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REPRODUCTIVE FLEXIBILITY IN SOUTH AMERICAN CAMELIDS: FIRST RECORDS OF ALTERNATIVE MATING TACTICS IN WILD GUANACOS (*Lama guanicoe*)

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ABSTRACT. Intraspecific variation in mating behavior has been documented in diverse taxa, including ungulates. Here, we report and describe for the first time the existence of alternative mating tactics in a wild guanaco (*Lama guanicoe*) partially migratory population. We document (1) a resource-defense tactic, widely reported for different populations; and (2) a clustered territorial tactic, adopted by the solo territorial males of this population. Our results highlight the reproductive flexibility of this species and its relationship with external factors that could be influencing it.

RESUMEN. Flexibilidad reproductiva en camélidos sudamericanos: primeros registros de tácticas de apareamiento alternativas en guanacos silvestres (*Lama guanicoe*). La variación intraespecífica en el comportamiento de apareamiento ha sido documentada en diversos taxones, incluyendo ungulados. Aquí reportamos y describimos por primera vez la existencia de tácticas alternativas de apareamiento en una población de guanacos silvestres (*Lama guanicoe*) parcialmente migratoria. Documentamos (1) una táctica de defensa de los recursos, ampliamente descrita para diferentes poblaciones; y (2) una táctica territorial agrupada, adoptada por los machos territoriales solitarios de esta población. Nuestros resultados destacan la flexibilidad reproductiva de esta especie y su relación con los factores externos que podrían estar influyendo en ella.

Key words: alternative reproductive tactics, intraspecific variation, *Lama guanicoe*, polygyny, reproduction.

Palabras clave: *Lama guanicoe*, poliginia, reproducción, tácticas alternativas de reproducción, variación intraespecífica.

It is well known that there is great variation in social behavior within a species, and often even within a population (Lott 1991), as a function of internal factors, such as age and body size, as well as external conditions, like population density or

environmental features (Isvaran 2005). One aspect of behavior that shows such extensive variation is mating behavior and examples exist in diverse taxa including arthropods, fish, birds and mammals (Lott 1991; Taborsky 1994; Isvaran 2005). Among

mammals, variation in mating behavior within populations is common in ungulates (Clutton-Brock et al. 1988; Bro-Jørgensen & Durant 2003; Isvaran 2005). Polygynous mating strategies in these species may vary among exclusive monopolization of females (e.g. harem-defense), the defense of territories containing resources that attract females (e.g. resource defense) or the defense of clustered territories (e.g. lek) (Bro-Jørgensen 2011).

In this study, we report for the first time discrete variation in mating behavior (i.e. alternative tactics; Brockmann 2001; Isvaran 2005) in a wild South-American camelid, the guanaco (*Lama guanicoe*) in La Payunia Reserve, Argentina. This species is the largest native herbivore in South America, and its populations can be either sedentary (i.e., family groups remain within their territories all year round) or migratory (i.e., after the reproductive season, individuals move collectively in large groups to their winter range) (Franklin 1983). Social units in guanacos are: (1) family-groups composed of a territorial adult male, several females and their offspring (this group type is defined upon composition and not relatedness, since member composition can change from day to day, i.e. they are “semi-open”); (2) solo territorial males that defend a small territory with females and young rarely present; (3) bachelor groups comprised of non-reproductive and non-territorial males of all age classes; (4) female groups consisting of individuals of all ages with or without offspring; and (5) mixed groups consisting of males and females of all ages (Franklin 1983; 2011).

So far, resource-defense polygyny has been described in guanaco populations (Franklin 1982; 1983), in which males establish territories and defend resources to attract mates during the reproductive season (Young & Franklin 2004a). Previous studies described that the males that contribute reproductively to the population are almost always territorial males from family groups and only under rare circumstances do solo territorial males or males in bachelor groups have an opportunity to mate (Jurgensen 1985; Young & Franklin 2004b). However, the observations made in our study area show that this may not be so for all populations. Here, we aim to document and describe the existence of alternative mating tactics in a wild partially migratory guanaco population.

This study was carried out in La Payunia Reserve (665 682 ha), located in west-central Argentina (36°36'S, 68°34'W). It harbors the largest population of guanacos of the region, which holds about 26,000 individuals in spring in the northern part of the

reserve (Schroeder et al. 2014). This partially migratory population has summer and winter ranges distant 85 km in average (Bolgeri 2016). During the reproductive season, winter migrants return to the NE, the most important breeding area (Sajj 2010). Family-groups and solo males establish their territories, and births and mating occur (Jurgensen 1985; Young & Franklin 2004a).

