

Social structure in a family group of Guanaco (*Lama guanicoe*, Ungulate): Is female hierarchy based on ‘prior attributes’ or ‘social dynamics’?

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ABSTRACT

Social life involves costs and benefits mostly associated with how individuals interact with each other. The formation of hierarchies inside social groups has evolved as a common strategy to avoid high costs stemming from social interactions. Hierarchical relationships seem to be associated with different features such as body size, body condition and/or age, which determine dominance ability (‘prior attributes’ hypothesis). In contrast, the ‘social dynamic’ hypothesis suggests that an initial social context is a determinant in the formation of the hierarchy, more so than specific individual attributes. Hierarchical rank places individuals in higher positions, which presumably increases resource accessibility to their benefit, including opportunities for reproduction. We evaluate the maintenance of hierarchy in a family group of guanacos (*Lama guanicoe*) and evaluate the possible mechanisms involved in the stability of these interactions and their consequences. We estimate the linearity of social hierarchy and their dynamics. We find evidence of the formation of a highly linear hierarchy among females with males positioned at the bottom of the hierarchy. This hierarchy is not affected by physical characteristics or age, suggesting that it is established only through intra-group interactions. Rank is not related with calves’ weight gain either; however, subordinated females, with lower rank, exhibit higher rates of allosuckling. We found no evidence of hierarchical structure in calves suggesting that hierarchical relationship in guanacos could be established during the formation of the family group. Hence, our results suggest that hierarchical dynamics could be related more to social dynamics than to prior attributes. We finally discuss the importance of hierarchies established by dominance and their role in minimizing social costs of interactions.

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1. Introduction

Life in society involves benefits and costs associated with group formation, which has profound impacts on the stability of the interactions among participants in the social group over time. Living as a group conveys benefits related to the optimization of scarce resources (including food, space and refuges) and/or measurable decreases in predation risks (Sherman et al., 1995; Ebensperger, 2001); increased parasitism and disease transmission; and competition for reproduction opportunities (Blumstein and Armitage, 1998). In addition, life in social groups has energetic costs associated with the frequency and complexity of the interactions within

groups (Alexander, 1974; Sherman et al., 1995). As a consequence, interacting animals need to develop specific behaviors to avoid such costs. Interactions between individuals can be seen as organizing processes that will ultimately define the social structure of the coalition (Kappeler and Van Schaik, 2002; Holand et al., 2004b; Veiberg et al., 2004). Hierarchy can also be understood as a by-product of the social rank formation process, given the differences in age, sex, body size, external ornaments, reproductive state, and/or by dominance interaction (Craig, 1986; Tölü et al., 2007). To explain these processes an ‘a priori attributes’ hypothesis has been suggested, which states that the position within the hierarchy is predetermined by differences among dominance abilities associated to phenotypic traits (Chase et al., 2002). Therefore, the relative importance of these attributes has yet to be established and seem to be highly idiosyncratic among different species of mammals (Côté, 2000; Holand et al., 2004a; Veiberg et al., 2004).

In its simplest form, social rank formation is based on dyadic interactions, the outcome of these interactions and the consistency

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of these outcomes in interactions with other members of the group (de Vries, 1995; de Vries et al., 2006). This dyad-based structure allows the establishment of linear hierarchies promoting stability of social structure. So, while the formation of hierarchical pairs may occur regardless of other members within the group, dominant and subordinate individuals will emerge depending on their explicit position within the group (Appleby, 1983). In contrast, more complex hierarchies arise with triad or more complex interactions (Appleby, 1983; Craig, 1986). While linear hierarchies are associated with stable relationships, complex hierarchies often convey unstable group structures and dynamics (de Villiers et al., 2003; Perry et al., 2004; Smith et al., 2008; Olson and Blumstein, 2009).

In ungulates, male hierarchy-by-dominance is generally established by competition for reproductive opportunities (Owen-Smith, 1993; Isvaran, 2005; Pelletier et al., 2006), whereas the establishment of female dominance hierarchies is thought to be mostly correlated with age (Thouless and Guinness, 1986; Côté, 2000), body size and/or body condition (Cassinello, 1996; Guilhem et al., 2002; Holand et al., 2004a; Veiberg et al., 2004; Vervaecke et al., 2007), and reproductive state (Lloyd and Rasa, 1989; Bebié and McElligott, 2006; Pluháček et al., 2006). In these cases, the consequences of social rank position are associated with access to particular environments. For example, access to higher quality grounds for food and refuge provide better conditions and care for calves (Cassinello, 1996; Holand et al., 2004a). In some ungulate species, while hierarchy is established early during ontogeny and maintained through adulthood, it is based on agonistic relationships between calves (Dennehy, 2001; Jennings et al., 2006; Favre et al., 2008), birth order, and/or body weight gain during lactation (Guilhem et al., 2002; Vervaecke et al., 2005; Pluháček et al., 2006; Dušek et al., 2007).

