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Male aggressiveness in a polygynous ungulate varies with social and ecological context

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Abstract

Aggression is a social behaviour which can be affected by numerous factors. The quality and quantity of food resources may play an important role in the aggressiveness of territorial ungulates as the defence of these resources influences female choice and mating opportunities. However, the relationship between food resources and aggression remains poorly understood. We assessed the ecological and social factors that influence aggression in *Lama guanicoe*, a territorial ungulate exhibiting resource-defence polygyny, during three periods (group-formation, mating and post-mating) in the reproductive seasons of 2014 and 2016. We recorded 460 focal observations of territorial (family groups, solitary) and non-territorial (mixed and bachelor groups) males. We performed analyses at the population level (including all focal observations) and at the group level (each social unit separately), to test whether the factors that influence aggression differ at these different scales. We also identified proxies of vegetation quality as potential predictors of aggression. At the population level, we found that the presence of aggressive behaviour peaked during the mating season and that post-mating aggression may have been driven by inter-annual environmental variations. For family groups and solitary males, variables reflecting high vegetation quality/quantity were predictors of aggressive behaviour, reflecting the resource-defence strategy of this species. Conversely, for mixed-group males, aggression may be more associated with social instability and group size, although this hypothesis has yet to be tested. Our research reinforces the idea that aggression can occur in multiple contexts depending on male status (e.g. territorial or non-territorial) and contributes to our understanding of how ecological (i.e. availability of food resources) and social factors influence aggression in a territorial ungulate.

KEYWORDS
aggression, agonistic behaviour, *Lama guanicoe*, polygyny, resource-defence ungulates, territoriality

1 | INTRODUCTION

Animals must adapt their physiology and behaviour to maximize fitness in response to changing environments (Wingfield et al., 2006). These adjustments require varying degrees of physiological and behavioural plasticity depending upon the extent to which the environment may change (Piersma & Drent, 2003). A key example of a plastic behaviour is aggression, which can be expressed to maintain a territory and defend specific resources (e.g. food or mates) or to retain social status within a group to access resources (Wingfield et al., 2006). There are many classifications of aggressive behaviour (Brain, 1979; Moyer, 1968; Wingfield et al., 2006), which reinforces the idea that it is a widespread social behaviour occurring in a broad variety of contexts (e.g. territoriality, dominance, competition for resources, mating) and serving many functions (Huntingford & Turner, 1987; Zumpe & Michael, 2001). Aggressive encounters include both offensive and defensive behaviours and can manifest in a wide range of displays, from threats to direct attacks (Huntingford & Turner, 1987).

Ecological factors such as seasonal changes in temperature, diurnal rhythms and distribution of food resources can all influence the development of aggressive interactions (Briffa & Sneddon, 2010; Fattorini, et al., 2018). Theory suggests two alternative relationships between aggressiveness and forage resources. Some have hypothesized that aggression levels may increase when resources are limited (Fattorini, et al., 2018; Lucherini, 1996; Nelson, 2006; Sirot, 2000) due to increased intraspecific competition (i.e. feeding interference). Alternatively, the energy allocated to aggressive interactions could increase with the value of a disputed resource (Enquist et al., 1985; Geist, 1978; Parker, 1974). Accordingly, individuals could invest more in body growth (e.g. weaponry), mating and social behaviours when there is greater availability of food resources (Caraco, 1979; Geist, 1978; Goss-Custard et al., 1984).

Previous research on ungulates has reported that aggressiveness can be related to several factors, including food quality/quantity (Fattorini, et al., 2018; Taillon & Côté, 2007), age (Fattorini, et al., 2018; Willisch & Neuhaus, 2010), group size (Fattorini, et al., 2018), social hierarchy or dominance (Lovari et al., 2015; Taillon & Côté, 2007; Ungerfeld & Freitas-de-Melo, 2014), weapon (e.g. horns) size (Hoem et al., 2007; Jennings et al., 2004) and seasonality (Clutton-Brock et al., 1982; Pereira et al., 2005; Willisch & Neuhaus, 2010). For territorial ungulates, most studies have focused on describing their behavioural patterns of aggression and towards non-territorial animals (Blank et al., 2015; Blank & Yang, 2014; Corlatti et al., 2013; Hoem et al., 2007; Marino, 2012), and the correlation between aggression and reproductive success (Festa-Bianchet et al., 1990; Fryxell, 1987). These studies suggest that greater levels of aggressiveness of territorial males lead to higher frequencies of courtship behaviours and more mating opportunities, but may also incur greater costs (e.g. increased risk of injury and energy demands, reduced food intake, increased parasite loads; Corlatti et al., 2013). For territorial males, the quality and quantity of food resources can also play an important role in aggressiveness since the defence of these resources influences female choice and mating opportunities (Emlen & Oring, 1977); however, the relationship between food resources and aggression remains poorly understood.

Guanacos (*Lama guanicoe*) are the largest native ungulates in South America, with a wide distribution ranging from Peru to Southern Argentina (Carmanchahi et al., 2019; Franklin, 1983; Raedeke, 1979). Guanaco populations can be either sedentary or migratory. Populations tend to be sedentary where forage resources are easily defensible, allowing territorial males to maintain their territories throughout the year. In contrast, where food and water are limited and weather conditions are adverse in some seasons, groups or individuals have seasonal territories and move collectively in large groups between summer and winter ranges (Bolgeri, 2016; Franklin, 1983; Franklin & Fritz, 1991; Raedeke, 1979). Guanacos have a complex social organization based on resource-defence polygyny (Franklin, 1983; Raedeke, 1979; Young & Franklin, 2004a), defined as a territorial system wherein males compete for access to food resources that are attractive to females. In this social mating system, the number of females that a male attracts is correlated with the quantity and quality of resources in its territory (Alcock, 1987; Emlen & Oring, 1977). Male guanacos can be found in one of four types of social units: family groups, solitary territorial males, bachelor male groups and mixed non-territorial groups (Franklin, 1983; Ortega & Franklin, 1995; see Methods for a detailed description). In both sedentary and migratory populations, these main social units are similar, with the exception that mixed groups are primarily found in migratory populations in varying proportions throughout the annual cycle (Franklin, 1983). This wild camelid has been successfully used as an ecological model of adaptation due to anatomical, physiological and behavioural traits that allow it to inhabit hostile environments (Franklin, 1983; González et al., 2006; Gregorio et al., 2019; Marino & Baldi, 2008; Ovejero et al., 2016; Taraborelli et al., 2012).

Previous research on South American camelids found that aggression peaked during the reproductive season (Jurgensen, 1985; Vilá, 1992; Wilson & Franklin, 1985) and that the most common aggressive display among male guanacos consisted of indirect interactions, such as ear threats (Wilson & Franklin, 1985). It has also been found that family groups had higher rates of agonistic interactions than bachelor groups (Lucherini, 1996). In sedentary populations in Patagonia, territorial males appear to display more aggressive interactions and with a higher level of aggression than bachelors, regardless of predation risk (Marino, 2012). By contrast, in migratory populations where males form seasonal territories and groups are stable only during the reproductive season (Franklin, 1982, 1983), studies assessing aggressive behaviour have been mainly descriptive and little is known about the different factors that modulate these behaviours (Wilson & Franklin, 1985).

