Territorial fidelity and behavior of male guanacos in the Patagonia of southern Chile

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Territorial fidelity and behavior of male guanacos in the Patagonia of southern Chile

by

Julie Kirsten Young

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Animal Ecology

Major Professor: William L. Franklin

Iowa State University

Ames, Iowa

2000

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Graduate College
Iowa State University

This is to certify that the Master's thesis of

Julie Kirsten Young

has met the thesis requirements of Iowa State University

Signatures have been redacted for privacy
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GENERAL INTRODUCTION

An increasing number of studies have focused on territorial behavior and movement of ungulates within the past few decades. Studies have ranged from general observations (Jarman 1974; Walther et al. 1983) to manipulative procedures (Carranza 1995). Few studies, however, used long-term data for analyses. This study examined territorial fidelity and behavior of an ungulate species, guanacos (Lama guanicoe), using both short- and long-term data sets.

Resource-defense polygyny is a commonly practiced territorial behavior, wherein males compete for access to resources required by females (Emlen and Oring 1977). Resource-defense systems occur in some species of ungulates (Koford 1957; Balmford et al. 1992; Carranza 1995). Some male ungulates establish territories based on the resources required by females, establishing either a year-round or seasonal territory (Estes 1991). Males that establish seasonal territories typically join mixed herds or male groups during the non-reproductive season (Emlen and Oring 1977). Little is known about the relationship between birth location, natal dispersal, adult movement patterns, and territoriality for ungulates that do not defend a territory year-round.

Most behavioral studies of male ungulates have focused on the rutting or reproductive periods (David 1978; Maher 1991). Many external factors could also influence behavioral patterns of polygynous, territorial male ungulates throughout the territorial season. Males have varying activity budgets based on predator protection, foraging, and reproductive needs. This variation in behaviors can help a male attract mates, secure a territory location, reduce predation risks, and increase foraging efficiency (Jarman 1974; Lipetz and Beckoff 1982; Walther et al. 1983; Goldsmith 1990).
Guanacos exhibit seasonal resource-defense polygyny (Franklin 1983). Territories are established during the austral spring (October) in preparation for the summer’s birthing and mating seasons. During the territorial season, reproductive-aged males are found as one of three social group type members: Family Group Territorial Males, Solo Territorial Males, and Male Groups (Franklin 1982; Ortega and Franklin 1995). Solo Territorial Males defend an established territory on which other guanacos are rarely present. Family Group Territorial Males defend an established territory; on which reproductive-aged females and some non-reproductive yearlings and chulengos (< 1 year old) occur. Male Groups consist of non-territorial males, including yearlings recently evicted from Family Groups, immature males, and old or injured males. In late fall (April/May), at the end of the territorial season, most males join females and young in mixed herds and migrate to their winter range (Bank 1997; Ortega and Franklin 1995; Franklin 1983).

The goal of this research was to study site-fidelity of territorial male guanacos and behaviors related to territoriality. The specific objectives were to determine: 1) territorial male use of area during the mating and non-mating territorial period within a given territorial season; 2) site specificity of territorial males from year to year; 3) territorial longevity; 4) differences in behaviors of territorial males based on social group type; and 5) other factors that influence behavioral patterns of territorial males.

Fieldwork

Data was collected between 1990 and 1999 for this study, with intensive work between 1997 and 1999. Previous assistants and graduate students collected data between 1990 and 1997 that was used in part for this project. In 1997, I conducted preliminary work to
fine-tune the methodology for the specific objectives. Three field assistants began working on this project in 1997 and I carried out fieldwork between August 1998 and June 1999. Field assistants also helped collect data during that period.

Thesis Organization

This thesis is organized into four chapters. The second and third chapters will be submitted to journals. The second chapter deals with the first three objectives, which are related to territorial fidelity of male guanacos. This paper will be submitted to the Journal of Mammalogy. The remaining two objectives regarding territorial guanaco behavior are presented in the third chapter. This chapter will be submitted to Acta Theriologica. The first and last chapters provide an overview of the material included within the two papers and the relevant literature.

References


TERRITORIAL FIDELITY OF MALE GUANACOS
IN THE PATAGONIA OF SOUTHERN CHILE

For submission to the Journal of Mammalogy

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ABSTRACT. --We investigated site-fidelity of territorial male guanacos (Lama guanicoe) in Torres del Paine National Park, Chile. The study took place over a 10-year period, with intensive work in the final years, 1997-1999. Guanacos have a social system of resource-defense polygyny with fluid movement of females between male territories. After the annual winter migration, males establish and maintain their territories from mid-spring until late fall. Territorial males can be classified as Solo Territorial Males and Family Group Territorial Males. We collected data on the type, location, size, and usage of territories for tagged, known-age males. We compared male territory fidelity between multiple years and between the mating (8 December - 11 January) and non-mating periods within the six-month territorial season each year (1 October - 15 March). Males used the same area within the 1997 and 1998 territorial seasons (n = 47). Most males (73%, n = 60) also returned to the same territory location from year to year. Males (27%) that shifted territorial locations showed no clear patterns in changes between Solo Territorial Male and Family Group Territorial Male.
High predictability of male territory sites within a given year and between years has short- and long-term benefits for management and conservation efforts.

