of time spent in vigilance significantly decreased as the number of adults in the group increased in the high predation risk population, ML, but this effect was insignificant in the predator-free population of C2B (Table 2, Fig. 1). Females in small groups spent significantly more time in vigilance in the high predation risk than in the predator-free site. Females in grasslands spent less time vigilant than females in shrublands in both populations, although this effect was not significant. The interaction between the number of adults and vegetation type was not significant, meaning that the effect of the number of adults was similar in shrublands and grasslands. There was no effect of season on female individual vigilance ($d = -0.2$, $t_{67} = -1.06$, $p = 0.293$) or of the interaction between season and the number of adults ($d = -0.12$, $t_{66} = -0.79$, $p = 0.429$). Finally, there were no differences in time spent in vigilance between mothers and females without dependent offspring in any population ($d = -0.22$, $t_{64} = -0.95$, $p = 0.347$). Regarding the random term, differences among females of the same group accounted for 40% of the observed variation in individual vigilance. The mean overlap between the time spent in vigilance and the time spent masticating vegetation was 27% (± 28); this overlap was higher in C2B but this difference was not significant ($d = 1.31$, $t_{68} = 1.78$, $p = 0.08$). There was no effect of the number of adults on the overlap between time spent in vigilance and masticating vegetation in ML ($d = 0.02$, $t_{65} = 0.34$, $p = 0.69$) nor in C2B ($d = -0.15$, $t_{65} = -1.56$, $p = 0.12$).

Although the number of adults had no effect on vigilance rate (vigilance bouts per minute), there were differences between sites and seasons (Table 2, Fig. 2). Vigilance rate was significantly higher in ML than in C2B (Table 2) and lower in post-reproductive than in reproductive season at both sites ($d = -0.10$, $t_{65} = 2.14$, $p = 0.036$).

Vigilance bouts length was highly variable between individuals and groups. A final model was selected after removal of an observation of one female in a group of two adults and one young in ML which spent 14.8 min (100% observation time) vigilant. Average length of vigilance bouts was higher in ML than in C2B and decreased with the

Table 2: Parameter estimates, standard error (SE), degrees of freedom for the error term (df) and t probability (t pr.). (*) indicates terms kept in the final model. Parameters for factors are differences between the reference level and the corresponding level and represent the intercepts of the models. Parameters for variables (number of adults) are the slopes of the regression lines corresponding to the reference level. For the interaction terms, estimates are differences between the reference and the corresponding level slopes. Reference levels (constant): grasslands at predator-free C2B

| Factors | Individual vigilance | | | Scanning rate | | | Vigilance bout length | | | Time spent walking | | | Aggression rate | | |
|--------------------------------|----------------------|------|-------|---------------|------|-------|-----------------------|------|-------|--------------------|------|-------|-----------------|-------|-------|
| | Est. | SE | t pr. | Est. | SE | t pr. | Est. | SE | t pr. | Est. | SE | t pr. | Est. | SE | t pr. |
| Constant (grasslands in C2B) | 1.96* | 0.41 | 0.000 | 0.44* | 0.05 | 0.000 | 2.08* | 0.25 | 0.000 | 0.97* | 0.11 | 0.000 | -2.81* | 0.88 | 0.000 |
| Differences between intercepts | | | | | | | | | | | | | | | |
| Site (ML) | 1.59* | 0.05 | 0.002 | 0.17* | 0.05 | 0.001 | 0.80* | 0.34 | 0.021 | 0.34* | 0.15 | 0.029 | 0.04 | 0.36 | 0.909 |
| Habitat type (shrublands) | 0.40 | 0.24 | 0.107 | 0.00 | 0.05 | 0.970 | 0.24 | 0.15 | 0.116 | 0.16 | 0.18 | 0.389 | 3.70* | 0.81 | 0.000 |
| Variables | | | | | | | | | | | | | | | |
| Number of adults | 0.02 | 0.05 | 0.694 | -0.01 | 0.01 | 0.327 | 0.00 | 0.03 | 0.882 | 0.03 | 0.04 | 0.68 | 0.12* | 0.06 | 0.040 |
| Differences between slopes | | | | | | | | | | | | | | | |
| Number of adults ML | -0.14* | 0.07 | 0.041 | 0.01 | 0.02 | 0.363 | -0.11* | 0.05 | 0.029 | -0.06 | 0.05 | 0.68 | 0.223 | 0.07 | 0.11 |
| Number of adults in shrublands | -0.09 | 0.08 | 0.275 | 0.02 | 0.02 | 0.317 | -0.08 | 0.05 | 0.130 | 0.01 | 0.06 | 0.64 | 0.874 | -0.19 | 0.25 |
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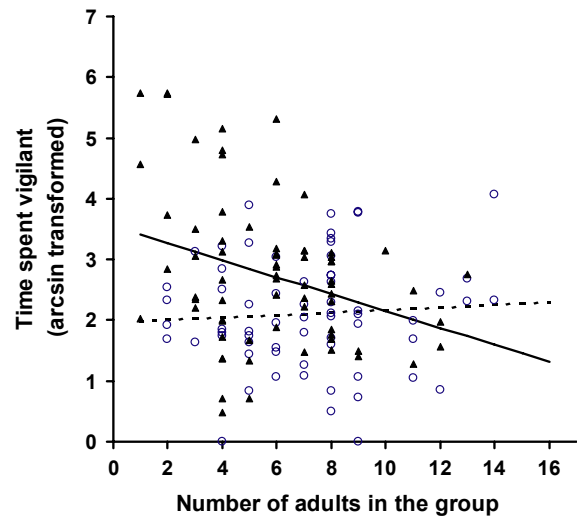