In this study, we examine the relationship between ecological and social factors and aggressive behaviour in male guanacos during the reproductive season, considering three periods (group-formation, mating and post-mating; see Methods for a detailed description). We evaluate this relationship in a wild, partially migratory population by estimating different measures of behaviour, which may

provide distinct information about the nature of social behaviour. First, because of the mating system and reproductive seasonality in migratory guanaco populations (Franklin, 1982, 1983; Young & Franklin, 2004a), we expected that the probability and frequency of aggressive interactions between male guanacos would peak during the mating period (Prediction I) and would be higher in males from family groups because of the behaviour's reproductive significance (Prediction II). Second, because resource-defence ungulates fight for territories which contain attractive food resources for females (Emlen & Oring, 1977; Franklin, 1983; Young & Franklin, 2004a, 2004b), we expected that the presence and the frequency of aggressive interactions in territorial males (family groups and solitary males) would be higher in areas of greater forage quality and productivity (Prediction III), given that territorial males can invest more energy in aggressive interactions where resources are higher (Enquist et al., 1985; Geist, 1978; Parker, 1974) and that they also have priority access to females and mating. Finally, because non-territorial males (bachelors and mixed groups) do not engage in reproduction, we expect that aggression in these social units will be linked to food resources (Fattorini, et al., 2018; Sirot, 2000) and will be higher in areas of lower forage quality and productivity due to increased competition (Prediction IV).

2 | METHODS

2.1 | Ethical note

The Directorate of Renewable Natural Resources of Mendoza Province (Resolution n°: 893/2013 and 1231/2016) provided the necessary permits to study guanacos in La Payunia Reserve. This study was conducted with wild free-ranging animals and was completely observational. Observations were conducted from a pick-up truck or elevated sites and therefore no handling of animals took place.

2.2 | Study area and population

The study area is located in west-central Argentina (between 36°00' and 36°36' S, and 68°34' and 69°23' W), including the northern part of the 665,000 ha La Payunia Reserve. It is characterized by gently undulating topography and vast flatlands in combination with areas with steeper hills and volcanic outcrops (Martínez Carretero, 2004). The climate is semiarid; mean temperatures in the study area range between 6°C in winter and 20°C in summer, with a mean annual precipitation of 198 mm (Candia et al., 1993; Martínez Carretero, 2004). Vegetation is xerophytic, with 58% plant cover, and corresponds to the La Payunia phytogeographic province (Martínez Carretero, 2004). Sandy plains are covered by herbaceous communities dominated by *Panicum urvilleanum*, *Stipa speciosa* and *Sporobolus rigens*, while slopes and basaltic scoria contain shrub communities mainly of *Neosparton aphyllum* and *Ephedra ochreata*

(Martínez Carretero, 2004). Guanacos use both types of habitats, and grasses (*Panicum*, *Poa* and *Hordeum*), as well as low shrubs (*Hyalis* and *Ephedra*), are important components of their diet. In addition, the proportions of plant groups (i.e. grasses and shrubs) in the guanaco diet show a positive association with changes in food availability (Puig et al., 1996, 1997). The main predator of guanacos is the puma (*Puma concolor*) and at La Payunia, predation is the most frequent cause of death for guanacos (Bolgeri & Novaro, 2015). The study area holds the largest population of *L. guanicoe* of the west-central region of Argentina, with about 26,000 individuals in spring in the northern part of the reserve (Schroeder et al., 2014). This is one of only a few guanaco populations that maintain annual migrations (Bolgeri, 2016).

Male guanacos can be found in one of four types of social units: (a) family groups composed of a territorial reproductive male, several females (2–15 individuals), and their offspring, forming highly cohesive and behaviourally synchronized units (hereafter referred to as "family groups"); (b) solitary territorial males, that defend a territory containing no other individuals, either males or females (hereafter, "solitary males"); (c) bachelor male groups comprised of non-reproductive and non-territorial males of all age classes (usually juveniles), with group size ranging from a few males to more than 50 (hereafter, "bachelor groups"); and (d) mixed non-territorial groups consisting of males and females of all ages, with variable group size, ranging from 15 to hundreds of animals (hereafter, "mixed groups") (Franklin, 1983; Ortega & Franklin, 1995).

We considered three periods within the guanaco reproductive or territorial season (Young & Franklin, 2004b): (a) group-formation (September–November), the time when animals that migrated begin to arrive at their spring and summer range and males separate from mixed groups to establish their territories (Fritz, 1985; Ortega, 1985; Wilson, 1982); (b) mating (December-January), considered the peak of the reproductive season, when social units are well established and births and mating occur, partially overlapping in time (Jurgensen, 1985; Young & Franklin, 2004b); and (c) post-mating (February), considered the end of the reproductive season, when groups begin to gather and prepare for migration to the winter range (Young & Franklin, 2004b).

2.3 | Behavioural records

We collected data daily from 8:00 to 20:00 hr over six 15-day surveys. Surveys were conducted during the reproductive season, spanning the three periods described above. On days when it was too hot (above 30°C), we did not conduct observations between 12:00 and 15:00 hr, as the animals were inactive. Surveys were performed in each period at two sites located in the NE (approximately 26 ha and 30 km of tracks; 36°8' S, 68°48' W) and NW (approximately 20 ha and 46 km of tracks; 36°4' S, 69°11' W) of the reserve during the reproductive seasons (mid-September – mid-February) of 2014 and 2016. We performed continuous focal-animal observations (Altman, 1974; Martin & Bateson, 2007)

of adult males belonging to different social units using a 60 mm spotting scope (20-60x; Bushnell Trophy XLT). At the beginning of each observation, we recorded the number of adults and offspring in the group, distinguished by body size. Groups were identified by excluding, at the beginning of each observation, individuals more than 300 m away from their neighbours. This was confirmed by noting animal movement during the observations (i.e. members of the same group moved together in the same direction, while the other individuals stayed in the same place or moved in another direction; Marino & Baldi, 2008; Taraborelli et al., 2012). We performed focal observations at 200–600 m distances from the animals. This range of observation distances was a compromise between minimizing disturbance, since observing animals from a short distance can induce an escape response (Taraborelli et al., 2012), and being able to observe and distinguish different behaviours with the optical device used. As there is no conspicuous sexual dimorphism in guanacos, sex was assessed by observing the testes (Franklin, 1983), which could be detected unequivocally from these observation distances. Since there were no marked individuals, we used scars, natural spots or moulting wool patterns to identify individuals and we looked for males belonging to other groups after each focal observation to prevent observing the same individual twice, that is daily pseudo-replication. Within each survey, the location selected for observing males was changed daily

in order to avoid watching the same groups on successive days and to minimize between-day pseudo-replication. Since at least a month passed between sampling periods, we considered each survey independent. When males were disturbed by our presence, observations were not initiated. We recorded 460 focal observations of 12-min duration (occasionally less when animals went out of sight for more than 30 s), using a digital recorder (Panasonic RR-US551), with 97.28 observation hours in total. Adjustments in sampling time were performed during the first survey using the minimum area method (Matteucci & Colma, 1982), which is estimated graphically and defined as the area at which the number of observed behaviours as a function of observation period reaches a plateau, or as the area at which an inflexion point of the curve is reached. According to the latter criterion, focal observations of less than 8 min were discarded (<85% of behaviours observed). During the observation time, we recorded all behaviours performed by the focal male. We defined aggressive interactions as all interactions between males of the same group or other groups involving a physical attack or a threat and included both direct and indirect forms of aggression (Lucherini, 1996; Wilson & Franklin, 1985). These interactions included low, medium and high aggression-level displays (see Table 1 for a description of aggressive behaviour patterns; Vilá, 1992; Wilson & Franklin, 1985), and were registered both when the focal male was the initiator or

