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# Pampas deer (*Ozotoceros bezoarticus*) social organization in semiarid grasslands of San Luis, Argentina

**Abstract:** Pampas deer (*Ozotoceros bezoarticus*) is a medium-sized South American cervid associated with savannas and grasslands in Argentina, Brazil, Bolivia, Uruguay, and Paraguay. Currently, four isolated population nuclei occur in Argentina, with the largest one located in the semiarid grasslands of San Luis Province. The aim of this work was to describe the social organization of this local population and to determine and analyze the factors that influence it. The most frequent groups found were mixed groups (34.82%), followed by solitary males (18.64%), and solitary females (15.00%). Differences in group type occurrence were found in three periods: dry, early rainy, and late rainy seasons. Mixed groups were more frequent during the dry season. The sexual segregation-aggregation statistic showed statistically significant segregation only in January and November. In addition, we analyzed the social grouping patterns during an annual cycle; the mean group size was  $2.49 \pm 0.46$  and Jarman's typical group size was  $3.84 \pm 1.08$  (individuals/group). A mixed-model nested ANOVA showed marked differences in terms of group sizes between habitat types and seasons. The social organization of the Pampas deer in San Luis is similar to that of the other populations of this species, despite occupying a different environment type and exhibiting disparate feeding styles and density values.

**Keywords:** grouping patterns; habitat type; sexual segregation; social structure; year season.

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## Introduction

The size and composition of groups in social ungulates are basic attributes of their social organization (Jarman 1974, Shi et al. 2005). Individuals gather in response to both the environment and the behavior of other individuals. Groups are not stable units. Instead, individuals gather and separate constantly (Rodrigues and Monteiro-Filho 1996, Gérard et al. 2002, Focardi and Pecchioli 2005).

Gregariousness is common among ruminants. Groups are formed by individuals that keep a short distance from each other and share activities, such as foraging, moving, and resting. Group size results from the balance between advantages and disadvantages of life in groups. An individual obtains benefits mainly related to reproduction and/or anti-predatory tactic. However, there are also disadvantages, such as the increase in intraspecific competition and disease transmission (Gueron et al. 1996). Changes in group size are influenced by the density and by ecological factors (type of habitat; quality, abundance and distribution of food; predatory risk) (Jarman 1974, Clutton-Brock et al. 1982, Barrette 1991, Focardi and Paveri-Fontana 1992).

With regard to group size, two trends have been identified in social ruminants. First, groups in open environments tend to be larger than those in closed environments. This difference could be due to the fact that large groups in open environments increase vigilance against predators. Among cervids, this trend was observed in the roe deer *Capreolus capreolus* Linnaeus, 1758 (Marchal et al. 1998) and the white-tailed deer *Odocoileus virginianus* Zimmermann, 1780 (Hirth 1977, Lagory 1986). Second, large grouping is linked to increasing density because it raises the probability of encounters among individuals (Barrette 1991, Gérard et al. 2002), as observed in the roe deer *C. capreolus* (Gérard et al. 1995, Marchal et al. 1998) and in bovid species, such as the bohor reedbuck *Redunca redunca* Pallas, 1767 (Wirtz and Lörcher 1983) and the alpine ibex *Capra ibex* Linnaeus, 1758 (Toïgo et al. 1996).

Jarman (1974) proposed that feeding habits also influence gregariousness, observing that in African bovids the

highly selective feeders tended to form very small groups, whereas the less selective feeders aggregated in larger groups.

Pampas deer (*Ozotoceros bezoarticus* Linnaeus, 1758) is a medium-sized South American cervid, associated with savannas and grasslands in Argentina, Brazil, Bolivia, Uruguay, and Paraguay (Jackson 1987, Merino et al. 1997). Until the mid-19th century, it occurred in north and central Argentina. Subsequently, it suffered a marked retraction due to the advance of agricultural activities. Currently, there are only four isolated population nuclei, and the largest one (>1000 individuals) inhabits the semi-arid grasslands in San Luis Province (Merino et al. 2011). This species is considered “near threatened” (NT) according to the IUCN Red List categorization (González and Merino 2008), but it is listed as “endangered” in Argentina (Pastore 2012).

