ARTICLE

Indirect measures of reproductive effort in a resource-defense polygynous ungulate: territorial defense by male guanacos

Andrea Marino

Abstract Trade-offs between reproductive effort and activities that are likely to enhance survival have been studied extensively in harem defense ungulates. However, among resource defense systems, ecological determinants of the variation in male reproductive effort are less understood. The aim of this study was to assess the extent of the effort devoted to territorial defense by male guanacos and how this is affected by predation risk. Time allocation to different activities and displays of aggressive behavior were compared between territorial and bachelor male guanacos within two populations with contrasting levels of predation risk. Territorial males devoted almost twice the time than bachelors to vigilance and moving, at the expense of foraging time. Aggressive interactions were more frequent and severe for territorial males than for bachelors, based on observation. These differences were larger during the reproductive season but remained statistically significant after this period, highlighting the extended effort towards territorial defense beyond the peak of reproductive activity. In contrast to previous observations on females of the same populations, there was no effect of predation risk level or group size on male time allocation, suggesting that under the ecological conditions of the study, intra-sexual competition entails a stronger influence on male individual behavior than predation risk level.

Introduction

Among mammals, a male's reproductive success is usually limited by the number of breeding females to which he can gain access (Clutton-Brock et al. 1982). A common male strategy is the defense of a resource that females require. If more than one female is likely to visit the resource vicinity, the effective result is polygyny (Vehrencamp and Bradbury 1984). A male capable of gaining and defending a territory that contains the required resource can enhance his fitness not only by an increased encounter rate with more than one receptive female but also by maximization of fertilization chances due to the exclusion of other males (Vehrencamp and Bradbury 1984). Territorial behavior can range from animals engaging in fierce combat along territory boundaries, with injury risk during the process, to more subtle defense methods, with individuals avoiding each other's signals (i.e., scent) (Gosling 1982). Both strategies require the owner to spend time and energy maintaining the territory at the expense of other potentially beneficial activities, such as feeding or resting (Davies and Houston 1984). A straightforward approach for analyzing the trade-offs between reproductive activities and those activities that are likely to enhance survival is to compare activity budgets among reproductive and non-reproductive individuals of the same sex.

In terms of ungulates, time-allocation correlates have been studied extensively with emphasis on factors affecting trade-offs between vigilance and foraging activities (Hunter and Skinner 1998; Childress and Lung 2003; Lung and

A. Marino (✉)
Unidad de Investigación Ecología Terrestre, Centro Nacional Patagónico, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Blvd. Brown 2915,
Puerto Madryn 9120, Chubut, Argentina
e-mail: marino@cenpat.edu.ar

Childress 2007). The aim of male vigilance may be the monitoring of the behavior of conspecifics to reduce risks associated with their proximity during the rut; this type of vigilance has been referred to as "social monitoring" (Lung and Childress 2007). Alternatively, vigilance might serve to reduce predation risk by enabling an approaching predator to be detected at a safe distance, thereby allowing escape; this is referred to "anti-predatory vigilance" (Pulliam and Caraco 1984). In this context, the correlation of vigilance with group size has been studied extensively since anti-predator benefits are expected to increase with group size (Pulliam 1973; Pulliam and Caraco 1984; Lima 1995). Animals living in a larger group may reduce predation-risk through the collective detection of predators and dilution and confusion effects (Pulliam and Caraco 1984). A decrease in vigilance effort with increasing group size is often observed in birds and mammals and thought to reflect the consequent reduction in the predation-risk perceived by each individual (Pulliam and Caraco 1984; Lima 1995).

Since both of these underlying processes are not mutually exclusive, it is difficult to isolate anti-predator vigilance from social vigilance. However, predictions based on behavioral correlates with particular ecological conditions can be derived in order to address the relative importance of predation-risk and intra-sexual competition in shaping male decisions about how to manage their time-budget. For example, anti-predatory vigilance is expected to decrease with increasing group size, whereas social monitoring is not (Beauchamp 2008). These processes have been well documented in some species of harem defense ungulates (Childress and Lung 2003; Lung and Childress 2007). Regarding territorial behavior, the monitoring of the behavior of peripheral individuals can be considered analogous to the "social monitoring vigilance" previously cited. To date, however, the effort devoted to territorial defense by resource-defense polygynous ungulates and how it is affected by predation risk has received relatively little attention.