The guanaco (*Lama guanicoe*) is one of four South-American camelid species, inhabiting high altitudes of the Andes mountain range, desert coastal low lands, and Patagonia. This species is characterized by a highly social organization based on a polygamous mating system, where males defend resources (Franklin, 1983; Bank et al., 2003; Young and Franklin, 2004; Sarno et al., 2006). During breeding season, three basic social units can be found: (1) territorial family harems, (2) non-reproductive male or female groups, and (3) solitary males (Bank et al., 2003). In natural conditions the size of family groups vary between 5 and 13 adults including a variable number of young with no obligated parental relationship between the male, females and young (Young and Franklin, 2004). While these groups have been widely described (e.g. Bank et al., 2003; Sarno et al., 2003, 2006), we lack a thorough description of the nature of interactions inside groups, in particular inside family groups. Here we evaluate social interactions and describe the social structure of a family group. We study the establishment of hierarchies among females, calves, and factors associated with events that give rise to these hierarchies. We hypothesize that hierarchy will be related to females quality measures like age, body weight and/or body condition; and that these could affect female care performance, measured by calve body mass gain.

2. Materials and methods

2.1. Study site

Observations were made at the “Centro Regional de Investigación y Estancia Ganadera Kampenaike” (52° 41' S and 70° 54' O), which is located 70km northwest of the city of Punta Arenas (Magellan region), in southern Chile. This ranch is associated with the National Institute of Agricultural Research (Instituto de Investigación Agropecuaria, INIA) and hosts large enclosures (~25 ha) for guanaco management allowing family groups to live in nearly wild conditions. Neither food nor water is provided which makes them fully dependent on natural conditions within the enclosure. Enclosures correspond to Patagonian vegetation characterized by scrub and herbs, including a transitional zone of shrub-like Mata Negra (*Senecio patagonicus*) and Calafate (*Berberis buxifolia*). The herb stratum is composed of Coirón (*Festuca gracillana*) and Murtilla (*Empetrum rubrum*).

2.2. Characteristics of the family group

We studied behavioral interactions in a family group composed of one adult male, six lactating adult females, two non-lactating adult females and six calves. Adults had been captured as partially dependent calves during different summer seasons between 1997 and 1999 on Tierra del Fuego Island. Exact ages are shown in Table 1. The original group was established in 1998 with one male and three females (older animals). However, new females were successively incorporated during the following 2 years. Young born in the group were removed every year at 6–10 months of age, prior to the birth of the next year's offspring. During this study all adults were captured to obtain measurements of total length, body length and thoracic girth. Pregnant females were individualized with color collars whereas non-pregnant females were individualized by numbered livestock tags (N-4 and N-8). New-born calves were weighed (hanging scale Neta® to ±0.25 kg) and individualized with the same color collar used for their mothers. To estimate daily weight gain, calves were captured and body weight was measured weekly, during eight weeks (60 days after birth).

2.3. Behavioral observations

To quantify social interactions we observed all members of a family group for a total of 176 h during 18 days during January and February of 2005, and recorded a total of 1232 interactions. The observations were made in two blocks, in the morning (9:00–12:00) and in the afternoon (14:00–18:00), using an ad libitum sampling protocol (Altmann, 1974). We quantified all agonistic interactions between individuals, recording the animal that was the initial confronter, the confronted animal and the winner of each interaction. In considering agonistic interactions they were classified in two types: (1) direct interactions, including

Table 1
Hierarchical index determination separated by classes of agonistic interactions (see text for details).

Interactions	h'	P	Steepness (Dij)	p	Absolute reciprocity R correlation	p
Females						
Direct	0.517	0.017	0.194	0.027	0.820	0.010
Indirect	0.658	0.002	0.094	0.202	0.110	0.145
Total	0.875	0.001	0.161	0.084	0.526	0.001
Calves						
Direct	0.429	0.505	0.067	0.341	0.798	0.015
Indirect	0.229	0.805	0.094	0.719	0.764	0.005
Total	0.429	0.475	0.008	0.495	0.891	0.001

front and lateral stroke, kicking, biting, spitting, chasing, chest-ramming, pinning, neck-wrestling, bringing down, and mount (or mount attempts) and (2) indirect interactions, including postural displays such as ear and tail positions, neck and leg movements, and vocalizations including snorting, grumbling threats, clicking, screaming and screeching. Total interactions do not necessarily correspond to the sum of direct and indirect interactions because some females showed both types of aggressive interactions at once. All interaction types were previously described by Franklin (1982). Interactions were separated by female–male, female–female and female–calf interactions, wherein interactions between females with their own or non-filial calves were also considered.

