

RELATIONSHIPS BETWEEN DIET QUALITY AND FECAL NITROGEN, FECAL DIAMINOPIMELIC ACID AND BEHAVIOR IN A CAPTIVE GROUP OF PRONGHORN.

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Abstract: Both behavior and fecal indices have been suggested as measures of diet quality of wild ruminants; however, their accuracy and applicability in measuring the diet quality of pronghorn have not been evaluated. We investigated the fecal and behavioral response of 10 captive pronghorn females (*Antilocapra americana*) to reductions in the availability of high quality forage. Low quality forage, consisting of over 98% mature cheatgrass brome (*Bromus tectorum*), was available in excess at all times. Intake of high quality forage was reflected in the total fecal output by the group and by the concentration of N and DAPA (diaminopimelic acid) in the feces. Fecal N and DAPA did not accurately reflect changes in body weight. However, fecal N and DAPA may be useful in monitoring trends in the diet quality of pronghorn. The rate of aggressive interactions was inversely related to diet quality. However, the relationship between the time devoted to feeding and the availability of high quality forage was more complex.

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Changes in body condition measures, such as body weight, are expressions of energy and matter balances and reflect attempts by animals to use resources to the best advantage (Gates and Hudson 1981). An accurate measure of diet quality for free-ranging ruminants has proved elusive (Leslie and Starkey 1985; Irwin et al. 1993; Wehausen 1995; Kucera 1997). Considerable effort has been directed towards the development of indices between population condition and diet and fecal nutrient levels (Holechek et al. 1982; Leslie and Starkey 1985).

Fecal nitrogen (N) is correlated with various measures of diet quality such as dietary N, energy, and intake and has been used to assess the quality of diets

of wild ruminants (e.g., Erasmus et al. 1978; Wofford et al. 1985; Osborn and Jenks 1998). However the reliability of fecal N as an index of diet quality may be compromised by secondary plant compounds such as tannins (Rhoades and Cates 1976; Zucker 1983; Freeland et al. 1985; Robbins et al. 1987) which can decrease N absorption and hence elevate fecal N.

Another fecal index is diaminopimelic acid (DAPA). DAPA is an amino acid found almost exclusively in bacterial cell walls (Work and Dewey 1953; Purser and Buechler 1966) and its concentration increases in the rumen pool as a function of increasing bacterial mass (Leslie et al. 1989). Low levels of dietary energy in the diet may limit microbial growth and hence should be detected by decreases in fecal DAPA. Fecal DAPA has been found to vary with season (Mauty et al. 1976; Kie and Burton 1984; Kucera 1997), species of ruminant (Leslie et al. 1989), and intake (Hodgman et al. 1996). Unlike fecal N, fecal DAPA is not thought to be compromised by factors such as secondary plant compounds (Nelson and Davitt 1984).

Implicit in the use of fecal indices is the assumption that daily fecal output is constant or that changes do not affect the concentration of the index in the feces (Leite and Stuth, 1990). However fecal progesterone concentrations in baboons (*Papio cynocephalus cynocephalus*) have been shown to be inversely related to the total fecal output (Wasser et al. 1993). Changes in total fecal output may occur due to either changes in diet composition or forage availability. In the presence of such changes, fecal indices may over- or underestimate dietary quality (Belonje and Van den Berg 1980; Leite and Stuth 1990; Miller et al. 1991; Kucera 1997). No information exists regarding the effect of total fecal output on the concentrations of N or DAPA in the feces of pronghorn (*Antilocapra americana*). Before the accuracy of fecal indices in measuring diet can be fully evaluated more knowledge relative to fecal output is required (Leite and Stuth 1990).

Social and non-social interactions may also influence or be influenced by nutrition. Any organism has a limited amount of resources and time available to devote to foraging, growth, maintenance and reproduction (Pianka 1994). Several researchers have reported increases in foraging behavior (and corresponding decreases in rumination and other behaviors) in various ruminants in response to decreases in forage availability (Arnold 1960a,b 1962; Miller 1971; Geist 1971) and quality (Arnold 1960b, Forchhammer 1995; Kronberg and Malechek 1997). The relationships between feeding and diet quality in pronghorn are largely unknown.

