THESIS

THE RELATEDNESS OF PHYSICAL TRAITS AND DOMINANCE RANK OF PRONGHORN BUCKS IN WINTER HERDS

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY SHARON GREATHOUSE ENTITLED "THE RELATEDNESS OF PHYSICAL TRAITS AND DOMINANCE RANK OF PRONGHORN BUCKS IN WINTER HERDS" BE ACCEPTED AS FULFILLING PARTIAL REQUIREMENTS FOR THE THESIS IN ZOOLOGY.

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Abstract

Physical traits of 13 pronghorn bucks (Antilocapra americana) were tested for correlation to dominance rank in a herd of 23 individuals that were reintroduced to Antelope Island, Great Salt Lake, on 28, January 1993. Horn length was found to be negatively related to dominance rank with both non-parametric Spearman r correlations and principle components analysis. All other physical traits including horn spread, horn base circumference, prong length, cheek patch dimensions, weight, and hind foot length were not correlated to dominance rank. Interactions were typically initiated by the eventual winner of the bout. Aggressive behavior was used almost equally to gain resources or establish and maintain rank . A new behavior, cheek rub - cheek rub, was also recorded.

Dominance is an attribute of a relationship between two individuals (Barrette and Vandal 1986). Dominance is usually the outcome of aggressive behaviors such as displays, threats, and fights, in which one individual submits or is displaced (Tomback et al. 1989). Many times dominance and rank are confused (Barrette and Vandal 1986). Dominance is control over another individual, whereas rank is defined as a relative position in a population. Dominance is often dependent on the individual's physical traits such as age, size, and horn length. Rank is greatly determined by the make up of the group (Barrette and Vandal 1986). For example, an individual who is the highest ranked in one herd may be ranked fifth in another herd depending on the characteristics of the males that are present. Rank order is also referred to as a dominance hierarchy. These hierarchies are established by aggressive-submissive relationships within the herd, and they are typically linear (Kitchen 1974; Fichter and Autenrieth 1978; Jackson and Winnegrad 1988; Rutberg and Greenberg 1990).

Being a dominant individual can have benefits. In territorial animals, the most dominant individuals hold the best territories, and therefore have higher mating success (Kitchen 1974). Dominant individuals also may have better access to resources such as food and bedding sites by being able to displace subordinate individuals.

Pronghorn (Antilocapra americana) are ideal animals to use in studying dominance hierarchies. Pronghorn are diurnal, they can be observed beyond flight distances, and their grassland and shrub habitat has few obstructions to hinder observations (Bromley 1991).

Pronghorn, as well as many other ungulates, have well-developed social hierarchies (Kitchen 1974; Fichter and Autenrieth 1978). In spring and summer, some pronghorn males establish territories. These territorial males tend to be high in the hierarchy (Fichter and Autenrieth 1978). Other males form bachelor herds in the spring and summer. In winter, fawns, females, bachelor males, and territorial males form large, mixed-sex herds, most likely to increase protection from predators (Kitchen 1974).

Winter observations offer an opportunity to observe relationships among males that may not encounter each other during the rest of the year. Thus, dominance status can be determined in the absence of ownership status. Therefore, winter observations may be used to determine dominance in relation to resource utilization, territorial males versus bachelor males, and the quality of territory held by territorial males.

Dominance rank may be related to physical attributes possessed by the individual. In mule deer and woodland caribou, antler size is related to rank (Barrette and Vandal 1986; Tomback et al. 1989). Kitchen (1974) stated that pronghorn buck hierarchies were based on age and weight. I predicted that horn characteristics and cheek patch dimensions may also be related to dominance rank in pronghorn because both are involved in dominance displays and are secondary sexual characteristics.

My objectives in this study were: 1) to determine if there was a dominance hierarchy present in the herd and check for linearity; 2) to determine if physical traits such as horn characteristics, cheek patch dimensions, hind foot length, and weight were correlated to dominance rank; 3) to determine whether bouts are more often initiated by the eventual winners or losers of the bout; and 4) to determine the context in which aggressive behavior was used.

The horn characteristics I examined were horn length, horn spread, prong length, and horn base circumference. Cheek patch dimensions measured were cheek patch length, cheek patch width, and cheek patch area. Weight, and hind foot length were used as indices of body size.