2.4. Hierarchy, dominance estimators, and social dynamics

We determined hierarchical level between two individuals by considering the degree of asymmetry in their interactions. This procedure consists of ranking the position individuals using a dominance matrix built from the number of victories as a function of all agonistic interactions between any two individuals confronting each other (Martin and Bateson, 1993, Interactions matrix are available in Supplementary Data 2). This information was used to determine the linearity of the hierarchy using the de Vries linearity index (h'), with 10,000 permutations to determine statistical significance. Values of the de Vries index h' , range from 0.0 to 1.0, where one represents a perfectly linear hierarchy among individuals and zero the lack of thereof (de Vries, 1995). To evaluate social structure we analyzed the steepness relationship among individuals with different hierarchical rank. The steepness (Dij) value ranges between 0.0 and 1.0, where one represents fully despotic relationships (involving steep and linear hierarchy) and 0 represents egalitarian relations among individuals (with weak and shallow hierarchy). This analysis was made with 10,000 permutations to determine significance. Hierarchical position was established using the normalized David's score (NDS, David, 1987; de Vries et al., 2006), which allows an evaluation of the degree of asymmetry in relationships. Similar NDS values represent more symmetrical relationships. Finally, reciprocity of interactions was evaluated using an absolute Mantel z-test (Hemelrijk, 1990), where high, positive correlation is known to indicate reciprocity in dyadic interactions (de Vries et al., 2006). All estimates of social interactions were independently calculated for females and calves using MATLAB (SOCPROG 2.4 routine; see Whitehead, 2009).

Social dynamics was estimated using Elo-rating following procedures described in Albers and de Vries (2001). Elo-rating considers the sequence in which interactions occur. All individuals start with a similar predefined rating score and after each interaction the rating of the participants in the interactions are updated. Winners gain a point and the loser loses one. The total points interchanged depend on the expectation of the outcome (Albers and de Vries, 2001; Neumann et al., 2011). Because Elo-ratings estimate competitive abilities by continuously updating individual's success, it allows following the temporal dynamics of interactions. To evaluate the hierarchical stability of relationships we additionally estimate the stability index (S) proposed by McDonald and Shizuka (2013), a modified version of the original index proposed by Neumann et al. (2011). Values of S close to zero indicate a low stability of relationship; in contrast, values close to 1 represent a high stability in social relationships (McDonald and Shizuka, 2013). Elo-rating and Neumann's stability index, S , were computed using scripts (R project) included in Neumann et al., 2011. S was then recalculated following McDonald and Shizuka (2013).

2.5. Female quality

Several approaches were used to evaluate female quality. First, we estimated adult body weight from thoracic girth using allometric equations (González et al., 2000) ($Wb = 5.69 \times 10^{-5} Tg^{3.04}$, $r^2 = 0.95$, where Wb is body mass and Tg is thoracic girth). Residuals of the linear regression between body weights and body lengths were then used as a proxy of body condition. Second, we estimated parental care quality by the daily weigh gain (DWG, the mean of difference between two successive body weight measures over the number of days between measurements). Third, we quantified allosuckling occurrence (ALLO) as the frequency of nursing a non-filial calf and the total number of nursing events (in relation to total frequency of occurrence). Specifically we refer ALLO to the percentage of allosuckling events of non-filial calves referred to the total number of sucking events (further details in Zapata et al., 2009a, 2010). Five of six caring females presented ALLO during this study. Fourth, the aversion toward non-filial calves was estimated by comparing the frequency of agonistic interactions between females and their own calf versus non-filial calves. We developed a calf aversion index (CAI), represented by the mean number of agonistic interaction to non-filial calves divided by all agonistic interactions with calves.

2.6. Statistical analysis

The relationship between social rank and mean daily interaction rate was established using a simple Spearman correlation. To further evaluate the relationship between females' attributes and hierarchical position, we used partial correlations between ages, body size, and body condition, DWG, ALLO and ACI across hierarchical positions (PCW, DS and NDS). Non-parametric Spearman partial correlations were assessed using Statistica 7.0 (StatSoft Inc., Tulsa, Oklahoma, USA).

3. Results

Dominance relationships among female guanacos were well resolved, highly linear, and significant (Table 1). Direct, indirect and total interactions presented a significant de Vries index, and total interactions showed the formation of maximal linear hierarchy (Fig. 1). These results suggest that the maximum linearity of hierarchies is established as a function of the combination of both classes of interactions, direct and indirect. Steepness index was significant only for direct interactions (Table 1), suggesting that despotic relationships are established only by direct interactions. Mantel test was significant for direct and total interactions (Table 1), showing in both cases the existence of a symmetrical relationship between individuals. In contrast, indirect interactions showed asymmetrical relationships between individuals. In calves no significant hierarchical relationship was observed (Table 1). Finally, steepness was not significant suggesting an egalitarian social structure for calves with highly correlated reciprocity in dyadic interactions (Table 1). Dynamics of social interactions were very stable during the observation period and a highly consistent rank order among the different classes of interactions was observed (Fig. 2). The stability index found in the three classes of interactions was nearly 1, suggesting little changes within hierarchical order among individuals.