Resource-defense polygyny is a territorial behavior, wherein males compete for access to resources required by females. Within this system, the number of females a male will attract is related to the quantity and quality of resources in his territory (Alcock, 1987; Emlen and Oring, 1977). While this social system is common and has been well studied in birds and insects (Alcock, 1987; Cristol, 1995; Dodson, 1997; Greenwood, 1980; Halliday, 1983; Lindstrom, 1996), resource-defense systems are still being discovered and studied in ungulates (Balmford et al., 1992; Carranza, 1995). Some ungulate species, such as wildebeest, (*Connochaetes taurinus*; Estes, 1969; Sinclair and Arcese, 1995), topi (*Damaliscus lunatus*, Vesey-Fitzgerald, 1955), springbok (*Antidorcas marsupialis*; Estes, 1991), and some pronghorn populations (*Antilocapra americana*; Byers, 1997; Kitchen, 1974), establish seasonal territories. In many of these species, adult males join mixed herds or male groups during the non-territorial, non-reproductive season.

When adult male ungulates hold territories, young males are often forced to leave the territorial areas before they reach reproductive age (Franklin, 1983; Walther et al., 1983). These expelled males disperse and join other family groups, remain solo, or join male herds. Although site fidelity exists in ungulates (Dubois et al., 1996; Greenwood, 1980), little is known about the relationship between site fidelity and seasonal territoriality.

Guanacos (*Lama guanicoe*) exhibit seasonal resource-defense polygyny (Franklin, 1983). Males establish territories during the austral spring (October) in preparation for the summer birthing and mating seasons. During the territorial season (1 October - 15 March), males are
typically found in one of three social group types (Franklin, 1982; Ortega and Franklin, 1995). Solo Territorial Males have an established territory with other guanacos rarely present. Family Groups consist of a territorial male, adult females, some yearlings (one to two years old), and chulengos (young <1 year old). There is no indication that females and their offspring are related to the territorial male. Male Groups consist of non-territorial males, including yearlings recently evicted from Family Groups, immature males, and old or injured males. Male Groups are found in distinct Male Group Zones, which include almost 20% of the entire summer range (Bank, 1997; Franklin, 1983). Family Group Territorial Males are typically the only males that mate (Franklin, 1982, 1983). There are no clear landscape patterns for Solo Territorial Male and Family Group Territorial Male locations as both are dispersed throughout the summer range (Fritz, 1985). Solo Territorial Males may have brief time periods with females present after the mating period ends (Jurgensen, 1985; Lawrence, 1990). In late fall (April/May), nearly all of the males in the population join females and young in mixed herds and migrate to their winter range (Fig. 1; bank, 1997; Franklin, 1983; Ortega and Franklin, 1995).

Each spring, males migrate 12-km from the wintering grounds back to the region containing territories (Ortega and Franklin, 1995). It is unclear if males establish territories in the same location they defended in previous years or in new areas, although preliminary work suggested that some males returned to the same territory location (Fritz, 1985). Only a few studies have shown examples of male ungulates returning to previously used mating sites after leaving the area through migration, dispersal, or territorial eviction by other males (Greenwood, 1980; Jarman, 1974; Skinner, 1994).
Although Family Group Territorial Males could benefit reproductively from returning to the same territory locations, it would seem unlikely that Solo Territorial Males would benefit from using the same strategy. It should be expected that Solo Territorial Males would change territorial locations completely or shift territorial boundaries in an effort to control part of a neighboring Family Group Territorial Male's territory in order to attract females. It has been shown in yellow-bellied marmots (Marmota flaviventris; Armitage, 1986) that solo males will shift to neighboring locations to defend an area that includes females.

The goal of this research was to study site fidelity of territorial male guanacos. Our specific objectives were to determine: 1) the areas used during the mating and non-mating period by territorial males; 2) territorial tenure and average territory size; and 3) male fidelity for the same territorial sites between years and its causes.

METHODS

Our study was conducted in Torres del Paine National Park (51° 3' S, 72° 55' W), an International Man and Biosphere Reserve in the Patagonia region of southern Chile. We used a 6,000-ha study site known as the Peninsula within the 240,000-ha park. The Peninsula was bordered by three lakes: Sarmiento on the south, Pehoe on the west, and Nordenskjöld on the north and west, and by the Goic sheep ranch on the east (Fig. 1). Dominant vegetation on the site included steppe grasses and shrubs (Pisano 1974). Distributed throughout the study site were grassy, marsh-like meadows called "vegas", the guanacos' preferred habitat (Lawrence, 1990; Ortega and Franklin, 1988; Pisano, 1974).
observing guanacos. Guanacos in this area were easily observed at close range without disturbance because of their habituation to humans (Franklin and Johnson, 1994).

Approximately 100 chulengos were hand-captured and tagged each year between 1987 and 1997 (Franklin and Johnson, 1994), enabling the identification of marked, known-age individuals. We collected data on location, group size and composition, and dominant habitat type for all tagged individuals between 1990 and 1999, two to six times per week on a year-round basis. From 1997-1999 we intensively focused on male territoriality and collected data five to six times per week during the territorial seasons. Over 5700 hours of observation were logged by three observers during the territorial seasons from 1997 to 1999. Tagged guanacos were observed by hiking three standardized transects that covered the Peninsula, enabling us to search the entire summer range during each field day. Solo Territorial Males and Family Group Territorial Males were found dispersed throughout most of the summer range.

In addition, we collected data on the overall composition of the guanaco population (tagged and untagged animals) by conducting population surveys in the summers of 1997 and 1998. Three to four observers hiked the entire Peninsula and Goic ranch in a single day and repeated the process the following day. The average number of guanacos observed between the two days was calculated for overall population size and social group composition.

