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ORIGINAL ARTICLE

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Quantitative variation in ecological and hormonal variables correlates with spatial organization of pronghorn (*Antilocapra americana*) males

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Abstract Whereas variation in pronghorn (*Antilocapra americana*) spatial organization is well documented, underlying ecological or physiological explanations are not well understood. This study quantitatively describes spacing systems of pronghorn males and correlates of their spatial organization. I collected behavioral data from two populations in South Dakota (Wind Cave) and Montana (Bar Diamond) to determine if males differed in space use, response to intruders, and behavior patterns indicative of area defense. I measured sex ratio and population density, and I examined characteristics of food resources, including forb species diversity, richness, coverage, biomass, and nitrogen content, and how they changed during the growing season. I also collected and analyzed fecal samples to determine if males differed in testosterone concentrations. Pronghorn males at Wind Cave were more territorial than males at Bar Diamond, although males at Bar Diamond became more territorial during the second year. The forb community at Wind Cave was more diverse, contained greater amounts of forbs later in summer, and had a higher nitrogen content later in summer. Population density was lower at Wind Cave, although density dropped at Bar Diamond during the second year, and sex ratios were skewed toward males at Bar Diamond. Finally, males at Wind Cave had higher testosterone concentrations than did Bar Diamond males, although differences were not statistically significant. With lower population density and higher forb abundance and quality, food resources were more economically defensible at Wind Cave, and males were more territorial there. Analyses using these and other pronghorn populations revealed that population density and sex ratio correlated weakly with spatial organization, whereas precipitation correlated most strongly, which suggests plant productivity has a powerful role in determining pronghorn territoriality.

Key words Territoriality · Ecological correlates · Intraspecific variation · Testosterone · Pronghorn

Introduction

Behavioral ecologists now recognize that animal social systems, including spatial organization, vary within species (Lott 1991). Animals of one population may maintain territories, whereas animals of another population may occupy undefended home ranges or form a dominance hierarchy (e.g., feral horses, *Equus caballus*: Rubenstein 1981; woodchucks, *Marmota monax*: Ferron and Ouellet 1989). Furthermore, animals in the same population may maintain territories at one point in time but switch to a different spacing system at another point (e.g., Anna's hummingbird, *Calypte anna*: Ewald and Carpenter 1978; red-backed vole, *Clethrionomys rufocanus*: Ims 1988).

A territory is worth maintaining only when an animal can maximize the benefits of territoriality (food, mates) while minimizing time and energy costs of defense (Brown 1964). Many experiments have demonstrated that when this cost/benefit ratio changes, animals shift toward or away from territoriality (e.g., Gill and Wolf 1975; Davies and Houston 1981; Wyman and Hotaling 1988; Grand and Grant 1994; Carranza et al. 1995). Ecological conditions can determine the relative costs and benefits of maintaining a particular spatial organization. Past research on animal spacing systems has relied heavily on qualitative assessments of ecological conditions (Maher and Lott 2000). For example, when food is "abundant," animals may not have to compete for access to it; thus, benefits of exclusive access to food do not outweigh the time and energy spent maintaining exclusive access to that food. Conversely, when food is "scarce," an animal may spend so much time searching and feeding that it has no time to devote to territorial ac-

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tivities, such as patrolling boundaries and chasing intruders (Jarman 1979; Woodward 1979). However, at “intermediate” levels of food abundance, benefits of territoriality could outweigh costs, and animals should maintain territories (Brown 1964). Likewise, “high” population density may preclude territoriality because animals spend too much time and energy repelling intruders (Brown 1964; Cole and Noakes 1980).

In a search for ecological factors influencing vertebrate spacing systems, Maher and Lott (2000) identified 20 variables. The most widely cited ecological factor is food, especially its abundance, distribution, and predictability (e.g., Bromley 1977; Ferguson et al. 1983; Grant and Guha 1993; Carranza et al. 1995). Since reproductive success can depend on food availability (e.g., Blanckenhorn 1991; Reznick and Yang 1993; Blumstein and Foggin 1997), food probably is an important resource to defend. Ungulates, in particular, invest a large proportion of time procuring food, suggesting food is a major determinant of spacing systems. Territoriality in impala (*Aepyceros melampus*) was strongly correlated with precipitation due to effects of rainfall on plant productivity. Males were territorial during the wet season, but as plant quality and abundance decreased in the dry season, territoriality declined (Jarman 1979). However, impala territoriality may shift with season independently of changes in the plant community. Even when rain in the dry season produced patches of green vegetation, males showed less vigorous defense of territories than during the wet season (Jarman 1979). A similar summer response to rainfall was seen in feral asses, *Equus asinus*, but forage availability was not measured in that study (Woodward 1979).

Food is one of the few ecological variables that has been manipulated experimentally, and causal relationships between food and spacing systems have been demonstrated. For example, clumped or predictable distributions of food resources increase defense and exclusive use of those resources (Grant and Guha 1993; Grand and Grant 1994). When red deer (*Cervus elaphus*) received supplemental food concentrated in particular locations, males defended those areas as territories, apparently because the locations then were attractive to females (Carranza et al. 1995).

In addition to food, habitat and population density often are cited as determinants of spacing systems (e.g., Ferron and Ouellet 1989; Biro et al. 1997; Basquill and Grant 1998). Population density of fallow deer (*Dama dama*) males was an important predictor of spatial organization. At densities <0.001 males/km^2, males were not territorial, but territoriality increased as density increased up to 0.005 males/km^2 (Langbein and Thirgood 1989). Although the authors measured ecological variables related to habitat structure, such as total area, tree cover, and woodland type, they did not assess food resources directly.

Whereas numerous studies have focused on relationships between ecological conditions and spatial organization, less attention has been placed on the proximate basis for differences in spacing systems. Hormones such as testosterone have been correlated with several aspects of social behavior, including spatial organization. Territorial males often have higher testosterone levels than nonterritorial males (e.g., Weddell seals, *Leptonychotes weddelli*: Bartsh et al. 1992; red-winged blackbirds, *Agelaius phoeniceus*: Beletsky et al. 1989), or males have higher testosterone levels when they are territorial compared to other times of the year (e.g., willow ptarmigan, *Lagopus lagopus*: Hannon and Wingfield 1990).