We found a significant correlation between social rank and the mean of aggressive interaction rates ($r_s = -0.671$, $p = 0.048$). A similar pattern was observed between social rank and indirect interactions ($r_s = -0.690$, $p = 0.04$), while no significant relationship between social rank and direct interactions was observed ($r_s = 0.367$, $p = 0.348$). These results suggest that individuals in more

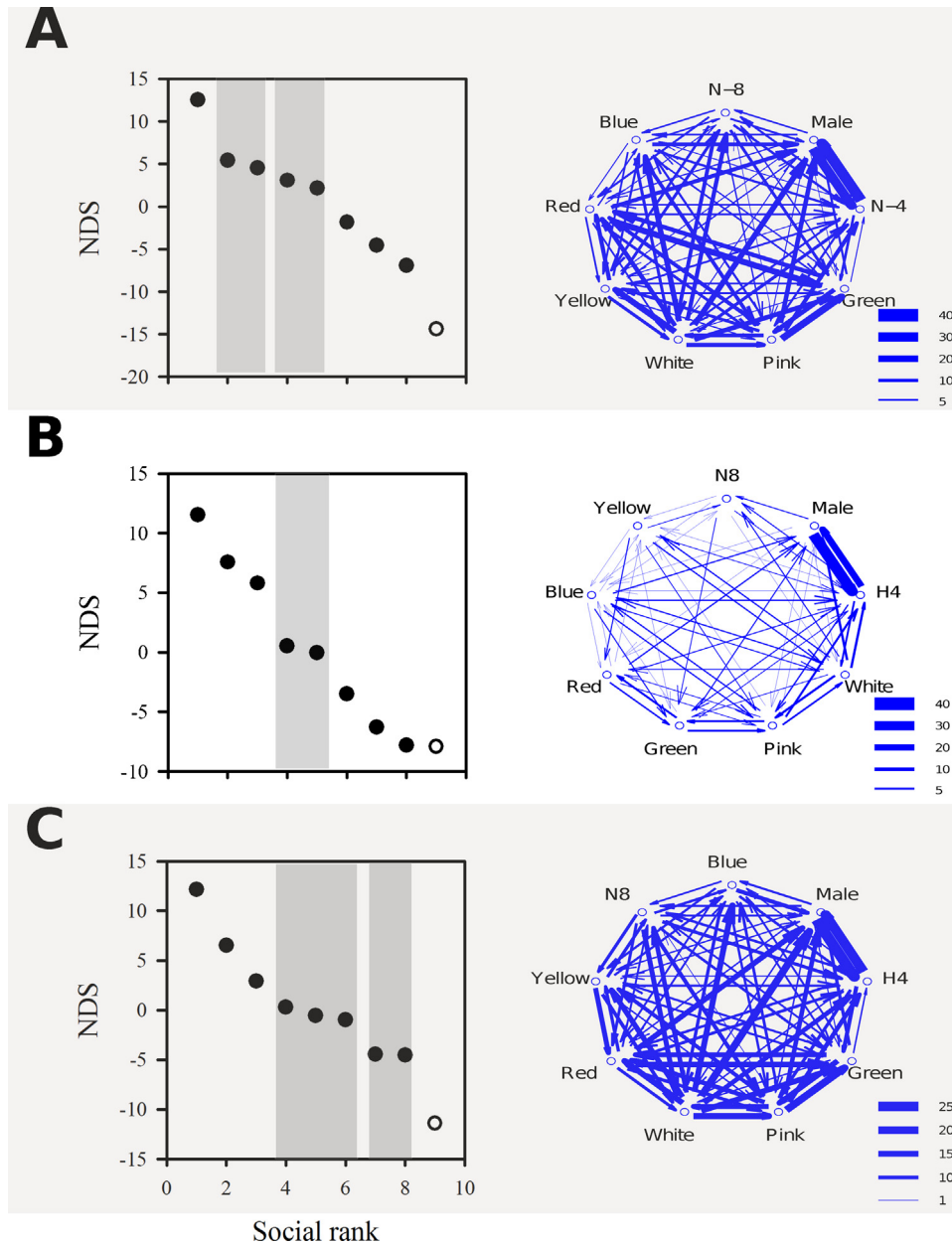


Fig. 1. Graphical representation of hierarchy estimated as relationship between normalized David's score (NDS) and rank position (left), and sociograms of interaction among adults (right). Gray zones represent animals with a NDS difference less than 1, indicating closed related individuals in the hierarchy. (A) Represents all interactions, (B) represents direct interaction and (C) represents indirect interactions. Legends of sociograms represent the number of interactions.

dominant positions use displays preferentially over direct interactions to maintain their social position within the hierarchy.