TABLE 1 Description of aggressive behaviour patterns (ethogram) in adult male guanacos. Descriptions are based on Wilson and Franklin (1985) and our observations. A classification of the aggression level of each behaviour is provided based on Vilá (1992): Low: there is no direct contact between males. Medium: the aggressive behaviour includes chases with both animals running, but no direct contact. High: there is direct contact between males

Behaviour type	Aggression level	Description
Ear threat	Low	The animal is standing with its head and neck upright, ears down, and attentively observing other animals in the area.
Raised tail	Low	The animal is standing or walking, with its head and neck upright, and its tail raised (perpendicular to the back). Occasionally, the tail may lie completely on the back. This behaviour can be observed in combination with the ear threat display.
Heading	Low	Rapid upward and downward movement of the head and neck. Usually lasts a few seconds.
Chase	Medium	The aggressor chases another male, with its head down and its neck in line with the back, and tries to kick and bite the opponent.
Neckwrestle	High	It is considered a tactic to unbalance the opponent. Two individuals twist their necks, sometimes accompanied by bites.
Chest-ram	High	Chest-to-chest frontal clash between two individuals standing on their hind legs.
Bite	High	It includes biting at the forelegs to unbalance an opponent, at the hind legs of a fleeing opponent, or at the neck as a tactic to impede movement.
Spit	High	Common display of the Camelidae observed as a subcomponent in intensive encounters. It may occur with the individual standing in place or combined with clashes or chases.
Mount	High	Sexual mount of another male, occasionally seen during this study.

the recipient of aggression. We subsequently used a digital audio editor to record the presence/absence of aggressive behaviour (presence was assigned when we observed at least one aggressive behaviour during the observation time) and calculate its frequency (total number of occurrences of aggressive behaviours during the observation time).

2.4 | Ecological variables

In each reproductive period, we identified ecological variables as factors that may have influenced aggressive behaviour. Vegetation type was categorized as grassland, shrubland or mixed steppe (low shrubland/grassland). In addition, six 500 × 500 m vegetation polygons, which are representative of areas used by guanacos in the study site, were selected to estimate the following features: (a) As a correlate of plant productivity, we estimated the mean value of the Enhanced Vegetation Index (EVI) derived from 250-m Moderate Resolution Imaging Spectroradiometer (MODIS) satellite images (lpdaac.usgs. gov; Reed et al., 1994). EVI is an enhanced version of the normalized difference vegetation index (NDVI; Pettorelli et al., 2005) and is adequate to model Patagonian steppe primary productivity, where vegetation cover is relatively low (Mohr Bell & Siebert, 2008). Each MODIS image is the result of a 16-day composite; therefore, we processed two images to obtain a mean EVI value per period. (b) Vegetation cover (%) was estimated using the point quadrat method (Daget & Poissonet, 1971) to obtain a proxy of food resource availability. Three transects were surveyed in each polygon, and the cover values were averaged. (c) In each transect, vegetation samples were taken from guanacos' main forage sources (_Panicum urvilleanum_, _Poa spp._, _Neosparton aphyllum_; Puig et al., 1996; Puig et al., 1997). The percent nitrogen (%N) of plants sampled in each transect was estimated using the micro-Kjeldahl analysis (AOAC, 1980) and then averaged to obtain a single value per polygon. We used %N as a proxy of high forage quality (Baron et al., 2002; Van der Wal et al., 2000). Given the homogeneity within each vegetation type (Martínez Carretero, 2004), we assumed that the sampled area and corresponding values provide a representative sample of the areas used by the observed male guanacos. For each focal observation, vegetation type was categorized and data were assigned from the nearest vegetation polygon, corresponding to the vegetation type where the male was found. For the latter, we registered the male's geographic location with a hand-held GPS (Garmin eTrex 10) after each focal observation and then used geographic information systems (QGis v2.18.12) to calculate the nearest vegetation polygon.

2.5 | Statistical analyses

To test our predictions, we performed analyses at two levels: a population level (for predictions I and II), in which we considered all focal observations (n = 460); and a group level (for predictions III and IV), in which we used different models for family groups (n = 114),

solitary males (n = 281) and mixed groups (n = 42). We did not fit models for bachelor groups due to low sample size (n = 23).

At both levels, we selected a sequential analysis approach that allowed us to integrate information from all the focal observations (Table S1; Mulero-Pázmány et al., 2017). First, we examined which factors determined the presence/absence of aggressive behaviour in male guanacos. For this, generalized linear models (McCullagh & Nelder, 1989) were fitted with a binomial error distribution and a logit link function. Next, we focused only on the observed males showing aggressive behaviour responses and analysed the frequency of these behaviours. We fitted generalized linear mixed models with a Poisson error distribution and log link function. We used total observation time (i.e. how long the individual was observed, expressed in minutes and log-transformed) of the focal observations as an offset to account for the different observation lengths for different males. We also used an observation level as a random factor to control for overdispersion. This term models the extra-Poisson variation in the response variable using a random effect with a unique level (id) for every data point (Harrison, 2014).

Initially, the predictor variables considered in the models at the population level were reproductive period (group-formation, mating, post-mating), sampling year (2014, 2016), site (NE, NW), mean EVI (range = 0.057–0.131) and type of social unit (solitary, family, bachelor, mixed). We also considered the interactions period*sampling year and mean EVI*sampling year to account for environmental variability between years, as the study site experiences high inter-annual variability (Candia et al., 1993; Martínez Carretero, 2004); period*social unit, considering that aggressive interactions during the three periods of the reproductive season could be manifested in different ways in territorial and non-territorial males; and mean EVI*social unit, to assess whether aggression in territorial and non-territorial males can be differentially influenced by resource availability (Table S1).

At the group level, we initially considered reproductive period, sampling year, site, mean EVI, % vegetation cover (range = 33.67–96.67), %N (range = 0.120–1.713) and vegetation type (shrubland, grassland, mixed steppe) as predictor variables to analyse how ecological features may affect aggressive interactions in territorial males (family groups and solitary males) and non-territorial males (mixed groups). We only considered the interaction period*sampling year in the binomial models developed for the solitary males because of the relatively low sample size of the other social units (Table S1).