Fig. 1: Predicted values for individual vigilance (proportion of time spent vigilant arcsine transformed) as a function of the number of adults in the group in the high predation risk population of ML (full line, black triangles) and in the predator-free population of C2B (dashed line, empty circles).

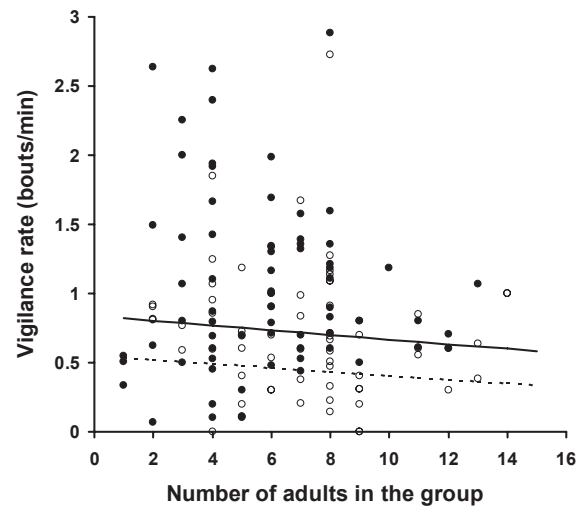


Fig. 2: Model predictions for vigilance rate (vigilance bouts/minute) as a function of the number of adults in the group in the high predation risk population of ML (full line, black circles) and in the predator-free population of C2B (dashed line, empty circles).

number of adults in the group in ML but not in C2B (Table 2, Fig. 3). There were no effects of vegetation type, nor season on vigilance bout length.

Time Spent Walking

The final model for time spent walking by individual females only included the differences between sites, showing that females in ML spent more time

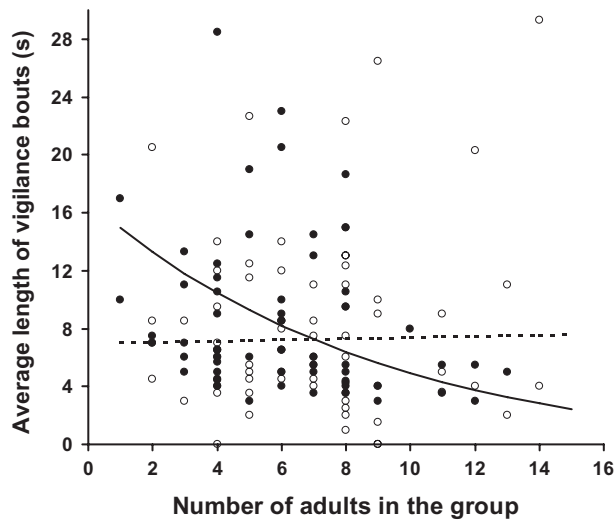


Fig. 3: Predicted length of vigilance bouts as a function of the number of adults in the group in the high predation risk population of ML (full line, black circles) and in the predator-free population of C2B (dashed line, empty circles).

walking than in C2B (Table 2). There was no effect of the number of adults in either population.