3.1. Relationship between hierarchy and female quality

The position of females within the hierarchy was not correlated with: age (PCW, $r_s = 0.009$, $p = 0.98$; DS, $r_s = -0.053$, $p = 0.89$; MDS, $r_s = -0.053$, $p = 0.89$, $n = 9$), body mass (PCW, $r_s = 0.383$, $p = 0.308$; DS, $r_s = 0.367$, $p = 0.332$; MDS, $r_s = 0.367$, $p = 0.332$, $n = 9$), or body condition (PCW, $r_s = -0.48$, $p = 0.911$, DS, $r_s = -0.24$, $p = 0.955$, MDS, $r_s = -0.24$, $p = 0.955$, $n = 9$). This suggests that these variables do not have significant incidence on the establishment of hierarchy within the group. Similarly, social position within the hierarchy was not correlated with calf daily weight gain (PCW, DS, MDS, $r_s = 0.522$, $p = 0.288$, $n = 6$), or ACI (PCW, DS, MDS, $r_s = -0.143$, $p = 0.787$, $n = 6$). However, a significant inverse relationship was observed with ALLO

(PCW, DS, MDS, $r_s = -0.899$, $p = 0.015$, $n = 6$), suggesting that hierarchical position may only be related with ALLO occurrence, wherein subordinate females are more prone to share their milk with other's calves.

4. Discussion

We found a significant dominance–subordination relationship among adults of a family group of guanacos in Patagonia. We also found that a significant linear hierarchy was established among females with a null reversion in agonistic interactions. This strongly suggests the existence of a stable dominance hierarchy structure within the family group. In addition, social dynamics presented high levels of stability during the period of observation suggesting insignificant changes in social order within the family group. However, intermediate hierarchical position showed similar NDS scores,

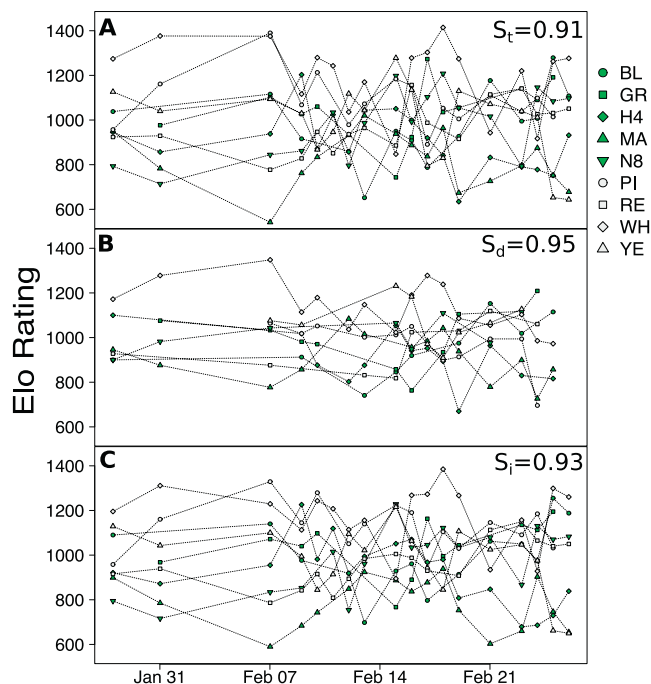


Fig. 2. Graphical Elo-rating contest among adults of a familiar group. Each line represents contest dynamic of each individual. In (A) are represented total interactions, (B) direct interactions and (C) indirect interactions. S represents a stability index. Animal codes correspond to females: BL, blue; GR, green; H4; N8; PI, pink; RE, red; WH, white; YE, yellow and MA, male.

a typical feature of unstable social relationships among a ranking position. Such results are clearly consistent with previous studies (Barrette and Vandal, 1985; Côté, 2000; Cafazzo et al., 2010). Hence, a decrease in competitive interactions between group members in non-adjacent hierarchical positions is indicative of a reduction in the number of interactions to avoid associated costs of social interactions (Côté, 2000; Cafazzo et al., 2010). Steepness and Mantel z -test suggested that indirect confrontations (displays) play a central role in hierarchical stability, more so than direct interactions. Moreover, dominant individuals show that interaction rates are mostly based on displays as compared to direct interactions. This situation is consistent with propositions stating that hierarchical societies decrease social costs by reducing direct interactions (Cafazzo et al., 2010). Therefore, visual cues and displays seem to be a sufficient agonistic interaction to maintain a stable social structure in a family group.