The primary interactions among pronghorn females involve assertions of dominance or aggressive takeover of feeding sites (Byers 1997). In the presence of seasonal variations in food abundance, the rate of agonistic interactions seems to be held constant in pronghorn groups through the modification of group sizes (Byers 1997). If this is the case, then in pronghorn groups of constant size, with temporally varying food abundance, we would expect to see changes in the

rate of agonistic interactions. In other species, under less than optimal conditions, it is often the low ranking animals which first show signs of impaired function such as lowered disease resistance or greater weight loss (Rowell 1966; Demarest et al. 1997). However among pronghorn females no significant fitness advantages of high social rank have been detected (Byers 1997; Dennehy 1997).

The possibility exists that in a species such as pronghorn, in which predation of healthy adults is low (Byers 1997), predator avoidance strategies may have a negligible effect on activity and therefore activity may accurately reflect habitat quality and population health.

The specific questions addressed by this study were: 1) are changes in the availability of high quality forage by pronghorn females reflected in changes in total fecal output, 2) are N and DAPA levels in feces good measures of diet quality in pronghorn females, 3) does the time devoted to feeding by pronghorn females vary inversely with the quality of their diet, 4) does diet quality influence the occurrence of other behaviors in pronghorn females, and 5) does social rank influence the quality of a female's diet?

METHODS

We conducted the study during June, July, and August 1998, at the Foothills Wildlife Research Facility, Fort Collins, Colorado. Ten captive female pronghorn were kept together in a 1.5ha pasture containing a wooden shelter, water and a trace mineral block. The animals ranged in age from seven to three years. All were bottle-raised in captivity. None of the animals were pregnant or had bred in the previous year. The animals' normal diet consisted of ad libitum alfalfa hay (approx. 0.35kg/animal/day) and a pelleted ration (approx. 1kg/animal/day; Baker and Hobbs 1985) fed at 0800h and distributed between 3 and 10 feeding troughs respectively. The pasture vegetation was composed almost entirely of mature cheatgrass brome (*Bromus tectorum*), and was specifically chosen for its unpalatable forage to provide as little additional nutrients as possible while allowing the animals, as far as is possible in captivity, the expression of their full suite of behaviors. The animals had been housed in the pasture in previous years and were allowed to adapt to the pasture for 3 days prior to the commencement of the study and to remove any palatable vegetation.

For sampling purposes, we divided the summer into 5 two-week periods or diets. The study consisted of two restricted feeding levels (75%, 50%) preceded and followed by ad libitum feeding. We measured the intake of alfalfa and pellets during the first ad libitum feeding and used it to calculate, by weight, the 75% and 50% feeding levels. The first week of each diet was an adjustment period (the first adjustment period was shortened to 3 days as the only change in their normal diet/lifestyle involved a change of pasture and the increased presence of a keeper in the field) and the second week was the sampling period during which time we measured, as described below, the forage composition, each animal's

body weight and behavior, and daily fecal output by the group. We also collected fecal samples from each animal.

We monitored the composition and abundance of pasture vegetation at weekly intervals using the canopy cover method (Daubenmire 1959). Forty 20 x 30cm plots were evenly spaced throughout the pasture and marked by tent pegs driven level with the ground. We then estimated the area of each plot, and hence the total pasture area, occupied by bare ground, cheatgrass, and non-cheatgrass forages.

The animals had previously been trained to stand on a platform for weighing and were weighed between 0500 and 0600h on the first day of the study and on the final day of each diet.

We collected samples of alfalfa and pellets in the middle of each sampling week and froze them for future analysis of nitrogen in the Wildlife Habitat Laboratory at Washington State University. We analyzed nitrogen levels using the Kjeldahl method according to AOAC guidelines (1990). We estimated dietary nitrogen (N) for the group each day based on the N content of the pellets and alfalfa. No estimate could be made of the contribution of pasture vegetation to dietary N intake.

