Influence of social dominance rank on diet quality of pronghorn females

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The relationship between social dominance rank and diet quality was examined in pronghorn (*Antilocapra americana*) females at the National Bison Range in Montana. Rank was ascertained by observation of agonistic interactions between study animals. Diet quality of the same individuals was quantified by measuring the concentration of the chemical indicator of forage quality, 2, 6 diaminopimelic acid (DAPA) present in feces. A significant, quadratic relationship was found in which high-ranked and low-ranked females showed high levels of DAPA, and middle-ranked females showed low levels of DAPA. This finding indicated that high and low-ranked females acquired better quality diets than middle- ranked females. I discuss possible explanations for this interesting result which, to my knowledge, has not been anticipated in the literature. *Key words:* DAPA, diet quality, dominance rank, pronghorn. *[Behav Ecol 12:177–181 (2001)]*

Social animals often aggressively intimidate or attack their conspecifics while competing for limited resources, such as mates or food. Often the outcomes of these interactions are predictable and consistent, which has led many observers to rank animals within a social group according to their competitive abilities. These hierarchies are most often inferred from the outcome of aggressive interactions, such as displays, threats, and fighting, in which one individual submits to or is displaced by another (Tomback et al., 1989). Although social dominance is commonly expressed through individual differences in priority of access to resources, it need not be; often animals contest dominance when there is no tangible resource to be acquired. The results of the pure expressions of dominance are thought to reinforce an animal's dominance status within the group (Byers, 1997).

Social dominance has been documented in many ungulate species, including woodland caribou, *Rangifer tarandus* (Barrette and Vandal, 1986), pronghorn (Fairbanks, 1994), bighorn sheep, *Ovis canadensis* (Festa-Bianchet, 1991), mountain goats, *Oreamnos americanus* (Masteller and Bailey, 1988), reindeer, *Rangifer tarandus* (Hirotani, 1990), and bison, *Bison bison* (Rutberg, 1986). Among most ungulate species, dominance confers advantages such as priority of access to food (Kojola, 1989; Masteller and Bailey, 1988; Prins, 1989; Rutberg, 1986), water (Leuthold, 1977), mates (Leuthold, 1977; Wilson, 1975), and territories (Wilson, 1975). Several factors have been associated with dominance rank in female ungulates, including body mass in reindeer (Hirotani, 1990), age in red deer, *Cervus elaphus* (Thouless, 1990), bighorn sheep (Festa-Bianchet, 1991), and bison (Rutberg, 1986); and antler size in caribou (Barrette and Vandal, 1986) and mule deer, *Odocoileus hemionus* (Tomback, et al., 1989).

Social dominance among pronghorn females is prominent (Byers, 1997; Fairbanks, 1994). Perhaps because they do not form stable, cohesive groups (i.e., group composition is dynamic, and no matrilineal or other social bonds exist), pronghorn females show more aggressive behavior than most other female ungulates (Byers, 1997; Fournier and Festa-Bianchet, 1995). Female pronghorn begin to contest social rank when they are less than one month old and form largely linear hierarchies (although triads do exist) within fawn social-groups by their third month of life (Byers, 1986, 1997). The social rank of each adult female is not based upon age (Fairbanks, 1994; Kitchen, 1974), agonistic interaction rate (Byers, 1997; Fairbanks, 1994), body mass (Byers, 1997), or horn size (Byers, 1997). Instead the rank status that a female attains as a fawn persists for her lifetime (Byers, 1997). Byers (1997) confirmed the stability of the linear hierarchies through focal samples of a number of individuals that he followed throughout their lifetimes. Moreover, rank transcends cohortship; high-ranking, young females may dominate low-ranking, older females. Although group composition changes frequently, the dominance status of individuals remains constant.

In several ungulate species, such as African buffalo, *Syncerus caffer* (Prins, 1989, 1996), bison (Rutberg, 1986), caribou (Barrette and Vandal, 1986), mountain goats (Masteller and Bailey, 1988), and red deer (Appleby, 1980; Thouless, 1990), dominant females have a foraging advantage. Byers (1997) was the first to test for a relationship between a pronghorn female's social rank and her foraging efficiency. He measured foraging efficiency by fine-grained focal observation of foraging behavior, and found that rank did not predict foraging efficiency. These findings present a paradox. Why do pronghorn females contest rank when they receive no advantage in foraging or, to my knowledge, any other benefit? One possible answer is that the observational measures of foraging efficiency (percent foraging time food processing, and processing time per step) failed to detect actual rank-related differences in diet quality. Perhaps subordinate females acquired lower quality diets, which could not be detected by observations of behavior. This hypothesis is plausible because pronghorn are selective browsers; measures of foraging efficiency that rely on processing time ignore possible differences in plant species composition in diet. I tested this hypothesis by measuring a chemical indicator of diet quality in a sample of pronghorn females that spanned a wide range of dominance ranks.