Chase et al. (2002) summarizes the major hypotheses explaining potential factors thought to determine the formation of linear hierarchies. They propose the “prior attribute” hypothesis where hierarchical positions are predetermined by individual attributes associated to dominance ability. In contrast, the “Social dynamic” hypothesis is put forward where social interactions among group members determine the linear hierarchy. Apparently, in most cases, both hypothesis are not mutually exclusive and can operate simultaneously in hierarchical interactions (Chase et al., 2002; Tanner et al., 2011). In guanacos, we found relatively high values for linear hierarchies ($h' = 0.875$) reinforcing the notion that high linear hierarchy is important to the social structure of our family group. In fact, high values are usually inferred when de Vries index values surpass 0.80 (Appleby, 1983; de Vries, 1995; de Vries et al., 2006). Such high hierarchy patterns have mostly been described in small social group systems, where strong knowledge of other individuals allegedly make high levels of interaction unnecessary to establish social relationships (Drews, 1993). Among ungulates, female hierarchy formation has also been associated

with age (Thouless and Guinness, 1986; Reason and Laird, 1988; Côté, 2000; Guilhem et al., 2002), body size and/or body condition (Cassinello, 1996; Guilhem et al., 2002; Holand et al., 2004a; Veiberg et al., 2004; Vervaecke et al., 2007), and reproductive state (Lloyd and Rasa, 1989; Bebié and McElligott, 2006; Pluháček et al., 2006). However, this seems not to be the case for guanacos as we failed to detect any significant effect of age, body size or body condition on hierarchical position during the observation period of this study, leading us to propose that linear hierarchy could be the only type of hierarchy established within the guanaco family here. On the other hand, adult position is known to be established through agonistic confrontations as calves (Dennehy, 2001; Jennings et al., 2006; Favre et al., 2008), and are thus highly influenced by calves' ages, and/or body weight gain during the nursing period (Guilhem et al., 2002; Vervaecke et al., 2005; Pluháček et al., 2006; Dušek et al., 2007). We also fail to find any social structure among calves and therefore no effect of age, sex or body weight gain over hierarchy formation as expected. This may be partly due to the fact that there was only one female calf within this particular family group, preventing us from evaluating the formation of hierarchy by female calf dominance interactions. These results suggest that among individuals with similar dominance attributes, social interaction could be explaining the observed linear relationships. Because social rank could be associated with better access to high quality grounds for food and refuge, thereby providing better conditions and care to calves for instance (Cassinello, 1996; Holand et al., 2004a), we expect dominant females to increase their reproductive success, perhaps, measured by calf survival and/or calf growth (Barroso et al., 2000). For similar reasons explained above, we did not find any calf mortality in the family group, and the relationship between hierarchical position and calves' growth cannot be estimated. In spite of this, we do find a significant inverse relationship between hierarchical position and allosuckling occurrence. Based on our findings and motivated by previous work in which allosuckling has been related to calves' opportunistic milk theft more than alloparental care by females (Zapata et al., 2009b), we propose that such relationship could be an indirect consequence of stressful conditions while interacting of lower hierarchical rank females (Lloyd and Rasa, 1989; Fournier and Festa-Bianchet, 1995). Consequently, agonistic relationships with other females should increase the vigilance and/or defence time and decrease the time dedicated to parental care and the discrimination between filial and non-filial calves.

Finally, as the family group is only one component of the guanaco's social organization (Bank et al., 2003), in future studies it will be essential to complement and confirm our conclusions. For instance, incorporating the social interactions of larger families and the dynamics of social interactions in non-reproductive male or female groups and solitary males will clearly improve our understanding of the ecological and evolutionary significance of hierarchy formation. We are confident that the results emerging from the experimental setting of our study strongly endorse the notion that hierarchical structure based on dominance establishes the nexus between different classes of social groups in guanacos described by Bank et al. (2003).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.plantsci.2004.08.011>.