We conducted four 15-days surveys during two reproductive seasons (2014 and 2016), at the peak (December-January) and the end (February) of the season, in the NE of the reserve (approximately 26 ha). At the beginning of each survey, we estimated guanaco densities following the line-transect method. For every group encountered, we recorded its size, composition and type of social unit. Guanaco densities (individuals/km²) were estimated using Distance 7.1 software (Buckland et al. 2001). For further details about methodology, see Carmanchahi et al. (2014).

To register mating behavior, we drove along existing tracks (total length: 30 km) and when we encountered a group, we performed *Ad Libitum* observations (Altman 1974; Martin & Bateson 2007) of adult males, using a spotting scope (20-60x; Bushnell Trophy XLT). We covered all the tracks every day to properly represent the entire area. At the beginning of each observation, we recorded the number of adults and offspring in the group, based on body size. Groups were identified by excluding individuals more than 300 m away from their neighbors; this was confirmed by animal movement (i.e. the members of the same group moved together while the other individuals stayed in the same place or moved in another direction; Marino & Baldi 2008, Taraborelli et al. 2012). Guanaco sex was assessed observing external sexual characters. For each mating observation, we recorded the date, location, duration, and social group. A copulation was defined as “complete” if it lasted at least 5 minutes without interruption (Jurgensen 1985). We also registered the male's geographic location with a GPS (Garmin eTrex 10) and then used Geographic Information Systems (QGIS v2.18.12) and the function heat map, that uses the Kernel Density Estimation, to map the observed males according to their social group throughout the reproductive season and identify clustering of males' location.

Guanaco densities were higher than 18 individuals/km² in every survey (Table 1). The social units most represented during the peak of the reproductive season were solo males (62.5%) and family groups (15%), followed by bachelors

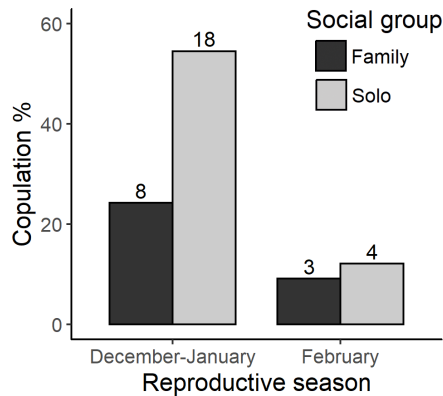


Fig. 1. Number of copulations (%) of territorial males in family-groups and solo males during the peak (December-January) and end (February) of the reproductive seasons of 2014 and 2016 in the NE area of La Payunia Reserve. The numbers above the bars indicate sample size.

(10.5%), mixed groups (8%) and female groups (4%). At the end of the season, percentages were 59.5%, 13%, 12.5%, 9.5% and 5.5%, for solo males, family, bachelors, mixed and female groups, respectively. Additionally, females were mostly found in family groups (80%) rather than in female groups (20%).

A total of 33 copulations were registered (average copulation time= 14.43 ± 6.77 minutes; range= 5-25 minutes) and 78.8% of these occurred during the peak of the reproductive season (Table 1; Fig. 1). Of the total, 11 were between males and females belonging to family groups. Additionally, 22 events were observed between females that were alone at that moment or in some cases together with their offspring (single females), and solo males. Of these, 86.3% (n=19) occurred in a particular site of the study area, the Zaino Valley (approximately 2.5 ha), an area of extensive grasslands where the great majority of solo territorial males were clustered (Table 1, Fig. 2). Solo territorial males were separated approximately 400 m, although this distance was highly variable since animals often moved around chasing females or interacting aggressively with other solo males. This territorial-defense displays usually included defecation and urination on dung piles that the solo males used to demarcate their territory (Panebianco 2019). None of the copulations between males and females from family groups was observed in the Zaino Valley. No males from bachelor groups were observed engaging in copulations.

Mating behavior between males and females in family groups was similar to what previously de-

scribed (Jurgensen 1985; Bank et al. 2003). It began with the pursuit of a female within the group until the female lied down and copulation occurred. Other members of the family group remained nearby while copulations happened and, when present, the offspring stayed close to the female. Groups were composed of 2-5 females, 1-2 yearlings and 1-3 offspring. Two of the registered copulations happened in the same group, with different females.