We collected fecal samples during each sampling week. During observation periods, defecation by individuals was recorded and, after the animal had moved a sufficient distance away to prevent undue disturbance, we collected approximately 20 grams of feces using forceps or latex gloves. The samples were stored in plastic Whirl Pak™ bags at -20°C within 4 hours of collection and later analyzed for nitrogen and DAPA (according to Davitt and Nelson 1984). Where possible, one fecal sample was collected per animal per day and only the last 3 fecal samples collected per diet from each animal were analyzed.

We monitored the daily total fecal output of the group by hand collecting and weighing all feces in the pasture prior to feeding the animals at 0800h. To test the accuracy of total fecal output estimates, an independent observer, at times unknown to the collector, watched the animals defecating and on a diagram noted the position of the sample in the pasture. The following morning, after the collection of feces from the pasture was completed, the number of missed samples was recorded. We calculated the total amount of N and DAPA excreted by the group per day by multiplying the mean fecal N or DAPA concentration (g/kg) for a particular day by the total amount of feces (kg) collected on that day.

We collected activity budget data during sampling weeks between 0600 and 2100h using instantaneous point sampling at 5-minute intervals for 1hour periods (Altmann 1974). Over the course of each sampling week a total of 45 hours of observations were collected and these consisted of three replicates of each hour (e.g., data was collected between 1500 and 1600h 3 times during

each sampling week). The total time spent Feeding, Reclining, and engaged in Other activities was measured. Feeding was further divided into feeding on alfalfa, pellets, or pasture vegetation. Other was further divided into moving, standing, interacting with others, and miscellaneous behaviors such as drinking and using the salt-lick.

All occurrence sampling of social interactions followed protocols established by Byers (1997). We noted the identity of animals involved in interactions and the loser was determined as the animal which conceded the resource in dispute or moved away. We recorded the form of the interaction as either nudge, spar, or butt and the interaction as either bedded, feeding, or simple displacement. Bedded displacement was recorded if an animal was forced to rise from reclining by another animal. Feeding displacement was recorded if an animal was forced to cease feeding by another animal. Simple displacement was recorded if no resource appeared to be contested.

We first calculated the dominance rank for each animal based on the percent of interactions won by each animal. However the dominance rank of an animal, calculated in this manner, may be elevated if she avoids interactions with animals dominant to her (Byers 1997). Hence we used a second method in which we ranked each animal depending on the number of animals which were subordinate to her minus the number which were dominant over her (DeVries 1993). We then evaluated the observed relationship between adjacent animals and if it was contradicted by that of the ranking scheme the position of the adjacent animals was switched. We compared the two resulting ranking schemes and the ten animals were then categorized as either high, intermediate, or low ranking animals.

Our analysis was limited by the fact that some variables could only be measured per animal (e.g., body weight, behavior) and some only for the entire group of animals per day (e.g., intake of high quality forage, dietary N, total fecal output, total fecal N, total fecal DAPA). Some variables could be calculated either per day or per animal (fecal N, fecal DAPA). We used Duncan's multiple range test to test for differences in each variable between diets. Unless otherwise stated a significance level of $\alpha = 0.05$ was used. We examined plots of residuals to ensure that data met the statistical assumptions. We used backward stepwise regression procedures of SAS (1990) to determine the combination of independent variables that best explained variation in the dependent variables. Variables were left in the models at a significance level of 0.1 unless otherwise stated. It should be remembered that the same animals were sampled repeatedly during the study. Therefore the p-values obtained in these analyses may be overly liberal i.e. significant relationships may be found where none exist. Spearman's correlation coefficient was used to test the relationship between the social rank of an animal and her age.