Aggression Rate

Final model terms for aggression rate were the number of adults and vegetation type (Table 2). Although aggression rate was almost null in grasslands, it was significantly higher in shrublands, and it increased significantly with the number of adults in the group (Table 2, Fig. 4). Even though the interaction between vegetation type and the number of adults was not significant, aggression events per hour increased from three in groups with two adults to 10 in groups with 12 adults when they were located in shrublands. In grasslands, however, aggression rate was almost zero in the former group-size range. Predicted values from these models – aggression rate in shrublands = $\text{EXP}(0.89 + 0.12 \times \text{number of adults})$; aggression rate in grasslands = $\text{EXP}(-2.81 + 0.12 \times \text{number of adults})$ – show that 24 adults in a group would be needed to have one aggression event per hour in grasslands. Family groups barely have more than 18 adults; thus, this range of values is located before the accelerated phase of exponential model in grasslands. As a result, aggression rate in grasslands is still very low, in spite of the number of adults. There were no differences in aggression rate between sites or in the effect of the number of adults between sites (Table 2). Finally, there was no effect of season on

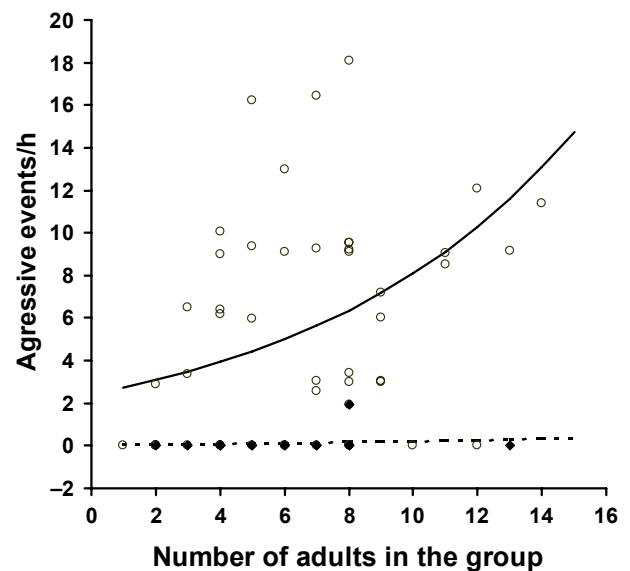


Fig. 4: Model predictions for aggression rate as a function of the number of adults in the group, for groups located in shrublands (full line, empty circles) and groups located in grasslands (dashed line, black circles).

aggression rate ($d = 0.06$, $t_{59} = 0.16$, $p = 0.873$) or of the interaction between season and the number of adults ($d = 0.08$, $t_{58} = 0.72$, $p = 0.474$).

Discussion

Individual Vigilance

Female guanacos showed great plasticity in the time invested in vigilance, ranging from 0% to nearly 80% of the observation time. Under predation risk, guanaco females showed higher scanning rates and a negative relationship between individual vigilance and group size (females in groups of more than 10 adults spent on average 50% less time in vigilance than females in pairs). This reduction in individual vigilance resulted from shorter scanning bouts in larger groups. As the overlap between time invested in vigilance and food handling was only partial and independent of group size, in addition to the lack of increase in travel time, vigilance reduction resulted in a net benefit in terms of time investment in forage cropping. The fact that the group-size effect is present in the predator exposed and absent in the predator-free population, plus the overall low individual vigilance observed in C2B, leads to the idea that guanacos are sensitive to predation risk and that the functional significance of group-size effect on individual vigilance is related to anti-predator responses. Guanacos from a low-density population

under predation risk by pumas also showed a strong reduction in individual vigilance with group size (Marino & Baldi 2008). Therefore, group-size effect on vigilance was absent in a predator-free population and occurred in two predator-exposed populations, reinforcing its functional significance as an anti-predator response. Higher levels of individual vigilance in response to increased predation pressure have been observed in other ungulates (Hunter & Skinner 1998; Childress & Lung 2003; Lung & Childress 2007), and the loss of group-size effects in isolation from predators has been observed in some macropodid marsupials (Blumstein & Daniel 2002).

During this study, ML was near the primary productivity peak whereas C2B was in the middle of the dry season. In addition to the lower annual productivity and higher guanaco density, dry season implies lower availability and poor-quality forage, suggesting that guanacos at the predator-free C2B may be exposed to higher competition pressure than those at ML. High levels of intraspecific competition among guanacos have been observed at C2B previously with lower population densities than those reported in this study (Cévoli 2005). Therefore, the scramble competition hypothesis, as an explanation for the reduction in individual vigilance as group size increases, was not supported at all as no group-size effect on vigilance or time spent walking was observed in the more extreme scenario of limiting resources. Although interference competition clearly rises as group size increases (see Aggression Rate subsection), it does not reduce individual vigilance in the predator-free population. Habitat quality is expected to covary with group size and home-range size, and to interact with group size-related scramble costs (Snaith & Chapman 2008). The lack of control of home-range size, territory quality and individual resting time during this study prevent discarding entirely the occurrence of scramble competition. However, these results indicate that even if scramble occurs, it is not responsible for the reduction in vigilance effort and support the hypothesis that group-size effect on female's vigilance reflects an anti-predator benefit of group living.

