A TEST OF LONG-TERM FECAL NITROGEN MONITORING TO EVALUATE NUTRITIONAL STATUS IN BIGHORN SHEEP

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Abstract: We analyzed 23 years of monitoring data from a bighorn sheep (*Ovis canadensis*) population to determine whether fecal nitrogen (FN), expected to reflect diet quality, can be used to track population nutritional status over the long term. We considered 3 measures of FN: its maximum value each spring (FN peak), the date of the peak, and the area under the curve relating julian date to summer FN (FN-total). We first determined the sources of variation in these 3 measures. Population density had a strong negative effect on FN-total while summer precipitation was positively related to FN-total, suggesting that diet quality declined with increasing density and improved with precipitation. Most sheep were recaptured every year, allowing us to assess FN as an indicator of nutritional condition by examining the relationships between summer mass gain and both FN peak and FN-total. The value of FN peak was not related to summer mass gain for any sex–age class, but FN-total was positively related to summer mass gain of nonlactating females and yearling females. Our results suggest that FN can be used as an index of forage quality over several years. Over several years, FN also reflects aspects of bighorn sheep body growth and is correlated with changes in density that may ultimately affect population performance. Short-term monitoring of FN, however, may not provide much useful information.

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A central concern in wildlife management is the assessment of how changes in population density affect population nutrition. Directly monitoring population size is difficult and costly (Gaillard 1988). Even when an effective census method is available, the relationship between population density and carrying capacity is difficult to determine because of possible time lags, interactive effects of density and weather, and nonlinear relationships between density and recruitment (Sæther 1997; Gaillard et al. 1998, 2000). Consequently, managers have used various indices to monitor individual condition, including body mass (Maillard et al. 1989, Gaillard et al. 1996), various blood parameters, several measures of fat content, and other physiological measurements (Ozoga and Verme 1978, Swihart et al. 1998). Body mass, however, may be subject to time lags and may not reflect current habitat condition (Sams et al. 1998). In addition, many of these indices require capturing or killing animals. Ungulate population dynamics often are correlated with changes in density and weather (Sæther 1997, Gaillard et al. 1998), both factors that may affect population growth through their effects on food resources. Dietary improvements can have a positive influence on pregnancy rates (Robinson 1996, Cook et al. 2001), size and viability of newborns (Sæther and Heime 1993, Robinson 1996), and milk yield (Hudson and Adamczewski 1990). An index of nutritional status would therefore be useful to monitor ungulate populations. Because fecal samples are easy to obtain and may reflect food quality, considerable attention has been devoted to potential fecal indices of nutritional status. Fecal nitrogen often has been calibrated in trials at the individual level (Hebert 1973, Brown et al. 1995, Hodgman et al. 1996) and has been commonly used to assess seasonal variation in food quality (Leslie and Starkey 1985). Brown et al. (1995), however, pointed out that further studies exploring the relationship between fecal indices and population parameters are "essential to validating indices as management tools." Some studies examined the relationship between mass gain and FN in captive animals (Gates and Hudson 1981, Holechek et al. 1982) while others measured the correlation between population

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density and FN (Sams et al. 1998, Asada and Ochiai 1999).

Very few studies, however, have tested the reliability of FN as an indicator of nutritional status over several years for 1 population (but see Kucera 1997). We analyzed 23 years of FN data in a marked bighorn sheep population to assess whether FN can be used to track population nutritional status over the long term. We expected that both sheep density and weather would affect year-to-year variation in FN. Because most of the individuals in this population were recaptured every year (Festa-Bianchet et al. 1996), we compared summer mass gain with 2 measures of FN to assess the reliability of FN as an indicator of nutritional status.

METHODS

Study Area and Captures

We studied bighorn sheep at Ram Mountain, Alberta, Canada (52°N, 115°W; elevation 1,700–2,200 m), an isolated outcrop about 30 km from the main Rocky Mountain Range. Since 1971, sheep have been captured in a corral trap baited with salt from late May to early October. Over 90% of sheep older than 1 year have been marked since 1975. We weighed captured sheep to the nearest 250 g with a Detecto spring scale (Cardinal Scale Manufacturing, Webb City, Missouri, USA). Ewe reproductive status was determined by udder examination at capture and by observing lambs suckle from marked ewes. Further details about the study area and capture methods are in Festa-Bianchet et al. (1996). We collected data for our current study from 1977 to 2000.