References

- Albers, P.C.H., de Vries, H., 2001. Elo-rating as a tool in the sequential estimation of dominance strengths. *Anim. Behav.* 61, 489–495.
- Alexander, R.D., 1974. The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 5, 325–383.
- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behavior* 49, 227–267.
- Appleby, M.C., 1983. The probability of linearity in hierarchies. *Anim. Behav.* 31, 600–608.
- Bank, M.S., Sarno, R.J., Franklin, W.L., 2003. Spatial distribution of guanaco mating sites in southern Chile: conservation implications. *Biol. Conserv.* 112, 427–434.
- Barrette, C., Vandal, D., 1985. Social rank, dominance, antler size and access to food in snow-bound wild woodland caribou. *Behaviour* 97, 118–146.
- Barroso, F.G., Alados, C.L., Boza, J., 2000. Social hierarchy in the domestic goat: effect on food habits and production. *Appl. Anim. Behav. Sci.* 69, 35–53.
- Bebié, N., McElligott, A.G., 2006. Female aggression in red deer: does it indicate competition for mates? *Mammal. Biol.* 71, 347–355.
- Blumstein, D.T., Armitage, K.B., 1998. Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. *Behav. Ecol.* 9, 8–19.
- Cafazzo, S., Valsecchi, P., Bonanni, R., Natoli, E., 2010. Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs. *Behav. Ecol.* 21, 443–455.
- Cassinello, J., 1996. High-ranking females bias their investment in favour of male calves in captive *Ammotragus lervia*. *Behav. Ecol. Sociobiol.* 38, 417–424.
- Chase, I.D., Tovey, C., Spangler-Martin, D., Manfredonia, M., 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proc. Natl. Acad. Sci. U.S.A.* 99, 5744–5749.
- Craig, J.V., 1986. Measuring social behaviour: social dominance. *J. Anim. Sci.* 62, 1120–1129.
- David, H.A., 1987. Ranking from unbalanced paired-comparison data. *Biometrika* 74, 432–436.
- de Villiers, M.S., Richardson, P.R.K., van Jaarsveld, A.S., 2003. Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (*Lycaon pictus*). *J. Zool.* 260, 377–389.
- de Vries, H., 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Anim. Behav.* 50, 1375–1389.
- de Vries, H., Stevens, J.M.G., Vervaecke, H., 2006. Measuring and testing the steepness of dominance hierarchies. *Anim. Behav.* 71, 585–592.
- Dennehy, J.J., 2001. Influence of social dominance rank on diet quality of pronghorn females. *Behav. Ecol.* 12, 177–181.
- Drews, C., 1993. The concept and definition of dominance in animal behaviour. *Behaviour* 125, 285–313.
- Dušek, A., Bartoš, L., Švecová, L., 2007. The effect of a mother's rank on her offspring's pre-weaning rank in farmed red deer. *Appl. Anim. Behav. Sci.* 103, 146–155.
- Ebensperger, L.A., 2001. A review of the evolutionary causes of rodent group-living. *Acta Theriol.* 46, 115–144.
- Favre, M., Martin, J.G.A., Festa-Bianchet, M., 2008. Determinants and life-history consequences of social dominance in bighorn ewes. *Anim. Behav.* 76, 1373–1380.
- Fournier, F., Festa-Bianchet, M., 1995. Social dominance relationships in adult female mountain goats. *Anim. Behav.* 49, 1449–1459.
- Franklin, W.L., 1982. Lama language: modes of communication in the South American camelids. *Llama World* 1, 5–11.
- Franklin, W.L., 1983. Contrasting socioecologies of South America's wild camelids: the vicuña and guanaco. In: Eisenberg, J.F., Kleiman, D. (Eds.), *Advances in the Study of Mammalian Behavior*, Spec. Pub. No. 7. American Society of Mammalogist, Lawrence, KS, USA, pp. 573–629.
- González, B., Zapata, B., Bonacic, C., Bas, F., 2000. Técnicas para el manejo del guanaco en cautiverio. In: González, B., Bas, F., Tala, C., Iriarte, A. (Eds.), *Manejo sustentable de la vicuña*. Servicio Agrícola y Ganadero, Pontificia Universidad Católica de Chile, Fundación para la Innovación Agraria, Santiago, Chile, pp. 143–163.
- Guilhem, C., Gerard, J.F., Bideau, E., 2002. Rank acquisition through birth order in mouflon sheep (*Ovis gmelini*) ewes. *Ethology* 108, 63–73.
- Hemelrijk, C.K., 1990. Models of, and tests for reciprocity, unidirectionality and other social interaction patterns at a group level. *Anim. Behav.* 39, 1013–1029.
- Holand, Ø., Gjøstein, H., Losvar, A., Kumpula, J., Smith, M.E., Røed, K.H., Nieminen, M., Weladji, R.B., 2004a. Social rank in females reindeer (*Rangifer tarandus*): effects of body mass, antler size and age. *J. Zool.* 263, 365–372.
- Holand, Ø., Weladji, R.B., Gjøstein, H., Kumpula, J., Smith, M.E., Nieminen, M., Røed, K.H., 2004b. Reproductive effort in relation to maternal social rank in reindeer (*Rangifer tarandus*). *Behav. Ecol. Sociobiol.* 57, 69–76.