Pampas deer are not markedly gregarious, showing a high rate of solitary individuals, and groups commonly do not exceed three individuals (Netto 1997, Moore 2001, Vila 2006). However, work on its social organization and grouping patterns are still scarce (Netto et al. 2000, Lacerda 2008, Cosse and González 2013).

Births in this species can occur throughout the year and usually a single fawn is born (Jackson 1987, Merino et al. 1997, González et al. 2010). In the San Luis population, birthing peaks during spring, especially from September to November (Jackson and Langguth 1987), corresponding to a rutting peak from February to April, as the gestation period is 7 months long.

The aim of this research is to describe the social organization of Pampas deer in the semiarid grasslands of San Luis and to determine and analyze the factors that influence it.

## Materials and methods

The Pampas deer population in San Luis inhabits the semiarid Pampean grasslands, a graminaceous steppe with small Chañar [*Geoffroea decorticans* (Gill. ex Hook. & Arn.) Burkart] patches (Anderson et al. 1970). Mean annual precipitation is 605 mm±204, about 80% of which falls between October and April, with lower precipitation in winter. The mean annual temperature is 17°C, with a strong continental effect: 43°C in summer and 15°C in winter (Anderson 1979). These seasonal rainfalls and temperatures cause marked fluctuations in forage availability.

We studied the Pampas deer population at “El Centenario” Ranch (34°10′ 2.57″S, 65°50′ 26.82″W). This cattle ranch covers 380 km<sup>2</sup>, and it hosts the largest Pampas deer

nucleus of the San Luis population (Dellafiore et al. 2003). Since the early 1990s, land use in the area has changed, with the introduction of exotic pastures, cattle rotation, and land subdivision. Currently, only 18% of the ranch has natural grasslands, whereas the exotics *Digitaria eriantha* Steudel (58%) and *Eragrostis curvula* (Schröd.) Nees (24%) occur in the rest of the grasslands. There are also small patches of soybean [*Glycine max* (L.) Merr.] crops (Merino et al. 2009, 2011).

We conducted monthly terrestrial censuses (n=12) from a vehicle between April 2006 and March 2007. Along fixed transects, we recorded the size and composition of groups classified according to the following age-sex classes: adult males and females (1 year old or older), fawns (up to 3 months of age) that still have the dot pattern on their dorso-lateral fur, and juveniles (between 3 and 12 months of age) with 3/4 adult size without spots of fawns (Moore 2001). For each observation, we also recorded dominant vegetation in the paddock (habitat type).

Groups were defined following Netto et al. (2000). According to their composition, the groups were classified into six types: solitary male/female (M/F); group of males (MM); group of females (FF), including fawns or juveniles; mixed group (MF), including fawns or juveniles; and female-fawn or juvenile dyad (F-F). We compared the frequency of group types during three main time periods using the  $\chi^2$ -test, owing to the clear differentiation between rainy and dry periods: dry season (June–September), when winter species grow among the dry dead standing tussocks of summer forage species; early rainy season (October–January), corresponding to the regrowth of summer forage species (almost exclusive formation of leaf tissue); and late rainy season (February–May), when summer forage species bloom and fructify. Sex and age ratios were also calculated for these three seasons.

We analyzed the sexual segregation or aggregation pattern using the sexual segregation-aggregation statistic (SSAS), following the protocol developed by Bonenfant et al. (2007) through the R program (R Development Core Team 2013).

For each census, we also calculated mean group size (MGS, the arithmetic mean of group sizes averaged across groups) and “crowding”, that is, the arithmetic mean of crowding values averaged across individuals (Reiczigel et al. 2008), to analyze the social grouping patterns during an annual cycle. Mean crowding equals Jarman’s typical group size (TGS) (Jarman 1974). TGS is the group size in which an individual lives, it characterizes the social environments of typical individuals, and it is larger than the MGS because individuals tend to live in groups larger than

average (Jarman 1974, Reiczigel et al. 2008). We compared the monthly group size distributions using the Kruskal-Wallis test.