To my knowledge, no study has examined the interrelationships of physiology, ecological conditions, and spacing systems simultaneously. Spacing systems in pronghorns (*Antilocapra americana*) provide an excellent opportunity to study these interactions. Characteristics of the food base, such as species diversity, coverage, abundance, and quality, can be quantified readily. Furthermore, technology now allows quantification of testosterone from feces rather than blood, making its measurement more feasible logistically. Finally, variation in pronghorn social organization is well documented, both between and within populations (reviewed in Maher 1992). Although several correlates have been proposed, including hunting pressure (Copeland 1980; Deblinger and Alldredge 1989), population age structure (Byers 1997; Byers and Kitchen 1988), and ecological conditions (Bromley 1991; Kitchen 1974; Maher 1991, 1994), the underlying basis for variation in pronghorn social organization is not well understood.

Pronghorn populations organized along a continuum of spatial organization, from territories to undefended home ranges, should show differences in behavior patterns, ecological conditions, and hormonal states. To untangle these relationships, I compared pronghorn males in two populations and addressed the following questions. (1) Do pronghorn males from two separate populations exhibit different spatial organization? (2) If so, do ecological conditions, including food abundance, quality, and species diversity, experienced by pronghorns differ in the two populations? (3) Do pronghorn male testosterone levels differ between populations? (4) If spacing systems differ, do population density and sex ratio correlate with those differences? I predicted that under more favorable conditions of food and population density, such as greater forb abundance and quality and low population density, males would exhibit more territoriality and higher concentrations of testosterone.

Methods

Definitions of territoriality

A “correct” definition of territoriality does not exist; authors studying variation in vertebrate spacing systems have proposed 48 different definitions of territoriality (reviewed in Maher and Lott 1995). However, I conceptually defined territory as a fixed, relatively exclusive space from which an individual actively excludes competitors for a specific resource or resources (Maher and Lott 1995). Thus, I included both ecological (exclusive area) and behavioral (defense) criteria in this definition.

For purposes of data collection, I developed an operational definition of territoriality. Exclusive area was gauged by examining the amount of home range overlap between pronghorn males: low amounts of overlap are indicative of exclusive areas (Bromley 1991). Males that defend exclusive areas respond to other males by staring, vocalizing with a snort wheeze call, approaching, interacting with, and, if necessary, chasing the intruder from the area (Kitchen and Bromley 1974). Males that show greater home range overlap engage in lower rates of snort wheeze vocalizations and scent marking (Maher 1994). To measure defense, therefore, I recorded the percentage of intruders approached, latency to approach intruders, and rates of specific behavior patterns, including scent marking, snort wheezing, and chases (which included cases in which the focal male chased another male or when he was chased by a male). Thus, I could compare these variables among males to determine if they differed in the criteria and, therefore, in their spacing systems.

Study sites and populations

I studied pronghorn social systems of two populations in 1994 and 1995. One population was located on the Bar Diamond Ranch, a privately owned cattle ranch situated on 6500 ha north of Billings, Montana, at 45°55’ N, 108°31’ W. The second population was located at Wind Cave National Park, 43°33’ N, 103°29’ W, situated on approximately 11,450 ha in the southern Black Hills of South Dakota.

These two study areas are macroscopically similar. Elevations average 1100 m at Bar Diamond and 1300 m at Wind Cave. Geographical features have been correlated with spacing systems in ungulates (e.g., Rubenstein 1981); however, topography is similar between the two locales. Open flats, gently rolling hills and steep canyons near drainages characterize both areas. Furthermore, pronghorns use similar habitats at both sites (C.R. Maher, unpublished data). Plant community composition is comparable between the two areas; habitats are primarily prairie grassland interspersed with ponderosa pine (*Pinus ponderosa*) forests at higher elevations. Although the study areas are approximately 500 km apart, climate patterns are similar. One exception is that Wind Cave receives more precipitation than Bar Diamond, perhaps because Wind Cave is at the southern edge of the Black Hills (D. Kinney, unpublished data). Grazing ungulates are present in both locations (domestic cattle, *Bos taurus*, at Bar Diamond; bison, *Bison bison*, at Wind Cave). Hunting is prohibited at Wind Cave, and it is minimal at Bar Diamond, where it occurs primarily after the breeding season.

Population densities and sex ratios were estimated using ground-based total counts (Lancia et al. 1996), and they differed between the two populations. In 1994, the density at Bar Diamond was estimated at 2.7 pronghorns/km^2, but it decreased to 1.8 pronghorns/km^2 in 1995. Wind Cave maintained an estimated population density of 1.0 pronghorn/km^2 in both years. The sex ratio at Bar Diamond showed a greater number of males relative to females: in 1994, the male:female sex ratio was estimated at 96:100 and it dropped to 81:100 in 1995 (C.R. Maher, unpublished data). The estimated sex ratio at Wind Cave remained near 45:100 in both years (C.R. Maher, unpublished data).

Behavioral observations

In 1994 and 1995, field assistants and I collected data from early May through September at Bar Diamond, and I collected data from late May to early September at Wind Cave. Sites were sampled with approximately equal intensity throughout the summer. I could not observe the rut at Wind Cave, so I only present data from days prior to the breeding season. When males maintain territories, they establish them in spring and usually maintain them through the breeding season; therefore, territoriality is expressed before the breeding season (Kitchen 1974). Over the 2 years, we recorded almost 500 focal hours of observations.