Guanacos (Lama guanicoe) are the largest wild ungulate in South America, and their mating system has been reported to be a resource-defense polygyny (Raedeke 1979; Franklin 1983). In this system, a group of females with their offspring of the year live within a territory that an adult male defends (Raedeke 1979; Franklin 1983; Bank et al. 2003; Young and Franklin 2004a, b). Territorial males engage in a series of time- and energy-consuming activities, such as being vigilant to detect potential intruders, patrolling borders, and reinforcing territory ownership through defecating–urinating displays directed towards neighbors and peripheral males (Franklin 1983; Young and Franklin 2004a). Eventually, outsiders cross territory boundaries, ultimately triggering chases and direct fights. Thus, territorial defense implies time-consuming activities that are undertaken at the expense of other mutually exclusive and potentially beneficial ones, such as feeding. The territorial defense effort has been assessed in family-group and solitary territorial male guanacos (Young and Franklin 2004a), but systematic comparisons between territorial males and males who are not engaged in reproductive activities are lacking. In contrast to territorial males, bachelors are mostly mature males who do not hold a territory and live within large male groups in which individuals enter and leave freely (Raedeke 1979; Franklin 1983). This distinction between territorial males and bachelors provides researchers with the opportunity to assess the magnitude of reproductive effort in terms of time allocation towards territorial defense.

The primary aim of this study was to compare time budgets and aggression rates between territorial males and non-reproductive bachelors in order to address the extent of the effort devoted to reproduction once a territory has been occupied. The main predictions tested were that (1) territorial males spend more time being vigilant and walking at the expense of time devoted to feeding activities, and (2) territorial males show higher aggression rates than bachelors. A secondary aim addressed the question of whether the behavioral trade-off between social vigilance and anti-predator vigilance is modified in the presence of a large predator. Thus, this study was carried out within two guanaco populations exposed to contrasting levels of puma predation (Puma concolor). At Monte León National Park puma activity is frequent (Pia and Novaro 2005; Travaini and Zanón Martínez 2008), and puma predation is a major cause of guanaco mortality; in contrast, the Cabo Dos Bahías Reserve has been free of guanaco predators for decades (Provincial wardens, personal communication). It was expected that (3) guanacos exposed to puma predation would invest relatively more time in vigilance than those from the predator-free population, and (4) predator-exposed males would show an inverse relationship between vigilance effort and group size, according to the theoretically enhanced anti-predator benefits derived from living in a larger group.

Materials and methods

Study locations

This study was conducted in two protected areas in Patagonia (Argentina): the Cabo Dos Bahías Provincial Reserve and Monte León National Park. Cabo Dos Bahías (C2B) is a small wildlife reserve (1,700 ha) 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 avellanedae* and *Lycium chilense* and grasslands by *Stipa tenuis* and *Poa ligularis* (Beeskow et al. 1987). Average annual precipitation is 250 mm (Beeskow et al. 1987). In terms of predation risk, there have been no guanaco predators reported in the area for more than 20 years (Provincial wardens, personal communication). As tourists frequently visit the reserve, guanacos are habituated to human presence and can be observed from short distances without an alteration in their behavior (A. Marino, personal observation).

Monte Leon National Park (ML) is located on the Patagonian coast, in Santa Cruz Province (50°06′S; 68°54′W). It comprises 60,000 ha of grasslands and shrublands. Shrublands are characterized by *Junellia tridens* and *Lepidophyllum cupressiforme*, whereas grasslands are characterized by *Festuca pallescens*, *Puccinellia sp.*, *Agrostis sp.*, and *Poa atropidiformis* (Oliva et al. 2006). Average annual precipitation is 240 mm. Pumas are common at ML (Pia and Novaro 2005), and guanacos are the major prey in their diet, accounting for 40% of prey biomass (Travaini and Zanón Martínez 2008). In order to minimize disturbance due 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.

Guanaco populations can be either sedentary (i.e., family groups remain within their territories all year round) or migratory (i.e., most individuals leave their territories after the reproductive season and move collectively to their winter range) (Raedeke 1979; Franklin 1983). Although there is no telemetry data available, several studies on guanaco ecology have been carried out at C2B (Baldi et al. 2001, 2004; Cévoli 2005; Marino 2010), and the lack of massive movements of animals, even before catastrophic mortalities (Cévoli 2005), suggests that the C2B population is sedentary. With respect to the ML population, population density estimates made during a 4-year period indicate that part of the population shows facultative migrations; however, such migrations were not observed during the year this study was carried out (A. Marino, unpublished data).