We also obtained the monthly TGS for males (TGSM) and females (TGSF), as well as the monthly typical number of individuals of equal sex category (TNM and TNF), and we compared these with a Mann-Whitney U-test. Kendall's coefficient was used to test whether the monthly patterns of TGSs and TNs varied in the same way.

Using Spearman correlation, we analyzed whether MGS was linked to monthly density, which was estimated with the DISTANCE 5.0 software (Merino et al. 2011). Moreover, a mixed-model nested ANOVA, with sector as a random factor and habitat type nested in sector, was used to examine whether group sizes (dependent variable) differed under the influence of the fixed factors, namely, seasons of the year (dry, early rainy and late rainy) and habitat type (vegetation present in the paddock: *Digitaria*, *Eragrostis* and natural grasslands), with subsequent Tukey's tests.

## Results

### Sex and age ratios

We observed a total of 1578 individuals ( $131.5 \pm 22.40$  Ind./census), 39.29% of which were male adults, 45.37% female adults, 12.18% juveniles, 2.02% fawns, and 1.14% undetermined. The mean adult male/female (sex) ratio, mean

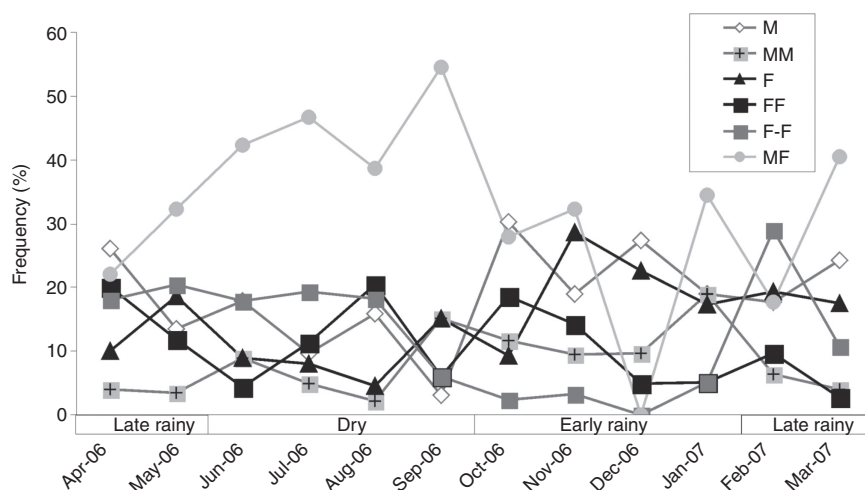
recruitment rate (juvenile/adult), and juvenile/female (age) ratios were  $0.91 \pm 0.35$ ,  $0.15 \pm 0.13$ , and  $0.26 \pm 0.21$ , respectively. The highest sex ratio ( $1.30 \pm 0.32$ ) occurred during the early rainy season, whereas the highest recruitment ( $0.22 \pm 0.06$ ) and juvenile/female ratio ( $0.38 \pm 0.1$ ) both occurred during the late rainy season.

### Group types according to their composition

A total of 652 groups were observed ( $54.33 \pm 12.26$  groups/census), with sizes between one and 17 individuals. Most of the groups were formed by three or less individuals (34.05% solitaires, 33.43% groups of two, and 14.42% groups of three). Group size distributions differed among months ( $H=34.039$ , 11 DF,  $p<0.0001$ ).

The most frequently observed groups were mixed groups (MF: 34.82%), followed by solitary males (M: 18.64%), solitary females (F: 15.00%), and female-fawn dyads (F-F: 12.52%), whereas the groups formed by individuals of the same sex were the least common (FF: 10.78% and MM: 8.24%).

The occurrence of group types was different among the three mentioned periods of the year ( $X^2=58.818$ , 10 DF,  $p<0.0001$ ). Mixed groups were frequent during the whole year, especially during the late rainy and dry seasons, peaking in September. During the early rainy season, the occurrence of mixed groups and of female groups and female-fawn dyads decreased. This trend coincided with an increase in the number of solitary individuals (both female and male) and male groups (Figure 1).