Methods

On 28 January 1993, 23 pronghorn were captured by the Utah Division of Parks and Recreation and the Division of Wildlife Resources with net guns fired from a helicopter, in Summit County, Utah, for reintroduction to Antelope Island State Park. Antelope Island is located 16 km from Salt Lake City and has an elevational range of 1280-2011 m over its 10,409 ha (Jones 1985; Utah Department of Natural Resources

1988). The island's habitat consists mainly of grassland with patches of sagebrush and minimal amounts of riparian and marsh habitat (Jones 1985). The island is also home to bison (Bison bison), mule deer, coyotes (Canis latrans), bobcats (Lynx rufus), and a large variety of raptors, songbirds, and shorebirds. Of the 23 pronghorn captured, there were 13 bucks, all determined by tooth replacement to be two years or older, and 10 does.

At the time of capture, I measured horns, cheek patch, and body size of all the males using a metric tape measure. Four different horn measurements were recorded: horn length (from the base of the horn to the tip following the curvature on the lateral side of the horn), base circumference, spread (the distance between the tips of the horns), and prong length (from the tip of the prong along its superior edge to where it meets the main horn shaft). The narrowest axis and the widest axis of the cheek patch were measured. Hind foot length (from the knee to the end of the hoof on the posterior side) was measured as a body size index. Twelve of the 13 pronghorn bucks were also weighed, however the accuracy of the weights was questionable due to the use of two different scales that were not equally calibrated. The pronghorn were then tagged with solar-powered radio transmitters mounted on ear tags (Advanced Telemetry

Systems Inc., Box 398, Isanti, MN 55040) and with colored livestock tags for relocation and identification of the pronghorn. The pronghorn were held on Antelope Island for three days for disease testing before their release on 31 January 1993. A male fawn was also released with the other 23 pronghorn, but he was not included in my study.

I conducted behavioral observations three to four days a week for approximately 20 hours a week from 6 February until 11 April 1993. The pronghorn were located using a Telonics radio receiver and a directional antenna. Observations were made using a vehicle as an artificial blind, using natural blinds, or in the open beyond flight distances. Behavioral observations were made using a 15-45 x 60 mm zoom spotting scope and 7 x 35 mm binoculars. Visual identification was based on neck patterns, horn characteristics, cheek patch shape, and tag color. Their physical descriptions were then matched to their radio frequency when the large winter herd began to disperse in the spring.

I recorded behaviors outlined by Kitchen (1974), including: non-contact patterns- 1) orientation, approach, and head lowered walk, 2) stare, 3) lowered head, 4) broadside display, 5) chase, 6) following-driving, 7) forcing up, 8) cheek patch display, 9) rump sniff, touch chest, attempt to mount, mount, 10) snort wheeze or buck roar, 11) urinate-

urinate; contact patterns- 1) butt, 2) touch horns or head, 3) sparring, 4) clashing, 5) fight; and submissive patterns-1) submissive posture - head up horns neutral, ears midway, 2) give way, walk off, run off, head twist, and other moves away.

An all occurrence sampling was conducted of male-male interactions. During my observations, I recorded the date and time they occurred and the individuals present by both radio frequency and sight. When an aggressive interaction occurred, I identified the individuals involved and described the action-reaction sequence. After the interaction I recorded the winner, the loser, and the initiator of the bout. The context of the interaction was also recorded as either a feeding displacement, bedding displacement, or non-displacement. An interaction was considered to be a displacement if a resource, such as food or bedding site, was relinquished to the more dominant individual. If no resources were involved in the interaction, it was considered a non-displacement.

A dominance matrix was constructed from the win-loss data. A hierarchy was developed by placing winners above losers in the matrix (Schein and Fohrman 1955). A coefficient of linearity (Appleby 1983) was calculated for the dominance hierarchy. The degree of linearity of the hierarchy is indicated by the coefficient K. The value of K can range from

1.0 to 0.0 with K=1.0 being the most linear, and K=0.0 showing a lack of linearity (Appleby 1983).

I compared dominance rank to each of the physical trait measurements using the nonparametric Spearman r correlation. A multivariant principle components analysis, including all physical measurements and dominance rank as variables, was used to describe variation among individual bucks and its relation to dominance rank.

I then compared the frequency of winner-initiated bouts to loser-initiated bouts using Chi-square analysis. I also compared the frequency of occurrence of displacements and non-displacement interactions using Chi-square.

Results

The dominance hierarchy, based on 39 interactions, contained three triangular relationships (Table 1). The coefficient of linearity for this hierarchy was low (K=0.06). Only 25 of a possible 78 dyads (32%), were resolved in the 39 interactions I observed, therefore linearity could not be tested statistically (Jackson and Winnegrad 1988).

In the univariant analysis, horn length was negatively correlated with dominance rank (Table 2). Horn base circumference, spread, prong length, cheek patch dimensions, hind foot length, and weight were not correlated with dominance rank (Table 2).

In the principle components analysis, the first principle component loaded heavily on the cheek patch dimensions (Table 3). The second principle component loaded heavily on horn length and dominance rank, with opposite signs. The first and second principle components together accounted for 51% of the variation among the bucks (Table 3).