Behavioral observations

Continuous focal watches (Altmann 1974) were conducted by three observers during January and March 2008 at ML, and by one observer at C2B during December 2007 and April 2008. Thus, both populations were observed during the early summer and autumn. Observations were conducted between 7:00 a.m. and 9:00 p.m. Guanacos were observed in family groups, which consist of an adult male (i.e., alpha male) and one or more females, with or without "chulengos" (offspring <1 year old). Bachelor groups comprise almost exclusively juvenile and adult males. These groups lack cohesion or clear hierarchies and appear to be loose aggregations, with animals entering and leaving continuously (Raedeke 1979). Whenever the size of the bachelor group could not be clearly determined, it was considered arbitrarily as the number of individuals within 50 m of each other. Operational family 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 remained closest to them. As there were no marked individuals, we used scars, natural spots, or molting wool patterns to identify individuals and avoid observing the same individual twice. Family groups in these populations are highly territorial, and group location is predictable between successive days, as has been observed in other populations during the reproductive season (Raedeke 1979; Franklin 1983). This characteristic 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 on 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 and never used twice within the same season. To observe the bachelors, we selected observation points that were at least 5 km apart, and focal watches were of short duration in order to minimize the chances of observing the same individuals repeatedly. Observations were made using 8.5×44 binoculars and a 60-mm spotting scope (at 30–500 m distant from the animals). When possible, one active (i.e., not resting) adult male from each bachelor group and the adult male and two adult females from each family group were continuously observed for ≤15 min until they went out of sight, laid down, or moved to another habitat type. Observations that lasted <3 min were discarded. Only male data are presented here.

During the focal watches, the observers used a voice-digital recorder to register the moment when the focal animal switched between successive behavioral states. These states were defined as "vigilant" (standing with the head in an upright position, even if the individual was handling or chewing vegetation), "moving" (either walking or running among adjacent vegetation patches), and "foraging" (either grazing or browsing). Other behavioral states that were less frequently observed were combined into the category "others" and included the proportion of time defecating/urinating, grooming, and wallowing in the dust. However, as this latter category represented <1% of the activity budget, it was considered negligible. Observation time was divided into these same categories, thus resulting in complementary proportions. Aggression events were defined as agonistic interactions between two individuals of the same group or neighboring groups that usually led one or both individuals to interrupt its feeding

bout. These interactions included threatening displays, such as eardown movements and head-up postures, and direct aggressions, such as spits, bites, and chases, and were registered both when the focal individual was the perpetrator or the victim, respectively. Most aggressive interactions observed lasted less than 3–4 s so they were considered as short events instead of behavioral states (Altmann 1974).The software package Etholog 2.2 (Ottoni 2000) was used to calculate the proportions of the observation time that the individual spent at each state. Aggression rate was expressed as the total number of agonistic events per hour of observation.

Independent variables

At the beginning of each observation, we recorded the number of adults and juveniles in the group. Seasons were defined as reproductive (December to early February), when most births and matings occur, and post-reproductive (March and April) (Bank et al. 2003). Thus, both populations were observed during both seasons, and this factor was considered to account for possible seasonal variations in behavioral responses. Other variables that were not directly related to former predictions were addressed to account for their possible influence on individual behavior. Previous studies among guanacos have shown that habitat structure might affect individual vigilance (Marino and Baldi 2008). Thus, vegetation physiognomy 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 at least 20% of shrub cover. Observer's location was also registered, and distance and azimuth from the group to the observer was measured with a laser range finder. These measures were used to determine the exact location of the observed individual. In order to account for differences in time allocation due to variations in patch quality, the enhanced vegetation index (EVI) derived from 250-m MODIS satellite images was used as an indicator of primary productivity (Pettorelli et al. 2005). These data are distributed by the Land Processes Distributed Active Archive Center (LP DAAC) (http://lpdaac.usgs.gov). Images corresponding to September and October were included in a geographic information system to account for the peak of primary productivity at each site. Pixel values from those locations where the focal individuals were observed were then extracted and re-scaled (i.e., the mean of the data set corresponding to each site was subtracted from each point value) in order to account for basal between-site differences in vegetation cover. Five records had to be removed from this analysis because individuals were located too close to the coast, resulting in mixed pixels with values out of range (Pettorelli et al. 2005).

Population surveys

Line-transect surveys of guanacos were conducted at C2B in November 2007 and at ML in April 2008, along all available dirt roads and tracks. Surveys were conducted from an open pick-up vehicle traveling at 10–30 km/h with two observers standing in the back, following the Distance Sampling method (Buckland et al. 1993). For every guanaco group encountered during the surveys, the vehicle was stopped and the distance and azimuth of the group to the transect line was measured using a laser rangefinder. Group size and composition was also recorded. Guanaco densities (individuals/km^2) were estimated using the Distance 5.0 software (Buckland et al. 1993).