**Figure 1** Monthly distribution of different types of Pampas deer groups in “El Centenario” Ranch (General Pedernera Department, San Luis). MF, mixed groups; M, solitary males; F, solitary females; F-F, female-fawn dyads; FF, female groups and MM, male groups. Seasons of year: dry, early rainy, late rainy.

## Sexual segregation

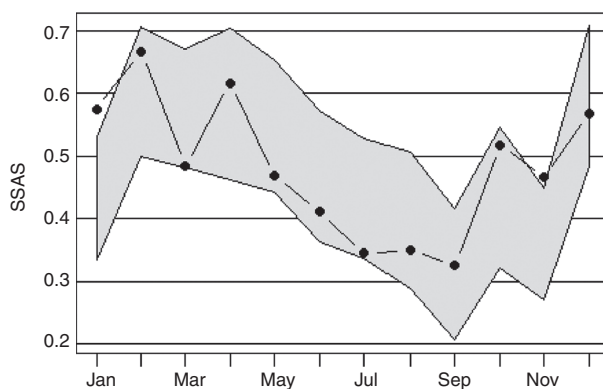
Through SSAS analysis, we detected a random male-female association pattern during almost all year, detecting statistically significant sexual segregation solely in January and November (Figure 2).

## MGS and TGS

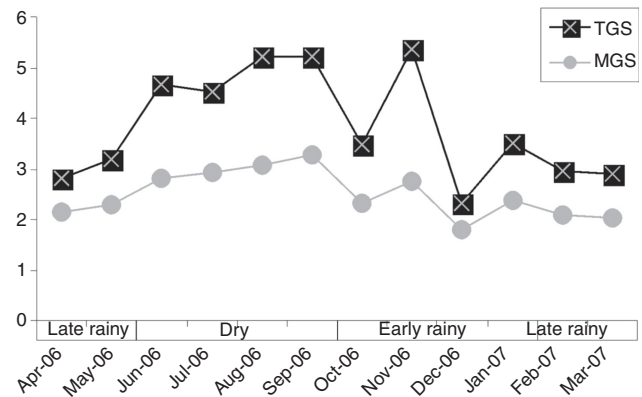
During the study period, MGS was  $2.49 \pm 0.46$  (Ind./group) and TGS was  $3.84 \pm 1.08$  (Ind./group). The largest groups occurred during the dry season ( $MGS = 3.02 \pm 0.20$ ;  $TGS = 4.90 \pm 0.37$ ), with maximum values in September ( $MGS = 3.27$ ;  $TGS = 5.20$ ) (Figure 3). During the early and late rainy seasons, gregariousness diminished, except in November ( $MGS_{ers} = 2.32 \pm 0.39$ ;  $TGS_{ers} = 3.67 \pm 1.25$  and  $MGS_{lrs} = 2.14 \pm 0.10$ ;  $TGS_{lrs} = 2.96 \pm 0.16$ ), with the lowest values observed in December ( $MGS = 1.80$  and  $TGS = 2.33$ ) (Figure 3).

No statistically significant differences in grouping occurred between males and females (TGSM vs. TGSF:  $U = 77$ ,  $p = 0.773$ ,  $n = 12$ ; and TNM vs. TNF:  $U = 69$ ,  $p = 0.862$ ,  $n = 12$ ).