RESULTS

Relationship between Intake and Output

Daily intake of high quality forage (pellets and alfalfa) and dietary N by the group of ten animals during the last 3 days of each diet differed significantly among all diets (Table 1; Fig 1). The proportion of fecal samples missed by the collector was found to be <1.5% (N = 42 pellet groups). Daily fecal output by the group also differed significantly with diet (Table 1; Fig 1). Daily fecal output (Output) by the group was related to their daily high quality forage intake (Intake) by the equation: Estimated Output = 3.01 + 0.507 Intake, ($R^2 = 0.569$, $P = 0.0012$, $N = 15$). Intake of pasture vegetation could not be measured during the study and hence its contribution to dietary N and fecal output remain unknown. However, from our observations, the animals only ingested very small quantities of the pasture vegetation with non-cheatgrass forages being preferred. We estimated that non-cheatgrass forages accounted for less than 0.5% of the total pasture area and less than 0.6% of the total vegetation cover in all diets, except in the first ad libitum when non-cheatgrass forages accounted for 6.5% of the total pasture area and 7.2% of the total vegetation. Throughout the study, bare ground and cheatgrass accounted for >10% and >75% of the total pasture area, respectively.

Diet Quality and Fecal N, DAPA

All but two animals lost weight during the 75% diet. By the end of the second ad libitum diet only two animals were more than 0.6 kg lighter than at the start of the study. All others were within 0.6 kg of their original weight (first ad libitum) or had exceeded it. By the end of the third ad libitum diet, all animals had regained weight lost during the 50% diet and all were heavier than at the commencement of the study.

Duncan's multiple range test identified significant differences in dietary N and in the mean fecal N and DAPA levels per animal per diet (Table 1; Fig 2). Body weight was only very poorly ($r^2 = 0.085$ $P = 0.1251$ $N = 50$) described by the equation: Estimated Body weight = 37.643 + 4.222 * (fecal N) – 8.934 * (fecal DAPA). We calculated mean daily fecal N and DAPA concentrations for the group for each of the last 3 days of each diet. We also calculated the total amount of fecal N and DAPA excreted, on those days (Fig 2). Caution should be used when interpreting mean daily values because it was not always possible to collect a fecal sample from each animal every day, hence the mean fecal N and DAPA levels for some days are based on samples from 7, 8, or 9 animals instead of 10. The best fitted line for daily dietary N ($r^2 = 0.194$ $P = 0.0014$ $N = 15$) using the variables measured per day, fecal N, fecal DAPA, total fecal N, and total fecal DAPA was found to be: Estimated Dietary N = - 4.97 + 2.264 * (fecal N) + 0.04387 * (fecal DAPA), where variables were left in the model at a significance level of $\alpha = 0.05$.

Table 1. Duncan's multiple range tests for significant differences in behavior and fecal indices with diet.

	Ad. Lib.1	75%	Ad. Lib. 2	50%	Ad. Lib. 3	Sample size	d.f.
Intake	A	B	C	D	E	N= 15	8
Dietary N	A	B	C	D	E	N= 15	8
Output	A	A	B	A	C	N= 15	8
Body weight	A	B	A	B	C	N=50	36
Fecal N ^a	A	B	A	B	A	N=50	36
Fecal DAPA ^a	A	B	A	C	B	N=50	36
Fecal N ^b	A	B	A	C	A	N=15	8
Fecal DAPA ^b	A	B	C	D	B,C	N=15	8
Total fecal N ^b	A	A	B	A	C	N=15	8
Total fecal DAPA ^b	A	A	B	A	C	N=15	8
Feeding	A,B	B,C	C	A	A,B	N=50	36
Reclining	A	A	A	A	B	N=50	36
Other	C	B	A	C	A,B	N=50	36
Feeding (pasture)	A	A	B	C	A	N=50	36
Other (standing)	A	B	C	D	C	N=50	36
Interactions	A,B	B	B	B	A	N=50	36

^a measured per animal, ^b measured per day.

N=50 Fecal N etc. values of all 10 animals * number of diets

N=15 Mean fecal N etc. on each of 3 days of each diet * the number of diets.