Copulations involving single females and solo males in the Zaino Valley generally occurred following a similar sequence of events. First, the female walked across the area where the solo males were found. When a solo male detected it, it began to chase the female by running. As the chase progressed, other solo males (usually between two or three) joined the pursuit, although some of them abandoned it quickly. If the pursuit was successful, one of the males mounted the female and mating occurred. When the copulation ended, the female walked away from the solo male and in some cases, it was again pursued by other solo males. This second sexual persecution ended with a second consecutive copulation in 75% (n=3) of the observed cases. On some occasions, other solo males approached the copulation and made vocalizations or remained vigilant until it ended to chase the female. After mating occurred, females walked away until we lost sight of them. Thus, we could not tell if they returned to female groups, family groups or stayed alone.

Based on ground surveys, the spatial distribution of family groups and solo males was different during the reproductive season. While the distribution of family-group males varied throughout the season, the distribution of solo males was more stable and was mostly concentrated in the Zaino Valley (Fig. 2). These social units were the most represented in another guanaco migratory population in Torres del Paine (Southern Chile; Ortega & Franklin 1995) and were also segregated in space. As in La Payunia, in this area of Chile both solo males and family-group males returned to the same areas for consecutive years (Young & Franklin 2004a). The authors argued that while the high potential for reproductive success is an obvious factor influencing family-group males to remain in the same place, it is unclear why more than 60% of solo males, who rarely have the opportunity to mate (Jurgensen 1985; Young & Franklin 2004b), returned annually to the same place. This same issue has long been raised in the guanaco population of La Payunia, although in this case, in contrast with the Torres del Paine population, we observed multiple cases of solo males

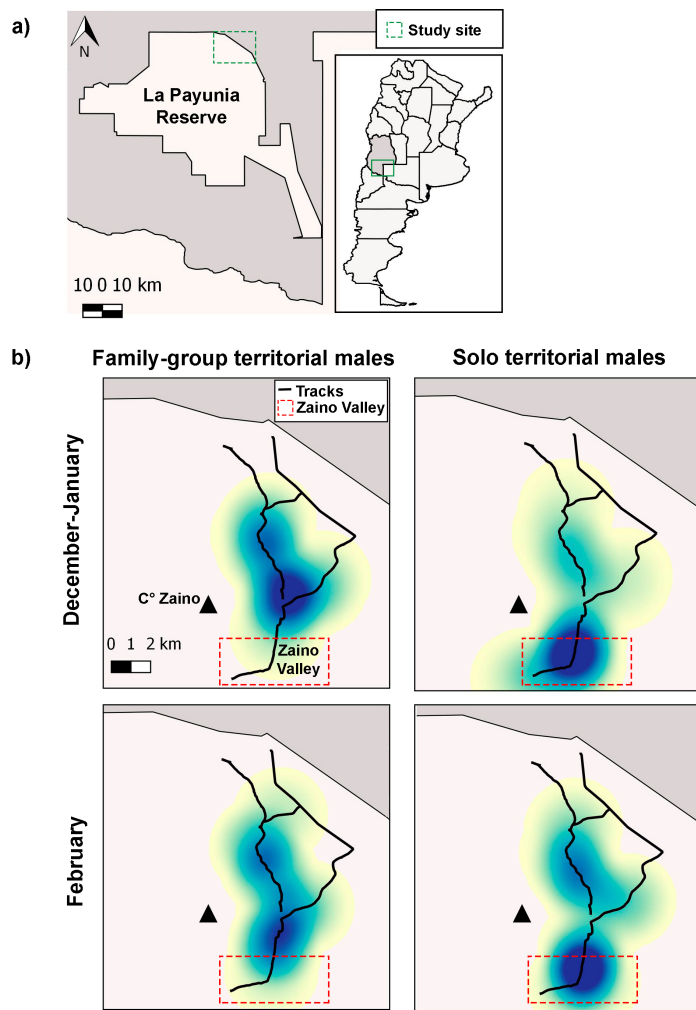


Fig. 2. a) Study area in the NE part of La Payunia Reserve, located in Mendoza province, west-central Argentina. b) Spatial distribution of territorial males in the NE area throughout the reproductive seasons 2014 and 2016. Data from both sampling seasons were plotted together for the peak (December-January) and end (February) of the reproductive season. A dotted red square indicates the Zaino Valley, which comprises around 10km of the surveyed tracks. A more intense blue color indicates a higher relative density of males, while light colors indicate a low relative density. The density was calculated based on the number of points in each location using the heatmap function in QGIS v2.18.12. and a radius of 3000 meters.