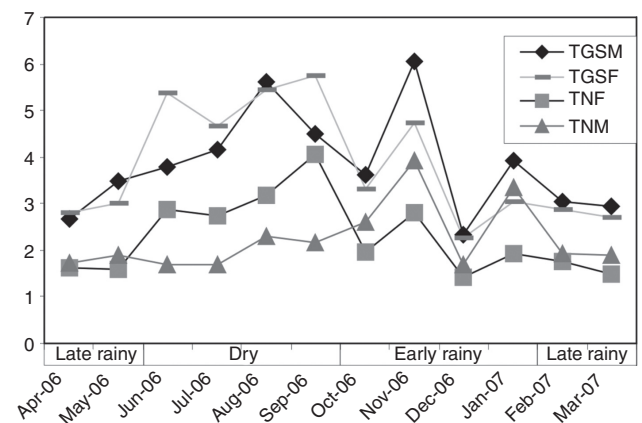
Kendall's coefficient ( $W = 0.758$ , 11 DF,  $p = 0.001$ ) indicated that the monthly patterns of TGSM and TGSF varied in the same way, i.e., both sexes tended to cluster together more often during the dry season and less during the late rainy season. Both trends were more marked in females (Figure 4). In contrast, no detectable correlation was observed between monthly TNF and TNM ( $W = 0.242$ , 11 DF,  $p = 0.304$ ). Females grouped with other females mainly during the dry season, whereas males grouped with other



**Figure 2** Annual patterns of sexual segregation/aggregation in Pampas deer analyzed using the sexual segregation-aggregation statistic (SSAS). The SSAS indicates statistically significant sexual segregation or aggregation if the observed value (dotted line) falls above or below the shaded area (at the 5% error level).



**Figure 3** Variation in Pampas deer mean group size (MGS) and "crowding" (TGS), from April 2006 to March 2007, in "El Centenario" Ranch (General Pedertera Department, San Luis). Seasons of year: dry, early rainy, late rainy.



**Figure 4** Variation in Pampas deer typical group size of males (TGSM), females (TGSF) and typical number of individuals of the same sex (TNM: males and TNF: females), from April 2006 to March 2007, in "El Centenario" Ranch (General Pedertera Department, San Luis). Seasons of year: dry, early rainy, late rainy.

males during both rainy seasons, especially the early one (Figure 4).

## Factors influencing group size

MGS was not correlated with monthly density ( $n = 12$ ; Spearman  $= -0.455$ ,  $p = 0.138$ ). Conversely, the mixed-model nested ANOVA revealed marked differences in the group size between habitat types within sectors (fourth-root transformed data;  $F_{2,526} = 8.56$ ,  $p = 0.014$ ) and seasons (fourth-root transformed data;  $F_{2,526} = 11.61$ ,  $p = 0.003$ ). The Tukey test indicated that the variability in group size was mostly due to differences between dry and late rainy seasons, and between *Digitaria* and *Eragrostis*.

## Discussion

The social organization of Pampas deer is characterized by small MGS and high rate of solitary individuals and groups of two, but groups that exceed 10 individuals are not frequent (Netto 1997, Netto et al. 2000, Vila 2006, Lacerda 2008). However, studies on grouping patterns to help elucidate the causes why this deer, typical of open environments, shows low aggregation values have been scarce so far. Some authors have proposed that this behavior could be due to the high flexibility of social organization in Pampas deer, in which dynamic groups merge and split constantly (Rodrigues and Monteiro-Filho 1996), or to very low population density (Jackson and Langguth 1987, Netto et al. 2000, Pereira et al. 2005).

The population of Pampas deer has been decreasing, both in terms of population size and distribution area, mainly because of anthropogenic pressure (González and Merino 2008). This trend is particularly evident in the populations in Argentina and Uruguay, which are clearly relictual.

The population of this deer in the semiarid grasslands of San Luis lives within a productive system on which this species would not exert any negative impact, and its population size is approximately 800 individuals in the study area ("El Centenario" Ranch) (Merino et al. 2011).

## Sex and age ratios

Sex and age ratios varied according to the seasons of the year. The early rainy season was the only period with more males than females and also with lower age ratios. This season coincides with the last stage of pregnancy and the beginning of fawn births (October), during which females

separate themselves from the group and seek better protection for their fawn (Jackson 1987, Jackson and Langguth 1987). The mean recruitment – an important estimation of population growth – was low ( $0.15 \pm 0.13$ ), although it is higher than that in the populations of Paraná (0.12) and Los Ajos (0.11) (Braga and Kuniyoshi 2010, Cosse and González 2013).