We used focal animal sampling and continuous recording (Martin and Bateson 1993) to collect behavioral and space use data. Males were recognized individually using natural markings, including neck bands, tail coloration patterns, and horn morphology (Bromley 1969; Kitchen 1974). To avoid biases in sampling effort, we established a schedule to search, either from a vehicle or on foot, specific areas on specific days during two time periods, morning (sunrise until approximately noon, or until shimmering heat waves prevented further observations) and late afternoon/evening. Each area was searched with nearly equal effort during each field season, and individual males were sampled equally throughout the day.

Upon locating a male, we determined his identity and recorded his location for later plotting on a topographic map, from which I calculated UTM coordinates for determining home ranges. Each male was observed, using a spotting scope when necessary, for 30 min. Males had to remain in view ≥10 min for the sample to be included in the analysis. The sample began once he habituated to the observer’s presence (e.g., he returned to his original activity). We recorded the amount of time the focal male spent in various activities (e.g., walking, reclining, feeding) and any interactions he had with females (e.g., courtship behavior patterns) and other males (e.g., chases, approaches). I converted activity variables to percentages because the sample did not always last 30 min. Interaction variables were converted to rates (number occurring/unit time). If another male entered the focal male’s home range within sight of the focal male, we recorded whether or not that intruding male was approached. We also recorded the latency between the moment when the focal male saw the intruder to the moment at which he moved in the direction of the intruder. Since we were conducting continuous recording of the focal male’s behavior patterns, we could identify clearly when the focal male saw another pronghorn: the male stared intently in a particular direction, and we could determine the object of his attention. Upon completion of one focal sample, we selected another male at random from those in view and continued sampling until all males were sampled or the group moved out of view. Individual males were sampled at intervals >24 h to ensure statistical independence.

I used the software package Wildtrak to calculate home ranges, using the minimum convex polygon technique (Todd 1992). We collected an average of ten locations for each male from the two populations. To determine the core area of a male’s home range, I examined a cumulative plot of the percent home range area versus percent minimum convex polygon size. The minimum value at which this curve reached a plateau indicated the size of the male’s core area. Core home range polygons ranged from 70 to 100% (mean=90%) of the total home range area. The computer program calculated amount of home range overlap between males that had the potential to overlap, i.e., they were in the same general area during the same time frame.

Ecological conditions

I used plot sampling (Krebs 1989) to assess plant communities of the two areas in late spring (late May/early June) and late summer (late August/early September) of each year. I used 1-m^2 rectangular plots (0.71×1.41 m) placed at 10-m intervals along 100-m transects, for a total of ten plots per transect. Since I was comparing conditions experienced by males, I limited transects to areas in which pronghorn males were commonly observed feeding. I randomly located both a starting point within an area and the direction of the transect.

Within each plot, I measured the percentage of three cover classes: bare ground, forbs, and grasses. Given the distances at which I observed males (as close as 10 m at Wind Cave but up to 1 km, particularly at Bar Diamond), I could not clearly ascertain the species that males ate. However, during summer, up to 90% of a pronghorn’s diet consists of forbs (Kitchen 1974; Stephenson et al. 1985; Wydeven and Dahlgren 1985; McInnis and Vavra 1987; Yoakum et al. 1996). Therefore, I identified all potential forb species eaten by pronghorns, counted the number of individuals of each species, collected all the palatable forbs, and froze the samples the same day they were collected. Many species reported to be important food items were present at one or both study sites, including cudweed sagewort (*Artemisia ludoviciana*), meadow salsify (*Tragopogon dubius*), scarlet globemallow (*Sphaeralcea coccinea*), stemless hymenoxys (*Hymenoxys acaulis*), purple milkvetch (*Vicia americana*), yellow sweetclover (*Melilotus officinalis*), aster (*Aster* spp.), blue lettuce (*Lactuca pulchella*), and common winterfat (*Tetradymia canescens*) (Cole 1956; Cole and Wilkins 1958; Stephenson et al. 1985). I later measured both fresh weight and dry weight of plants collected from each plot to indicate biomass present in each population. I calculated species richness and the Shannon-Wiener index (Krebs 1989) to measure species diversity in both seasons for both populations, and I tested for differences in species diversity between communities using a *t*-test (Zar 1984).

Finally, I used percent total nitrogen as an index of plant quality, and I restricted analysis to leaf tissue. True proteins comprise 60–80% of total plant nitrogen, and leaf proteins are the highest quality proteins (Van Soest 1994). Soluble nonprotein nitrogen, including nitrate, peptides, and amino acids, may comprise 15–40% of total plant nitrogen (Van Soest 1994). Nitrogenous secondary plant compounds, when present (Hazlett and Sawyer 1998), represent a very small component of total nitrogen (Van Soest 1994). Leaf material was separated from stems and flowers in the dried samples and then ground to a fine powder using a coffee grinder. Ground samples were digested in sulfuric acid with a copper sulfate catalyst using a Lachat BD-46 Block Digestor. Digests were sent to the University of Maine Soils Analysis Laboratory, where nitrogen concentrations were determined by colorimetric analysis.

Testosterone levels

Many researchers now routinely track hormone levels of free-ranging animals using noninvasive techniques, such as fecal hormone analysis (e.g., Kirkpatrick et al. 1990, 1996; Komers et al. 1994; White et al. 1995; Creel et al. 1996, 1997; Stoops et al. 1999; Strier et al. 1999). Since pronghorns are not amenable to traditional capture and restraint methods (Dotson 1992), I collected fecal samples to measure testosterone levels. When a known male defecated during an observation period, I noted the location so fecal material could be collected once he left the area, usually within 30–60 min after defecation. When I could locate the fresh (i.e., moist) samples, I collected them in reclosable plastic bags, placed them on ice in a small cooler, then froze them within 2 h of collection.