The territorial mating period was from 8 December to 11 January when a combined average for the 1997 and 1998 territorial seasons included 91% of all observed copulations (n = 88; Fig. 2). The remaining copulations were observed from 12 January to 16 February (4%) or before 8 December (5%). The non-mating territorial period was, therefore, from 1 October to 7 December and 12 January to 15 March.
Territorial seasons (hereafter referred to by their starting year) were divided into mating and non-mating periods for 1997-1998 and 1998-1999. Coordinates for the mating versus non-mating periods were analyzed by Multiple Response Permutation Procedure (MRPP) for each territorial male guanaco. This test would establish any differences in territorial space used by individual male guanacos between the mating and non-mating period (Mielke et al., 1976; Van Dyke et al., 1998). Male territory locations within 1997 and 1998 were also compared with one another by MRPP to determine if known territory locations were spatially discrete.

Territorial tenure was determined by identifying all years that individual males held a territory between 1994 and 1998. This 5-year time period was used to avoid excluding males that established a territory in our final year of study, as it is likely that some of these males would continue to defend territories in 1999. Average territory size was determined for the 1998 season. Territory size was defined as the 95% minimum convex polygon for territorial males observed ≥10 times during the territorial season (Kitchen, 1974; White and Garrott, 1990).

For male guanacos that held a territory for ≥2 years (n = 95), we calculated harmonic center of activity coordinates in each territorial year (Hayne, 1949; Smith et al., 1973). Each male's harmonic centers of activity were then used to determine if territorial males held a spatially discrete territorial location over time by MRPP.

Male guanacos that held a territory for ≥2 consecutive years were further analyzed (n = 60). All observed x- y-coordinates within a given territorial season were used to examine a male's territorial location. MRPP compared territorial locations of individual males between years, to determine if males returned to the same territorial location in consecutive years.
The level of significance was set at 0.001 through a Bonferroni adjustment for independent tests. We also calculated the average linear distance between territorial centers of activity for each territorial male in all subsequent years.

Dominant social group type for each male was defined as the type most commonly observed during the mating period (Solo Territorial Male or Family Group Territorial Male ≥75% of observations) in each territorial year. Over the 10 years of observations, territorial male guanacos were classified as (1) having not changed social group type; (2) changed one time; (3) changed two times; or (4) only observed within the territorial season, but only outside of the mating period (unknown). We compared the social group type classifications and any linear distances moved between territorial centers of activity by ANOVA (SAS, 1990). We also compared the age that males first established a territory and subsequent linear distances between centers of activity by ANOVA (SAS, 1990).

We analyzed birth weight and territorial patterns of individual adult males. Logistic regressions were used to compare a male's original birth weight and the age it first established a territory and if it was initially a Solo Territorial Male or Family Group Territorial Male. Logistic regression was also used to compare the age that males first established a territory and if they were initially Solo Territorial Males or Family Group Territorial Males (SAS, 1990).

RESULTS

Between 1990 and 1999, 150-tagged male guanacos were observed as Family Group Territorial Males or Solo Territorial Males. During the intensive study period from 1997 to 1999, the average number of Solo Territorial Males (28%) and Family Group Territorial
Males (22%) observed during population surveys were relatively equal, although most males were found in Male Groups (56%; Table 1). Numbers of tagged Solo Territorial Males and Family Group Territorial Males were roughly equal to the proportion seen during the population surveys.

Individual males used the same area within a given territorial year. There was no significant difference in location between the mating and non-mating territorial periods (P > 0.001, 45 of 47 males; Fig. 3). Male territory locations were spatially discrete in 1997 (P < 0.001, n = 42) and 1998 (P < 0.001, n = 41). Individual male territorial locations were constant and did not overlap within a given territorial season.

Between 1994 and 1998, males held a territory an average of 2.3 years (± 0.02 SE, n = 117). Most males held a territory for only one year (42%), although some males held territories for two (26%), three (27%), four (11%), or five (11%) years. Within our 10-year study, we observed males defending territories for up to eight years. The average territory size in 1998 was 24.9 ha (± 1.6 SE, n = 28) and the median was 13.2 ha. The median represented a normal territory size because the range was quite large (1.8 - 86.3 ha).

Male territory locations were spatially discrete over the 10-year study period (P < 0.001, n = 95). Most males returned to the same territory location between years (73%, P > 0.001, n = 60). Male guanacos with a significant difference in territory location between years (27%, P < 0.001, n = 60) still showed tremendous overlap in territory sites between years (Fig. 4). Over 80% of the males established territories within 1 km of previously held territories (Fig. 5). Within two consecutive years, males adjusted territorial centers of activity an average of 0.66 km (± 0.15 SE, n = 135).
Male guanacos that were initially Family Group Territorial Males established territories at the same locations in consecutive years. Males observed with a significantly different territory location between years were initially Solo Territorial Males or unknown (P ≤ 0.001, 16 of 60 males; Table 2). There was a significant difference between Solo Territorial Males and Family Group Territorial Males in the distance between territorial centers of activity in two consecutive years (F_{1,59} = 2.25, P < 0.05, n = 129). Family Group Territorial Males shifted territorial center of activity coordinates by a least square mean of 0.56 km, while Solo Territorial Males shifted locations by a least square mean of 0.74 km.

Between years, we found most male guanacos in the same social group type (Solo Territorial Male or Family Group Territorial Male). Most males did not change between Family Group Territorial Males and Solo Territorial Males between territorial years (57%, n = 60), although some males changed social group type one (38%) or two (5%) times. Only seven of the 26 males (27%) that were originally Solo territorial Males or unknown became Family Group Territorial Males (Table 2). While 21 males were Family Group Territorial Males after leaving Male Groups, only seven males were ever Family Group Territorial Males after being a Solo Territorial Male (Table 2).