MATERIALS AND METHODS

I studied pronghorn at the National Bison Range (NBR) in northwestern, Montana, USA. The NBR is a 7504 ha National Wildlife Refuge enclosed by a perimeter fence. The plant community on the NBR is endemic prairie with a number of exotic plant species. The elevation range is 770–1490 m. Further descriptive details appear in Byers (1997). I observed the behavior of and collected fecal samples from pronghorn fe-

males from 3 June 1996 to 16 August 1996. The female prong-horn population as of August 1996 numbered 61 females and 46 males. During previous studies, Byers (1997) marked with colored plastic ear-tags 10 of my 19 study individuals. I identified the remaining nine individuals by variation in natural markings.

Pronghorn at the NBR are habituated to vehicles. In a vehicle, I approached groups to within 30 m, then used binoculars or a telescope to verify the identities of individuals. If study animals were present, I conducted all occurrence sampling (Altmann, 1974) of dominance interactions that involved any of them. For each interaction, I recorded the winner and loser, defining loser as the female that ended the interaction by moving away. For eight individuals, I combined my data on dominance interactions with those that Byers (1997) collected in previous years on the same individual females. Because dominance status of individuals is constant throughout life (Byers, 1997), combining data from different years is acceptable. I verified this by comparing the rank of each of these eight females in 1996 to their rank in years previous. All females retained the same ranking regardless of whether I used the 1996 data or the combined data. I ranked each individual by her percent wins in all aggressive encounters. Byers (1997) showed that ranking by percent wins gives the same result as when ranking by the number of other females dominated. Byers (1997) came to this conclusion by calculating the correlation between the percentage of interactions a female won and the proportion of females with which she interacted that she dominated, and running correlations for varying minimum numbers of other interactants (from 3 to 26). In this analysis, Byers (1997) found that all correlation coefficients exceeded 0.91, which shows that percent wins is a sensitive indicator of overall dominance rank.

Frequently, I observed study animals defecating while I was observing social interactions. When a study animal defecated, I mentally marked the site. After the animals traveled a sufficient distance away, I approached the sample on foot and, using latex gloves, collected approximately 20 g of the feces. Because I only collected feces from females I actually observed defecating, and since fresh feces are warm and moist, the likelihood of collecting feces from the wrong female was negligible. I placed the feces into plastic Whirl Paks labeled with a sample number, identification of female, time, date, and location. I stored the samples in a $-30°C$ freezer within 4 h of collection. To control for seasonal variation in forage quality, I collected fecal samples from each female at least once a month during the study period.

I used 2, 6 diaminopimelic acid (DAPA) extracted from the feces to quantify diet quality. The general rationale is as follows: more than 80% of a ruminant's energy from food comes from volatile fatty acids produced by bacterial fermentation in the rumen. DAPA is a cell wall component of nearly all rumen bacteria, and is not found in fungi, yeast, protozoa (Work and Dewey, 1953), animals (Mason and White, 1971) or plants (Czerkawski, 1974; Hutton et al., 1971; Ling and Buttery, 1978; Weller, 1958). DAPA remains attached to indigestible bacterial residues (Mason and White, 1971), and is a constant 4.1% of the dried rumen bacterial mass (Davitt and Nelson, 1984). The concentration of DAPA in feces is an index of the rate of bacterial growth in the rumen and hence is an index of the rate at which energy is delivered to the rumen.

Several authors reported finding DAPA in plants (Czerkawski, 1974; Theurer, 1982), but these studies are likely flawed. Theurer (1982) reported that bacterial contamination of feedstuffs ranged from 8% to 18%, which could account for the DAPA reportedly found in plant matter. Second, each study used regular ninhydrin instead of the more specific acid ninhydrin to elute DAPA. Thus, the DAPA reportedly found in plant material in these studies most likely results from the elution of acids other than DAPA. The absence of DAPA from plant material was confirmed by Ibrahim et al. (1970), Hutton et al. (1971) and Ling and Buttery (1978); all of who used acid ninhydrin instead of regular ninhydrin and found no discernable evidence of DAPA in feedstuffs.