Fecal testosterone was extracted and measured at Deaconess Research Institute in Billings, Montana. Fecal samples were thawed, then 0.5 g was weighed and placed into a preweighed scintillation vial containing 10 ml of ethyl acetate:hexane (3:2 v/v). The organic material was decanted, then air dried at 37°C for 2–3 h, and the resulting residue was resuspended in 1.0 ml phosphate buffer. Remaining fecal material from each extraction was air dried and weighed, and concentrations were indexed to dried fecal weights (Rachlow et al. 1998). Samples were then analyzed using a commercial radioimmunoassay kit (Coat-a-Count, Diagnostic Products Corporation; Berkeley et al. 1997). Cross-reactivities were: aldosterone, not detectable; androstenedione, 0.5%; corticosterone, 0.002%; cortisol, 0.005%; cortisone, 0.02%; 5α-dihydrotestosterone, 3.4%; estradiol, 0.02%; estrone, 0.01%; 19-hydroxytestosterone, 2.0%; 11-ketotestosterone, 16%; methyltestosterone, 1.7%; progesterone, not detectable; 11ß-hydroxytestosterone, 1.2% (J. Goodman, personal communication). To measure parallelism to the standard curve, successively halved dilutions of selected samples were assayed, then values were graphed against the standard curve. In this laboratory, intra-assay coefficients of variation for fecal hormone analyses ranged from 5.7 to 10%, and interassay coefficients of variation ranged from 8 to 16.4% (Kirkpatrick et al. 1990, 1993, 1996; White et al. 1995).

Because I compared male activity and spatial organization prior to breeding, in this analysis I only included samples collected before the rut. Most males were sampled once, but several males were sampled more than once (mean number of samples=1.6). In the latter cases, I calculated a mean value for each male and used that value in the analysis.

Statistical analyses

For each variable, I calculated a mean value for each male for the season; thus, individual males constituted the independent sampling units used in the analysis. Since the behavioral and hormonal data were not normally distributed, I analyzed those data with nonparametric statistics, using SYSTAT (Systat 1992). To measure relationships between spacing systems and environmental and demographic variables, I used JMP (SAS 1994) to calculate correlations and multiple regression. Significance was set at $P \leq 0.05$.

Results

Do males differ in their spacing systems?

Home range sizes were not significantly different in the two populations in either 1994 or 1995. In 1994, the mean (±SE) core home range size was 138.7±32.7 ha at Bar Diamond (n=39 males) and 63.0±11.3 ha at Wind Cave (n=27 males, P>0.11). Furthermore, home range size did not change between years (P>0.65). In 1995, Bar Diamond males had a mean core home range size of 81.0±15.3 ha (n=16), and Wind Cave males had a mean core home range size of 61.2±8.7 ha (n=27, P>0.22).

In 1994, males at Wind Cave had significantly less home range overlap with other males (3.0±1.0%, n=24) compared to Bar Diamond males (8.1±1.4%, n=35, U=647, P<0.001). Furthermore, at Bar Diamond, most males' home ranges overlapped with at least one other male, whereas at Wind Cave, many males' home ranges did not overlap with any other males. Yet, in 1995, I found no significant differences in amount of home range overlap between Wind Cave males (5.25±1.51%, n=26) and Bar Diamond males (3.62±0.98%, n=15, P>0.85). Indeed, Bar Diamond males occupied more exclusive areas in 1995 compared to 1994 (U=353.5, P=0.05).

I witnessed a sufficient number of encounters with intruders to compare males in 1995. Males at Wind Cave had significantly shorter latencies to approach intruders compared to males at Bar Diamond (Wind Cave: median=16.0 s, n=12; Bar Diamond: median=1800 s, n=8; U=80.5, P=0.011). In addition, males at Wind Cave approached a significantly greater percentage of intruders that entered their areas (Wind Cave: 88.5±8.31%, n=13; Bar Diamond: 40.7±16.5%, n=9; U=27, P=0.013). In 1995, males at Wind Cave also approached males at higher rates than did males at Bar Diamond (U=272.5, P=0.02), but in 1994, the difference was not significant (U=726.5, P=0.073; Table 1).

Scent marking has been interpreted as males informing other pronghorns of the identity of the male in the area (Kitchen 1974). Males at Wind Cave spent significantly greater percentages of time marking vegetation with their cheek patches (where scent glands are located) in both 1994 (U=544, P=0.005) and 1995 (U=224.5,

Table 1 Mean (±SE) values of behavior patterns for pronghorn males at Wind Cave and Bar Diamond prior to rut, 1994 and 1995. Sample sizes represent number of males

Population	Approach intruders (number/h)	Cheek marking (% time)	Linked urination defecation (number/h)	Snort wheeze (number/h)	Chase (number/h)
1994					
Bar Diamond (n=47)	0.040±0.024	0.90±0.16**	0.88±0.15*	0.049±0.024***	0.25±0.12
Wind Cave (n=36)	0.12±0.046	1.41±0.17**	1.49±0.19*	0.29±0.067***	0.76±0.61
1995					
Bar Diamond (n=22)	0.39±0.36*	1.31±0.36**	1.69±0.49	0.11±0.050*	0.079±0.048
Wind Cave (n=35)	0.93±0.51*	2.32±0.34**	2.07±0.28	0.31±0.080*	0.14±0.049

*P<0.05; **P<0.01; ***P<0.001

Table 2 Plant community characteristics for Bar Diamond and Wind Cave in late spring (late May/early June) and late summer (late August/early September). Sample sizes listed are number of transects sampled (ten plots/transect), and values reported for coverage, dry weight, and nitrogen are the mean±SE

Population	Species diversity (H′)	Species richness	Forb coverage (%)	Dry weight (g)	Leaf nitrogen (% total Kjeldahl nitrogen)
Spring 1994					
Bar Diamond (n=5)	1.29	54	–	–	–
Wind Cave (n=6)	1.28	54	20.53±1.68	14.2±1.47	2.85±0.28
Summer 1994					
Bar Diamond (n=6)	0.82	11	5.28±1.72**	3.76±1.44*	1.34±0.56
Wind Cave (n=6)	1.19	35	20.19±5.40**	17.7±6.30*	2.10±0.23
Spring 1995					
Bar Diamond (n=5)	0.61	40	23.68±2.57	30.5±2.80**	2.16±0.23
Wind Cave (n=8)	1.38	63	24.40±3.85	13.0±2.09**	2.48±0.082
Summer 1995					
Bar Diamond (n=5)	0.66	9	3.90±1.53**	5.01±3.64**	0.50±0.31**
Wind Cave (n=8)	1.20	40	33.86±6.44**	37.9±8.05**	2.07±0.18**

*P<0.05; **P≤0.01

P=0.008; Table 1). Another form of scent marking is linked urination defecation (LUD). Again, males at Wind Cave performed LUD at greater rates than males at Bar Diamond in 1994 (U=561, P=0.008), but the difference was not statistically significant in 1995 (U=274.5, P=0.07; Table 1).