Out of a total of 37 bouts, 92% were initiated by the eventual winner (X^2=26.0; df=1; P<0.01). Fifty-nine percent of the interactions I observed were non-displacements, and 41% were displacements (X^2=1.3; df=1; P>0.10).

I observed a new interaction not previously reported in winter herds. I named this behavior cheek rub - cheek rub. In this interaction, one buck rubs his cheek patch on a bush. In itself, this behavior has been described and involves the deposition of scent for marking territories (Kitchen 1974). However, I observed that ocassionally another buck marks the same bush immediately after the first buck leaves the bush. If the second buck is dominant, the behavior ends here. If the first buck chases off the second buck and remarks the bush, the first buck is considered the winner. The second buck is always the initiator of the interaction. I observed this interaction on three different occasions. Three different bucks were involved, but the interaction was initiated and won by the same buck on all three occasions. Two of the interactions were considered marking site displacements. The other one was a non-displacement interaction since the first buck had already moved away from the bush, but observed the second buck marking it. All three incidents were observed on 2 and 3 April 1993 in groups that were predominately female, containing nine and fifteen pronghorn, respectively.

Discussion

The dominance hierarchy I constructed was based on only 39 interactions, some of which were repeated interactions of the same dyad. Since only 25 of the possible 78 dyads (32%) were resolved, a statistical test of linearity was not appropriate. Hierarchies with incomplete information have an increased probability of appearing linear (Appleby 1983). Jackson and Winnegrad (1987) suggest only conducting linearity tests on hierarchies in which 80% or more of the dyadic relationships were determined.

Horn length was the only characteristic that supported my hypothesis that physical characteristics are correlated to dominance rank. Horn length was negatively correlated to rank since the most dominant individuals have the lowest rank number and the longest horns. This correlation between horn length and rank is supported by research on other ungulate species such as mule deer and woodland caribou (Barrette and Vandal 1986; Tomback et al. 1989). Longer horns may be beneficial in sparring thus leading to higher rank.

All other horn characteristics, such as spread, base circumference, and prong length, did not support my hypothesis. These other horn characteristics may not increase sparring ability or dominance, but may be attractive to females. Since base circumference varied little between individuals, this may be a possible explanation why it was not related to rank. However there was a high degree of variability in prong length and horn spread among bucks.

The relationship between dominance rank and horn characteristics, as measured in this study, may be confounded by horn sheath shedding. Pronghorn shed their horn sheaths between late October and mid-November each year, thus their horns were still growing when I measured them in January. The time each buck casts his sheaths is related to the cycle of the testes (O'Gara et al. 1971). Territorial males cast their horns earlier than bachelors . Since there is no notable difference in growth rates of horn between age groups (Kitchen 1974), territorial bucks possibly have longer horns through the winter since they have a head start in regrowth .

However, even though there are no differences in growth rates between age groups, there may be differences in growth rates between individuals. Therefore, some individuals can grow longer horns.

Horn sheath shedding may also account for the lack of social interaction in the beginning of my study period (Kitchen 1974). When the horn measurements were taken, their horns were soft and flexible at the tips. Prong length was also affected by the horn sheath shedding. Some of the bucks did not have a prong when we took the measurements, but were noted as developing prongs later in the year. Therefore, these early measurements may not have been very representative of later prong lengths which might have been more related to dominance rank. Since all of the horn measurements continued to grow throughout the winter, it may not be accurate to compare measurements from early winter to a hierarchy based on a majority of interactions from late winter and early spring.

Even though there was a lot of variation in cheek patch dimensions between the bucks, cheek patch dimensions were not correlated to dominance rank. The cheek patch is used to a greater degree in display to females and marking of territories during rut than in winter dominance interactions (Kitchen 1974). The variation in cheek patches may be more important in female mate choice than male-male competition.

Weight and hind foot length were not related to dominance rank. With the weights, the use of two different scales makes my results questionable. There was very little variation seen among bucks in their hind foot lengths. This lack of variation easily explains why rank would not be related to hind foot length. These results are contradictory to some research, while they support others. Kitchen (1974) predicted dominance rank to be based on weight and age. Dominant feral pony mares (Equus caballus) had greater rump heights than subordinant mares (Rutberg and Greenberg 1990). However, rank was poorly associated with height in highland pony (Clutton-Brock et al. 1976), and dominance rank was not related to weight in bison cows (Rutberg 1983).