In order to confirm that puma predation was a relevant source of mortality at ML and negligible at C2B, dead guanacos found opportunistically while conducting population surveys and behavioral observations were recorded. Park wardens also helped finding dead animals recording their locations during their daily surveys. Large bones fractured, canine-like punctures in the neck or throat, puma tracks and scats, among other signs associated to a carcass were used to assign puma predation as the cause of death (Logan and Irwin 1985). Whenever the carcass was too decomposed to assess cause of death properly, it was recorded as undetermined.

Statistical analysis

As group sizes of families and bachelors are markedly different, predation-risk predictions were tested separately for each category. A first set of linear models was fit to the proportion of time spent in vigilance by territorial males and bachelors, previously arcsine transformed to meet model assumptions (Sokal and Rohlf 1995), obtaining a final model for each category. The terms included in these models were "predation risk-level" (predator exposed vs. predator free site), "group size", and the interaction term "predation-risk level × group size". For territorial males, the effect of the "number of adult females" in the group was also tested. The variable "vegetation type" (shrublands vs. open grasslands) was also considered. Parameters for factors are expressed as differences between factor levels, considering one of the treatments as the reference level. Parameters for variables are the slopes of the regression lines corresponding to the reference level. Then, estimated standard errors were used to test if the difference between the reference level and the other levels was significantly different from zero using t tests, considering an alpha level of 0.05 (Crawley 1993).

To assess the significance of the differences between territorial males and bachelors in time allocation, linear models were fitted to the proportion of time spent in

vigilance, walking, and foraging by males of both social categories. These proportions has been previously arcsine transformed to meet model assumptions (Sokal and Rohlf 1995). The terms considered in this second set of models were "reproductive state", with two levels (territorial males vs. bachelors), "season" (reproductive vs. post-reproductive), and the "reproductive state × season" interaction. The variable "scaled EVI" was also included in these models as an indicator of primary productivity of the observed locations.

The number of agonistic interactions recorded during the watches was related to the total observation time on that individual. Aggression rate was defined as the number of agonistic interactions per hour of observation, obtaining a sample of 94 males. A set of generalized linear models assuming a negative binomial distribution for the error term and a logarithmic link function were fitted to the aggression-rate 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 were bounded below (Crawley 2007). A second analysis was conducted on the aggression data. Each focal observation was coded as a binary response, with a value of zero if no agonistic interaction was observed, and one if at least one aggression event occurred. The probability of observing at least one aggressive event during a focal watch was then modeled, assuming a binomial distribution of the variance structure, using a complementary log–log link function (Crawley 2007) and the same fixed factors as in the previous set of models. This type of response variable is less influenced by extreme values and variance heterogeneities that commonly arise in aggression-rate data and may be a more reliable variable for testing current predictions. Model fitting was performed using Genstat 7.1 software (Lawes Agricultural Trust-VSN Int, Rothamstead, UK).

Finally, green index (EVI) values corresponding to the locations of the focal individuals were compared between territorial males and bachelors. A linear mixed model (Crawley 2007) was fitted to the EVI data, including "reproductive state" (territorial vs. bachelor) as a fixed term and "site" as a random term, in order to account for between-site basal differences in plant cover. In this case, model fitting was performed using R 2.9.2 (The R Foundation for Statistical Computing, Vienna, Austria) software.

Results

Population density, group size, and mortality

Population density at C2B was 55.2 ± 10.0 guanacos/km^2, family groups comprised on average 6.61 adults [standard deviation (SD) 1.1]—i.e., one adult male and 5.61 adult females—and bachelor groups comprised on average 17.3 individuals (SD 11.7). Only six carcasses were found at C2B during the study: two chulengos died tangled in wire fences, two chulengos and a juvenile died from unknown causes, and an old female died presumably due to parturition-related problems. Neither carcasses with predation signs nor any evidence of activity of pumas or other guanaco predators (i.e., dogs) were found at C2B during this study.

Population density at ML was 24.13 ± 6.6 guanacos/km^2, family groups comprised on average 7.8 adults (SD 5.3), and bachelor groups comprised on average 30.9 individuals (SD 18.2). A total of 57 carcasses were found during the study. Puma predation accounted for 29 (76%) of the 38 carcasses for which cause of death could be determined. Puma kills are usually misreported since carcasses are generally too decomposed to assess cause of death properly. Therefore, the contribution of predation to guanaco mortality is probably underestimated. In addition to guanaco-predated carcasses, other signs of puma activity were frequent at ML, such as scats, tracks, and other prey-species remains. Although predation risk was not systematically measured, these signs confirm that during the study period, predation risk at ML was clearly high, whereas at C2B it was null or at least negligible.