Wind Cave males snort wheezed more frequently than Bar Diamond males in 1994 (U=539, P<0.001) and 1995 (U=278.5, P=0.049; Table 1), even though population density was lower at Wind Cave. Furthermore, Bar Diamond males altered their behavior between years. In 1995, they snort wheezed at greater rates than they did in 1994 (U=427, P=0.058).

In 1994, the data suggest males at Wind Cave chased males at greater rates than males at Bar Diamond (U=697.5, P=0.069); however, in 1995, those differences disappeared (U=331.5, P=0.233; Table 1). In 1994 at Wind Cave, I often saw two specific males chasing other males, but those males were not present in 1995; they may have contributed disproportionately to the high rates in 1994, yet the difference between years at Wind Cave was not significant.

Do ecological conditions and hormonal concentrations differ between the two populations?

Plant species diversity did not differ significantly between the two sites at any season (P>0.10; Table 2). By late summer each year, Wind Cave retained greater numbers of forb species in the plant community, probably due to greater amounts of precipitation through the summer. At Bar Diamond, most forbs were desiccated and dead by the end of August, thus reducing species richness.

In June, 1995, Bar Diamond and Wind Cave did not differ in percent coverage of forbs (P>0.88), but by August of 1994 and 1995, Wind Cave had significantly greater percent forb coverage (1994: U=2, P=0.01, n=6, 6 transects; 1995: U<0.01, P =0.003, n=5, 8 transects; Table 2). Coverage data were not available for Bar Diamond in June 1994.

In June 1995, Bar Diamond had significantly more plant biomass as measured by dry weights (U=29.0, P=0.003, n=5, 8 transects), but by August of both years, Wind Cave contained more forbs (1994: U=1.0, P=0.016; 1995: U=1.0, P=0.005; Table 2).

Table 3 Mean (±SE) concentration of fecal testosterone in males at Bar Diamond and Wind Cave in 1994 and 1995

Population	Testosterone concentration (ng/g dry feces)
Bar Diamond, 1994 (*n*=4 males)	1566.8±640.9
Bar Diamond, 1995 (*n*=4 males)	1405.9±662.8
Wind Cave, 1994 (*n*=19 males)	2582.3±359.6
Wind Cave, 1995 (*n*=15 males)	2600.6±355.9

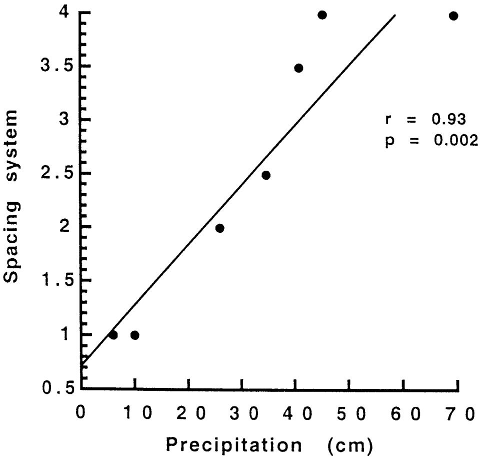

Fig. 1 Relationship between spacing system and precipitation for pronghorn populations in Nevada (*n*=1), California (*n*=2), Montana (*n*=2), and South Dakota (*n*=2)

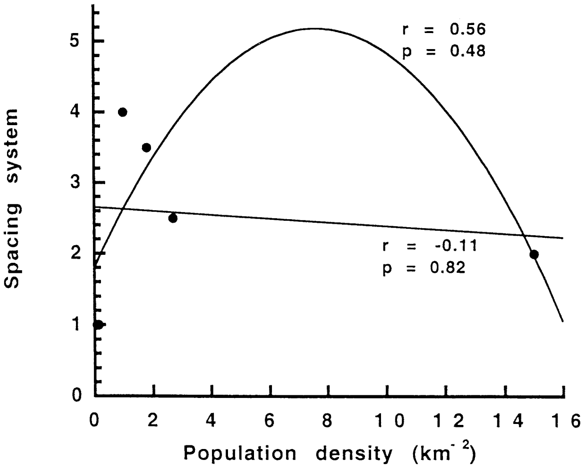

Fig. 2 Relationship between spacing system and population density for pronghorn populations in Nevada, California, Montana, and South Dakota. Sample sizes are given in the legend to Fig. 1

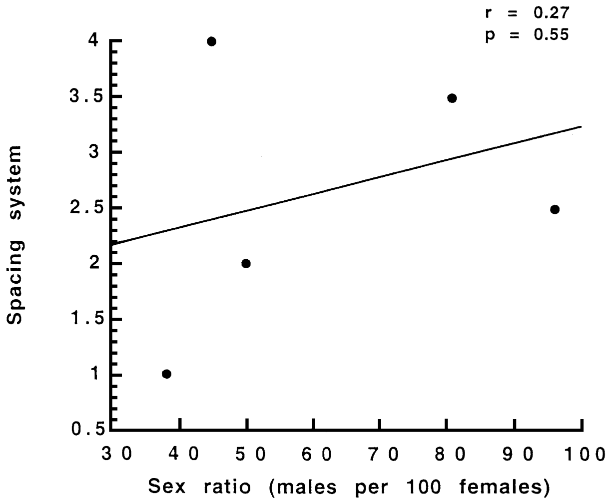

Fig. 3 Relationship between spacing system and sex ratio for pronghorn populations in Nevada, California, Montana, and South Dakota. Sample sizes are given in the legend to Fig. 1

In June 1995, plant nitrogen content was not significantly different between the two sites (*P*>0.12; Table 2). However, by August each year, forbs at Wind Cave had higher leaf nitrogen concentrations (1994: *U*=7.0, *P*=0.077; 1995: *U*<0.01, *P*=0.003). Within each site, plant tissue nitrogen declined from June to August, and Bar Diamond experienced a more dramatic decline (1995: *U*=25, *P*=0.008) than Wind Cave (1994: *U*=29, *P*=0.077; 1995: *U*=49, *P*=0.074).