Numerous studies have documented the efficacy of DAPA as an indicator of diet quality. In feeding trials on domestic sheep, *Ovis aries,* Nelson et al. (1982) showed that fecal DAPA was closely correlated with diet digestible energy. Several studies showed that fecal DAPA levels fluctuated to reflect seasonal changes in forage quality in free-ranging moose, *Alces alces* and white-tailed deer, *Odocoileus virginianus* (Leslie et al., 1989), mule deer (Kie and Burton, 1984), and elk *Cervus canadensis,* (Nelson and Davitt, 1984). Kucera (1997) also found that fecal DAPA was significantly correlated with condition indices such as kidney fat index in mule deer. Leslie et al. (1989) showed that fecal DAPA concentration was closely correlated with fecal nitrogen in free-ranging white-tailed deer and moose. Fecal nitrogen is frequently used as an assay of diet quality (Kie and Burton, 1984; Leslie and Starkey, 1987; Wehausen, 1995). Hodgman et al. (1996) examined the relationship between several chemical constituents of mule deer feces (including fecal nitrogen, fecal DAPA, fecal neutral detergent fiber, fecal acid detergent fiber and fecal acid detergent lignin) and diet quality. In trials that controlled digestible energy intake, Hodgman et al. (1996) showed that the indices of microbial origin (fecal DAPA, fecal nitrogen) were the best indices of diet quality.

Finally, the significant seasonal decline in DAPA in my study (see results) suggested that DAPA was a sensitive indicator of diet quality. Population DAPA was highest in late May, when there was much new green plant growth on the NBR, and declined steadily as the summer progressed and forage plants became senescent. Smith and Malechek (1974) also demonstrated across-summer decline in pronghorn forage quality in Utah.

I extracted fecal DAPA according to the protocols established by Davitt and Nelson (1984). I dried and ground each sample. I then hydrolyzed 0.35 g of the ground sample, filtered it through diatomaceous earth to remove particulate debris, concentrated it, and passed it through an ion-exchange column filled with Amberlite resin to extract the DAPA. I reacted the extracted DAPA with acid ninhydrin and determined the DAPA concentration spectrophotometrically.

To ensure that my methodology for measuring the DAPA concentration of the feces of study animals was precise, I repeated the assay on 20 randomly chosen samples and performed a regression analysis of the first against the second results. To assess the relationship between DAPA and rank, DAPA and age, and DAPA and date, I performed simple and polynomial regression analyses of the relevant data. Finally I conducted an analysis of variance (ANOVA) to confirm my results. For the ANOVAs rank was divided into three categories, age into two categories, and DAPA samples into two time periods. All data were analyzed using StatView®5 (SAS Institute, 1998) for Macintosh.

RESULTS

I recorded at least six and as many as 84 aggressive encounters for each study animal. Percent wins ranged from 17% to 94% (Table 1). I collected at least three and as many as 25 fecal samples from each individual, for a total of 167 fecal samples. To measure the precision of the fecal DAPA assay, I repeated the assay on 20 randomly chosen samples. Linear regression

Table 1

Age and rank status of study animals

Female	Age (years)	Age category for ANOVA	Wins	Losses	Percent wins	Rank category for ANOVA
BR[a]	6	1	3	15	17	3
SEP[b]	13	2	9	36	20	3
ON[b]	11	2	19	63	23	3
NEP[b]	13	2	13	40	25	3
ROE[a]	6	1	2	6	25	3
RV[a]	6	1	7	11	39	3
MAR[b]	8	2	33	43	43	2
NG[b]	11	2	38	46	45	2
VY[a]	6	1	12	14	46	2
NIF[b]	11	2	30	33	48	2
RB2[a]	5	1	3	3	50	2
ROG[a]	6	1	6	6	50	2
HAC[b]	10	2	35	32	52	2
EKG[a]	4	1	9	8	53	2
UTE[b]	11	2	37	30	55	2
YB[a]	6	1	12	7	63	1
OC[a]	11	2	6	3	67	1
AB2[a]	5	1	5	2	71	1
RUB[a]	13	2	17	1	94	1

[a] Data collected by Dennehy, NBR (summer 1996).

[b] Combined data from Dennehy, NBR (summer 1996) and Byers (1997).

of first against second results indicated close agreement between results obtained at different times ($r^2 = .95$, $p < .001$).

