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Time Allocation during the Reproductive Season in Vicuñas

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Abstract

Vicuñas (*Vicugna vicugna*) are wild South American camelids that live in high-altitude grasslands (Puna). Their social organization is based on family and bachelor groups. The amount of time they allocated to walking, running, lying, grazing and alert behaviour was studied in Abrapampa, northwestern Argentina, during the 1988–1990 reproductive seasons. Females and yearlings spent significantly more time grazing, and less time walking, running and alert than territorial males and bachelors. This result suggests that females maximized the time spent foraging to fulfil the energetic demands of reproduction. The alertness of the territorial males increased and the grazing decreased with the number of females in the families, suggesting that males that incurred a higher cost of lost feeding time through vigilance activities increased their mating success.

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Introduction

Time is frequently a limited resource and animals must allocate it between different behaviours in order to take in enough energy for growth, maintenance and reproduction (S. A. ALTMANN 1974; BEKOFF & WELLS 1981; HERBERS 1981). During the reproductive season, there is an increase in energetic demands (SADLIER 1969; OFTEDAL 1985) and the way animals allocate their time during this period can determine their reproductive success (CLUTTON-BROCK et al. 1982; SALATHE & BOY 1987). In arid environments, such as where vicuñas live, ungulates satisfy their energetic requirements by investing most of their time in foraging, and a positive relationship was found between time spent grazing and energy intake (ALLEN & WITTAKER 1970; STOBBS 1970). Even in these extreme conditions, however, differences in time allocation between the sexes and between age classes

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are expected because their reproductive success is influenced by different factors (EISENBERG 1966; WILSON 1975; CLUTTON-BROCK et al. 1982).

Ungulate female reproductive success depends on the survival of their calves to independence, which is related to birth weight and growth (CLUTTON-BROCK et al. 1988). Therefore, female strategies are based upon maximizing investment of energy in pregnancy, lactation and offspring care (CLUTTON-BROCK et al. 1982, 1988; GOSLING 1986). The resultant increase in female energy demands during the reproductive stage leads females to spend the majority of their time feeding or ruminating (GOSLING 1986).

In contrast, no paternal care is shown by most male ungulates, and male reproductive success depends primarily on intrasexual competition (CLUTTON-BROCK et al. 1982; GOSLING 1986). Male strategies are based on the defence of a resource that females need and/or on the retention of females, in other words a male 'must establish itself as an owner' (GOSLING 1986). In ungulates with a territorial social organization, one cost of male reproduction that has frequently been measured is the time devoted to the maintenance of the territory (OWEN-SMITH 1977; KLEIMAN 1981).

The vicuña (*Vicugna vicugna*) is a wild South American camelid that lives in high-altitude grasslands of the Puna Region of Bolivia, Perú, Chile and Argentina. They live in family groups that occupy areas defended by males throughout the year (KOFORD 1957; FRANKLIN 1974, 1983). Mean family composition is one male, three or four females and two offspring (VILA & ROIG 1992). There are also bachelor groups which vary in location, size and composition (KOFORD 1957; FRANKLIN 1974, 1983). Most females breed for the first time at 2 yr old or older; 1 or 2 wk after parturition, females come into oestrus; gestation takes 11 mo, while lactation lasts between 6 and 9 mo, and females nurse while pregnant (KOFORD 1957; FRANKLIN 1974, 1983). When they are about 10 mo old, most calves are chased away from the families by territorial males before the following calving season. Only a few yearlings remain with their families for a long time. In Abrapampa, sexual activity peaks in early–mid Mar. (VILA 1990). Calving season starts at the end of the summer (Feb.–Mar.) (KOFORD 1957; FRANKLIN 1983; GLADE & CATTAN 1987; VILA 1990).