Finally, males at Wind Cave did not have significantly greater concentrations of fecal testosterone than males at Bar Diamond in 1994 (*U*=22, *P*=0.194, *n*=19, 4 males) and in 1995 (*U*=12, *P*=0.072, *n*=15, 4 males; Table 3).

Correlates of spacing systems in pronghorn populations

Several characteristics of the forage base differed in the two populations. Because food resources, population density, and sex ratio are potential determinants of spacing systems and they covary in populations, I examined data from previous studies in an attempt to disentangle these variables. I have observed pronghorn populations in California (Maher 1994), Nevada (Maher 1991), Montana and South Dakota (this study), and used similar methodology in each study. I ranked the degree of home range overlap and rates of snort wheezing and scent marking across those populations. Then I calculated a composite score for each population, and I assigned each population to a spacing system that ranged from undefended home range with no evidence of territorial behavior (1) to strongly territorial (4), based on those scores. I did not have plant productivity data from each study, so I used precipitation as an indirect measure of plant productivity because precipitation is well correlated with productivity (Sneva and Hyder 1962).

Spacing system was strongly correlated with the amount of precipitation (*r*=0.93, *P*=0.002, *n*=7 populations; Fig. 1), and precipitation explained 87% of the variation in the data. Population density did not correlate as strongly with spacing system, either as a linear function (*r*=0.11, *P*=0.82) or as a second-order polynomial function (*r*=0.56, *P*=0.48; Fig. 2), nor did it explain as much of the variance (r^2=0.31 for the second-order polynomial function). Finally, sex ratio also did not correlate strongly with spacing system (*r*=0.27, *P*=0.55; Fig. 3), and it explained just 7.4% of the variation in the data. Multiple-regression results confirmed the univariate analyses (*F*=7.243, *P*=0.069, *df*=6); the only statistically significant regression coefficient was precipitation (*b*=0.915, *P*=0.022; population density: *b*=–0.052, *P*=0.813; sex ratio: *b*=0.070, *P*=0.759).

Discussion

Spatial organization and ecological conditions

Pronghorn males in these two populations occupied different regions of a continuum that can range from an undefended home range to a territory. Males at Wind Cave retained more exclusive areas, they were more responsive to intruders, and they performed scent-marking activities and vocalizations at higher rates compared to males at Bar Diamond (Table 4). Thus, based on my operational definition, Wind Cave males were located closer to the territoriality end of the continuum than Bar Diamond males.

Several features, including hunting pressure, age structure, and ecological conditions, have been proposed to explain variable spatial organization in pronghorn populations. In Idaho and Colorado, hunters displaced pronghorn males from territories, causing males to abandon those areas and form multimale, multifemale groups during the breeding season (Copeland 1980; Deblinger and Alldredge 1989). However, my study occurred prior to the breeding season, and hunting pressure was nonexistent.

In 1977–1978, a harsh winter killed older (>4 years) males at the National Bison Range (NBR), Montana. Surviving younger males established territories in spring, but they stopped defending those areas later in summer. After several years, they no longer maintained territories, even for a short time. Young males apparently could not hold territories effectively against incursions by other males, whereas older males, being larger and more experienced, were better at defense (Byers and Kitchen 1988). Unfortunately, I do not know the age structure of males at Wind Cave and Bar Diamond. However, these populations are well established and no large-scale disturbances have been reported, suggesting a normal age distribution. Although minimal hunting occurred at Bar Diamond after the breeding season, it probably did not affect age distribution significantly, since horn size usually does not correlate with age in adult pronghorn males (C.D. Mitchell and C.R. Maher, unpublished data).

Differences in pronghorn spacing systems at Wind Cave and Bar Diamond may be related to differences in the food base (Table 4). Theoretically, territories are maintained when resources within the territory are economically defensible (Brown 1964). Forbs are the primary food source for pronghorns during much of the year (Kitchen and O'Gara 1982), and the plant community at Wind Cave tended to have higher forb diversity and richness, especially later in the summer. Wind Cave also contained more forbs later in the summer, both in terms of coverage and biomass, compared to Bar Diamond. These differences could be due to differences in precipitation and habitat management. Wind Cave had higher amounts of rainfall than Bar Diamond in summer 1995 and in August 1994. Bar Diamond also experienced greater amounts of rainfall in 1995 compared to 1994 (Billings Office, National Weather Service, personal communication). Furthermore, Bar Diamond is a working cattle ranch, managed primarily for one species of grazing ungulate, whereas Wind Cave is managed to house a more diverse prairie community that includes browsing and grazing mammals.