There was a significant difference in the distance between territorial centers of activity by year (F_{7,127} = 8.06, P < 0.05, n = 135). Male guanacos that established territories in 1990 and again in 1991 shifted territorial center of activities the most (Fig.6). Males also differed in the distance between territorial center of activities and the age that first territories were established (F_{4,51} = 14.04, P < 0.05, n = 97). Males that first established a territory at three years old (1.9 km, n = 10) shifted territorial center of activities significantly more than males that were four (0.56 km, P < 0.05, n = 14) or six years old (0.8 km, P < 0.05, n = 26).
Initial social group type was not related to the age that a male first established a territory ($r^2 = 0.05, P > 0.05, n = 38$) and there was also no relationship between the age that a male first established a territory and birth weight ($r^2 = 0.001, P > 0.05, n = 35$). Similarly, there was no relationship between territorial social group type and birth weight ($r^2 = 0.009, P > 0.05, n = 37$).

**DISCUSSION**

In 1997 and 1998, an equal number of males established Solo Male and Family Group territories. Most males, however, never established a territory but remained in Male Groups within a given territorial season. The tagged population surveys resulted in a similar distribution of males.

**Territorial Size and Tenure**

The median territory size (13.2 ha) was almost two times larger than the 7.2-ha average territory size observed by Jurgensen (1985) when the total population was smaller. The increase in population size that occurred until mid-1990, forced guanacos to either remain at a higher density within the park or roam outside of the park and compete with sheep and other domestic animals for forage (Franklin et al., 1997). At the beginning of the 1998 territorial season, guanacos began moving out of the Peninsula and into the northwestern region of the park, Laguna Azul. Since males were observed with larger territory sizes when the Peninsula population was decreasing, it is likely that male guanacos trying to establish a first territory in 1998 were part of the population that moved to Laguna Azul.

Some males continued to hold territories for up to eight years. It is evident that male guanacos will attempt to establish and hold territories for as long as possible, even though
most males (78%) will only establish a territory for three years or less. Most males stopped establishing territories because they either died or returned to Male Groups primarily due to old age or injuries (Bank, 1997).

**Territorial Fidelity**

We found that males had high site fidelity within a territorial season. This location remains constant prior to, during and after the mating period. Along with a constant territorial location, males established territories that were spatially discrete from other territorial male guanacos.

Most male guanacos also displayed high territorial-fidelity from year to year. After each winter migration, 73% of the territorial males returned to the same location to re-establish territories. There was spatial overlap in territory sites by all territorial males, including those territorial male guanacos that held territories in significantly different locations between years (27%). High site-fidelity was accompanied by distinct spatial separation of individual territorial male sites. Most males returned to familiar, well-established locations.

While the high potential for repeated reproductive success should be an obvious factor influencing Family Group Territorial Males to remain at the same territorial location, it is unclear why over 60% of the Solo Territorial Males that extremely rarely would have an opportunity to mate returned to the same territory site annually. Although over 40% of the male guanaco population established territories each year, only a small number of these males contributed to the breeding population. This suggests that a male's drive to establish a territory is stronger than the drive to remain in a Male Group for added predator protection (Bank, 1997). It would appear that selective pressures cause males to continue establishing
territories, similar to Thomson’s (*Gazella thomsonii*) and Grant’s gazelles (*Gazella granti*) that hold territories regardless of female availability (Walther et al., 1983).

Comparable to female topi (Balmford et al., 1992), female guanacos move freely between male territories, especially in the post-mating period (Jurgensen, 1985). Even though Family Group Territorial Males encounter the most mating opportunities, it is possible that Solo Territorial Males have a small chance to copulate in the post-mating season with the few females that reach their reproductive readiness late. Solo Territorial Males would benefit from returning to a familiar location that might allow late season access to females.

We had expected Solo Territorial Males would shift territory sites to establish territories within neighboring Family Group Territorial Male locations. After one or more years, over half of the male yellow-bellied marmots that held territories that bordered territories with female colonies were successful in shifting their territorial boundaries to contain these colonies (Armitage, 1986). Male guanacos that were initially Family Group Territorial Males returned to the same territory location in the following years, whereas 30% of the males that were initially Solo Territorial Males showed a significant change in territorial locations in the following years. Unlike yellow-bellied marmots, less than half of the males that changed territorial locations gained mating opportunities as Family Group Territorial Males (Table 2). This uncertainty in future reproductive success, coupled with the disadvantages associated with establishing a territory in an unfamiliar location, could result in males returning to the same territorial location.

Familiarity to an area could play a key role in site-fidelity of territorial male guanacos. Site-fidelity in elk (*Cervus elaphus*) herds is related to the benefits provided by previous knowledge of the area (Edge and Marcum, 1985; Edge et al., 1985). In guanacos, habitat
familiarity, neighboring territorial males, and female movement patterns could have a strong influence on male guanacos, as evidenced by more than 80% of the territorial males that establish a territory within 1-km of its previous territory.

We found that the age a male first established a territory was a good predictor of the distance between centers of activity in two consecutive territorial years. Older males held more localized territories between years, while males that first established a territory when three years old shifted their territorial center of activity more. The age a male first established a territory did not determine if it was a Solo Territorial Male or Family Group Territorial Male.