Aggression Rate

Aggression rate increased with the number of adults in the group in both populations, and the lack of differences between sites suggests that predation risk has no effect on intragroup agonistic interactions. However, habitat structure did affect aggression rate noticeably. Aggression rate was almost null when groups were feeding in open grasslands. In

contrast, when groups were located in shrublands, aggression rate was higher and increased rapidly with group size. The patchy distribution of shrubs seems to play a fundamental role given that individuals concentrate around them and their interaction rates increase. This seems to happen even when they are feeding on grasses and not on shrubs. In many occasions, focal individuals were clearly chewing grass after lifting their heads from a patch of shrubs. Shrub patches concentrate nutrients and promote the establishment of herbaceous plants (Bisigato & Bertiller 2004) and result in biotic refuges for grasses with low anti-herbivore defense (Pazos et al. 2007). Therefore, even if they are not feeding on them, woody plants act like hot spots containing high density of grasses, turning grass distribution from homogeneous to heterogeneous. Patchy distribution of forage in shrublands seems to be the major determinant of increased aggression rate. Most of these interactions imply an apparently dominant female that threatens another that was previously feeding on the shrub patch, with the consequent displacement of the subordinate. Predicting fitness costs of these interactions is difficult but they might range from reduced foraging efficiency by the interruption of the feeding bout for one or both members, to more extreme consequences (Huntingford & Turner 1987; Sansom et al. 2008). Even small wounds, as those resulting from conspecific bites, can have dramatic outcomes during the Patagonian summer. Myiasis (i.e. the infestation with dipterous larvae that feed upon tissues of live animals) can extend from a small wound which is progressively enlarged and deepened, resulting in extensive tissue destruction and even promoting lethal bacterial infections (Lane & Crosskey 1995). Increased interference competition in larger groups mediated by agonistic interactions has been observed in cervids with drastic consequences (Clutton-Brock et al. 1982) and in macropods (Blumstein et al. 2002), indicating that these costs derived from group living might be widespread among social herbivores.

Implications for Grouping Patterns

The costs/benefits approach to group-size variation suggests the existence of an optimal or equilibrium group size but, as Pulliam & Caraco (1984) pointed out, combining costs and benefits into a single metric presents serious methodological problems. The overall aggression rate among female guanacos is relatively low, and the proportion of time they invest in agonistic interactions may be a poor predictor of

the associated costs. However, assuming that anti-predator benefits and aggression costs are main factors determining group sizes, some qualitative inferences about the direction of group-size differences between contrasting scenarios can be derived. For example, as in shrublands competition costs in terms of aggression are relatively high and increase rapidly with the number of adults in the group, but they are almost null in grasslands, smaller group sizes can be expected in the former habitat type. Mean number of adults in family groups from a population survey conducted at ML (with predators) on Jan. 2008 are in agreement with this prediction, with $5.67(\pm 2.3)$ members for groups located in shrublands and $9.00(\pm 5.3)$ in those located in grasslands. On the other hand, as guanacos seem to perceive risk reduction where predators have been absent for a long time, smaller group sizes might be found in predator-free populations to minimize aggression costs, in agreement with mean group sizes stated in Table 1. However, group-size differences observed in these populations seem relatively small. Why would family groups in a predator-free population be as large as six given the competition costs? It has been suggested that some anti-predator behaviors may be more phenotypically plastic than others, and the rate at which a species can lose an anti-predator behavior after predator eradication depends on the degree to which the behavior is experience dependent and, ultimately, on its cost (Blumstein & Daniel 2002). In this context, time allocation may be highly experience-dependent (Hunter & Skinner 1998; Blumstein & Daniel 2005) whereas grouping patterns may be less flexible and likely constrained by other grounds besides predation avoidance. Territorial males gain obvious mating benefits with increasing harem size. Regarding females, other factors such as protection from sexual harassment by bachelor males (Cappozzo et al. 2008) and access to high-quality forage might still favor female aggregation into male territories, even in absence of predators. Further processes might also add to the costs of group living, such as increased pathogen transmission (Pulliam & Caraco 1984) and/or decreased forage quality in larger groups. These processes probably interact with the male's particular ability to defend a territory and maintain group cohesion, to ultimately determine the upper limit to group size. These factors are not mutually exclusive and likely to operate simultaneously. Future studies on guanaco grouping patterns will allow for testing these hypotheses, assessing the relative importance of these factors in shaping group-size variation within and between pop-

ulations, and to address the potential of habitat heterogeneity for limiting group-based anti-predator responses. Overall, the individual patterns observed in this study show that females are able to perceive predation pressure relaxation and adjust time allocation in accordance and suggest that predation risk and habitat structure are among the major determinants of costs/benefits balance of group living for territorial guanacos.

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