At Wind Cave, the quality of the food source appeared higher in summer than in spring. Total nitrogen measures all forms of nitrogen, including lignified nitrogen and nonprotein nitrogen. However, true protein comprises 60–80% of all plant nitrogen, and these proteins are high quality (Van Soest 1994). These conditions may be important to males because more abundant, higher-

Table 4 Summary of statistically significant differences in behavior patterns, resource characteristics in August, and demographics for Wind Cave National Park, South Dakota (WICA) and Bar Diamond Ranch, Montana (BADI) prognorn populations in 1994 and 1995 (*n.s.*: *P*>0.05)

Criterion	Population comparison	
	1994	1995
Home range overlap	WICA<BADI BADI 1994>BADI 1995	n.s.
Latency to approach intruders	–	WICA<BADI
Percent intruders approached	–	WICA>BADI
Total rate of approaches	n.s.	WICA>BADI
Percent time scent marking	WICA>BADI	WICA>BADI
Rate of linked urination defecation	WICA>BADI	n.s.
Rate of snort wheezing	WICA>BADI BADI 1994<BADI 1995	WICA>BADI
Testosterone	n.s.	n.s.
Forb species diversity	WICA>BADI	WICA>BADI
Forb species richness	WICA>BADI	WICA>BADI
Percent forb coverage	WICA>BADI	WICA>BADI
Forb biomass	WICA>BADI	WICA>BADI
Forb nitrogen content	n.s.	WICA>BADI
Pronghorn population density	WICA<BADI BADI 1994>BADI 1995	WICA<BADI
Pronghorn sex ratio	Skewed toward males at BADI in both years	

quality food may attract more females at the end of summer, which coincides with the start of the breeding season.

Food resources are often cited as correlates of territoriality, but few studies quantify food resources (Jarman 1979; Woodward 1979; Rubenstein 1981; Carranza et al. 1990). Carranza and colleagues have quantified food resources under natural conditions and have experimentally manipulated food resources for red deer. High levels of green vegetation inside areas maintained as territories correlated with a higher proportion of territorial males and higher female densities held by those males (Carranza et al. 1996). Furthermore, experimental addition of food at specific locations enticed females to those areas, which males then defended (Carranza et al. 1995). An earlier study of pronghorns at Wind Cave found that food was twice as abundant on grassland defended as territories compared to a nearby prairie dog town that was not used by pronghorns. However, nearby grassland also had abundant forage, yet pronghorns did not defend those areas (Bromley 1991). Pronghorn territories at NBR contained more forbs than nonterritorial areas, and the most heavily used areas of males' territories had higher forage productivity and higher amounts of crude protein than the edges (Kitchen 1974; unpublished data). In Alberta, more pronghorn groups occurred on burned prairie, which contained newly growing green forage, than unburned prairie, which contained brown, desiccated plants (Courtney 1989).

My study did not compare populations during the breeding season because time constraints did not allow me to observe the rut at Wind Cave. However, Kitchen (1974) reported that pronghorn females seemed to be attracted to areas with higher plant quality, measured as fresh weight, and moisture. Female group sizes were largest in the best areas of a territory, and lactating females spent more time foraging in those areas (D.W. Kitchen, unpublished data). Females thus appear to assess forb quality, move into areas that still contain the highest-quality forage (i.e., high moisture content) as the range dries out in late summer, then breed with the male whose territory is used most extensively late in summer (D.W. Kitchen, unpublished data). Territory quality, measured as succulence and protein content in forbs and shrubs, was positively correlated with the number of copulations achieved by that territory holder (D.W. Kitchen, unpublished data).

At Wind Cave, not only was food perhaps worth defending in terms of abundance and quality, but intruder pressure was low enough that it could be defended with less effort. In addition to favorable resource conditions, pronghorn density was lower at Wind Cave than at Bar Diamond. Indeed, lower population density may have contributed to more favorable resource conditions. Population density is reported widely as a determinant of territoriality (Cole and Noakes 1980; Ferron and Ouellet 1989; Langbein and Thirgood 1989; Rolando et al. 1995). Intruder pressure alters resource defensibility, e.g., higher intruder pressure increases costs of maintaining access to food resources (Chapman and Kramer 1996).

Male and female density, as well as cover availability, were the strongest correlates of territoriality in fallow deer. Male and female densities <0.05/ha precluded territoriality. As densities increased, the number of territories increased, but the highest male density was <0.5/ha (Langbein and Thirgood 1989). In a nonterritorial population of fallow deer, however, an increase in population density from 0.76/ha to 0.94/ha did not lead to an increase in territoriality (San Jose and Braza 1997). Perhaps intruder pressure was too high at these densities to warrant defense of areas, or perhaps other variables had more important effects on spatial organization. The authors did not measure characteristics of the food resources in this study, and food may have been a more important constraint on defense than population density.

Sex ratios also may have affected spatial organization at Wind Cave and Bar Diamond. Sex ratios at Bar Diamond were 96:100 and 81:100 in 1994 and 1995, respectively, whereas the sex ratio at Wind Cave remained near 45:100. Therefore, defense of exclusive areas at Bar Diamond also could have been more difficult due to the greater percentage of males, i.e., potential intruders, in the population.

Besides differences in territoriality between the two populations, I witnessed changes within the same population; males at Bar Diamond shifted closer to the territoriality end of the continuum in 1995, when they had lower amounts of home range overlap and higher rates of territorial vocalizations. These changes may be related to changes in the food base and population density. May and June were wetter months in 1995, so forbs were probably more abundant that year, especially since productivity and precipitation are positively related (Sneva and Hyder 1962). Casual observations suggested the range was greener in 1995 compared to 1994, and biomass measured as dry weight actually was higher at Bar Diamond versus Wind Cave in spring 1995. Yet, by August, quality and quantity declined to the same level in both years. Also, for unknown reasons, population density at Bar Diamond declined from 2.7 pronghorns/km^2 to 1.8/km^2, and fewer males were present in the study population. These changes may have made defense more feasible in 1995.

Although Bar Diamond males were more territorial in summer 1995 leading up to the breeding season, when the rut began they again changed their spatial organization. Males no longer appeared to maintain territories. Instead, they moved to areas where females were present. The combination of a biased sex ratio, lack of females in many parts of the study site, and lower-quality, less abundant food may have contributed to the decline of territoriality in the 1995 rut (C.R. Maher, unpublished data).

Byers (1997) recently rejected resources (specifically, food) as an explanation for territoriality in pronghorns at NBR. Unfortunately, his description of the spatial organization of the population is qualitative, which makes direct comparisons to other populations difficult. He compares behavior patterns such as site faithfulness, scent marking, snort wheezing, chases, and exclusion of intruders, but he categorizes these variables as simply present or absent. Although males may exhibit the same behavior patterns, e.g., snort wheezing, the rate at which particular patterns occur is an important indicator of the degree to which territoriality exists in a population (Maher 1994; this study).