CONCLUSIONS

We found that most territorial male guanacos in Torres del Paine National Park returned to the same territorial location between years. High territorial-fidelity of migratory ungulates has rarely been reported in the literature (Greenwood, 1980; Skinner, 1994). Studies on ungulates with high site-fidelity can help our understanding of the evolutionary and ecological consequences of a resource-defense mating strategy. It is likely that a multitude of factors affect an individual's ability to obtain mating opportunities as evidenced by the high site fidelity of both mating and non-mating guanacos.

ACKNOWLEDGEMENTS

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Wlodarski, and M. Dougherty provided field assistance. P. Dixon, D. Nordman, and K. Jovaag provided statistical assistance. We thank B. Bowen and C. Vleck for reviewing earlier drafts of the manuscript. Patagonia Research Expeditions (through Hidden Corners) and the University of Connecticut supported this study.

LITERATURE CITED


Table 1. Percent of male guanacos found in each social group type during the 1997 and 1998 territorial seasons from the tagged and entire male population within the Peninsula of Torres del Paine National Park.

<table>
<thead>
<tr>
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<td>20</td>
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<td>Male Group</td>
<td>58</td>
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<td>54</td>
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</table>
Table 2. Total number of Solo Territorial Males (STM), Family Group Territorial Males (FGTM), and unknown (UNK) found in each social group type from 1990 to 1999. Male guanacos that were observed within the territorial season but not during the mating period were classified as unknown. Original social group type for all territorial males are given (n).

<table>
<thead>
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<tr>
<td></td>
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<tr>
<td>STM (n = 36)</td>
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</tr>
<tr>
<td>UNK (n = 3)</td>
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</tr>
</tbody>
</table>

* One male returned to STM status
** Two males returned to STM status
Figure 1. The main region used by guanacos in the 6,000 ha Peninsula at Torres del Paine National Park, Chile. Nearly all summer male territories and Male Groups were located within the 4,000 ha eastern region from mid-spring until late fall.
Figure 2. Guanaco copulations observed during the 1997 and 1998 mating seasons (n = 88) from 1 December to 18 January.
Figure 3. Coordinates for Solo Territorial Male (# 283) seen 35 times from 1 October to 10 March during the 1998 territorial season. A local x-y-coordinate system (80 m per coordinate) was used to determine the male's movement during the breeding (8 December - 11 January) and non-breeding (1 October - 15 March, excluding breeding dates) periods.
Figure 4. Home-range of two territorial male guanacos (093 and 873) over a five year period. Male 093 significantly differed in territorial location between years, while male 873 returned to the same location. Each x-y-coordinate is 80 meters.
Figure 5. Frequency distribution of distances between territorial centers of activity in two consecutive years for tagged territorial males. Over 82% of the distances were less than one kilometer (n = 112 for 60 males).
Figure 6. Average linear distance between centers of activity for males that held a territory in two consecutive years, between 1990 and 1999. Males adjusted territorial center of activity locations the most between 1990 and 1991. The number of males observed for each two-year period is in parenthesis and the second year is noted for the x-axis.
ACTIVITY BUDGET PATTERNS IN MATING AND NON-MATING TERRITORIAL MALE GUANACOS

For submission to Acta Theriologica

JULIE K. YOUNG AND WILLIAM L. FRANKLIN

ABSTRACT

Behavioral patterns of territorial male guanacos (*Lama guanicoe*) were recorded in Torres del Paine National Park, Chile. Both Solo Territorial Males and Family Group Territorial Males were observed to compare the activity time budgets of males (n = 27) in differing social groups and habitats. We found no difference in the activity time budgets of males based on social group type, total number of females present, total guanacos present, or age of the territorial males. There was a difference in time spent alert (to other guanacos and vigilant) and in other (defecation, alertness to observer, and scratching) activities based on habitat type. It is likely that territorial male guanaco behaviors are related to the resources defended rather than any direct ability to attract potential mates.
INTRODUCTION

Behavioral patterns of polygynous, territorial male ungulates can be influenced by external factors. Predator avoidance, foraging, and reproductive needs may influence male activity budgets. This variation in behavior can help a male attract mates, secure a territory location, reduce predation risks, and increase foraging efficiency (Goldsmith 1990; Walther et al. 1983; Lipetz and Beckoff 1982; Jarman 1974).

While some territorial ungulate males budget a large proportion of time to attract mates (Estes 1991), others rely on resource-defense (Emlen and Oring 1977). Territorial male guanacos (*Lama guanicoe*) in Torres del Paine National Park, Chile, defend resources to attract mates through resource-defense polygyny (Franklin 1983; 1982). From spring through late fall, reproductive-aged males are found in one of three social group types: Family Group Territorial Males, Solo Territorial Males, and Male Groups (Ortega and Franklin 1995; Franklin 1983). Family Group Territorial Males establish a territory, which is occupied by reproductive-aged females, yearlings and chulengos (< 1 year old) present. Females, yearlings, and chulengos present are rarely related to the territorial males. Solo Territorial Males have an established territory with females and young rarely present. The remaining non-territorial males are found in Male Groups (Ortega and Franklin 1995; Franklin 1983; 1982).

Those males that mate are almost always found in Family Groups. Only under rare circumstances do males that are Solo Territorial Males or in Male Groups have an opportunity to mate (Jurgensen 1985). The lack of mating opportunities, combined with the lack of other guanacos present, suggests that Solo Territorial Males should behave differently than Family Group Territorial Males.
We observed territorial male guanacos to examine potential differences between activity time budgets of Solo Territorial Males and Family Group Territorial Males. Our main objectives were to determine if there were differences in the activity budgets of territorial males based on social group type and to identify other factors that influence behavioral patterns of territorial males.