Forage quality, as indicated by milligrams of DAPA per gram of feces, declined significantly over the course of the study period (Figure 1, $F_{1, 166} = 35.5$, $p < .0001$). The mean DAPA concentration in feces from each female was significantly related to her rank (Figure 2, $F_{1, 18} = 3.7$, $p < .05$). The relationship was best explained by an upwardly concave parabola where high-ranked and low-ranked females showed high levels of DAPA and middle-ranked females showed low levels of DAPA. This indicates that high and low-ranked females con-

sumed higher quality diets than middle-ranked females. As an additional test of this result, I contrasted the high and low-ranked females against the middle-ranked females using an ANOVA, and the results were significant ($F_{1, 19} = 6.01$, $p < .025$).

I found no relationship between age and fecal DAPA concentration ($F_{1, 19} = 0.44$, ns). Dividing age into two categories and running an ANOVA of DAPA versus age supported this result ($F_{1, 19} = 0.35$, ns).

DISCUSSION

As the polynomial regression indicated, high- and low-ranked females excreted significantly greater amounts of DAPA than did middle-ranked females, indicating that they consumed better quality diets. To my knowledge, no other study has presented similar findings, nor has any body of theory anticipated this result. Below, I consider several alternative hypotheses to explain my findings.

Several reports (Appleby, 1980; Barrette and Vandal, 1986; Festa-Bianchet, 1991; Fournier and Festa-Bianchet, 1995; Fraser, 1968; Masteller and Bailey, 1988; Prins, 1989; Rutberg, 1986; Thouless, 1990) indicate that high-ranked individuals acquire better quality resources than do their lower ranked conspecifics. Little explanation is necessary for these findings because, in contemporary behavioral theory, high-ranked individuals are expected reap the benefits of their superior competitive abilities (Wilson, 1975).

The finding that low-ranked females obtained better quality diets than their middle-ranked conspecifics is unprecedented, and begs an explanation. One hypothesis is that subordinate females are able to acquire better quality diets because they spend less time contesting dominance and more time foraging than do their higher ranked conspecifics. Indeed Byers (1997) showed that a pronghorn female's overall rate of dominance striving is weakly influenced by her rank; subordinate females tend to avoid interactions with other females, while dominant females show elevated rates of agonistic interactions with conspecifics. Perhaps this behavioral shift allows low-ranked females to compensate for the loss of priority of access to resources.
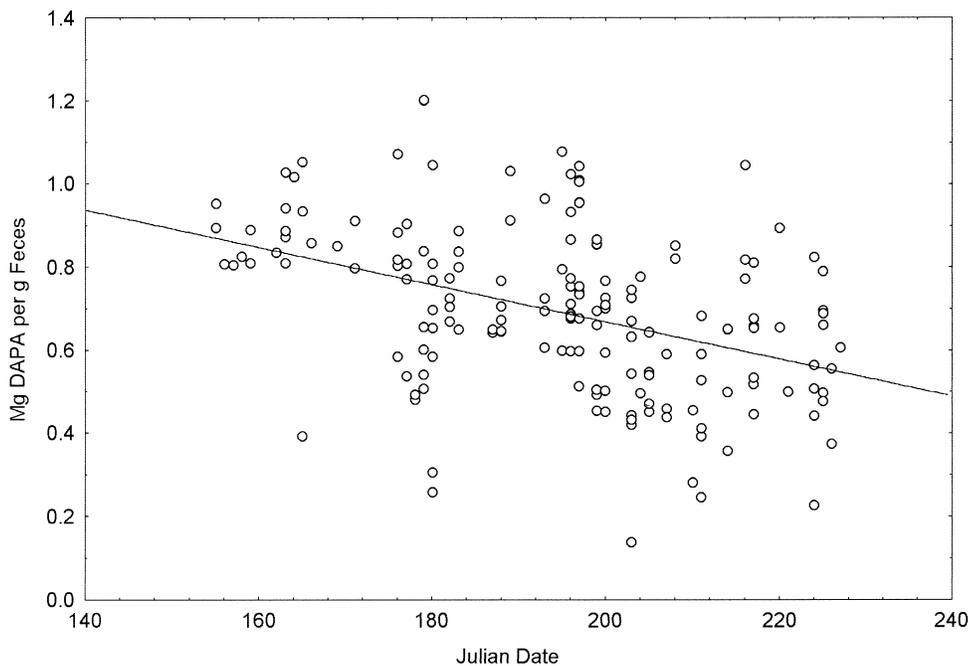