As one alternative to the importance of food resources, Byers (1997) suggests low and high population density preclude defense of areas due to low benefits and high costs, respectively. However, the population density at NBR did not change significantly before and after the shift in spacing systems. During years in which males were described as territorial, 1969–1978, density was 1.25±0.08 pronghorns/km^2, and when males were described as occupying undefended home ranges, 1982–1994, density was 1.38±0.20 pronghorns/km^2 (Mann Whitney *U*-test: $\chi^2=1.50$, $P=0.22$). However, sex ratio during nonterritorial years was significantly skewed toward females (1969–1978: 99.0±4.19:100; 1982–1994: 70.7±2.84:100; $\chi^2=11.43$, $P=0.0007$), which suggests sex ratio may have been more important than population density in affecting the spatial organization of this population. Interestingly, although density recovered soon after the harsh winter of 1977–1978, the sex ratio has remained biased toward females in this population.

Because I have studied several pronghorn populations in different areas, I could examine correlations between population density, sex ratios, plant productivity (measured indirectly by precipitation), and spatial organization. The populations I examined were not organized in the same ways. Although the Bar Diamond population was less territorial than the Wind Cave population, Bar Diamond males were not located at the far end of the continuum, occupying completely undefended home ranges. Thus, Bar Diamond in 1994 falls within the middle of the continuum, and Bar Diamond in 1995 shifted closer to the far end. A previous study of a California population found that males had an average home range overlap of 30.6% (Maher 1994), higher than the overlap at Wind Cave and Bar Diamond. These California males also very rarely snort wheezed (Maher 1994), whereas rates at Bar Diamond and Wind Cave were higher. In California, food conditions were extremely poor due to drought conditions, and population density was quite low because the population was recently translocated and because recruitment was low, probably due to a combination of predation and drought (Maher 1994). Thus, the California population was located much closer to the undefended home range end of the continuum than the Bar Diamond and Wind Cave populations.

For populations in California, Nevada, South Dakota, and Montana, sex ratio and population density were weakly correlated with spacing system and explained just 7% and 31% of the variation in the data, respectively. Precipitation was strongly correlated and explained much of the variance. Forage is an important resource for pronghorns, and its characteristics are important correlates of a male's tendency to defend an exclusive area. Animal spacing systems are probably determined by more than one ecological and (or) demographic variable (Maher and Lott, 2000), and multivariate approaches can often clarify these complex relationships. Population density and sex ratio may be important in pronghorn populations; yet, over the range of values and the set of variables I measured, precipitation, and therefore plant productivity, appears to be a more powerful predictor of their spatial organization. Future studies could manipulate these variables experimentally to determine if the relationships actually are causal.

Spatial organization and testosterone

Spacing systems are affected as much by the animals' internal state, i.e., physiology, as by external conditions, e.g., population density and food abundance. Physiological condition is reflected in metabolic processes and hormone levels, and hormones have important effects on reproduction and aggression (e.g., Poole et al. 1984). Higher testosterone concentrations are associated with higher activity levels (e.g., mountain spiny lizards, *Sceloporus jarrovi*: Marler and Moore 1989), higher energy consumption (e.g., Marler et al. 1995), dominance status (e.g., house mice, *Mus musculus*: Zielinski and Vandenbergh 1993; sugar gliders, *Petaurus breviceps*: Bradley and Stoddart 1997), more aggressive behavior patterns (e.g., rabbits, *Oryctolagus cuniculus*: Girolami et al. 1997), larger home ranges (e.g., dark-eyed juncos, *Junco hyemalis*: Chandler et al. 1994), and higher mating success (e.g., Harris sparrows, *Zonotrichia querula*: Rohwer and Rohwer 1978; song sparrows, *Melospiza melodia*, and white-throated sparrows, *Zonotrichia leucophrys*: Wingfield 1984; satin bowerbirds, *Ptilonorhynchus violaceus*: Borgia and Wingfield 1991).

Higher testosterone levels may have similar effects in pronghorns. Perhaps because sample sizes were small, differences in testosterone levels were not statistically significant; however, the data suggest that testosterone levels reflect the spacing systems observed in these two populations. Males at Wind Cave were more territorial than Bar Diamond males, and Wind Cave males engaged in higher rates of snort wheezes, scent marking, and chases. However, due to the correlative nature of the relationship, I do not know if testosterone caused higher levels of activity or if interactions between males increased testosterone concentrations. For many species, a baseline level of testosterone is necessary for the expression of particular behavior patterns, such as aggression, but social interactions, such as fights among males, lead to further increases in testosterone above baseline levels (Wingfield et al. 1990; Sapolsky 1997).

Nutrition is also related to testosterone levels. Animals experiencing poor nutritional conditions have lower testis weights (Boussès and Chapuis 1998) and exhibit lower testosterone levels when exposed to estrous females (Walkden-Brown et al. 1994) compared to animals eating higher-quality diets. Bar Diamond had lower-quality food resources than Wind Cave, and this could contribute to lower testosterone levels. Experimental manipulations would be necessary to determine the causal relationship of testosterone, nutrition, and spatial organization in pronghorns.

Conclusions

Pronghorn males are not simply "territorial" or "nonterritorial." Males exhibit different degrees of defense of exclusive areas, and this defense appears related to characteristics of their food source, population density, and sex ratio, perhaps through the mediating influence of testosterone. By operationally defining territoriality for pronghorns and quantifying behavior patterns, home ranges, ecological and physiological variables, I could develop a clearer picture of spatial organization for this species, and I could detect subtle changes within a population between years. Closer examination of other behaviorally flexible species may reveal similar subtleties in spatial organization, and experimental manipulations will allow us to determine causal relationships between spacing systems and ecological and demographic conditions.

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