Sample Collection and Measures of Diet Quality

We collected fresh and clean fecal samples from sheep older than 1 year during captures or in the field. Collection dates were spaced <18 days apart until 19 June, and <1 month apart until mid-September. We considered only samples collected 31 May–18 September (n = 32–181 samples/year) to maximize the number of years that could be included in the analyses. These dates correspond approximately to the time of year during which bighorn sheep gain mass in our study area (Festa-Bianchet et al. 1996). We air-dried samples in paper bags and determined total nitrogen content by the Kjeldahl method (Drew 1970).

To develop an index of nutritional quality over most of the period when sheep gain mass, we estimated the area under the curve relating Julian date to the natural log of FN content from 31 May to 18 September (Fig. 1). That area represents {$\log_e$ [fecal nitrogen]-days}, and we refer to it as "FN-total." We used the $\log_e$ of FN to linearize the relationship between FN and apparent digestibility (Wehausen 1995).

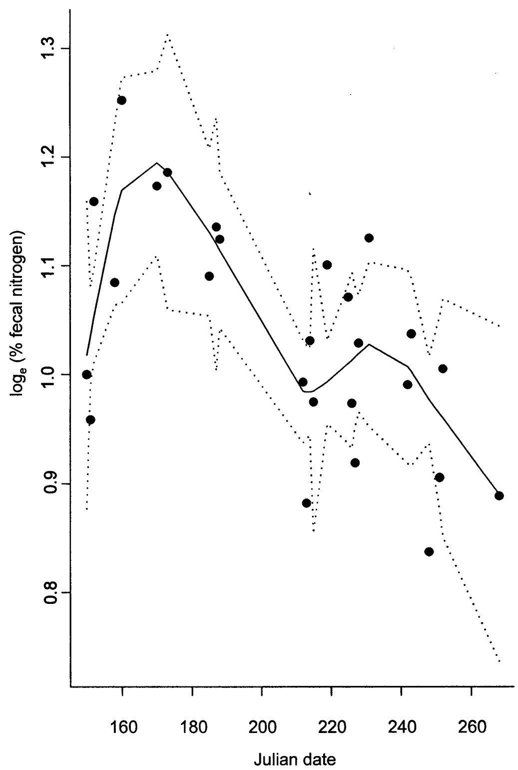

Fig. 1. The nitrogen content of bighorn sheep feces during summer 1995 at Ram Mountain, Alberta, Canada. The solid line is a cubic spline smoother, the dotted lines show the 95% CI. Each point represents the average nitrogen content of fecal pellets collected from 1 to 12 sheep during a single day.

We used 3 annual measures of diet quality: FN peak, the date of the peak, and FN-total. Because many studies emphasize the role of spring nutrition on population parameters (e.g. Festa-Bianchet 1988*a*, Côté and Festa-Bianchet 2001), we determined the peak value of FN and the date of that peak each year. We expected that the date of FN peak would be correlated with onset of green-up, while the peak FN value would reflect vegetation quality during the spring green-up. We used cubic spline smoothing (Shipley and Hunt 1996) to estimate the maximum of the curve (therefore, the FN peak on the y-axis and its date on the x-axis). We calculated FN-total each year using an image analyzer and Agvision software (Decagon Devices, Pullman, Washington, USA).

We did not consider FN-total for 1 year when sampling began after 31 May and 1 when the last collection was before 18 September. The FN peak was calculated for those 2 years, but not for 6 years when FN content was already decreasing by 31 May, suggesting that the peak may have occurred before the first samples were collected. Samples collected in 1987 were excluded from all analyses because FN values were abnormally low and had an unusual seasonal pattern compared to other years. We suspect that problems occurred with the laboratory analyses of samples collected that year.

Density and Weather Data

Because population density and weather can affect vegetation quality, we expected them to influence our 3 measures of diet quality. We used the number of adult ewes in June to measure population density, consistent with previous studies of this population (Jorgenson et al. 1998) and with other studies of sexually dimorphic ungulates (Kruuk et al. 1999, Côté and Festa-Bianchet 2001).

We assessed the relationships between FN-total, FN peak, and peak date (dependent variables) and population density, temperature, and precipitation (independent variables) using linear or natural logarithmic regressions. Because of missing weather data, fewer years were available to analyze the effects of weather than those of population density.

Weather data were collected by Environment Canada at Nordegg, Alberta, about 20 km west of our study area, at 1,326 m elevation. We examined the relationships between spring weather (15 May–10 Jun; total precipitation and average daily maximum temperatures) and FN peak and peak date. We used precipitation and temperature data over a longer interval (1 May–31 Jul) to analyze weather effects on FN-total, which should be affected by vegetation quality over much of the summer.

