Short Note

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Dung-pile use by guanacos in eastern Patagonia

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Abstract: Previous studies on guanacos have reported that only territorial males create and maintain dung-piles. The aim of this analysis was to compare dung-pile use by territorial males with the use by females and young in family groups, and by bachelor males. Although territorial males showed the highest dung-pile use, all individuals dropped feces on piles frequently, in contrast to what was previously observed within other guanaco populations. Besides stressing the behavioral plasticity of guanacos, these results suggest an additional adaptive function of localized-defecation other than demarcating territory ownership by the territorial male.

Keywords: dung-piles; guanaco; localized defecation; territory defense; ungulates.

Territorial defense is a widespread feature among polygynous ungulates (Jarman 1974) and many of these territorial species create permanent defecation sites, called dung-piles that serve an important scent-marking role (Estes 1991). It has been reported that both males and females create these localized defecation sites among certain species, such as bushbuck (*Tragelaphus scriptus*, Pallas 1766) (Wronski et al. 2006). However, in other species, only territorial males are reported to create and maintain dung-piles in order to demarcate territory ownership whereas the rest of the sex and age categories often produce single fecal pellet groups (Walther et al. 1983, Estes 1991, Ezenwa 2008).

Guanacos (*Lama guanicoe*, Müller 1776) and vicuñas (*Vicugna vicugna*, Molina 1782) are the two species of wild camelids that inhabit the South American arid lands. Both species have been reported to conduct localized defecation, forming conspicuous dung-piles (Franklin 1983). Guanaco social organization is arranged into territorial family groups and large non-territorial bachelor or mixed groups and solo males (Franklin 1983). Family groups are composed of an adult male that defends a territory and one or more females with their yearly offspring called chulengos. Females usually remain with the male in the same territory all year round in sedentary populations and at least seasonally in migratory ones. Since Franklin's seminal studies on guanaco ecology and behavior (Franklin 1982, 1983) it has been accepted that dung-piles are only used frequently by guanaco males and rarely by females, and that the main function of this behavior is related to males' territorial displays. As guanacos have a wide distribution range across contrasting ecological conditions and show great plasticity in various behavioral aspects (Franklin 1983, Puig and Videla 1995, Marino 2010), between-population variation in defecation patterns can be expected. The aim of this analysis was to compare dung-pile use by territorial males with females and young in family groups, and with bachelor males, within two guanaco populations located in eastern Patagonia. If dung-pile use is only related to the males' territorial displays, only territorial males should use them frequently, as previously reported.

Data on dung-pile use was recorded during sampling surveys oriented to a behavioral and parasitological study in two wildlife reserves located on the Eastern coast of Patagonia, Argentina: Reserva Provincial Cabo Dos Bahías (C2B) and Monte León National Park (ML) (see Marino 2010 for study area and general methodology description). Focal observations were conducted by three observers, during January and March 2008 at ML, and by one observer at C2B during December 2007 and April, August and October 2008. We observed guanacos in family and bachelor groups. Each time a defecating individual was observed, sex and age category and group type were recorded, as well as whether feces were or were not dropped in a pile. Piles were clearly distinguished because old feces became progressively dry and light gray whereas fresh feces are dark brown and wet. Generally, piles are 1–2 m in diameter and appear as large, circular dung accumulations, darker in the middle and progressively lighter to the periphery. As fecal samples were collected, whether feces were dropped in a pile or as single pellets was assessed *in situ*. A total of 160 defecating individuals

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Table 1: Comparisons of the proportion of defecating events in which feces were dropped in piles out of the total defecating events, among social categories, seasons and sites.