METHODS

We collected data on previously tagged, known-age territorial male guanacos in Torres del Paine National Park, Chile (Franklin and Johnson 1994). The park is home to one of the largest wild populations in existence (Torres 1992; 1985). These guanacos are habituated to humans, which made observing natural behaviors at close range possible. Observations were conducted by three field researchers during the territorial season (October 1998 – March 1999) between the hours of 0930 and 1600. Males were selected at random and observed for two, 15-minute focal samples (Altmann 1974). The observer took a five-minute break between each focal sample. Focal samples were treated as independent samples so that a total of 27 males were observed during 120 focal samples. Although most males were only observed on one day (12), through random selection of territorial males for observation some males were observed on two (6), three (2), four (4), five (1), or seven (2) separate days. We collected focal sample data for a total of 30 hours of observation. Data collected included territory location, initial and final group type, group composition, female and chulengo activity (when present), initial and final habitat type, time of day, and timed behavioral observations.
Behaviors were divided into seven major categories: resting (all inactive periods not associated with a second behavior except regurgitation), bathing (any dust bath or self-grooming), eating (feeding bouts), alert (all scanning of surroundings or staring at other animals/objects in the area), aggression (all aggressive behavior towards other guanacos), moving (walking or running), and other. Multiple behaviors were recorded if observed at the same time, but the foremost behavior was used for timing. We encountered other behaviors that had to be dealt with when males were first observed. Alert behavior towards the observer was not categorized as alert but as other. During aggression periods, the sex of other guanacos involved was recorded. Moving did not include any walking or running that was associated with a second behavior (e.g. if a male was walking towards another guanaco aggressively, then the behavior was categorized as aggression). Other activities included such behaviors as scratching, non-aggressive defecation, and alertness to the observer.

Habitat types were categorized based on dominant vegetation and slope. Vegetation types included Calafate (*Berberis buxifolia*), Mata Negra (*Senecio patagonicus*), Mata Barrossa (*Mulinum spinosum*), Coiron (*Festuca gracillana*), and meadow-like "vegas" (dominated by *Holcus lanatus* and *Hordeum comosum*; Lawrence 1990; Ortega and Franklin 1988; Pisano 1974). Slopes were categorized as hilltop, hillside, or flat.

Data was analyzed using analyses of variance (ANOVA) with Bonferroni adjustments for multiple tests (SAS 1990). Some males were observed multiple times, so we nested the behavioral effects by individual males. However, to test the effects of habitat type, each focal sample was treated as an individual sample for analyses because each male had multiple habitats within the territory in which it could be located.
We looked at the effect of social territory type (Solo Territorial Males versus Family Group Territorial Males) and the proportion of time spent per activity by ANOVA. We further categorized males into one of three classes based on number of reproductive-aged females present. Only behavioral observation periods during which the number of females present remained constant were used in the analysis. Males were observed with an average of 1.6 (4.4 SD) reproductive-aged females present. Male observations were classified as: (1) Solo Territorial Males with no females present; (2) Family Group Territorial Males with 1-6 females present; or (3) Family Group Territorial Males with ≥7 females present.

When females were present, their activity was recorded but not timed. For those observations with females present, we calculated the percentage of observations when each specific activity was recorded.

Territorial male activity budgets were also analyzed by total number of guanacos present, including the territorial male, females, yearlings, and chulengos. The average group size for all territories observed was 3.4 (6.1 SD). We categorized male territory locations as having ≤2, 3-9 or ≥10 total guanacos present.

We placed observation periods into three time categories. Males were observed in the morning from 0930-1200, mid-day from 1200-1400, and late afternoon from 1400-1600. We also analyzed the behavioral time budgets of territorial males by the dominant habitat type and by the sex of the second guanaco involved in all aggression activities.

For statistical significance we accepted a p-value for each ANOVA at ≤ 0.007 based on the Bonferroni adjustment. This value was determined by dividing 0.05 p-value by the number of independent tests for each behavior (7).
RESULTS

There were significant differences in the time spent per activity within all territorial male observations ($F_{6,833} = 237, P < 0.001, n = 120$). Territorial males spent most of their time eating (65%). Alert (14%) and resting (12%) were also observed regularly, but for less time than eating (Fig. 1).

We found no difference in the activity time budgets between Solo Territorial Males and Family Group Territorial Males (Table 1). The time spent in each of the seven activities did not vary between Solo Territorial Males and Family Group Territorial Males ($P > 0.007$, Table 1). There was also no effect of the total number of females present on the proportion of time spent per activity ($P > 0.007$, Table 1).

In the territorial observations with females present ($n = 46$), females were mainly found eating (in 89% of observations) and resting (in 43% of observations). Females were also found alert (26%), followed by moving (15%), aggression (11%), other (9%), and bathing (7%).

We found no significant effect of overall group size on activity time budgets for males ($P > 0.007$, Table 1). There was also no effect of time of day on the activity time budgets of male guanacos ($P > 0.007$, Table 1).

Territorial males were observed in a variety of habitats, but most frequently were found at vegas (54% of the time, Table 2). There was a significant effect of habitat type on the time spent in aggression ($F_{2,71} = 15.17, P < 0.007, n = 81$; Table 1), with most aggressive encounters occurring on Mata Barrossa hilltops (38%). No aggression behavior occurred in Calafate flat areas, vegas and Coiron hilltops. There was a significant effect of habitat type on the time budgeted for other ($F_{2,71} = 6.17, P < 0.007, n = 81$; Table 1), with this class of
activity occurring mostly on Mata Barrossa hilltops (10%). Males spent no time in other activities while in Mata Barrossa and Coiron flat areas. There was no significant effect of habitat type on the proportion of time resting, bathing, eating, alert or moving (P > 0.007, Table 1).