Mass Gain

We used the rate of summer mass gain as a measure of nutritional status. Autumn body mass correlates with winter survival for lambs and old ewes (Festa-Bianchet et al. 1997) and with ewe reproductive success (Festa-Bianchet et al. 1998).

To assess the reliability of FN as an index of nutritional status, we first examined the relationships of FN-total and FN peak to mass gain from 5 June (15 Jun for lambs) to 15 September for lambs, yearlings, and rams aged 2–3 years. We adjusted mass to these dates for each individual from repeated captures (Festa-Bianchet et al. 1996) and compared average gain to FN values using linear regressions. Older rams rarely are caught more than once a year, and therefore we could not estimate their mass gain. Summer mass gain by individual ewes was negatively correlated with mass on 5 June (Festa-Bianchet et al. 1996). Consequently, for ewes, we compared our 2 measures of FN with the residuals of the regression of summer mass gain on mass on 5 June. We distinguished ewes according to whether or not they were lactating. To account for within-year variability in adjusted mass gain, we also compared FN-total and average yearly mass gain weighed by the inverse of its variance. We performed statistical analyses using S-plus (Venables and Ripley 1999).

RESULTS

Interannual Variability in Fecal Nitrogen

Excluding the 6 years when FN peak occurred before sample collection started (27–29 May), the average date of FN peak was 21 June (n = 17 yr). The latest peak occurred in 2000, on 8 July.

The mean value of FN peak was 3.56% (range: 3.09–4.50%; n = 17 yr, CV = 8.3%). The average value of FN-total was 114.2 (range: 95.9–129.3; n = 21 yr, CV = 7.6%).

Population Density and Weather

We found that FN peak date was later with cool spring temperatures (n = 13; r^2 = 0.61, P = 0.002, slope = –2.31 ± 0.5 [SE]) and higher spring precipitation (n = 13; r^2 = 0.24, P = 0.092, slope = 0.09 ± 0.05). The date of FN peak did not vary with population density (P = 0.59). The value of FN peak was not correlated with temperature, precipitation, or population density (all $P > 0.15$).

FN-total showed a strongly negative relationship with population density (Fig. 2), while it was positively correlated with FN-totalsummer precipitation (n = 14, r^2 = 0.37, P = 0.02, slope = 0.05 ± 0.02). We found no correlation between FN-total and temperature (P = 0.36).

Mass Gain

The value of the FN peak was weakly related to average summer mass gain for nonlactating ewes (r^2 = 0.25, n = 14, P = 0.07, slope = 2.38 ± 1.12), but we found no significant relationships for any

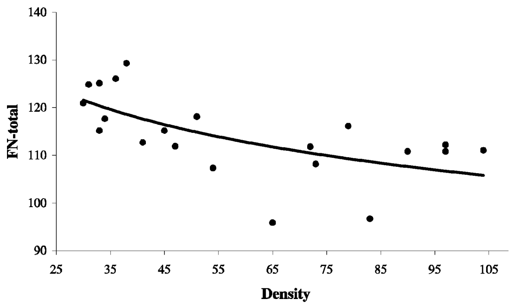

Fig. 2. Fecal nitrogen-days (FN-total; area under the curve relating fecal nitrogen content to Julian date) compared to the number of adult females in the Ram Mountain (Alberta, Canada) population of bighorn sheep, 1977–2000. Each point represents 1 year ({y = 164.7 – 12.7 [SE = 3.5] log[x]}; r^2 = 0.41, F = 13.1, P = 0.002, n = 21).

other sex–age class ($P > 0.15$). The value of FN-total was positively correlated with average mass gain by yearling females (n = 21; r^2 = 0.26, P = 0.02, slope = 0.0016 ± 0.001) and nonlactating ewes (Fig. 3). However, FN-total was unrelated to average summer mass gain of other sex–age classes ($P > 0.38$). We obtained very similar results to those presented in Fig. 3 when data on mass gain were weighed by the inverse of their variance ({y = –4.19 + 0.04 [SE 0.02]x}; r^2 = 0.33, F = 8.78, P = 0.008).