Principle components analysis allows comparison of all the physical characteristics and rank simultaneously by combining them into one variable and plotting it on a hypothetical axis. The cheek patch dimensions were weighted the most heavily on the first principle component, so cheek patch dimensions accounted for the most variation between the bucks. Rank loaded very little on the first principle component. Even though there was a great deal of difference in cheek patch dimensions, it was not related to dominance. The second principle component shows horn length and dominance rank loaded heavily, but with opposite signs. This shows horn length and dominance rank to be negatively related, so individuals with lower rank numbers tend to have longer horns. These results support the univariant correlation between horn length and dominance and lack of correlation between cheek patch dimensions and dominance.

As among the bucks in this study, more dominant caribou bulls initiated more interactions (Barrette and Vandal 1986). Kitchen (1974) also states that dominant pronghorn bucks initiated 93% of all interactions. Energy costs may explain why eventual winners initiate more bouts. It would cost more energy to attempt to move up in rank than to hold a position, due to the likelihood that he would have to escalate the interaction. Barrette and Vandal (1986) found that when subordinant bucks initiated an interaction it escalated more often than if a dominant individual initiated the interaction. Even though low-ranking individuals escalated the interaction, the success rate was still low.

Context in which winter aggression occurred was fairly evenly divided between displacements and non-displacements. Displacements can serve two purposes. They allow dominant individuals access to better resources and can establish or maintain a dominance relationship at the same time. These displacements may become more important in winters where food and other resources are scarce. The pronghorn on Antelope Island did not appear to be malnourished, and no winter mortality occurred during the study.

One aspect that I think merits further study is the relatedness of dominance rank to plasma testosterone. Initially, I included this in my study, but was forced to abandon this idea due to the lack of funding to pay for the testosterone assays. Testosterone levels may be correlated to dominance rank due to its relationship to other characteristics such as horn growth, size, weight, and pronghorn cheek patch dimensions. All of these characteristics are male secondary sexual characteristics, and therefore are dependent on testosterone for development. Testosterone levels may also be related to an individual's aggressiveness. High levels of testosterone in other animals cause increased aggressiveness (Guyton 1991). Could increased aggressiveness due to high levels of testosterone increase an individual buck's chance of becoming dominant?

Dominance rank is most likely based on a combination of many traits, possibly involving the traits I examined including horn characteristics, cheek patch dimensions, hind foot length, weight, and others such as testosterone levels that I did not include. Determinants of dominance rank are difficult to identify in large, free-ranging mammals. However, such research is important in understanding social organizations and the evolution of sexually-selected traits.

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Table 1. Antelope Island winter buck dominance hierarchy. Rank number increases as you move towards the right or downward in the table. The number of interactions won are listed horizontally, and the number lost are listed vertically. The interactions that occur below the diagonal may indicate triangular relationships between the bucks.

	462	264	333	507	434	536	475	564	445	495	243	391	423	tot. wins
462	-	3	0	0	0	1	0	0	0	0	4	0	0	8
264		-	2	0	2	0	0	0	0	1	1	0	0	6
333			-	0	2	0	0	0	0	0	0	0	1	3
507				-	1	0	0	0	0	0	0	1	0	2
434					-	1	0	0	0	0	0	1	0	2
536						-	2	0	0	1	3	0	0	6
475							-	0	0	1	1	0	0	2
564								-	1	0	0	0	0	1
445									-	1	0	0	1	2
495										-	2	0	0	2
243				1						1	-	1	0	3
391								1				-	1	2
423													-	0
tot. loss	0	3	2	1	5	2	2	1	1	5	11	3	3	39

Table 2: Univariate correlations between winter dominance rank and physical characeristics of pronghorn bucks. The lower the rank, the more dominant the individual.

Physical Characteristic	Spearman r	P
Horn Length	-0.62	<0.05
Horn Spread	-0.10	>0.10
Horn Base Circumference	-0.09	>0.10
Prong Length	-0.14	>0.10
Cheek Patch Length	0.10	>0.10
Cheek Patch Width	-0.49	<0.10
Cheek Patch Area	0.37	>0.05
Hind Foot Length	-0.06	>0.10
Weight	-0.25	>0.10

Table 3: Principle components analysis of pronghorn buck physical characteristics and dominance. PC1 is the combination that explains the most variation amoung the bucks, while PC2 explains the next most variation.

Physical Characteristic	PC 1	PC 2
Weight	0.06	0.29
Hind Foot	0.15	0.29
Cheek Patch Length	0.46	-0.02
Cheek Patch Width	0.50	-0.14
Cheek Patch Area	0.54	-0.11
Horn Length	0.13	0.61
Prong Length	-0.17	0.24
Horn Base Circumference	0.13	0.22
Horn Spread	0.39	0.07
Dominance Rank	0.04	-0.56
Percent of Variation Explained	31%	19%