We evaluated the multicollinearity of predictor variables by calculating the generalized variance inflation factor (GVIF; Fox & Monette, 1992), which is a generalization of the variance inflation factor (VIF). GVIF is applied to measure the collinearity among covariates, such as dummy regressors from a categorical variable. Fox and Monette (1992) suggest reporting the adjusted generalized variance inflation factors $AGVIF = GVIF^{1/(2df)}$, where _df_ is the number of degrees of freedom associated with the term and is analogous to reporting the square root of the VIF for a single coefficient. As a rule of thumb, AGVIF values greater than 2.236 (analogous to VIF > 5) were considered an indication of collinearity (Zuur et al., 2007). At the population level, we excluded the terms mean EVI*sampling

year (AGVIF = 7.60), mean EVI*social unit (AGVIF = 3.10) and mean EVI (AGVIF = 3.23) from the binomial model. We excluded the terms mean EVI*sampling year (AGVIF = 7.96), mean EVI*social unit (AGVIF = 3.24), mean EVI (AGVIF = 2.63) and social unit*period (AGVIF = 2.49) from the frequency model. At the group level, we excluded the term vegetation cover from all the binomial models since AGVIF > 2.236. Mean EVI was also excluded from the binomial models for solitary males (AGVIF = 3.42) and mixed groups (AGVIF = 7.50). We excluded mean EVI from the frequency models performed for family groups (AGVIF = 2.41) and solitary males (AGVIF = 2.59). Due to the low sample size at the group level, we also considered exploratory analyses between independent and response variables and model fit to include the predictors in the models (Table S1).

We used a Bayesian framework with non-informative priors to obtain 95% credible intervals (CrI) around the mean, representing the uncertainty around our estimates. We considered an effect to be statistically meaningful when the posterior probability of the mean difference between compared estimates was higher than 0.95 or when the estimated CrI did not include zero (for further details on statistical inference, see Korner-Nievergelt et al., 2015). We also analysed model residuals using graphical methods (i.e. qqplots of residuals fitted values versus residuals) for homogeneity of variance or other departures from model assumptions and model fit. All modelling was performed with the software R v3.4.3 (R Core Team, 2016), using the packages "car" (Fox & Weisberg, 2019),

"bbmle" (Bolker, 2017), "lme4" (Bates et al., 2018) and "arm" (Gelman et al., 2018).

3 | RESULTS

3.1 | Factors influencing aggressive behaviour at the population level

The probability of aggressive behaviour in males was greater during the mating period, compared to the group-formation period (Figure 1a; Table 2). In the mating and post-mating periods, the presence of aggressive behaviour was higher in 2014 than in 2016 (Figure 1a; Table 2). There were no differences in aggressive behaviour between sites (Table 2). In addition, the presence of aggressive behaviour was higher in males from family groups and mixed groups, compared with solitary males (Figure 1b; Table 2). The interaction between period and type of social unit was not meaningful (Figure S1; Table 2). The frequency of aggressive interactions in males was similar during the group-formation and the mating periods (Figure 1c; Table 2) and across sites (Table 2). In the post-mating period, the frequency of aggressive interactions was higher in 2014 than in 2016 (Figure 1c; Table 2). In addition, the frequency of aggressive behaviour was higher in males from family groups and mixed groups, compared to solitary males (Figure 1d; Table 2).
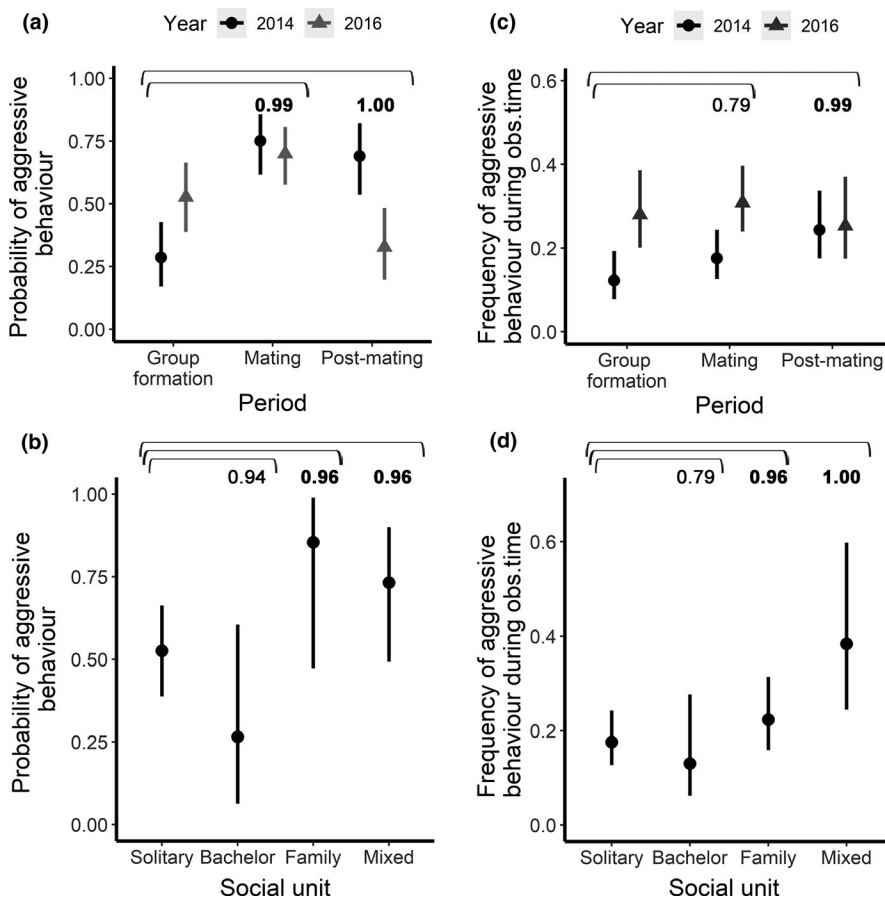

FIGURE 1 Relationship between the probability/ the frequency of aggressive behaviour during the observation time and the period of the reproductive season and the year sampled (a; c), and the social unit of the observed males (b; d). Black dots and grey triangles represent mean estimates of the models; the vertical bars represent the 95% CrI. Numbers represent the posterior probability of a mean difference between compared estimates. A statistically meaningful effect (presented in bold) can be assumed when the posterior probability of the mean difference between compared estimates is higher than 0.95

TABLE 2 Results from linear models estimating the effects of predictors on the presence and frequency of aggressive behaviour in male guanacos. We present estimates of the parameters with their 95% credible intervals (CrI) in parentheses. A statistically meaningful effect of a fixed factor (presented in bold) can be assumed when the posterior probability (Post P.) of the mean difference between compared estimates is higher than 0.95 or when the estimated CrI does not include zero