Our objective was to analyse the time budget of vicuñas, including comparisons between age classes, pregnant and non-pregnant females, and males with different numbers of females. Females were expected to graze more frequently than animals in the other categories because of the high costs of reproduction (similarly pregnant females were expected to graze more than non-pregnant ones). Males were expected to graze less frequently and to walk and run more frequently than other categories as a way of maximizing their time spent in territory and group maintenance, and males with more females in the group were expected to spend less time grazing and more time being vigilant than males with fewer females.

Methods

The study was conducted at the Abrapampa Experimental Station of the National Institute of

Agricultural Technology (INTA), Jujuy Province, north-western Argentina, from Feb. to Apr., 1988, from Feb. to Mar. 1989, and in Jan. 1990. A total of 294 h of vicuña observation were recorded. The area is part of the Puna or Altiplano Region, a high, dry grassland dominated by tall perennial bunchgrasses and rhizomatous grasses (for details of the study site, see VILA 1992). A total of 600 vicuñas were held with protection from poaching and with almost no management activities. They were kept in a 400-ha field, with natural pasture and bordered by a wire fence which prevented sheep and llamas from entering the field, but which vicuñas could easily jump.

Observations were conducted from 0800 to 1800 h, from a 6.5-m high observation hut with 8 × 30 binoculars and 20 × 40 telescope. Observations were concentrated on vicuñas living around the observation hut (at least 10 families). Behaviours were classified as: (a) grazing, when the animal was standing or walking very slowly with its head close to the ground, (b) walking, or low displacement with head up, (c) running, (d) lying, and (f) alert, when standing with the head raised high and ears erect.

1988: Focal identified males. In 1988, six males were individually identified by natural marks and a tag attached to the left ear. These males and their family composition (males : females : yearlings : calves) were: A: (1 : 1 : 2 : 1); B: (1 : 3 : 0 : 0); C: (1 : 3 : 0 : 2); D: (1 : 4 : 1 : 2); E: (1 : 5 : 0 : 1) and F: (1 : 7 : 1 : 3). Focal males were selected on a random basis and followed for 30 min. Behaviour was recorded using the 'zero–one occurrence' sampling method (J. ALTMANN 1974), i.e. the occurrence or non-occurrence of the activities in every 1-min interval was recorded. Results were expressed as mean probabilities of occurrence per 1-min interval. Because of its relatively short duration, alert behaviour was recorded using the 'all occurrence' sampling method (J. ALTMANN 1974), and results expressed in mean number of occurrences per 1-min interval.

1989: Male scans. Scans were carried out every 30 min, and the number of females in the family group and the behaviour of the males scanned was recorded. A total of 1269 scans were conducted. Groups were identified before the first scan. Between scans they were viewed continuously in order to identify the territorial males, which were sometimes at some distance from their families.

1990: Focal males, females, yearlings and bachelors. The behaviour of males, females, yearlings and bachelors was recorded using the same focal method as in 1988. Because individuals were not individually recognizable, special care was taken to avoid sampling the same animals each day. Females were classified as 'pregnant' when their bellies were distended, enlarged and with the curve of the abdomen far towards their rear. At the time of the study females were in their last month of pregnancy so the difference between pregnant and non-pregnant animals was easily noticeable.

Results

1988: Focal Identified Males

Regression analyses were conducted, using the mean number of occurrences per 1-min interval and mean probability of occurrence per 1-min interval of alert, grazing, walking and running activities as dependent variables, and the number of females per male as the independent variable (Table 1). Lying behaviour was omitted from these due to its infrequent occurrence. Alert behaviour showed a significant positive regression coefficient (Fig. 1 a) suggesting that males with more females were more vigilant than males with small groups. Grazing behaviour showed a trend to decreasing values when the number of females increased (Fig. 1 a), but this tendency was not statistically significant, probably due to the small sample size. Walking and running were not related to group size (Table 1).