- Isvaran, K., 2005. Variation in male mating behavior within ungulate populations: patterns and processes. *Curr. Sci.* 89, 1192–1199.
- Jennings, D.J., Gammell, M.P., Carlin, C.M., Hayden, T.J., 2006. Is difference in body weight, antler length, age or dominance rank related to the number of fights between fallow deer (*Dama dama*)? *Ethology* 112, 258–269.
- Kappeler, P.M., Van Schaik, C.P., 2002. Evolution of primate social systems. *Int. J. Primatol.* 23, 707–740.
- Lloyd, P.H., Rasa, O.A.E., 1989. Status, reproductive success and fitness in Cape mountain zebra (*Equus zebra zebra*). *Behav. Ecol. Sociobiol.* 25, 411–420.
- Martin, P., Bateson, P., 1993. *Measuring Behaviour, an Introductory Guide*. Cambridge University Press, Cambridge.
- McDonald, D.B., Shizuka, D., 2013. Comparative transitive and temporal orderliness in dominance networks. *Behav. Ecol.* 24, 511–520.
- Neumann, C., Dubocq, J., Dubuc, C., Ginting, A., Irwan, A.M., Agil, M., Widdig, A., Engelhardt, A., 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Anim. Behav.* 82, 911–921.
- Olson, L.E., Blumstein, D.T., 2009. A trait-based approach to understand the evolution of complex coalitions in male mammals. *Behav. Ecol.* 20, 624–632.
- Owen-Smith, N., 1993. Age, size, dominance and reproduction among male kudus: mating enhancement by attrition of rivals. *Behav. Ecol. Sociobiol.* 32, 177–184.
- Pelletier, F., Hogg, J., Festa-Bianchet, M., 2006. Male mating effort in a polygynous ungulate. *Behav. Ecol. Sociobiol.* 60, 645–654.
- Perry, S., Barrett, H.C., Manson, J.H., 2004. White-faced capuchin monkeys show triadic awareness in their choice of allies. *Anim. Behav.* 67, 165–170.
- Pluháček, J., Bartoš, L., Čulík, L., 2006. High-ranking mares of captive plains zebra *Equus burchelli* have greater reproductive success than low-ranking mares. *Appl. Anim. Behav. Sci.* 99, 315–329.
- Reason, R.C., Laird, E.W., 1988. Determinants of dominance in captive female addax (*Addax nasomaculatus*). *J. Mammal.* 69, 375–377.
- Sarno, R.J., Bank, M.S., Franklin, W.L., 2003. Forced dispersal of juvenile guanacos (*Lama guanicoe*): causes, variation, and fates of individuals dispersing at different times. *Behav. Ecol. Sociobiol.* 54, 22–29.
- Sarno, R.J., Bank, M.S., Stern, H.S., Franklin, W.L., 2006. Effects of age, sex, season, and social dynamics on juvenile guanaco subordinate behavior. *J. Mammal.* 67, 41–47.
- Sherman, P.W., Lacey, E.A., Reeve, H.K., Keller, L., 1995. The eusociality continuum. *Behav. Ecol.* 6, 102–108.
- Smith, J.E., Kolowski, J.M., Graham, K.E., Dawes, S.E., Holekamp, K.E., 2008. Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Anim. Behav.* 76, 619–636.
- Tanner, C.J., Salali, G.D., Jackson, A.L., 2011. The ghost of social environments past: dominance relationships include current interactions and experience carried over from previous groups. *Biol. Lett.* 7, 818–821.
- Thouless, C.R., Guinness, F.E., 1986. Conflict between red deer hinds: the winner always wins. *Anim. Behav.* 34, 1166–1171.
- Tölü, C., Savaş, T., Thomsen, H., 2007. Effects of goat social rank on kid gender. *Czech J. Anim. Sci.* 52, 77–82.
- Veiberg, V., Loe, L.E., Mysterud, A., Langvatn, R., Stenseth, N.C., 2004. Social rank, feeding and winter weight loss in red deer: any evidence of interference competition? *Oecologia* 138, 135–142.
- Vervaecke, H., Roden, C., de Vries, H., 2005. Dominance, fatness and fitness in female American bison, *Bison bison*. *Anim. Behav.* 70, 763–770.
- Vervaecke, H., Stevens, J., Vandemoortele, H., Sigurjónsdóttir, H., de Vries, H., 2007. Aggression and dominance in matched groups of subadult Icelandic horses (*Equus caballus*). *J. Ethol.* 25, 239–248.
- Whitehead, H., 2009. SOCPROG programs: analyzing animal social structures. *Behav. Ecol. Sociobiol.* 63, 765–778.
- Young, J.K., Franklin, W.L., 2004. Activity budgets patterns in family-group and solitary territorial male guanacos. *Rev. Chil. Hist. Nat.* 77, 617–625.
- Zapata, B., Gaete, G., Correa, L., González, B., Ebensperger, L., 2009a. A case of allo-suckling in wild guanacos (*Lama guanicoe*). *J. Ethol.* 27, 295–297.
- Zapata, B., González, B.A., Ebensperger, L.A., 2009b. Allonursing in captive guanacos, *Lama guanicoe*: milk theft or misdirected parental care? *Ethology* 115, 731–737.
- Zapata, B., Correa, L., Soto-Gamboa, M., Latorre, E., González, B.A., Ebensperger, L.A., 2010. Allonursing allows growing offspring to compensate for insufficient maternal milk in farmed guanacos (*Lama guanicoe*). *Appl. Anim. Behav. Sci.* 122, 119–126.
- Côté, S.D., 2000. Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour* 137, 1541–1566.