Significantly different diet means are assigned different letters

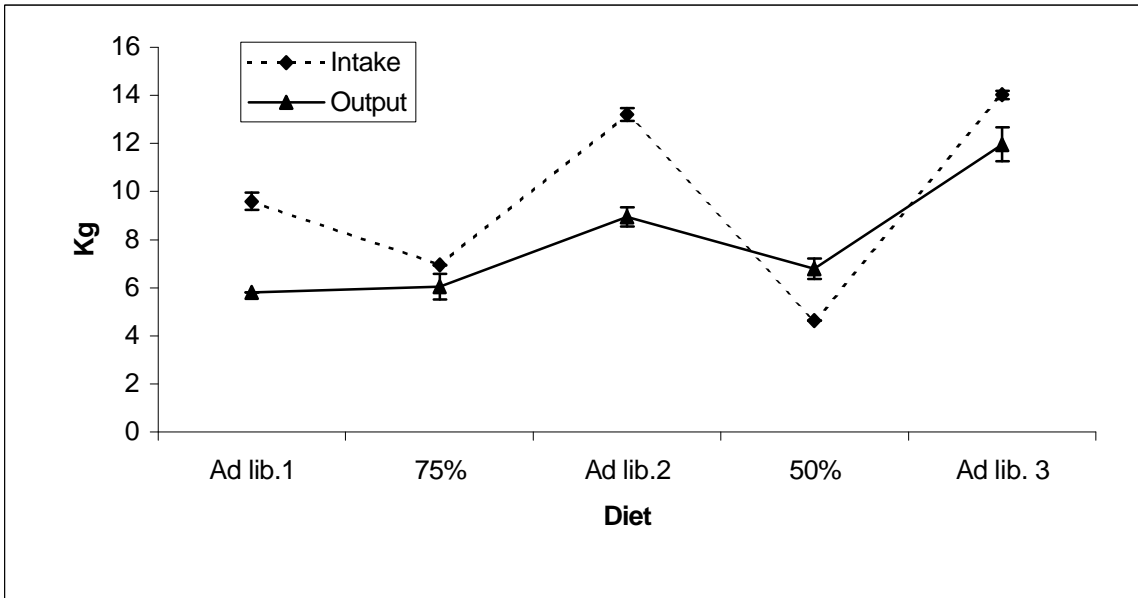


Figure 1: Mean daily fecal output and mean daily intake of high quality forage (pellets and alfalfa) with diet. Bars represent standard errors.

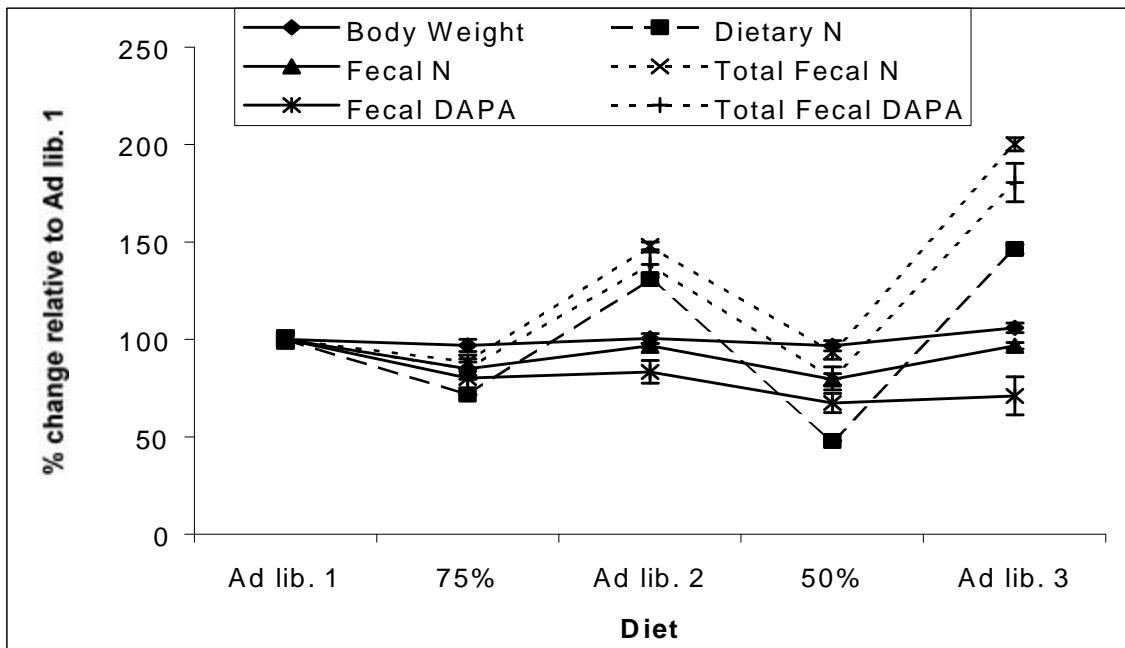


Figure 2: Measures of diet quality in pronghorn compared. All measures, except body weight, were calculated as the mean daily values for the group per diet. Body weight is the mean body weight of the group at the end of each diet. Bars represent standard errors.