	Estimate	Standard error	z-Value	Pr(>|z|)
Constant (territorial males, non-reproductive season at C2B)	2.31	0.61	3.80	0.000
Differences				
Females and young in family groups	−0.86	0.62	−1.40	0.162
Bachelor males	−1.37	0.68	−2.02	0.044
Reproductive season	0.88	0.47	1.87	0.061
Site ML	−0.67	0.46	−1.46	0.144

Parameters are expressed as differences between the reference level (territorial males, non-reproductive season, at C2B) and the corresponding level. Residual deviance: 7.501 on 7 degrees of freedom.

were observed and they were classified according to age class as adults or young (i.e. individuals younger than 2 years, either juveniles or chulengos). Observations were conducted during the reproductive season, when mating and births occur (October–January), and after the peak of reproductive activity (March–August). To compare dung-pile use among social categories, the proportion of defecating events in which feces were dropped in piles out of the total defecating events observed in each category (territorial males, females and young pooled as only one class, and bachelors) was calculated. Occasionally, several guanacos in a group were observed using the same dung-pile but only one defecating event per group was considered in order to minimize data dependence. These proportions were computed for each season within each site, obtaining a set of 12 values for the response variable "proportion of individuals using dung-piles" in each category.

A generalized linear model with binomial error and logit link was fit to the proportion data. Social category, with three levels (territorial males, females and young in family groups, and bachelors); season, with two levels (reproductive and non-reproductive); and site (ML and C2B), were the factors included in the model. Chi-square tests were used to test if differences between factor levels were statistically significant with an alpha level of 0.05 (Crawley 2007). Model fitting was performed using R 2.9.2 (The R Foundation for Statistical Computing) software.

On average, territorial males defecated in piles 90% of the time and the difference between seasons in the use of dung-piles was not statistically significant (Table 1, Figure 1). Females and young in family groups also used dung piles frequently (average 80% of the defecating events, Figure 1) and there were no significant differences in dung-pile use with territorial males (Table 1). Finally, territorial males used piles more often than the non-territorial bachelors but this difference was only marginally significant (Table 1). These non-territorial males dropped

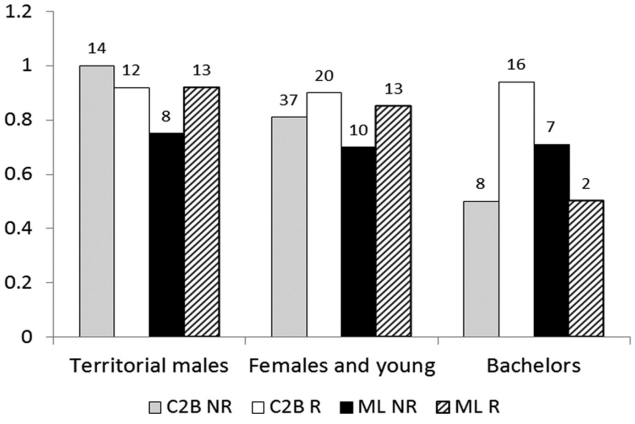

Figure 1: Proportion of defecating events in which feces were dropped in piles out of the total defecating events observed in each social category, site (C2B and ML) and season: reproductive season (R) and non-reproductive season (NR).
Sample sizes are shown above corresponding bars.

feces in piles on average 70% of the time (Figure 1), in contrast to the previously reported almost exclusive use by territorial males (Franklin 1983). The differences between guanaco defecation patterns observed in this study and those previously observed in Torres del Paine and Tierra del Fuego emphasize guanaco behavioral plasticity and raise questions about the adaptive function of localized defecation. Dung-pile use cannot be considered only as a territorial display to demarcate territory ownership because females and young do not participate in territorial defense but show a high frequency of dung-pile use in the populations studied here. It has been reported that, in contrast to guanacos, vicuñas of all age classes and both sexes defecated only in piles, this species being one of the few ungulates that always use traditional piles for defecation and urination (Franklin 1983, Vilá 1994). In the vicuña case, the authors suggested that dung-piles may not only be related to male territorial displays but also may serve to