Predictors	Presence of aggressive behaviour		Frequency of aggressive behaviour	
	Estimate (95% CrI)	Post P.	Estimate (95% CrI)	Post P.
Intercept	**−0.94 (−1.58; −0.29)**	**0.99**	**−2.09 (−2.55; −1.64)**	**1.00**
Year:2016[a]	**1.04 (0.29; 1.79)**	**0.99**	**0.82 (0.30; 1.35)**	**0.99**
Period: mating[b]	**2.07 (1.25; 2.89)**	**1.00**	0.36 (−0.15; 0.86)	0.91
Period: post-mating	**1.77 (0.91; 2.64)**	**0.99**	**0.68 (0.17; 1.21)**	**0.99**
Site: NE[c]	−0.19 (−0.62; 0.23)	0.81	0.13 (−0.10; 0.36)	0.86
Social unit: bachelor[d]	−1.26 (−2.85; 0.32)	0.94	−0.30 (−1.00; 0.42)	0.79
Social unit: family[d]	**2.11 (−0.20; 4.38)**	**0.96**	**0.24 (−0.02; 0.51)**	**0.96**
Social unit: mixed[d]	**0.97 (−0.13;2.07)**	**0.96**	**0.78 (0.45; 1.11)**	**1.00**
Year:2016*Period:mating	**−1.32 (−2.33; −0.29)**	**0.99**	−0.26 (−0.88; 0.36)	0.79
Year:2016*Period: post-mating	**−2.62 (−3.69; −1.53)**	**1.00**	**−0.78 (−1.48; −0.10)**	**0.99**
Period: mating*social unit: bachelor	1.43 (−1.36; 4.27)	0.84	--	--
Period: post-mating*social unit: bachelor	1.15 (−1.36; 3.71)	0.81	--	--
Period: mating*social unit: family	−1.94 (−4.28; 0.48)	0.94	--	--
Period: post-mating*social unit: family	−1.75 (−4.14; 0.71)	0.92	--	--
Period: mating*social unit: mixed	−0.12 (−2.05; 1.80)	0.54	--	--
Period: post-mating*social unit: mixed	2.02 (−0.44; 4.44)	0.94	--	--

[a]Reference level of "Year" variable: 2014.
[b]Reference level of "Period" variable: group-formation.
[c]Reference level of "Site" variable: NW.
[d]Reference level of "Social unit" variable: solitary male.

3.2 | Factors influencing aggressive behaviour at the group level

The probability of aggressive behaviour in territorial males (family groups and solitary males) was influenced by some of the ecological variables tested (Figure 2; Table 3). In males from family groups, %N of vegetation had no ecologically meaningful effect on the probability of aggressive behaviour (Figure 2a; Table 3). In contrast, aggressive behaviour increased with greater mean EVI (Table 3). In solitary males, the presence of aggressive behaviour increased in areas with higher %N of the vegetation (Figure 2b; Table 3). In solitary males, the presence of aggressive behaviour was also lower in grasslands compared to shrublands (Table 3). In the case of non-territorial males (i.e. mixed groups), the %N did not influence the probability of aggressive behaviour (Figure 2c; Table 3).

The frequency of aggressive behaviour in males from family groups was higher in grasslands, compared to shrublands (Table 4). In contrast, neither %N nor vegetation cover influenced the frequency of aggression (Figure 3a,b, Table 4). In solitary males, the frequency of aggressive interactions increased with higher vegetation cover, while %N had no ecologically meaningful effect (Figure 3c,d; Table 4). In the case of mixed groups, the frequency of aggressive interactions was not affected by any of the ecological variables examined (Figure 3e,f; Table 4).

4 | DISCUSSION

4.1 | Aggressive behaviour at the population level

Our results showed that aggressive interactions in male guanacos varied among the group-formation, mating and post-mating periods,
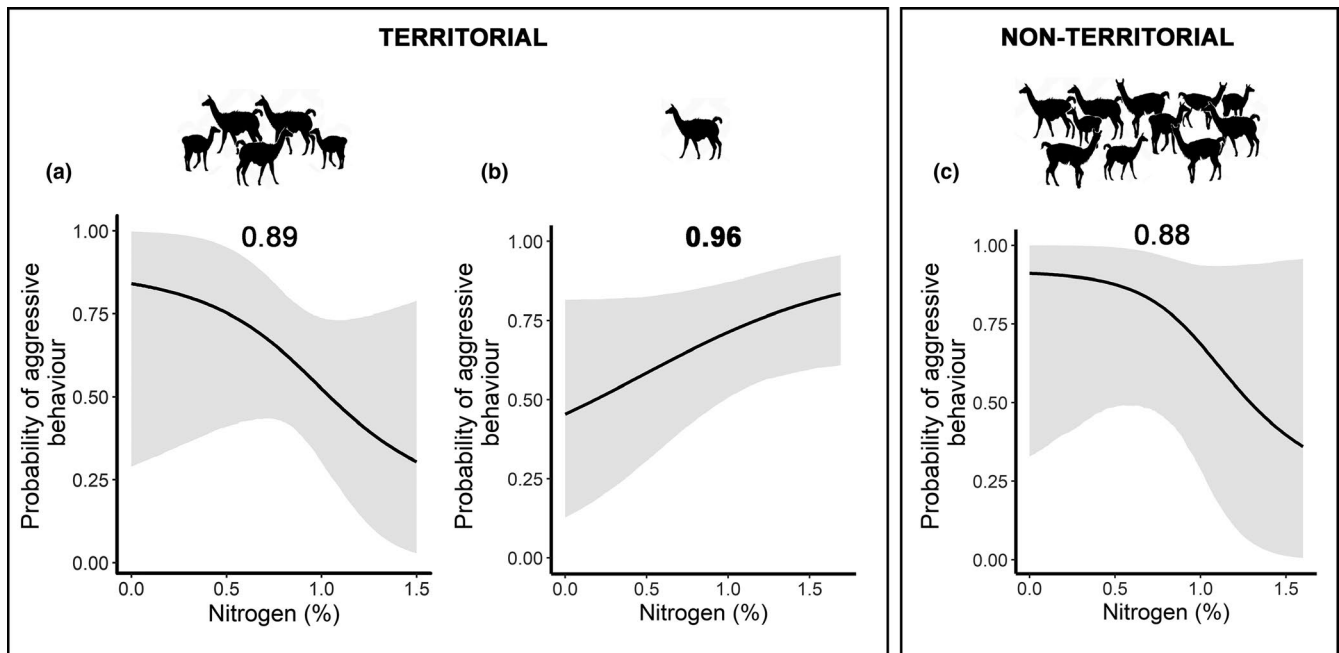
FIGURE 2 Relationship between the probability of aggressive behaviour and the percentage of nitrogen in plants in males belonging to different social units. We used different models for each social unit: males from family groups (a), solitary males (b) and males from mixed groups (c). Black lines represent mean estimates of the models, and grey bands represent 95% CrI. Numbers represent the posterior probability of a mean difference between compared estimates. A statistically meaningful effect (presented in bold) can be assumed when the posterior probability of the mean difference between compared estimates is higher than 0.95

suggesting that seasonality during the reproductive season is an important determinant of variation in this social behaviour. The presence of aggressive behaviour peaked during the mating period, as we predicted (Prediction I). These findings are similar to those found in other populations of guanacos in Chile and Argentina, especially for territorial males (Marino, 2012; Wilson & Franklin, 1985). Moreover, a wide variety of vertebrate taxa display similar patterns, including other wild South American camelids (*Vicugna vicugna*, Vilá, 1992), ungulates (*Antilocapra americana*, Kitchen, 1974; *Cervus elaphus*, Clutton-Brock et al., 1982; *Aepyceros melampus*, Murray, 1982; *Gazella subgutturosa*, Blank et al., 2015), primates (Cavigelli & Pereira, 2000; Ostner et al., 2002) and birds (Wingfield et al., 1987, 2001).