Aggression behaviors were observed in 16 of the 27 territorial males during 31 of the 120 focal sample periods. There was no significant difference in the time budgeted for any of the activities based on the sex of the other guanaco involved (P > 0.007, Table 1).

DISCUSSION

Territorial male guanacos spent most of their time eating (65%), followed by alert (14%) and resting (12%). Jurgensen (1985) also found that territorial male guanacos within Torres del Paine spent a large amount of time eating (54%). Similar behavioral patterns have been observed in other territorial ungulate species including the bontebok (Antidorcas marsupialis; David 1978) and pronghorn (Antilocapra americana; Byers 1997).

Time budgets of territorial males did not vary with social group type, the number of females present, or the total number of guanacos present. It was surprising that the time budgeted for alert and feeding did not vary between Family Group Territorial Males and Solo Territorial Males. Although Lagory (1986) found that white-tailed deer (Odocoileus virginianus) groups of different sizes did not use different anti-predator strategies, many polygynous ungulates decrease the amount of time each individual spends vigilant as group size increases (Jarman 1974). Most individuals within pronghorns and white-tailed deer populations decrease the amount of time alert as group size increases (Lipetz and Beckoff 1982; Lagory 1986). Female and juvenile mountain goats (Oreamnos americanus) not only
decrease the amount of time alert, but also increase the amount of time spent feeding as
group size increases (Risenhoover and Bailey 1985); this alteration of time budgets with
group size increases feeding efficiency without decreasing the overall time spent alert
because the group compensates for the individual differences.

However, Maher (1991) found that pronghorn males decrease the time spent feeding
once rutting season begins and previously solitary males are found with females. Under
these circumstances pronghorn males spend more time in behaviors related to attracting a
mate and mating (Maher 1991). This time spent interacting with other conspecifics can lead
to a decrease in the amount of time spent feeding (Risenhoover and Bailey 1985). Some
ungulates, such as red deer (Cervus elaphus), are more frequently interrupted by conspecifics
when group size increases (Clutton-Brock et al. 1982), and individual moose increase the
time spent alert as group size increases (Molvar and Bowyer 1994). In guanacos, it is
possible that there was no effect of social group type on the time spent alert because Solo
Territorial Males may spend more time alert to potential predators whereas Family Group
Territorial Males spend more time alert to conspecifics.

It should be noted that our study did not differentiate between anti-predator alert
behavior (vigilance) and alert behavior directed towards guanacos and other non-predator
species. Because territorial male guanacos play a distinct role in the social system of
guanacos, it is possible that females and young guanacos obtain anti-predator benefits even
though territorial males do not. Females were only spending time alert in 26% of the
territories where they were present (n=46), whereas 91% of the males that held territories
with females present were showing alert behavior.
We found no difference in behavioral time budgets based on the time of day. The guanaco's only predators, mountain lions (*Felis concolor*), are most active at dawn and dusk (Franklin et al. 1999). We had hypothesized that males would decrease the time spent on non-alert behaviors, such as bathing and resting, in the early time period because of their increased vulnerability to predation at this time. However, we found no effects of time of day on male guanaco time budgets.

There were some differences in male territorial guanaco behaviors based on habitat type. Males spent more time in aggression and other on Mata Barrossa hilltops. This shrub rarely grows taller than 0.5 meters (Pisano 1974). Use of these open hilltop areas for aggressive behaviors could be advantageous to the males. From a hilltop, guanacos in this low-lying vegetation have an extensive view and are relatively safe from ambush attacks by mountain lions (Iriarte 1991). Since mountain lions are typically found in areas with trees or high cover density (> 3 meters tall; Franklin et al. 1999), males can invest more time in non-alert activities without increasing predation risks.

Although a Mata Barrossa hilltop does not provide females with a high quality food resource (Lawrence 1990), it could act as geographically important display grounds during fights. It is possible that other males observe these fights and compare their own ability based upon these observations. David (1978) noted that aggressive chasing of other males by territorial springbok is a method of advertising their territorial status. Some red deer establish territories with lower quality swards in areas that females use as routes to better territorial habitats (Carranza 1995). Although hilltops may not be on direct routes used by female guanacos, aggressive behavior between two males on hilltops could provide female
guanacos with knowledge of the male territories. From a hilltop, territorial males would also be able to oversee their territory while engaged in aggressive behaviors.

Family Group Territorial Male and Solo Territorial Male guanacos did differ in the amount of time budgeted for other behaviors. Mountain goats increase their time alert as they feed closer to timberline, an area of higher predation risk (Romeo and Lovari 1996). Similarly, Goldsmith (1990) noted that female pronghorn vigilance behavior increased in habitats with low visibility (tall vegetation). Although mountain lions in Torres del Paine National Park are most successful when hunting guanacos from elevated and hidden positions (Wilson 1984), there was no difference in alert behavior between the habitat types where territorial males were observed.