DISCUSSION

Yearly differences in summer FN were correlated with changes in population density and weather

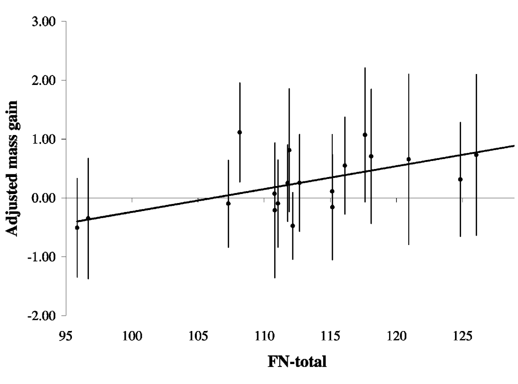

Fig. 3. Fecal nitrogen-days (FN-total; area under the curve relating fecal nitrogen content to Julian date) during summer and the residual rate of mass gain by nonlactating bighorn ewes, after accounting for individual mass in June, at Ram Mountain, Alberta, Canada, 1977–2000. We calculated residual mass gain from a regression including all ewes, because we found no interaction between reproductive status and body mass in June affecting summer mass gain. Each point is the yearly average residual ± SD ({y = –4.12 + 0.04 [SE = 0.01] x}; r^2 = 0.38, F = 11.3, P = 0.003, n = 20).

that likely affect individual nutrition and were correlated with yearly differences in mass gain by nonreproductive females. Therefore, fecal nitrogen values collected over many years can be used to monitor forage quality for populations of bighorn sheep and ultimately may be useful to assess nutritional condition. Yearly differences in mass gain by most sex–age classes, however, were independent of variation in FN.

Refinements of the FN analyses likely would improve the performance of FN as an index of nutritional quality. Bighorns are usually grazers (Hofmann 1989), and therefore FN content is less likely to be affected by varying amounts of tannins in the diet. Tannin-rich diets may increase FN content without a corresponding increase in diet quality (Robbins et al. 1987). A strong correlation between FN and dietary protein has been reported several times in bighorn sheep (Hebert 1973, Irwin et al. 1993). Wehausen (1995) demonstrated that the reliability of FN as a measure of forage nutritional quality can be increased by accounting for variability in ash content. In particular, bighorn sheep may produce fecal pellets with very high ash content after using natural mineral licks and ingesting large quantities of soil or dust (Wehausen 1995). Unfortunately, we did not measure ash content during our study. We do not know of any natural licks used by this population, and therefore we think that fecal samples did not have very high ash content.

Several studies of ungulates stressed the importance of vegetation quality in the spring, particularly in mountainous areas (Albon and Langvatn 1992, Côté and Festa-Bianchet 2001). In our study, the value of FN-total was a stronger correlate of summer mass gain than the FN peak. Yearly variability in FN-total was correlated with changes in sheep population density and summer precipitation. In turn, high values of FN-days were associated with higher mass gain by yearling and nonlactating females. The yearly FN peak was not related to mass gain by any sex–age class, population density, or weather variables. In mountainous areas, where the growing season lasts only a few weeks, forage digestibility starts to decline soon after green-up (Illius 1985, Festa-Bianchet 1988*b*, Albon and Langvatn 1992, Côté 1998).

We did not have information on FN content from October to mid-May at Ram Mountain, but in the Sheep River study area (approx 150 km to the south) FN levels remained at about 1.2–1.5% from late November to early May (Festa-Bianchet

1987). Therefore, our measure of FN-total likely included most of the period when FN values were above the winter minimum.

Yearly differences in vegetation phenology likely are important for ungulates in these highly seasonal environments because small differences in plant digestibility can have a marked effect on mass gain (White 1983). Our measure of FN-total was affected by both the peak nitrogen value and subsequent changes over the summer—particularly the rate of decline in nitrogen content—which presumably reflected the decline in diet quality over the period when most bighorns normally gain mass. Measures of vegetation quality limited to spring green-up provide valuable information on when mass gain may begin, but not necessarily on forage quality over the entire mass-accumulation season. Bighorn ewes at Ram Mountain gain mass until September, and lambs and yearlings gain weight until at least October (Festa-Bianchet et al. 1996).

The delay in FN peak in years with cool and wet springs (see also Beaubien and Freeland 2000) is not surprising because the growing season cannot begin until the snow has melted. At Ram Mountain, most spring precipitation falls as snow, delaying green-up. Osborn and Jenks (1998) also reported a negative relationships between snow and FN levels in white-tailed deer (*Odocoileus virginianus*). Côté and Festa-Bianchet (2001) reported a strong effect of FN in early June on midsummer mass of mountain goat (*Oreamnos americanus*) kids, possibly because yearly variations in timing of snow melt (and therefore on timing of green-up) were greater in their study area than at Ram Mountain.

The positive correlation between summer precipitation and FN-total also was expected. Drought can affect the demography of herbivorous mammals by limiting forage availability (Frank and McNaughton 1992). Precipitation is an important determinant of plant longevity and productivity, since lack of water promotes senescence (Muraoka et al. 1997, Yang et al. 2001) and decreases growth (Macklon et al. 1996). Precipitation also can determine the nitrogen concentration in leaves; mineral nutrients must be in solution to be taken up through the roots, and drying of the upper layers of the soil rapidly decreases nitrogen availability for plants (Lemaire and Denoix 1987, Onillon et al. 1995).