Table 1 shows the comparative data for several populations. This information can be used to discuss the social organization of this species. The San Luis Pampas deer population is characterized by having solitary individuals or pairs as the basic social units (34.05% and 33.43% of the total groups, respectively). This behavior was also observed in the remaining populations of this species (Table 1). The Pampas deer population of San Luis showed a MGS of  $2.49 \pm 0.46$  and a TGS of  $3.84 \pm 1.08$ . Both indices are the highest for the species, with the exception of the Los Ajos population, which has undergone a strong process of geographic retraction and is currently confined to a small area of 25 km<sup>2</sup> under intensive livestock use with high deer density (Cosse 2010).

## Grouping patterns

On the basis of our results, we conclude that the Pampas deer population in San Luis has a seasonal dynamic that affects the size and composition of groups, with a clear grouping trend during the dry season when the available foraging sources diminish and the deer gather in patches of stubble soybean (Merino et al. 2009). A similar situation was observed in fire-affected areas in Das Emas National Park (Netto et al. 2000), as well as in rice crops in Los Ajos de Rocha, Uruguay (Cosse Larghero 2002).

**Table 1** Population parameters of *O. bezoarticus*, concerning its social organization and type of environment.

Populations	Brazil		Argentina		Uruguay
	P.N. Emas <sup>a</sup>	Pantanal <sup>b</sup>	Bahía SB <sup>c</sup>	San Luis <sup>d</sup>	Los Ajos <sup>e</sup>
MGS	2.11±0.07	2.13±1.45	1.91±1.15	2.49±0.46	2.4±3.56
TGS	3.10	3.11±0.01	–	3.84±1.08	7.18±7.9
Groups of 1	44%	42%	43%	34.05%	40%
Groups of 2	29%	30%	35%	33.43%	35%
Groups of ≥3	29%	28%	22%	32.52%	25%
Environment	Cerrado savanna	Pantanal wetland	Grassland	Grassland	Grassland
Density (ind/km <sup>2</sup> )	1	0.2	0.51–1.38	1.95±0.25	11±0.98
Area km <sup>2</sup>	1318	140000	285	380	25
Feeding style	Dicot feeder	Mix dicot feeder	Mixed grass feeder	Mixed grass feeder	Mixed grass feeder

References: <sup>a</sup>Netto et al. 2000; Rodrigues 1996; <sup>b</sup>Mourão et al. 2000; Lacerda 2008; <sup>c</sup>Vila 2006; <sup>d</sup>Present work; <sup>e</sup>Cosse and González 2013. Feeding style follows Merino and Rossi (2010).

During the early rainy season, vegetation begins to grow and the distribution of foraging sources becomes homogeneous. Thus, individuals are not so gregarious and groups tend to be smaller. Groups begin to split and the frequency of solitary individuals increases, especially because this period coincides with the last stage of pregnancy and females separate themselves from the group, as previously reported (Jackson 1987). In turn, males during this season, prior to the rut (which begins in late February or early March), show their antlers in velvet (Jackson 1986) and remain solitary or cluster with other males. As a result, the percentage of mixed groups decreases.

During the late rainy season, males, now showing their polished antlers, become less gregarious as the rut begins, and solitary males begin to search for a mate. This behavior results in a high proportion of small mixed groups formed either by a male and a female, or by a male, a female and a juvenile, with the males displaying clear pre-copulatory behavior (Jackson 1985, Pereira et al. 2005).

Mixed groups are very frequent all year long, with a slight decrease in the early rainy season, when females enter the final stage of pregnancy. Our results suggest that there is no sexual segregation in the Pampas deer population of San Luis. It is corroborated by the results of the SSAS analysis, which revealed sexual segregation in January and November only (Figure 2).

The causes of sexual segregation in ungulates have been widely discussed in the literature, with those hypotheses concerning predation risk, forage selection, and activity budget standing out (Main et al. 1996, Ruckstuhl and Neuhaus 2000, 2002, Ruckstuhl 2007). The arguments of these hypotheses are based on sexual dimorphism. Pampas deer have small differences in terms of body size (Merino et al. 2005, Cassini et al. 2014) and low degree of sexual segregation compared with the other cervid species with strong sexual size dimorphism (Putman and Flueck 2011).