Contrary to our expectations, the frequency of aggressive interactions did not differ between the group-formation and the mating periods (Figure 1c). Previous research in South American camelids has reported contrasting results. Studies carried out in another migratory guanaco population in southern Patagonia reported that the rate of aggressive encounters between territorial males was higher in December, during the mating period, compared to January or February (Jurgensen, 1985). However, aggression rates between group-formation and the mating periods were not contrasted. On the other hand, Vilá (1992) reported similar results to those found in our study regarding the frequency of aggressive behaviours in vicuñas. The similar frequency of aggressive interactions between these two periods could be related to male defence of territories during the reproductive season, which begins during the group-formation period and continues through the mating period.

Considering that aggressiveness is influenced by resource availability (Fattorini, et al., 2018; Sirot, 2000; Taillon & Côté, 2007), the difference in aggressive behaviour between 2014 and 2016 during the group-formation and post-mating periods could be due to inter-annual environmental variability and differences in forage availability. During the reproductive season of 2014, primary productivity and vegetation cover were 26.2% lower than in the reproductive season of 2016 (see Tables S2 and S3) and this difference could have led to greater competition for forage in 2014. In this sense, the increased presence and frequency of aggressive behaviour observed during the 2014 post-mating period could have been more related to competition for forage than to reproductive concerns, irrespective of males' social unit. The nearly complete absence of copulations during the post-mating period supports this argument (Jurgensen, 1985; Panebianco, 2019; Young & Franklin, 2004b). Further evidence in favour of this argument comes from the relatively high concentration of faecal cortisol metabolites observed in guanaco males during the post-mating period of 2014 (Panebianco, 2019), suggesting that individuals had higher energy demands during this time (Gregorio et al., 2019; Romero et al., 2009). Similarly, in other ungulate species, such as Apennine chamois (*Rupicapra pyrenaica ornata*) and white-tailed deer (*Odocoileus virginianus*), food depletion influenced intraspecific social behaviour by increasing aggression (Fattorini, et al., 2018; Taillon & Côté, 2007) and endocrine correlates (Fattorini, et al., 2018), in accordance with competition theory (Sirot, 2000).

Our results supported that aggressive behaviour is higher in males from family groups (Prediction II). Both the probability and the frequency of aggressive behaviour were higher in males

TABLE 3 Results from linear models estimating the effects of predictors on the presence of aggressive behaviour in male guanacos belonging to different social units. We used different models for each social unit. We present estimates of the parameters with their 95% credible intervals (CrI) in parentheses. A statistically meaningful effect of a fixed factor (presented in bold) can be assumed when the posterior probability (Post P.) of the mean difference between compared estimates is higher than 0.95 or when the estimated CrI does not include zero

| | Territorial males | | | | Non-territorial males | |
| | Family group | | Solitary male | | Mixed group | |
Predictors	Estimate (95% CrI)	Post. P	Estimate (95% CrI)	Post. P	Estimate (95% CrI)	Post. P
Intercept	**−5.42 (0.07; 10.79)**	**0.98**	**−2.22 (−4.17; −0.31)**	**0.99**	5.29 (−2.38; 12.89)	0.91
Year:2016[a]	**−3.91 (−6.36; −1.43)**	**0.99**	**1.78 (0.73; 2.83)**	**0.99**	−1.42 (−4.75; 1.91)	0.80
Period: mating[b]	−2.33 (−5.56; 0.86)	0.92	**2.48 (1.47; 3.52)**	**1.00**	1.11 (−0.96; 3.22)	0.85
Period: post-mating	**−3.90 (−7.39; −0.46)**	**0.99**	**1.85 (0.35; 3.34)**	**1.00**	1.97 (−0.54; 4.49)	0.94
Site: NE[c]	−0.72 (−1.71; 0.27)	0.92	0.27 (−0.36; 0.89)	0.80	--	--
Mean EVI	**69.33 (14.00; 124.71)**	**0.99**	--	--	--	--
Nitrogen percentage	−2.33 (−6.09; 1.46)	0.89	**1.17 (−0.21; 2.57)**	**0.96**	−3.16 (−8.28; 1.96)	0.88
Vegetation type: mixed steppe[d]	−0.12 (−1.50; 1.23)	0.57	−0.47 (−1.36; 0.42)	0.86	0.91 (−3.22; 1.37)	0.78
Vegetation type: grassland[d]	−0.13 (−1.69; 1.45)	0.57	**−0.91 (−1.73; −0.11)**	**0.99**	−1.08 (−3.61; 1.45)	0.80
Year:2016*Period:mating	--	--	**−1.75 (−3.06; −0.41)**	**0.99**	--	--
Year:2016*Period: post-mating	--	--	**−3.24 (−4.63; −1.87)**	**1.00**	--	--

[a]Reference level of "Year" variable: 2014.

[b]Reference level of "Period" variable: group-formation.

[c]Reference level of "Site" variable: NW.

[d]Reference level of "vegetation type" variable: shrubland.

TABLE 4 Results from linear models estimating the effects of predictors on the frequency of aggressive behaviour in male guanacos belonging to different social units. We used different models for each social unit. We present estimates of the parameters with their 95% credible intervals (CrI) in parentheses A statistically meaningful effect of a fixed factor (presented in bold) can be assumed when the posterior probability (Post P.) of the mean difference between compared estimates is higher than 0.95 or when the estimated CrI does not include zero

| | Territorial males | | | | Non-territorial males | |
| | Family group | | Solitary male | | Mixed group | |
Predictors	Estimate (95% CrI)	Post. P	Estimate (95% CrI)	Post. P	Estimate (95% CrI)	Post. P
Intercept	**−1.92 (−3.54; −0.26)**	**0.99**	**−1.99(−2.87; −1.14)**	**1.00**	−0.87 (−2.78; 1.03)	0.81
Year:2016[a]	0.34 (−0.18; 0.88)	0.90	**0.56 (0.21; 0.92)**	**0.99**	--	--
Period: mating[b]	0.25 (−0.82; 1.31)	0.68	0.10 (−0.29; 0.49)	0.70	--	--
Period: post-mating	0.22 (−0.81; 1.22)	0.67	0.29 (−0.14; 0.73)	0.90	--	--
Vegetation cover	0.01 (−0.01; 0.01)	0.53	**0.01 (−0.00;0.02)**	**0.97**	0.02 (−0.01; 0.04)	0.85
Nitrogen percentage	0.24 (−0.86; 1.34)	0.66	−0.08 (−0.56; 0.73)	0.59	−0.36 (−1.64; 0.93)	0.70
Vegetation type: mixed steppe[d]	0.21 (−0.33; 0.74)	0.77	−0.22 (−0.67; 0.23)	0.83	--	--
Vegetation type: grassland[d]	**0.52 (−0.010; 1.12)**	**0.95**	−0.02 (−0.40; 0.36)	0.55	--	--

[a] Reference level of "Year" variable: 2014.