Predation risk and male vigilance effort

A total of 94 males were observed: 26 territorial males and 27 bachelors at C2B and 31 territorial males and ten bachelors at ML. There were no differences between sites (predator exposed vs. predator free site) in vigilance effort of territorial males nor of bachelors. Neither was any significant relationship found between vigilance effort and group size or harem size, and these results were consistent for both populations studied. Only vegetation type appeared to have some influence, with a decrease in vigilance effort when bachelor males were located in open grasslands in the predator-exposed ML population, but this difference was not statistically significant. Parameter estimates and statistics are detailed in Table 1.

Male reproductive state, time allocation, and aggressive behavior

Territorial males invested significantly more time in vigilance than bachelors during the reproductive season, and this difference remained during the post-reproductive season, although it was then significantly smaller (Fig. 1a). Territorial males also spent more time walking than bachelors, but both social classes moved significantly less after the reproductive season (Fig. 1c). Parameter estimates

Table 1 Parameter estimates corresponding to the proportion of time spent being vigilant by territorial males and bachelors

Factors	Territorial males				Bachelor males			
	Estimates	SE	df	t pr.	Estimates	SE	df	t pr.
Constant (predator-free C2B, shrublands)	2.93	0.22	54	0.000	1.5	0.16	36	0.000
Differences between intercepts								
Site (predator exposed ML)	0.06	0.31	54	0.844	0.14	0.31	36	0.661
Vegetation type (grasslands)	−0.03	0.35	54	0.926	0.05	0.30	36	0.874
Grasslands in ML (vegetation type × site)	−0.75	0.71	52	0.295	−1.2	0.67	34	0.094
Group size	0.04	0.03	53	0.271	−0.01	0.02	35	0.418
Number of females in the group	0.04	0.05	53	0.476	–	–	–	–
Differences between slopes								
Group size in ML (group size × site)	0.05	0.70	52	0.486	0.00	0.04	34	0.868

SE Standard error, *df* degrees of freedom for the error term, *t (pr.)* probability by *t* test, *C2B* Cabo Dos Bahías Provincial Reserve, *ML* Monte León National Park

Reference levels (constant): shrublands in the predator-free site (C2B)

Fig. 1 Percentage of time devoted by territorial males (*black bars*) and bachelor males (*white bars*) to vigilance (**a**), foraging (**b**), walking (**c**), and proportion of observations with at least one aggressive interaction (**d**). *Error bars* Standard errors. Significant differences are indicated by a *single asterisk* if *p* < 0.05 or by *double asterisks* if *p* < 0.001
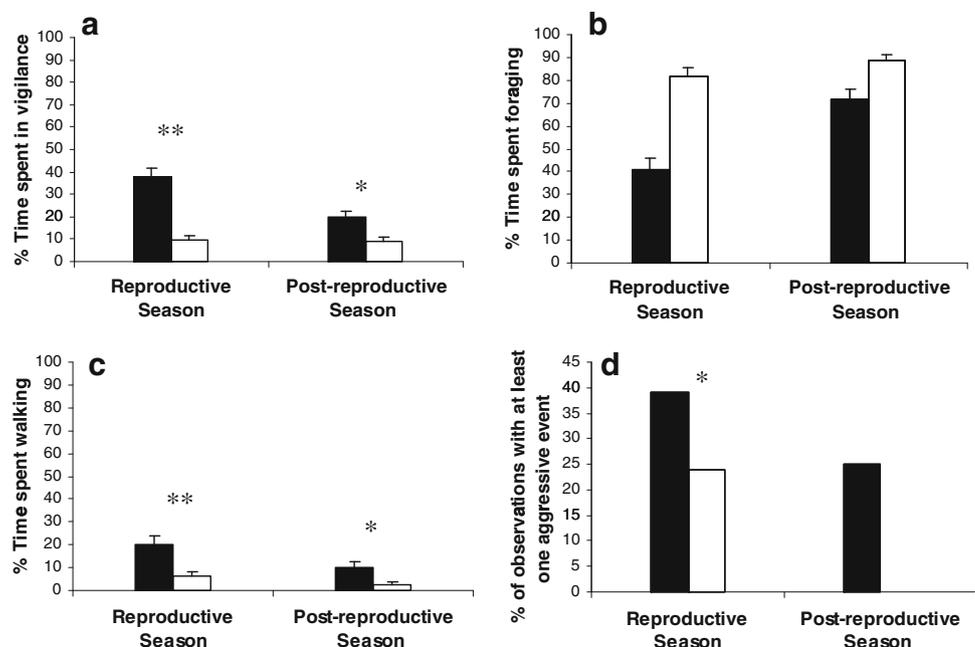
and statistics are given in detail in Table 2. Bachelors spent more time foraging than territorial males and showed no differences in foraging effort between seasons. In contrast, territorial males invested more time in foraging after the reproductive season, but even during this period they foraged less than bachelors (Fig. 1b). As these three proportions are complementary, previous analyses are not independent of each other. Foraging results are essentially derived from vigilance/walking results and, consequently, they are statistically invalid. However, estimated parameters have been included in Table 2 and Fig. 1b to illustrate that vigilant effort was inversely correlated with foraging effort.