Observations made for other Pampas deer populations are in agreement with our findings because previous authors also detected sexual segregation associated with birth period, as in Los Ajos (Cosse and González 2013), Pantanal (Netto 1997, Lacerda 2008), and Emas (Rodrigues 1996). According to Ruckstuhl (2007), the isolation of females in the beginning of births could be due to the lack of mobility in neonates that are not able to flee, and to a need for individual recognition between mother and fawn. This pattern of sexual segregation associated with births also could be linked to the “predation risk hypothesis” (Ruckstuhl and Neuhaus 2000), and is related to habitat availability where females and small fawns stay

in safer habitats while males look for better quality pastures to meet their nutritional requirements during antler development. This crucial event in their biological cycle could play an important role in the grouping patterns of Pampas deer. Further studies are required to improve our knowledge of sexual segregation patterns.

## Factors that influence gregariousness

Consequently, it could be assumed that the group patterns observed in Pampas deer in the semiarid grasslands of San Luis are influenced by two factors: season of the year and type of habitat (plant species). The environmental variables (temperature, precipitation, photoperiod, etc.) determine the phenological state of the vegetation. Hence, both the supply and the spatial distribution of foraging resources have an influence on group patterns. This trend becomes evident with the formation of temporary groups of up to 17 individuals during periods of high concentration of food supply in some patches.

The life cycle of Pampas deer also has an influence on its group patterns, as reflected in the variations in group size and composition according to the reproductive period and its seasonal events (mating, pregnancy, and birth). In conclusion, the group patterns of Pampas deer depend both on the seasons of the year and on the life cycle of individuals. Similar conclusions were drawn from the local populations of Pampas deer in Pantanal and Los Ajos (Lacerda 2008, Cosse and González 2013).

The MGS of the Pampas deer population in San Luis was not linked to their monthly density. Coincidentally, Cosse and González (2013) did not observe a correlation between both parameters in the population of Los Ajos (Uruguay), or between the MGS and densities of different populations in Argentina, Brazil, and Uruguay. Thus, density would not have an influence on the gregariousness of Pampas deer.

Moreover, the type of environment would not influence the gregariousness of this species, which has a wide distribution range and lives in a large variety of environments, but exhibits a similar social organization formed by basic units of solitary individuals or dyads, both in closed environments (savanna of the Brazilian Cerrado) and open grasslands of Uruguay and Argentina. The lack of relationship between gregariousness and density or type of environment has been recently suggested by Lacerda (2008), Cosse (2010), and Cosse and González (2013).

Another factor that would affect gregariousness is feeding style, as proposed by Jarman (1974) for bovids

and, later by Putman (1988) for cervids. According to these authors, highly selective feeders form very small groups, whereas less selective feeders can be a part of larger groups. The Pampas deer has wide geographical ranges and lives in a great variety of habitats. This characteristic favors its trophic behavior diversity, which includes varied feeding types ranging from mainly dicotyledons, as in the Brazilian Cerrado (“dicot feeder”) and the Pantanal (“mixed dicot feeder”), to mainly grasses (“mixed grass feeder”), as in San Luis, Bahia Samborombón (Argentina) and Rocha (Uruguay) (Merino and Rossi 2010) (Table 1). In all of these populations, Pampas deer shows no variation concerning its social organization, despite displaying several feeding tactics. Consequently, these various feeding styles would not have influence on the gregariousness of this species.

Another issue to be explored is the predatory pressure affecting different populations of Pampas deer and its relationship with gregariousness. In South America, several predators, such as the jaguar (*Panthera onca* Linnaeus, 1758), the cougar (*Puma concolor* Linnaeus, 1771), and the maned wolf (*Chrysocyon brachyurus* Illiger, 1815), coexist with this species in different environments. In the study area, only the cougar is present, but its potential impact on the local population of Pampas deer is unknown because the population density of this feline is quite low.

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