[b]Reference level of "Period" variable: group-formation.

[c]Reference level of "Site" variable: NW.

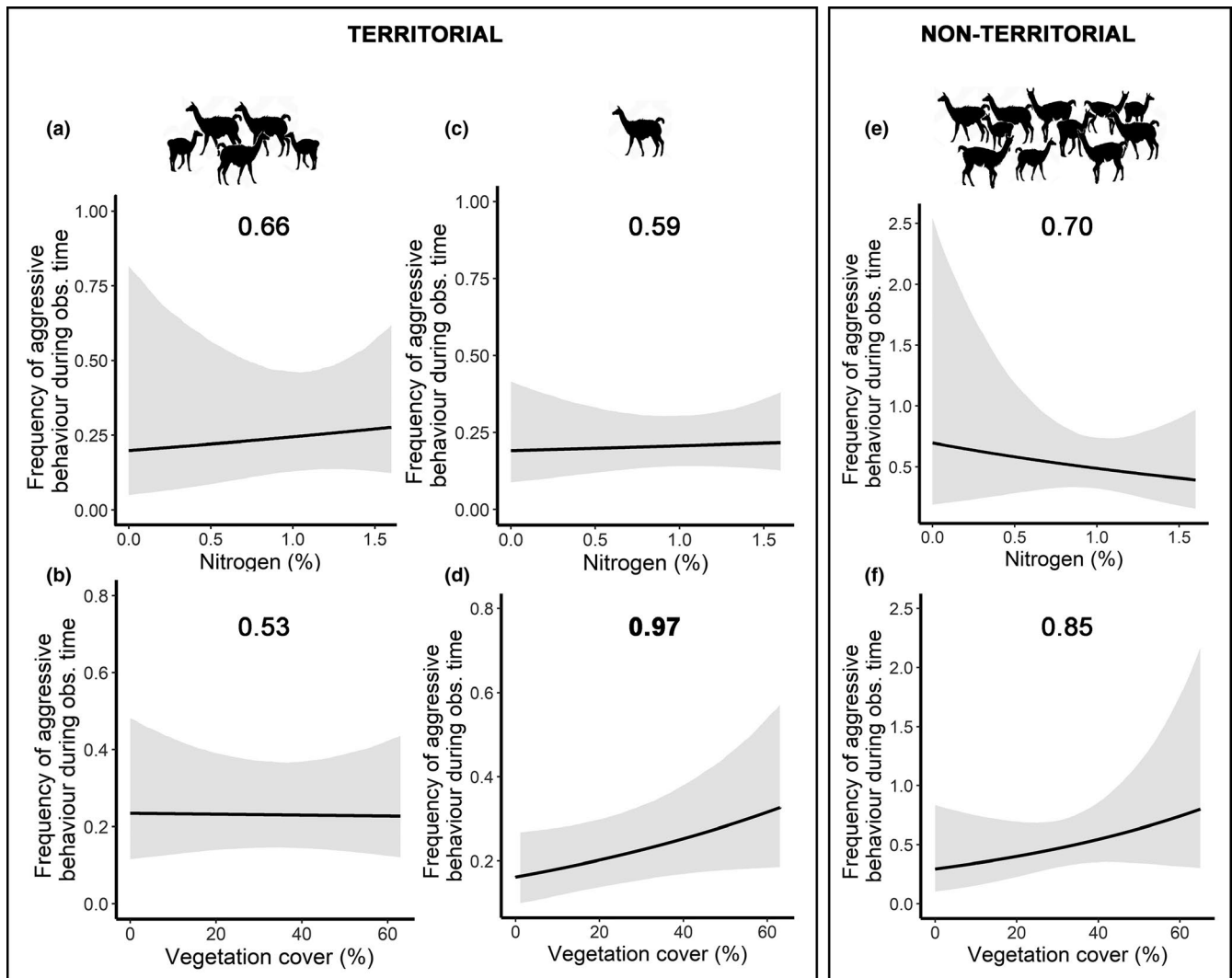[d]Reference level of "vegetation type" variable: shrubland.

FIGURE 3 Relationship between the frequency of aggressive behaviour during the observation time, the percentage of nitrogen in plants and vegetation cover in males belonging to different social units. We used different models for each social unit: males from family groups (a, b), solitary males (c, d) and males from mixed groups (e, f). Black lines represent mean estimates of the models, and grey bands represent 95% CrI. Numbers represent the posterior probability of a mean difference between compared estimates. A statistically meaningful effect (presented in bold) can be assumed when the posterior probability of the mean difference between compared estimates is higher than 0.95

from family groups. Similar results were found in previous studies (Lucherini, 1996; Marino, 2012) and likely reflect the social organization of wild South American camelids, where families defend food resources and therefore play a main role in aggressive interactions within the population. In accordance with Lucherini (1996), our data also suggest that family groups of wild South American camelids, at least during the summer (i.e. reproductive season), live in a stable and predictable social environment in which superfluous agonistic interactions between males are avoided, as they are energetically costly and potentially dangerous (guanacos and vicuñas can use canines teeth during fights). In fact, in our study, males from family groups did not engage in high aggression-level displays (Table 1) and performed mostly low to medium aggression-level behaviours, such as ear threats or chases. These indirect displays may be sufficient for the defence of territories in this social context. Additionally, males may use other strategies that could be equally successful,

such as active vigilance (i.e. social vigilance; Marino & Baldi, 2008), which has been recorded in other ungulate species (Kitchen, 1974; Maher, 2000).

Alternatively, phenotypic traits (e.g. antler size, body mass, body size, colour) are commonly used in ungulates as signals of rank in agonistic behaviour to assess fighting ability of opponents (Clutton-Brock & Albon, 1979; Hoem et al., 2007; Lovari et al., 2015; Taillon & Côté, 2007; West & Packer, 2002; Zahavi, 1987). Guanacos may retain some kind of rank signal, like body mass or colour (Lovari et al., 2015), that allows low-ranking individuals to avoid territorial males without the need to involve in high aggression-level interactions. However, this hypothesis has yet to be tested.