Aggressive behavior

Heterogeneity in aggression-rate data prevented fitting a final model with acceptable residual patterns. However, average values were in accordance with predicted differences between territorial males and bachelors. The probability of observing an aggressive event was significantly higher during territorial-male watches than during bachelor watches and decreased after the reproductive season (Fig. 1d). Actually, no aggressive interactions occurred while conducting observations on bachelors during the post-reproductive season. However, while 100% of the aggressive events recorded for territorial males at C2B were

Table 2 Parameter estimates corresponding to the comparison between territorial males and bachelors for time spent being vigilant, walking, foraging, and probability of observing at least one aggressive event

Factors	Time spent vigilant				Time spent walking				Time spent foraging				Probability of observing at least one aggressive event		
	Estimates	SE	df	t pr.	Estimates	SE	df	t pr.	Estimates	SE	df	t pr.	Estimates	SE[a]	t pr.
Constant (bachelor males in reproductive season)	1.54	0.19	91	<0.001	1.29	0.19	92	<0.001	5.15	0.22	91	–	−1.40	0.46	0.002
Differences between intercepts															
Territorial males	1.81	0.26	91	<0.001	0.85	0.23	92	<0.001	−1.85	0.29	91	–	1.10	0.54	0.042
Season (post-reproductive)	0.00	0.33	91	0.990	−0.6	0.23	92	0.008	0.25	0.38	91	–	−1.45	0.54	0.053
Territorial males in post-reproductive season	−0.97	0.42	91	0.023	−0.1	0.48	91	0.797	1.23	0.48	91	–			
EVI (green index)	−5.55	7.3	85	0.448	7.74	8.13	86	0.344	0.21	8.51	85	–	10.8	17.2	0.531

EVI Enhanced vegetation index

Reference levels (constant): bachelor males during reproductive season

[a] SE are based on dispersion parameter with value 1

Table 3 Aggression rate (average values)

Social category	Season	Aggressive events/h (SE)
Territorial males	Reproductive	5.16 (1.63)
	Post-reproductive	3.33 (1.47)
Bachelors	Reproductive	3.77 (1.85)
	Post-reproductive	0.00

directed towards neighboring groups, at ML only 20% of the aggressions were directed towards other males during the reproductive season. At ML, 80% of the aggressive events recorded in family groups during the reproductive season and 100% of those recorded during post-reproductive season involved hostility between the focal male and his harem females and/or their offspring. Parameter estimates and statistics are given in detail in Table 2.

Vigilance effort, time spent walking or foraging, and the probability of observing aggressive interactions were not correlated with the scaled green index (EVI) (Table 2). Of the observed variation in EVI data, 52% was explained by between-site differences, with within-site variation accounting for the remaining 48%. However, there were no significant differences between locations of territorial and bachelor males once between-site variation was accounted for (estimate = 0.00, SE 0.00, df = 87, t pr. = 0.188) (Table 3).

Discussion

Male reproductive effort

During the reproductive season, bachelor males spent on average twice as much time foraging as territorial males; in turn, the latter spent almost 60% of their time on activities that are likely linked to territorial defense, such as vigilance and moving. Even though these differences in time allocation between territorial males and bachelors decreased significantly after the reproductive season, territorial males still spent almost 20% more of their time in vigilance and walking activities after the mating season than did bachelors, and these activities came at the expense of foraging time. In addition, both territorial males and bachelors engaged in aggressive behavior during the reproductive season, but territorial males did so significantly more often and, in contrast to bachelors, remained aggressive post-reproductive season. These results suggest that, in addition to the substantial costs of territorial defense during the peak of reproductive activity, territory ownership entails costs beyond the mating season; they are also in accordance with the observation of family groups staying within their territories at least until winter. Vicuña (*Vicugna vicugna*) territorial males, the other species of South American wild camelids, shows a similar frequency of agonistic interactions during the mating season and thereafter, but the level of aggressiveness is highest during

the mating season (Vilá 1992). In our study, aggression intensity differed between social categories: whereas the agonistic interactions of bachelors consisted of threat displays, such as ear-down movements and feeding-patch displacements, territorial males were involved in chases and fights in 48% of the observed aggressive events. It is remarkable that a high proportion of the aggressive interactions recorded at ML involved territorial males being aggressive with their harem females, particularly after the mating season. In most of these interactions, the territorial male apparently tried to expel a female from the group. The possibility of territorial males aggressively regulating harem size may be an additional dimension of reproductive effort that has to be considered. However, more studies are needed to determine whether this regulation exists and under what conditions.