Figure 1

The concentration of DAPA in each sample collected plotted against the date of collection.
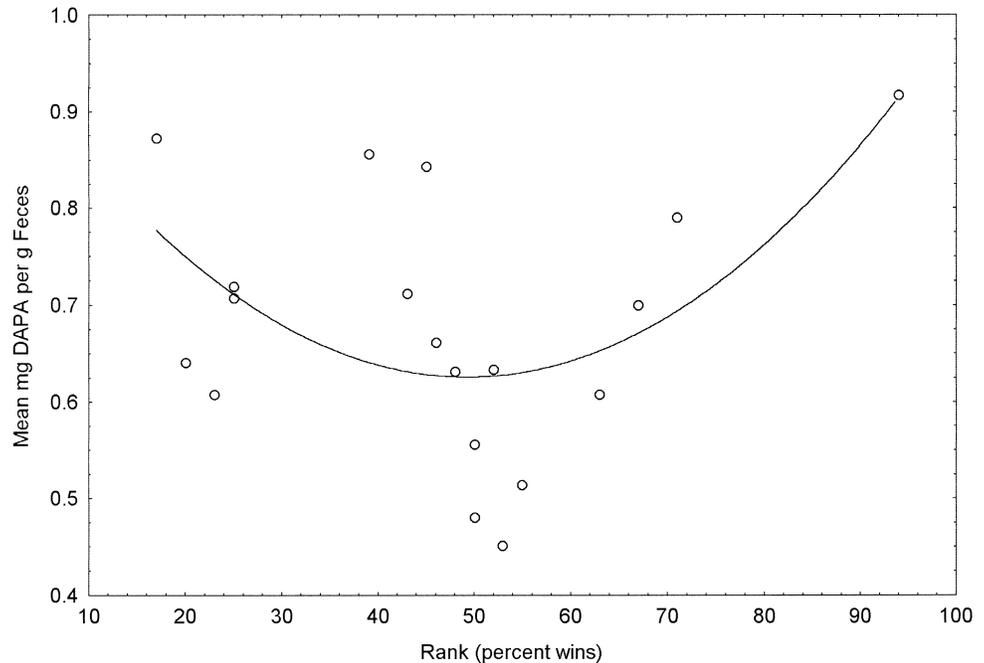
Figure 2
Mean fecal concentration of DAPA for each female plotted against her dominance ranking.

Alternatively, low-ranked females may be those who spend less time being vigilant, thus are able to acquire greater resources than their more vigilant conspecifics. A closer look at pronghorn female activity budgets and the trade-offs associated with vigilance and feeding is required.

Another hypothesis follows the fact that low-ranking female pronghorn are often ostracized from social groups and tend to be entirely solitary. Segregation among habitats may be induced among classes of individuals by dominance, resulting in local or regional geographic segregation of subpopulations (Langen and Rabenold 1994). The consequences of this segregation may result in subordinates acquiring better quality diets because of less competition for forage. Support for this conjecture comes from Baker et al. (1981), who found that socially low-ranked birds performed no better foraging in flocks than alone. In fact, subordinates were often able to acquire more food while foraging alone. For these subordinates, the benefits of foraging in flocks were two-fold: they minimized the risk of predation and reduced the probability of not finding forage at all (Thompson et al., 1974). Since these considerations do not apply to the pronghorn I studied, they too could be acquiring the benefits of being solitary.

In the presence of predators, being solitary could be fatal as pronghorn depend on groups to mitigate their exposure to predation (Hamilton, 1971). However, since pronghorn adults at the NBR presently lack significant predation pressure (Byers, 1997), this strategy may, in fact, be beneficial by reducing exposure to stressful, interspecific aggression and by allowing ostracized females to devote more time to foraging and food processing. In this situation, middle-ranked individuals may be surrendering access to quality forage to their higher ranked conspecifics in return for access to the center of a foraging group, but they are not gaining the benefits of their central position (i.e., reduction of predation). Instead, they suffer the concomitant reduction of diet quality.

In summary, sociality, behavior, and survival are largely context dependent. Contemporary theory works admirably for organisms that are under conflicting, but stable, ecological pressures to acquire food and avoid predators. When conditions are relaxed, social organization and the correlates of dominance may undergo upheaval. Anomalous social patterns may give rise to unusual results, such as my finding that low-ranked females acquire better quality diets than do their middle-ranked conspecifics.

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