copulating with single females that were moving through the area in the Zaino Valley. The differences

found between these populations suggest that the reproductive tactics adopted by males in La Payunia are more plastic than those described so far in the literature (Franklin 1983). In this sense, resource-defense polygyny would be one of the reproductive tactics of this species, and perhaps the most frequent in all populations, but it would not be the only one, as occurs in the other wild South American camelid, the vicuña (*Vicugna vicugna*), where both territorial defense and females defense were reported (Vilá 1992; Arzamendia et al. 2018). The solo territorial males of the Zaino Valley are adult individuals, relatively grouped in space, defending small homogeneous territories (Panebianco 2019) and are spatially separated from other social units such as family groups (Table 1; Fig. 2). Considering the observed mating success of solo males, estimated from the frequency of copulations, along with the space use and territorial defense displays, we propose that these males would be adopting an alternative reproductive tactic, such as clustered territories (Thirgood et al. 1999). We support this argument on the fact that the guanaco population of La Payunia shares characteristics with other wild populations that display clustered territories (Clutton-Brock et al. 1993). These are: 1) individuals inhabit environments where resources are spatially unpredictable. In this sense, La Payunia is characterized by the occurrence of prolonged periods of drought and highly localized rainfall and grassland fires in summer (Candia et al. 1993; Martínez Carretero 2004). 2) Females have large home ranges and fe-

Table 1

Summary of guanaco density (\pm standard error), copulations (n=33), and relative abundance of family groups and solo males during the reproductive seasons of 2014 and 2016 in the NE area of La Payunia Reserve, which includes Zaino Valley (ZV).

| Reproductive season | Period of the season | Density (ind./km ²) | Social group ^a | Number of copulations | Copulation % in ZV ^b | % of groups in ZV (n) ^c |
|---------------------|----------------------|---------------------------------|---------------------------|-----------------------|---------------------------------|------------------------------------|
| 2014 | Peak | 21.22 \pm 3.66 | Family | 3 | 0 | 20 (25) |
| | | | Solo | 5 | 100 | 74 (98) |
| | End | 18.74 \pm 3.25 | Family | 2 | 0 | 38 (18) |
| | | | Solo | 2 | 100 | 71 (80) |
| 2016 | Peak | 25.86 \pm 5.27 | Family | 5 | 0 | 30 (20) |
| | | | Solo | 13 | 85 | 67 (90) |
| | End | 21.45 \pm 4.10 | Family | 1 | 0 | 31 (16) |
| | | | Solo | 2 | 50 | 59 (75) |

^a It refers to the social group where the male was observed

^b Percentage calculated based on the number of copulations in each row.

^c Percentage calculated based on the number of groups (solo or family as appropriate) according to the total number of groups of the same social unit observed during population surveys (n).

male groups are large and loose. Seasonal home ranges were estimated as part of a study on the migratory patterns of the guanaco population of La Payunia (Bolgeri 2016), and female summer areas ranged between 7.72 and 50.44 km² (Bolgeri, unpublished data). These values are much higher than those described in other southern (0.35-1.86 km²; Moraga et al. 2014) and central ((0.08-0.23 km²; Contreras et al. 2006) Chilean populations. These larger areas could be related to the absence of fences and physical barriers in La Payunia, which favors the movement of individuals. Furthermore, the social system described in guanacos is “semi-open” (Franklin 1983), in which females of family groups can come and go of different groups without male interference. 3) Population density is high. The density of the guanaco population in the NE of La Payunia was estimated between 18.74 and 25.86 individuals/km² in summer (Table 1), and was higher compared to the Torres del Paine population in the same period (15.4 individuals/km² Ortega & Franklin 1995).

In conclusion, we registered mating behavior in a partially migratory guanaco population inhabiting La Payunia during the reproductive season and described two coexisting reproductive tactics. On the one hand, a resource-defense tactic widely documented for this species and reported in different populations (Franklin 1983; Marino 2012). On the other hand, a clustered territorial tactic, adopted by the solo males of this population. Additional work, including marking individuals, remains to be done to understand more deeply which internal and external factors influence the development and maintenance

of this tactic and how spread it is in other guanaco populations. Furthermore, it will be necessary to address questions that include assessing the costs and benefits of these alternative tactics to assess their impact on fitness (Isvaran 2005) and the proximate underlying mechanisms.

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