Feeding, Reclining, and Other activities

Feeding on pasture vegetation accounted for over 51% of total feeding in all diets except during the second ad libitum diet when feeding on pasture decreased to 30%. Feeding and Other activities differed significantly with diet (Table 1; Fig 3).

Standing accounted for over 63% of Other activities during all diets. Feeding, Other, and Reclining activities were related by the equation: Estimated Feeding = 12.05 - 1.01 * (Other) - 1.01* (Reclining), ($r^2 = 0.998$ P = 0.0001 N = 50). Differences in body weight, fecal N per animal, and fecal DAPA per animal did not explain variation in Feeding, Other, or Reclining activities, as all were removed from the model at the significance level of $\alpha = 0.1$.

The total number of interactions in the third ad libitum diet was significantly lower than all other diets except ad libitum 1 (Table 1; Fig 4). Simple displacement was most often the cause of interactions (51%), while feeding displacement (44%) and bed displacement (5%) accounted for the remainder. Interactions most often took the form of nudging, which accounted for over 75% of all interactions. Of the three diet quality measures, dietary N, fecal N, and fecal DAPA, only the relationship between the total number of interactions per animal and fecal N approached significance: Estimated total interactions = 85.669 - 19.227 * (fecal N), ($r^2 = 0.14$, P = 0.079, N = 50).

Effects of Dominance

We found close agreement in the dominance ranking schemes identified by the two methods used. Dominance status was unrelated to age (Spearman's correlation coefficient P > 0.38, N=10), social and non-social behaviors, body weight, fecal N, and fecal DAPA (Repeated measures ANOVA, P > 0.05, N = 50).

DISCUSSION

Ad libitum intake increased during the study. Several possible reasons exist for this. First, the duration of the second and third ad libitum diets may have been insufficient to allow full recovery of the animals from the preceding restriction diets. However, body weight changes do not seem to support this conclusion as almost all animals had regained, or added to, their pre-restriction weight. Alternately the increase observed could have been a reaction by the animals to the sudden unpredictability of high quality forage availability.

A second possibility is that pasture vegetation may have contributed more to the diet than initially thought. Non-cheatgrass forages were in greatest abundance during the first ad libitum diet. Hence ad libitum intake of pellets and alfalfa during the first diet may have been depressed. However, non-cheatgrass forages remained at negligible levels for the remainder of the study and therefore cannot explain the differences seen in ad libitum intake.