1989: Male Scans

Data for all daily scans of the males were tabulated according to the behaviour observed and the group size. The null hypothesis that the frequencies of behaviours were equal for each group size was tested using a contingency table analysis. This

Table 1: Statistical analyses of the relationship between the behaviour of resident males and the number of females in their territories. 1988: Regression analyses of the mean values of the activities of six individually identified males. 1989: Partitioned contingency tables of the data from 1269 scans, with Bonferroni adjustments of acceptable p levels

	Focal males, 1988			Scans, 1989	
Activities	r^2	F	p	χ^2	p
Alert	0.735	11.1	0.029	18.96	0.004
Graze	0.591	4.33	0.13	22.25	0.001
Run	0.022	0.09	0.78	2.15	0.91
Walk	0.151	0.71	0.44	3.36	0.76

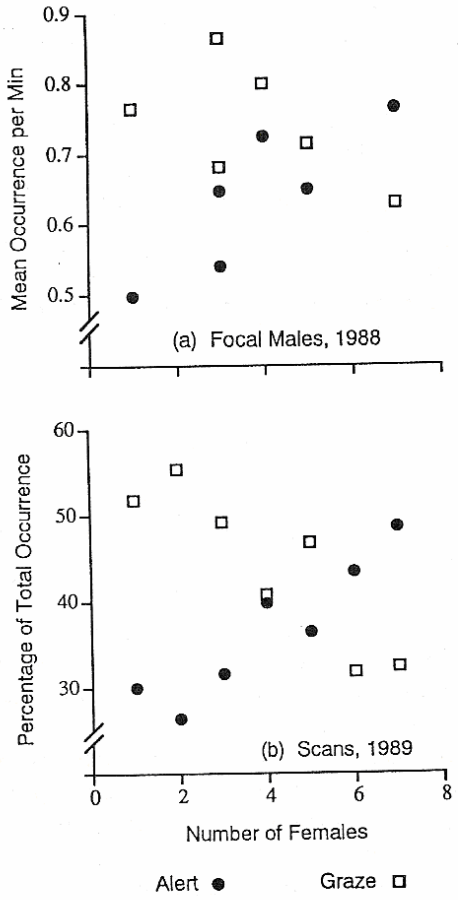

Fig. 1: a. Mean number of occurrences of male alert behaviour and mean probability of occurrences of male grazing behaviour in relation to number of females; each point corresponds to a territorial male followed in 1988 season. b. Percentage of total occurrence of alert and grazing behaviours in relation to the number of females, from scans recorded in 1989 season. Statistical analyses in Table 1

Table 2: Mean probabilities of occurrence (SE) of walking, running, grazing and lying, and mean number of occurrences of alert behaviour for the different categories of vicuñas. An arcsin transformation was applied to the data and one-way ANOVAs were conducted, comparing categories for each activity (df = 3, 16). Symbols =, < and > indicate non-significant ($p > 0.05$), significant negative, and significant positive differences with the Fisher PLSD test ($p < 0.05$), respectively

	Bachelors		Territorial males		Females		Yearlings	F-value (p-value)
Walk	0.336	>	0.237	>	0.164	=	0.208	6.92
	(0.04)		(0.02)		(0.01)		(0.02)	(0.0002)
Run	0.094	>	0.034	>	0.01	=	0.024	13.36
	(0.02)		(0.07)		(0.003)		(0.007)	(0.0001)
Alert	0.716	=	0.616	>	0.195	=	0.194	14.94
	(0.23)		(0.071)		(0.037)		(0.035)	(0.0001)
Graze	0.425	=	0.52	<	0.56	=	0.57	2.855
	(0.06)		(0.03)		(0.02)		(0.03)	(0.03)
Lie	0.003	=	0.038	=	0.046	=	0.064	0.624
	(0.002)		(0.021)		(0.017)		(0.027)	(0.6)
n	12		35		68		35	

revealed a highly significant overall association ($\chi^2 = 29.68$, df = 18, $p = 0.041$). The table was then partitioned into its constituent rows, each corresponding to a behavioural type, with the remaining behaviours aggregated. Separate tests were then carried out for the null hypothesis that the proportion of each behaviour did not vary with group size. As for 1988 data, lying behaviour was eliminated from the analysis because of its low frequency of occurrence. These analyses showed that the frequencies of alert and grazing behaviour differed significantly with group size while there was no evidence of variation in the frequency of walking and running (Table 1). The significant differences were overwhelmingly attributable to an increase in vigilant behaviour with group size at the expense of grazing (Fig. 1 b).