A larger territory may be more costly to defend. Systematic knowledge of territory size and quality would help to account for extra variation in the data in order to assess more precisely the extent of male reproductive effort, but unfortunately this information is lacking for the studied populations. In contrast to what was observed in other populations, where bachelors are pushed to marginal habitats (Franklin 1983), primary productivity indicators (EVI) indexed for locations where focal observations took place were not different between family groups and bachelors. Although precise measures of preferred forage availability are still required, according to these results it would appear unlikely that the relative increase foraging effort by bachelors is compensation for lower forage quality.

Among highly dimorphic ungulates with harem defense systems, such as red deer, a dramatic decline in the proportion of time spent grazing has been observed in harem-holders during the rut (Clutton-Brock et al. 1982). As a result of the high energy costs of rutting and reduced food intake, the body weight and condition of rutting stags decline noticeably during this short period. However, this decline in foraging effort is quickly reversed when the stag ceases to hold an harem (Clutton-Brock et al. 1982). In sedentary populations, guanaco territorial males are generally in poorer condition than the non-territorial males throughout the entire year (Raedeke 1979). The tremendous physiological cost of year-long territorial defense could make a smaller body size a selective advantage for males faced with reduced foraging effort because of the consequent lower total nutrient requirement (Raedeke 1979). This extended investment in reproduction by resource-defense males has been suggested as an explanation for the lack of sexual dimorphism in guanaco body size, as opposed to the typical dimorphic pattern observed among polygynous ungulates (Franklin 1983).

Male vigilance and predation risk

The lack of differences between locations in the time spent in vigilance by both bachelors and territorial males suggests that predation-risk level was not influential enough to force significant changes in male time allocation. Bachelors in the predator exposed ML were found in groups of ≥12 individuals. Anti-predator benefits of grouping probably have reached an asymptote within these group sizes since vigilance effort remained invariably low, regardless of the predation-risk level. Therefore, bachelors, which presumably lack group-size constraints inherent to territorial defense, may compensate for increased predation risk by living in larger groups without the need of increased vigilance effort. Alternatively, it is intriguing that territorial males showed high levels of vigilance effort regardless of predation pressure or the number of females in their groups. A previous study on guanaco vigilance patterns in a low-density population exposed to puma predation showed that territorial males reduced their vigilance effort as the number of females in their harems increased (Marino and Baldi 2008), as would be expected under the anti-predatory vigilance hypothesis. As Raedeke (1979) previously suggested, at a low population density, territorial defense may be suspended since it may not be necessary. Within a low competition context, expected patterns of anti-predatory vigilance may be exposed. Both populations studied here occur at high density, and it is possible that intra-sexual competition has been intense enough to mask the effect of predation risk. If this were to be the case, territorial males with harems large enough to compensate for reduced anti-predator vigilance still might need to be vigilant to defend their territories. The fact that the females of the same populations did respond to increased predation risk with higher vigilance effort and significant group-size effects on time allocation (Marino 2010) supports the hypothesis that guanacos are able to perceive this level of predation-risk variation. Therefore, the pattern observed in this study is presumably linked to specific male behavior under these defined ecological conditions. Whereas female vigilance seems to be directed towards reducing predation risk, under high-density conditions vigilance by territorial males seems to be directed towards keeping other guanacos out of the territory. Lung and Childress (2007) found that the primary benefit of vigilance for female elk is to detect potential predators, whereas for male elk it is to monitor conspecifics during the mating season. Given the differential interests of males and females, analogous differences between the sexes in the functional significance of vigilance might be expected among other polygynous ungulates regardless of whether the resource defended is the harem or the territory.