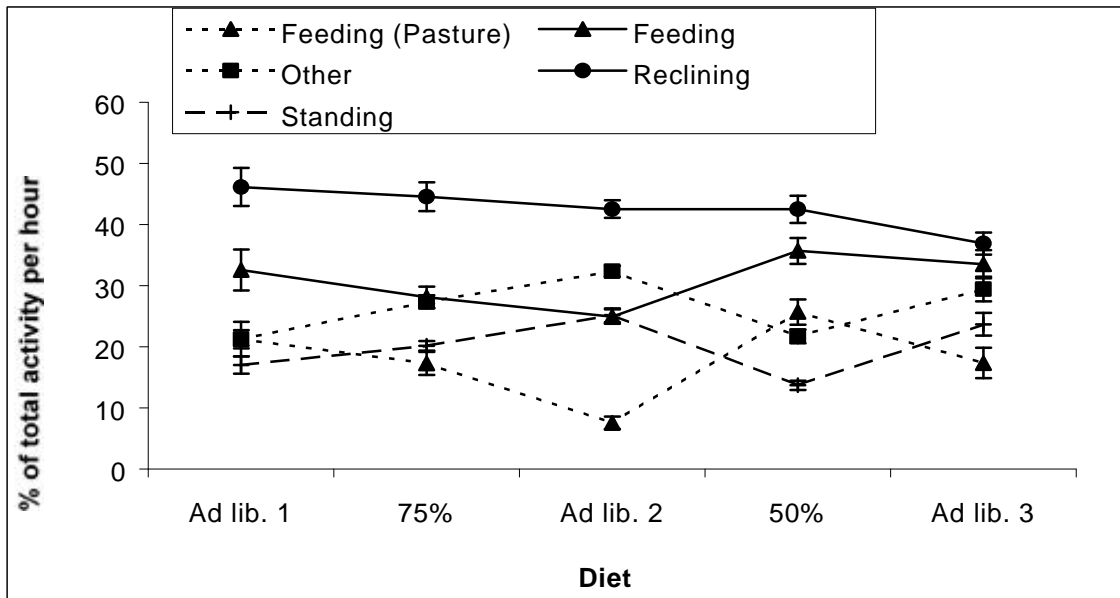


Figure 3: Change in non-social behaviors with diet. Bars represent standard errors.

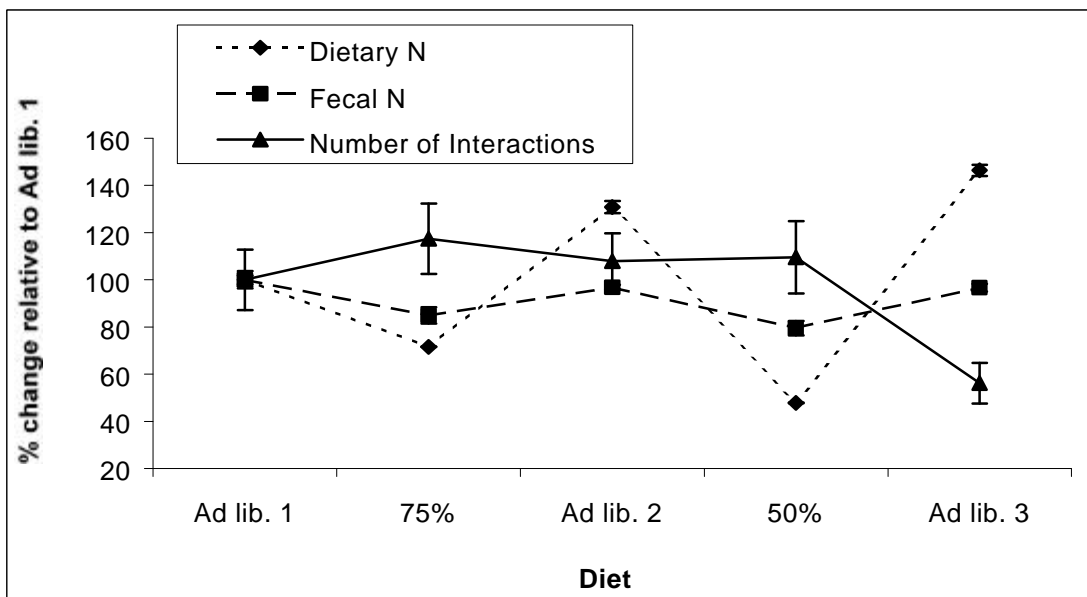


Figure 4: Change in rate of interactions with diet. Bars represent standard errors.

Third, daily temperature may have influenced intake. High summer temperatures have been shown to reduce intake in captive white-tailed deer (Wheaton and Brown 1983). Daily temperature means for each of the diets were 63.5, 72, 75, 69, 79⁰ F respectively. As the first ad libitum diet coincided with the coolest mean temperature and the third ad libitum diet with the highest, if temperature influenced intake, we would expect the opposite relationship to that observed. Hence temperature is not thought to be responsible for the changes seen in intake.

Fourth, seasonal variations in intake and body weight have been documented in many ruminant species (e.g. Ozoga and Verme 1970; Loudon 1991), even in captivity where food is provided ad libitum in pens (Moen 1978; Wheaton and Brown 1983; Wild unpublished data). Intake for non-reproducing female white-tailed deer has been shown to reach a minimum in early June and peak in December (Moen 1978). Therefore, dietary intake may have increased over the summer as part of normal seasonal variation.