1990: Focal Males, Females, Yearlings and Bachelors

There were no significant differences between pregnant (n = 34) and non-pregnant female samples (n = 34) in any of the five activities (Student's t-test, t-values < 1.07, p values > 0.28) Therefore, in the following analyses we grouped the data for females in one category.

Table 2 presents the mean probabilities of occurrence per 1-min interval of grazing, walking, running, and lying and the mean number of occurrences per 1-min interval of alert behaviour for territorial males, females, members of bachelor groups and yearlings. One-way ANOVA indicated significant differences between age and sex categories for all activities except lying. Post-hoc multiple comparisons between means were conducted, using the Fisher PLSD method. Bachelors walked and ran with a higher probability ($p < 0.05$) than other animal categories, followed by territorial males, which performed these behaviours more frequently than

females ($p < 0.05$). There was no significant difference in the frequency of alert behaviour between bachelors and territorial males ($p > 0.05$) and both were more frequently alert than females ($p < 0.05$). Females grazed more than territorial males and bachelors (p values < 0.05). The yearlings, which were associated with families, showed a time budget similar to that of females, and no significant differences were found between their mean probabilities of occurrence per 1-min interval and those of the females (p values > 0.05).

Discussion

BOSCH & SVENDSEN (1987) found that lactating female vicuñas grazed more frequently than non-lactating ones, but we did not find significant differences in the occurrence of this activity between pregnant and non-pregnant females. OFTEDAL (1985) showed that wild female ungulates need to increase energy intake by only one-third of the maintenance level for pregnancy, but must double this for lactation. Thus, gestation is much less costly than lactation, and its effects on a female's time budget might therefore be insufficient to produce significant differences in the amount of time allocated to foraging.

Females showed a very similar time allocation pattern to that of yearlings in the families, with both investing a high proportion of time in foraging. This may be because the quality of the food is very low in the Puna, so the high energetic and nutritional costs of both reproduction and growth would necessitate maximizing foraging time.

As in other vicuña populations, bachelors spent most of their time in marginal areas separated from areas where families established territories (KOFORD 1957; FRANKLIN 1983; CAJAL 1985). The entire observation area was occupied by family territories, so bachelors using this area could move only between families, or stay temporarily in a sector which had been vacated by a family which had gone to drink. This may explain the high frequencies of running, walking and alert behaviour of bachelors, as well as the lower time spent grazing. Previous work in this study area showed that bachelors are chased frequently by territorial males (VILA 1992).

Ungulate males incur three principal costs associated with reproduction (BERGER 1986): (1) losses in feeding time through activities related to vigilance ('time costs'), (2) costs incurred through walking, running, chasing and fighting for females ('energetic costs'), and (3) costs associated with injuries or death during fights ('injury costs'). Male vicuñas allocated less time than females and yearlings to maintenance activities and more time to movements and vigilance. The resulting decrease in net energy intake rate was probably part of the 'time' and 'energetic' costs of territorial defence. Males spent more time in vigilant behaviour and less time grazing when the number of females in their territories increased, indicating an additional 'time' cost associated with female defence. Family groups and territories were relatively stable all year and copulation occurred within these territories (FRANKLIN 1974, 1983). Consequently, the number of females in the territory is a relatively good measure of mating success of male vicuñas (VILA

1990). Therefore, the observed male cost of losing foraging time through vigilance can be interpreted as a cost invested in increased reproductive success. Interestingly, there were no relationships between the occurrence of either walking or running and group size, suggesting the lack of significant extra costs of the 'energetic' type associated with female protection.