References

Altmann J (1974) Observational study of behaviour: sampling methods. Behaviour 49:227–267

Baldi R, Albon SD, Elston DA (2001) Guanacos and sheep: evidence for continuing competition in arid Patagonia. Oecologia 129:561–570

Baldi R, Pelliza Sbriller A, Elston D, Albon SD (2004) High potential for competition between guanacos and sheep in Patagonia. J Wildl Manag 68:924–938

Bank MS, Sarno RJ, Franklin WL (2003) Spatial distribution of guanaco mating sites in southern Chile: conservation implications. Biol Conserv 112:427–434

Beauchamp G (2008) What is the magnitude of the group-size effect on vigilance? Behav Ecol 19:1361–1368

Beeskow AM, Del Valle HF, Rostagno CM (1987) Los sistemas fisiográficos de la región árida y semiárida de la Provincia de Chubut. Publicación Especial, Secretaría de Ciencia y Técnica, Buenos Aires

Buckland ST, Anderson DR, Burnham KP, Laake JL (1993) Distance Sampling: estimating abundance of biological populations. Chapman & Hall, London

Cévoli SR (2005) Dinámica de la población de guanacos (*Lama guanicoe*, Müller) de la reserva Cabo Dos Bahías, Chubut. PhD thesis. Universidad Nacional de la Patagonia, Patagonia

Childress MJ, Lung MA (2003) Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? Anim Behav 66:389–398

Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behaviour and ecology of two sexes. University of Chicago Press, Chicago

Crawley MJ (1993) GLIM for ecologists. Blackwell, Cambridge

Crawley MJ (2007) The R book. Wiley, Chichester

Davies NB, Houston AI (1984) Territory economics. In: Krebs CJ, Davies NB (eds) Behavioural ecology. Blackwell Scientific Publications, Oxford, pp 148–169

Franklin WL (1983) Contrasting socioecologies of South America's wild camelids: the vicuña and the guanaco. Am Soc Mam Spec Publ 7:573–628

Gosling LM (1982) A reassessment of the function of scent marking in territories. Z Tierpsychol 60:89–118

Hunter L, Skinner JD (1998) Vigilance behavior in African ungulates: the role of predation pressure. Behaviour 135:195–211

Lima SL (1995) Back to the basics of anti-predatory vigilance: the group size effect. Anim Behav 49:11–20

Logan KA, Irwin LL (1985) Mountain lion habitats in the Bighorn Mountains, Wyoming. Wild Soc Bull 13:257–262

Lung MA, Childress MJ (2007) The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. Behav Ecol 18:12–20

Marino A (2010) Costs and benefits of sociality differ between female guanacos living in contrasting ecological conditions. Ethology 116:1–12

Marino A, Baldi R (2008) Vigilance patterns of territorial guanacos (*Lama guanicoe*): the role of reproductive interests and predation risk. Ethology 114:413–423

Oliva G, Humano G, Rial P, González L, Paredes P, Mascó M, Kofalt R, Ferrante D, Franchini C, Vivar E (2006) Estudio de línea de base y plan de monitoreo de la biodiversidad vegetal del Parque Nacional Monte León. INTA, Santa Cruz

Ottoni EB (2000) EthoLog 2.2: a tool for the transcription and timing of behavior observation sessions. Behav Res Methods Instrum Comput 32:446–449

Pettorelli N, Olav Vik J, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends Ecol Evol 20:503–510

Pia MV, Novaro AJ (2005) Monitoreo de poblaciones de carnívoros y análisis de alternativas para reducir conflictos con la ganadería en el área circundante al Parque Nacional Monte León. Fundación Patagonia Natural, Administración de Parques Nacionales, Argentina

Pulliam RH (1973) On the advantage of flocking. J Theor Biol 38:419–422

Pulliam RH, Caraco T (1984) Living in groups: is there an optimal group size? In: Krebs CJ, Davies NB (eds) Behavioural ecology. Blackwell Scientific Publications, Oxford, pp 122–147

Raedeke KJ (1979) Population dynamics and socioecology of the guanaco (*Lama guanicoe*) of Magallanes, Chile. PhD thesis. University of Washington, Seattle

Sokal RR, Rohlf FJ (1995) Biometry: the principles and practices of statistics in biological research. WH Freeman, New York

Travaini A, Zanón Martínez JI (2008) Puesta a prueba de la extinción ecológica de presas autóctonas del puma (*Puma concolor*) en Patagonia. UNPA, Puerto Deseado

Vehrencamp SL, Bradbury JW (1984) Mating systems and ecology. In: Krebs CJ, Davies NB (eds) Behavioural ecology. Blackwell Scientific Publications, Oxford, pp 251–278

Vilá BL (1992) Vicuñas (*Vicugna vicugna*) agonistic behaviour during the reproductive season. In: Spitz F, Janeau G, Gonzalez G, Aulagnier S (eds) Ongules/Ungulates/91, ProcInt Symp. SFEPM/IRGM, Toulouse, pp 475-482

Young JK, Franklin WL (2004a) Activity budget patterns in family-group and solitary territorial male guanacos. Rev Chil Hist Nat 77:617–625

Young JK, Franklin WL (2004b) Territorial fidelity of male guanacos in the Patagonia of Southern Chile. J Mammal 85:72–78