The negative relationship with population density suggests that FN-total measures summer forage quality, integrating the effects of weather and density on food resources. Our estimates of population size are accurate because nearly all individuals were seen every year (estimate of capture probability close to 1; Jorgenson et al. 1997). As density increases, competition for high-quality forage also increases, so that the best food items are rapidly depleted and the average diet is of poorer quality (Choquenot 1991, Mduma et al. 1999). A negative correlation of FN and population density also has been reported for white-tailed deer (Sams et al. 1998) and Sika deer (*Cervus nippon*; Asada and Ochiai 1999).

The mass gain of yearling females and non-lactating ewes was related to FN-total, but yearly variation in FN-total had no apparent effect on mass gain by lambs, lactating ewes, or young rams. During our study, population density more than tripled, providing clear evidence of resource limitation; yearling female mortality (Jorgenson et al. 1997), and age at primiparity (Jorgenson et al. 1993) increased, while winter lamb survival (Portier et al. 1998) and horn growth in males (Jorgenson et al. 1998) declined. Among ungulates, juveniles are more sensitive to changes in environmental quality than adults (Gaillard et al. 1998, 2000). The lack of correlation between FN and mass gain for lactating ewes suggests that they may compensate for decreased forage quality by increasing intake or modifying their resource allocation strategy. Ewes decrease maternal effort when population density increases, so that mass gain by lactating ewes is density-independent (Festa-Bianchet and Jorgenson 1998). Ewes could similarly decrease maternal effort in year of low forage quality.

In the Ram Mountain bighorn sheep population, density did not affect adult female survival (Jorgenson et al. 1997) and had a weak effect on summer mass gain of lactating females, whereas mass gain and winter survival of lambs were strongly density-dependent (Festa-Bianchet and Jorgenson 1998, Portier et al. 1998). Mass gain by nonlactating ewes increased in years with higher FN-total (Fig. 3). Mass gain by nonlactating ewes appeared to be directly related with FN-total, while the relationship between FN-total and mass gain for lactating ewes was complicated by the conversion of a variable amount of forage protein into milk. Surprisingly, however, lamb mass gain was not related to any FN measure. Possibly, in years with poor forage, more small lambs died before weaning and were therefore not included in our calculations of summer mass gain. Parameters other than food resources may play a role in milk yield, such as stress resulting from high density (stress can inhibit lactation in cattle; Breuer et al. 2000, Silanikove et al. 2000).

Mass gain by yearlings was related to FN-total only for females. Young females are particularly sensitive to changes in density in this population; survival of yearling females was density-dependent, while survival of yearling males was not (Jorgenson et al. 1997). Female age at first reproduction was the first demographic parameter to respond to changes in density Festa-Bianchet et al. 1995). These results are surprising because in dimorphic mammals, young males have higher metabolic requirements than young females and usually are believed to be more sensitive to environmental conditions (Clutton-Brock et al. 1985). On the other hand, mothers may increase milk production for sons in years when forage quality is poor, as suggested by the increasing relative fitness costs of sons over daughters at high population density (Bérubé et al. 1996).

MANAGEMENT IMPLICATIONS

Our results suggest that FN can be used as an index of bighorn sheep forage quality over the long term and would be particularly useful in populations for which data on density, body mass gain, and weather are not available. Because many factors may affect FN, monitoring FN for only a few years may not be sufficient to assess trends in forage quality that may ultimately affect nutritional status and population performance. We showed a relationship between FN and mass gain of yearling and nonlactating female bighorn sheep despite missing the start and end of the growing season, and despite relatively low year-to-year variability in FN. Consequently, seasonal measures of FN could be even more useful in environments with greater variability in onset of vegetation growth and in forage productivity.

Although mass gain by lactating ewes was independent of FN, FN was negatively related to population density, which in turn was associated with decreased recruitment (Festa-Bianchet et al. 1995, Portier et al. 1998) and ram horn growth (Jorgenson et al. 1998). Lower FN values corresponded to years of high population density and low precipitation, 2 factors that have a negative effect on population demography. Our results do not imply that FN could be used to compare different populations (Hobbs 1987). Within a population, however, long-term monitoring of fecal indices such as FN, or possibly a combination of several indices such as Neutral Detergent Fiber (Brown et al. 1995), could help managers monitor how changes in weather and density affect ungulate food quality and decide whether increases in density have an impact on forage quality and consequently warrant increased harvest levels.

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