We found a significant relationship between daily fecal output and intake of high quality forage. In this study the availability of high quality forage was limiting but at no time were the animals limited in their access to forage per se due to the presence of pasture vegetation. Palatability of forages has been shown to influence intake, and limitations to intake, due to palatability, are known to differ between animal species (Dynes 1996). Therefore, in pronghorn, forage palatability, and not simply its availability, may be of greater importance and hence fecal output may be more variable in pronghorn than in less discerning ruminants. A cholesterol metabolite, cholestanone, in the feces of female baboons is positively correlated with dietary fiber and Wasser et al (1993) suggested that, in the presence of profound variations in dietary fiber, it may be appropriate to express fecal progestogens, and presumably other fecal measures, by cholestanone concentrations. We did not test for the presence of cholestanone in pronghorn feces.

Fecal N and DAPA levels were poor predictors of body weight but moderately good predictors of daily dietary N. The inability of fecal N and DAPA to monitor body weight agrees with findings by Kucera (1997). Kucera (1997) suggested that fecal indices reflect what an animal ate recently and body condition measures, such as body weight, reflect dietary and energetic factors over months or even between seasons. Therefore, it may be naive to expect fecal indices measured over short periods of time to reflect population condition at that time. Kucera (1997) did find that fecal N and DAPA reflected growth of vegetation and this seems to be supported by our findings that fecal N and DAPA are related to dietary N. We may have found a stronger relationship between dietary N and fecal N and DAPA had the contribution of pasture vegetation been included in our estimates of dietary N. Expressing fecal N and DAPA levels as the total amount excreted by the group did not improve the predictive equations. This may suggest that N and DAPA excretion rates change in response to

changes in fecal output and hence their concentrations in the feces are independent of changes in fecal output.

We hypothesized that the time devoted to feeding would be inversely related to the availability of high quality forage. This however was not the case. The time devoted to feeding during the 75% diet appears to have been limited by the time devoted to standing. One possibility for this limitation is that the 75% diet coincided with the fourth of July celebrations. Events such as a hot air balloon race and fireworks may have lead to a heightened alertness among the animals resulting in them spending more time standing and alert. Alternately, when on the 75% diet, the best energetic strategy for the animals may have been to conserve energy. The 50% diet may have been sufficiently severe that they could not conserve enough energy by standing and so were forced to forage resulting in the feeding/standing pattern observed. The results of this study suggest that there is a threshold level of nutrition at which feeding behavior is modified.

In wild pronghorn groups, interaction rates appear to be relatively constant (Byers 1997). We found that the total number of interactions did appear to vary with diet and were best described by fecal N levels ($p = 0.079$). Similar to findings by Byers (1997) high ranking females appear to have slightly, although non-significantly, elevated rates of interactions relative to subordinates. This suggests that subordinates may avoid interactions and/or dominant animals may seek interactions. No clear relationship occurred between rank and body weight, dietary N, or fecal indices. This suggests that high social status does not confer greater fitness on the individual and agrees with results of previous studies (Byers 1997; Dennehy 1997).

MANAGEMENT IMPLICATIONS

The results of this study suggest that the assumption of constant total fecal output, in selective feeders such as pronghorn, may be invalid. Further research should focus on measuring more fully the relationship between intake and fecal output levels, the existence of such a relationship in the wild, and the influence of this relationship on specific fecal indices. Based on the results of this study it appears that fecal N and DAPA may be useful in monitoring diet quality in pronghorn. However, the resultant effects of diets of varying quality on the health of wild pronghorn populations requires further study.

The rate of energy intake (or feeding) has been suggested as a measure of the relative fitness of a forager (Hanks 1981; Morse and Fritz 1987). If, as suggested by the results of this study, there is a threshold level of nutrition at which feeding behavior is modified then the measurement of feeding or any other behavior as an index of diet quality may only be possible where extreme or sudden changes in diet quality occur.

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