BOSCH & SVENDSEN (1987) reported that male vicuñas spent less time grazing than females during the reproductive season in Pampa Galeras Perú. However other studies (MENARD 1982; GLADE & CATTAN 1987) found no differences in time allocation between males and females. Differences in time budgets between the sexes in vicuñas might not be detected statistically if the sampling method has a coarse grain, because all age–sex classes spend most of their time foraging. However, even small differences in time allocated to foraging might have a great impact upon the probability of survival because the reproductive season coincides with the short annual period of plant growth in the Puna (PFISTER et al. 1989).

The pattern reported here, with females spending more daylight time grazing, and males spending more time moving and being alert, has been found in several other ungulates during the reproductive season, including giraffes, *Giraffa camelopardalis*, gerenuks, *Litocranius walleri* (LEUTHOLD & LEUTHOLD 1978), impalas, *Aepyceros melampus* (JARMAN & JARMAN 1973), roe deer, *Capreolus capreolus* (CEDERLUND 1981), white-tailed deer, *Odocoileus virginianus* (BIER & MCCULLOUGH 1989) and feral horses, *Equus caballus* (DUNCAN 1980; BERGER 1986; RUBENSTEIN 1986).

A relationship between fighting success and the number of females that males manage to hold has been found in other ungulates, including gazelles, *Gazella* spp. (WALTHER et al. 1983) and red deer (CLUTTON-BROCK et al. 1982). In a previous study on the aggressive behaviour of vicuñas conducted in the same study site in summer 1987, VILA (1992) also found a positive relationship between the aggressive interactions in which resident males were engaged and the number of females in their territories. However, our study appears to be the first one in ungulates which shows a positive correlation between the male reproductive 'time' cost and the number of females present in male territories. Previous studies, such as BOSCH & SVENDSEN's (1987) in vicuñas and BERGER's (1986) in wild horses, did not find this relationship.

The vicuñas' mating system was originally described as pure 'resource defense polygyny' (FRANKLIN 1983); that is, males defend territories containing resources that attract females (EMLEN & ORING 1977). During the reproductive season, resident males were observed preventing intruding males that approached females and herding females that moved away from their territories (KOFORD 1957; FRANKLIN 1974). Based on these observations, BOSCH & SVENDSEN (1987) proposed that territory defence should be complemented with direct defence of females and predicted that the amount of time that resident males spent in territorial behaviour varied with number of females in the group. However, they did not find that large multi-female groups required more time spent in defence.

The difference between our results and those of other studies could be due to different methodological approaches (i.e. different categories of behaviour) or,

more probably, to actual differences of mating patterns between populations, associated with different environmental pressures. Differences between populations in mating patterns can be found in other ungulates, such as horses (RUBENSTEIN 1986), white-tailed deer, (HIRTH 1977; MILLER 1981), red deer, *Cervus elaphus* (CARRANZA et al. 1990), sika deer, *Cervus nippon* (MIURA 1984) and fallow deer, *Dama dama* (LANGBEIN & THIRGOOD 1989). Variation in mating systems should be expected as they are the outcome of the reproductive strategies of individuals and not of species (CLUTTON-BROCK 1989; DAVIES 1991; LOTT 1991; AHNESJO et al. 1993). In Pampa Galeras, Perú, and Parque Nacional Lauca, Chile, the most favourable pastures for vicuñas showed a heterogeneous distribution, frequently concentrated along the margins of the rivers, facilitating resource defence. Males that can monopolize such an area will attract more females to their territories and increase their mating success. In Abrapampa the grassland is highly homogeneous (see VILA 1992 for a detailed description of the study site). Therefore, resident males could only increase the attractiveness of their territories by (1) increasing the size of the defended area or (2) minimizing the disturbance to female activities by more actively scanning for intruders. Both hypotheses predict the observed increase in time invested in vigilance. Future studies should be conducted to test these hypotheses, and that of the effect of resource distribution on differences in the vicuñas' mating system between populations.

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