keep group members within the territory, serving as reference points to all social categories, helping to organize the spatial distribution of individuals without incurring excessive agonistic interactions (Franklin 1983, Vilá 1994). This idea is consistent with the observation that dung-piles do not keep outsiders out in the absence of the territorial male and his group (Franklin 1983). This process might be operating in the guanaco populations studied here, in which other behavioral aspects, such as a more rigid social structure, higher group cohesion and aggressiveness by territorial males towards group members (Marino 2011), and year-round territoriality (Burgi 2005, Marino et al. 2014), are more similar to those reported in vicuña studies than to the descriptions of migratory guanaco populations of Torres del Paine, and may explain the more frequent use of piles by all social categories. In migratory populations, all group members or some of them leave the territory after the reproductive season and join large mixed groups were all social and age classes congregate, social organization is less rigid and females often can join and leave the groups freely (Franklin 1983). In contrast, territorial males in sedentary populations may attack or chase females willing to leave or outsiders willing to enter into the territory (Marino 2012). Thus, in sedentary populations dung-piles could be important reference points for all social categories, including subordinate individuals, to minimize aggressive interactions. Presumably, the quantity of feces required for the maintenance of the numerous piles in a territory may exceed the deposition capability of the territorial male and the use of piles by all group members could help to produce enough fecal biomass to sustain this system. In this regard, Franklin (1983) stated that because only adult males used dung-piles in the migratory population of Torres del Paine, dung-piles were smaller and less abundant than those observed in vicuña studies. It is worth mentioning that guanacos at ML used piles on average a 10% less than in C2B. Although this difference was not statistically significant (Table 1) it was consistent across social categories. Previous studies on density and social structure have shown that a fraction of the ML population show migratory movements in certain years, in contrast to C2B which seems to be completely sedentary every year (Marino 2011). This difference may suggest some correlation between dung-pile use and the level of sedentarism of the population. However, further between-population comparisons are required to address this issue.

In addition to their scent-marking role, other factors have been considered to explore the adaptive significance of dung-pile formation by large herbivores. Permanent defecation sites have been suggested to result from an anti-parasitic behavior because they may serve to sequester fecal-oral transmitted parasites by selective clustering feces in a given space, allowing subsequent avoidance during foraging (Taylor 1954). This process is likely to benefit all group members resulting in an adaptive advantage beyond territorial displays, and might explain the occurrence of localized defecation in other social categories than territorial males. However, there is some evidence among African *Bovidae* suggesting that dung-piles would actually increase infection risk (Ezenwa 2008). Some fecal-oral transmitted parasites might be significant stressing factors for wild guanaco populations (Beldomenico et al. 2003) but the consequences of dung-pile formation in terms of parasite transmission among the South American camelids are also little known. If dung avoidance while grazing results from an anti-parasitic behavior, dung-piling would be advantageous due to the maximization of the feeding area within the territories, and this effect could be enhanced by selecting particular poor patches to do so (Victoria Rodríguez, pers.com). Also, there are some reports on the effects of dung-pilling behavior on the surrounding habitat, resulting in greater soil depth, plant-species diversity, and increased forage production due to the localized input of organic matter and nutrients. This pattern was particularly striking in vicuña studies in which the fertilizing effects of nutrient downhill washing by precipitation caused densely vegetated strips or belts around dung-piles (Franklin 1983). These vegetation patches underwent various successional stages and topsoil depth increased by 2 cm with each succeeding stage (Franklin 1983). Other studies suggest that guanaco dung-piles offer favorable sites for seedling establishment and their role as seed sources could accelerate the process of colonization (Henriquez 2004). These belts of un-grazed vigorous plants surrounding dung-piles are frequently observed in populations of sedentary guanacos and suggest that dung-avoidance while grazing, combined with the localized input of organic matter and nutrients, may have relevant consequences for vegetation and soil dynamics. A positive impact on vegetation by localized defecation has been reported for other herbivore species (Putman et al. 1991, Zalba and Loydi 2014). In the current desertification context, the potential adaptive significance of this herbivore-vegetation feedback across the arid and semi-arid environments where the South American camelids have evolved deserves particular attention. Future studies accounting for between-population variability in defecating patterns, parasite loads, and effects on vegetation and soil will allow testing these hypotheses.

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