Despite the energy costs of aggression (Clutton-Brock et al., 1979; Huntingford & Turner, 1987), males from family groups frequently engaged in aggressive interactions. These repeated aggressive displays could be interpreted as signals of individual

condition. Territorial and top-ranking males of many species signal their individual quality and fighting ability to other competitors through repetitive aggressive displays even in stable social groups (Parker, 1974; Payne & Pagel, 1997), including goitered gazelle (Blank et al., 2015), Himalayan tahr (*Hemitragus jemlahicus*; Lovari et al., 2015) and goats (*Capra hircus*; et al., 2000). This behaviour is also a cue of their willingness to fight, which can affect the decision-making processes of the other males involved (Blank et al., 2015).

The probability and frequency of aggressive interactions in males from mixed groups was also high, which was unexpected. These results could be related to many factors such as group size and composition (i.e. different age/sex class), and social instability. In our study, mixed groups had a mean size of 42 individuals (Figure 4) and contained multiple adult males. In this scenario, the encounter rate among individual animals (e.g. competitors and potential mates) is likely high (Knell, 2009; Vander Wal et al., 2012), leading to an increase in aggressive encounters and intrasexual competition. Additionally, it could be argued that mixed groups during the reproductive season are socially unstable units and lack a social hierarchy, because the composition and size of these associations can vary considerably in the short term, as animals can come and go at will, and they are remnant groups from migration. Consequently, this social instability could induce higher levels of aggressiveness (Teichroeb & Sicotte, 2008). Similarly, studies in other ungulate species reported that aggressiveness was enhanced after regrouping experiments (goats, Andersen et al., 2008; *Ozotoceros bezoarticus*, Villagrán et al., 2020). The lack of stable social bonds and changes in group composition may have negative consequences, such as reduced access to food resources (Andersen et al., 2008) and lower food intake and growth (Stookey & Gonyou, 1994), so further research is needed to assess the potential consequences of aggression in mixed groups.
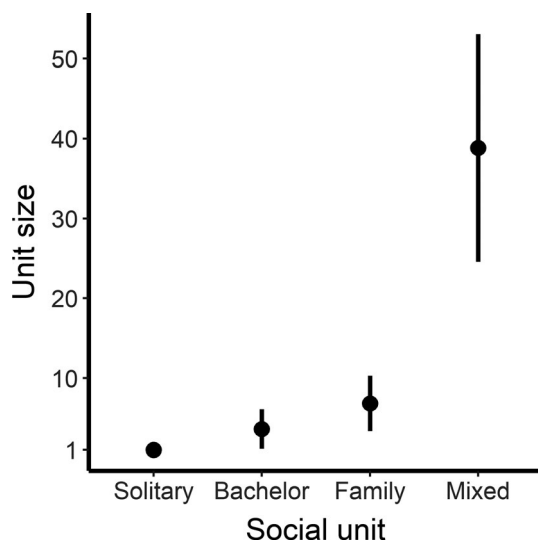
4.2 | Aggressive interactions at the group level

Our results showed that the probability and the frequency of aggressive interactions increased with higher quantity (higher mean EVI; higher vegetation cover) and/or quality (higher %N of vegetation) of food resources in territorial males (partially supporting Prediction III), but not in non-territorial males (Tables 3 and 4). In general, most aggressive interactions relate to conflict over food and mating, and territoriality is often a combination of these two contexts (Parker, 1974). If we also consider that one of the main drivers of fighting behaviour in males is resource value and that animals adjust fighting to variation in resource value (Arnott & Elwood, 2008; Barroso et al., 2000; Koenig et al., 2004; Taillon & Côté, 2007), the defence of high-quality food resources by territorial male guanacos may provide access to better forage and enhance probability of mating with females in their territory. This possibility may also apply to solitary males. Although solitary males are not associated with other individuals, they were seen copulating with females at least as often as males from family groups (Panebianco et al., 2020). In this sense, resource value may be influenced by both extrinsic factors linked to absolute properties of the resource unit (i.e. forage quality), and intrinsic factors related to the subjective value an individual assigns to the resource (i.e. mating opportunity) (Enquist & Leimar, 1987; Lane & Briffa, 2018). Accordingly, as the value of the resource increases, so does the cost that an animal is willing to pay for that resource, for example, in terms of contest duration or energy allocation (Arnott & Elwood, 2008; Enquist & Leimar, 1987; Maynard Smith, 1982). This trade-off should be the subject of future research because it may improve our understanding of the adaptive value aggressive behaviour.

The relationship between resource value and aggressiveness has been studied and confirmed in other species (Barroso et al., 2000; Clutton-Brock et al., 1979; Fattorini, et al., 2018; Hoem et al., 2007). For instance, when nursing effort is the highest, female Apennine chamois select nutritious food patches to cope with the heavy energetic demands. This in turn leads to increased rates of aggression (Fattorini, et al., 2018). In this way, our study in guanacos combined with previous evidence suggests that differences in the assessment of resources are related to mating strategies (i.e. harem-defence or resource-defence) and the resource at stake (Jennings & Gammell, 2013). A potential caveat is that sample sizes at the group level were relatively small. Further research evaluating the intrinsic (e.g. male age) and extrinsic (e.g. size and quality of the territory assessed by measuring other attributes such as fibre content or crude protein) factors influencing value of resources (Lane & Briffa, 2018) in territorial male guanacos is needed to better understand potential impacts on aggressive behaviour.

In contrast to Prediction IV, aggression in non-territorial mixed groups was not associated with the quality and/or quantity of food resources, and this may be because competitive interactions between individuals are not expected to increase when food is abundant (Sirot, 2000), as they are during the reproductive season. A lack of an association between aggressive behaviour and high availability of food resources has been reported in guanacos previously

FIGURE 4 Mean ± standard deviation of unit size in relation to the social unit to which the focal males belonged

(Marino, 2012). In this sense, the greater aggressiveness recorded in mixed sex groups at the population level may not be associated with contest over food. While this aggressiveness may be due to social instability and group size, as previously discussed, further research will be necessary to understand in more depth the factors affecting aggression in these social units. For instance, the assessment of aggressive interactions outside the reproductive season, when mixed groups comprise a large proportion of the population and forage resources decrease, could further clarify the relationships among these factors.

5 | CONCLUSIONS

We assessed ecological and social factors that could influence aggressive interactions in male guanacos using different measures of behaviour. At the population level, our results revealed that the presence of aggressive interactions peaks during the mating season and that aggressiveness might vary with inter-annual environmental fluctuations. At the group level, our results showed that the factors influencing aggression might be different for territorial and non-territorial males. For family groups and solitary males, high food resource quality and/or quantity were predictors of aggressive interactions, findings that may be related to the resource-defence strategy of this species. Conversely, male aggression in mixed sex groups may be associated with social instability and group size. Overall, our research reinforced the hypothesis that aggression can occur in multiple contexts depending on male status (e.g. territorial or non-territorial), and contributed to our understanding of how food availability and social factors influence aggression in a resource-defence ungulate. Further research is needed to better understand the relationship between territoriality, resource value assessment and reproduction in wild guanacos.

Relatively little effort has been devoted to understanding how ecological factors influence aggression in resource-defence ungulates compared to other mating systems (e.g. harem-defence). Thus, our research represents an important contribution to the study of this social behaviour during the reproductive season.

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SUPPORTING INFORMATION

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