In many territorial mammals, there are differences in male behavioral patterns that directly affect an individual's mating success (Rachlow et al. 1998). In guanacos, the lack of variation in individual behavioral time budgets, makes it difficult to interpret variation in reproductive success. Territorial behavior of other male ungulates is frequently used to attract and secure mates (Rachlow et al. 1998; Gosling 1986; David 1978; Owen-Smith 1977), but in this population of guanacos, males attract mates through resource-defense rather than through differences in behavior (Franklin 1983). The habitats in which male guanacos establish territories act as the main resource to attract females. Although some studies have cast doubt on whether female choice is based solely on a male's defended resources (Balmford et al. 1992; Ostfeld 1987), the lack of behavioral differences between mating and non-mating males favors the argument that resources act as a strong attractant for female guanacos.
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REFERENCES


Wilson, W. 1984. Puma predation on guanacos in Torres del Paine National Park, Chile.

Table 1. F-statistics from ANOVA for the proportion of time spent by territorial male guanacos in Torres del Paine National Park, Chile.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Resting</th>
<th>Bathing</th>
<th>Eating</th>
<th>Alert</th>
<th>Aggression</th>
<th>Moving</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>FGTM versus STM</td>
<td>21</td>
<td>0.03</td>
<td>0.26</td>
<td>0.06</td>
<td>0.00</td>
<td>0.03</td>
<td>0.16</td>
<td>0.02</td>
</tr>
<tr>
<td>Females present</td>
<td>22</td>
<td>0.02</td>
<td>0.31</td>
<td>1.44</td>
<td>2.94</td>
<td>0.30</td>
<td>0.27</td>
<td>2.01</td>
</tr>
<tr>
<td>Total group size</td>
<td>22</td>
<td>0.15</td>
<td>0.72</td>
<td>1.50</td>
<td>2.87</td>
<td>0.25</td>
<td>0.24</td>
<td>2.17</td>
</tr>
<tr>
<td>Time of day</td>
<td>23</td>
<td>0.22</td>
<td>1.89</td>
<td>2.29</td>
<td>1.98</td>
<td>4.09</td>
<td>1.46</td>
<td>0.77</td>
</tr>
<tr>
<td>Habitat</td>
<td>81</td>
<td>0.30</td>
<td>0.04</td>
<td>0.39</td>
<td>0.22</td>
<td>15.17*</td>
<td>0.18</td>
<td>6.17*</td>
</tr>
<tr>
<td>Fighting interaction</td>
<td>16</td>
<td>0.85</td>
<td>1.53</td>
<td>0.17</td>
<td>0.08</td>
<td>0.98</td>
<td>0.63</td>
<td>1.48</td>
</tr>
</tbody>
</table>

P < 0.007 (Bonferroni adjustment value)*
Table 2. Habitat and slope types used by territorial male guanacos during the 1998-1999 season. The total number of times males occurred within each habitat are shown for focal samples (when males remained in the same habitat type) in Torres del Paine National Park, Chile (n = 81).

<table>
<thead>
<tr>
<th></th>
<th>Hillside</th>
<th>Hilltop</th>
<th>Flat area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mata Barrossa</td>
<td>13</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Mata Negra</td>
<td>2</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Calafate</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>Coiron</td>
<td>4</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Vega</td>
<td>-</td>
<td>-</td>
<td>43</td>
</tr>
</tbody>
</table>
Figure 1. Activity time budget for focal samples of Solo Territorial Male guanacos (n = 68) and Family Group Territorial Male guanacos (n = 39) observed between October 1998 and March 1999, for a total of 30 hours in Torres del Paine National Park, Chile.
GENERAL CONCLUSIONS

Guanaco territory locations and even more importantly, potential breeding locations are highly predictable. Most territorial male guanacos use the same sites both within and between years. This high site-fidelity was observed in both Solo Territorial Males and Family Group Territorial Males, although some Solo Territorial Males will adjust territory locations between years.

Not only did Solo Territorial Males and Family Group Territorial Males show similarities in site-fidelity, but they also had similar behavioral activity budgets. Differences in behavior were only observed when habitat type was evaluated. Although territorial behavior of male ungulates is typically used to attract and secure mates (Owen-Smith 1977; David 1978; Gosling 1986; Rachlow et al. 1998), this population of guanacos attracts mates mainly through resource-defense (Franklin 1983). Even though some studies doubt that female choice is based solely on a male’s defended resources (Ostfeld 1987; Balmford et al. 1992), habitat type was the only definite factor that influenced male behavior. The lack of behavioral differences between breeding and non-breeding males favors the argument that resources act as a strong attracting force for females.

This study showed that male territory locations are predictable, but that territorial male behaviors cannot be used as indicators of breeding potential or success. Predictable use of space by territorial male guanacos can aid research and management of guanaco populations and the land. Standardized routes can be used for population surveys, both within a given survey and over years. The accuracy of these surveys can aid land management and harvesting decisions.
Because uncontrolled wildlife utilization practices are often detrimental to otherwise viable wildlife populations (Gardner 1991), the information gathered here should play an important role in decision-making, regarding management and harvesting of guanaco populations. Over-harvesting of guanacos caused the species to be placed on CITES Appendix II (CITES 1985), and only in recent years have guanacos seen an increase in local population sizes. To continue seeing local populations thrive, most Solo Territorial Males and all Family Group Territorial Males should be excluded from any harvesting practices.

Recommendations for Future Research

More research needs to be conducted to further understand territorial fidelity of male guanacos. Information regarding female movement over space and time is invaluable to completely understanding the ultimate implications of male site-fidelity. Research on guanaco relatedness would also help our understanding of territorial behavior, fidelity, and female territorial use. The information obtained needs to be made available to Park Service employees and land managers throughout the regions of South America where guanacos are found.

References


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