Bienn. Symp. North Wild Sheep
and Goat Counc. 8:279-292.

THE ROLE OF PRECIPITATION AND TEMPERATURE IN THE WINTER RANGE DIET QUALITY OF MOUNTAIN SHEEP OF THE MOUNT BAXTER HERD, SIERRA NEVADA

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Abstract: The study of population ecology of wild ungulates often has emphasized the role of nutrition relative to demography, notably reproduction and survival. Consequently, diet quality is an important consideration in modeling such populations. An assessment of the principle environmental variables driving winter range diet quality of mountain sheep from the Mount Baxter population in the Sierra Nevada was made using 14 years of fecal crude protein data. Fecal crude protein, a measure of diet digestibility, should reflect the availability of growing plant tissues, which in turn should reflect the role of temperature and precipitation. The amount of winter precipitation proved to be a relatively unimportant influence, while the timing of the first major storm that initiated plant growth was very important. Second in importance was temperature. These results are discussed in the context of application to demographic models.

Diet quality has long been considered an important parameter in the population ecology of wild ungulates (Leopold 1933). Most studies have approached diet quality from the standpoint of the quantity of available forage and resultant resource competition when forage quantity is in short supply. This approach has been influenced strongly by work on winter ranges where forage quantity is obviously limiting to the ungulate population(s). Fundamental concepts and models of density-dependence, as a negative feedback loop regulating herbivore populations, have been derived from such environments (McCullough 1979). Such simple population models may adequately represent ungulates whose populations are limited by the availability of nutrients on a winter range, and whose winter range affords no opportunities for forage growth during the winter months due to low temperatures. However, such models will become increasingly less able to predict population parameters as more variables influence diet quality. Warm arid ecosystems of variable precipitation input, in which the quality of winter diets may be influenced by active plant growth, in addition to forage available from a previous growing season, are an example (Wehausen et al. 1987).

Because of the frequent warm winter daytime temperatures, the eastern base of the Sierra Nevada in Owens Valley may be such an ecosystem. On the basis of fecal crude protein (FCP) curves, Wehausen (1980) noted substantial differences for 1976-78 in both winter and summer range diet quality of the Mount Baxter mountain sheep (*Ovis canadensis*) population in the Sierra Nevada. Winter range diet quality was hypothesized to be influenced by the timing of the first winter storms. This paper reexamines the factors underlying the winter range diet quality of the Mount Baxter population based on FCP data from 14 different winters.

These analyses are made in the context of attempting to derive a predictive model of winter range diet quality that can be incorporated in a demographic model.

Wehausen (unpubl.) has shown that FCP measures apparent digestibility of the diet rather than other quality parameters, which are measured only to the extent that they are correlated with digestibility. For herbivores, forage digestibility is inversely related to the amount of plant structural components in the diet, especially lignin (Van Soest 1982). In general, the more rapidly plant tissues are growing, the lower their content of structural components, and the higher their digestibility. For a foraging sheep, the more growing plant tissue there is around them, the better they will be able to select a diet high in digestibility.

Of various factors potentially influencing plant growth, water and temperature were hypothesized to account for much of the variation in winter range plant growth and, hence, forage digestibility and FCP values. Precipitation was expected to be the major influence on FCP levels through both the timing and amount of winter rain; the latter should determine the length of the growing season through soil moisture reserves. No plant growth and, thus, no rise in FCP was expected prior to the first soaking winter rain. Temperature was expected to influence forage growth and sheep diet quality in 2 ways. First, there is a temporal sequence in the initiation of growth among the plant species present, beginning with the most cold tolerant (e.g., grasses) and ending with the most cold intolerant (various shrubs). As the growing season becomes progressively warmer, there will be more species growing and more from which sheep can choose; additionally, some of the species that initiate growth later produce higher quality forage (Wehausen 1980). Second, within any period of the growing season, year-to-year variation in temperature was expected to influence diet quality through the rate at which plants produced new growth.

The Los Angeles Department of Water and Power provided the precipitation and temperature data used. Support for this research has come from: The California Dept. of Fish & Game; The University of California, White Mountain Research Station; The National Park Service; The U. S. Forest Service; and The Foundation for North American Wild Sheep; and was conducted as part of the California Dept. of Fish & Game Bighorn Sheep Program. V. C. Bleich and S. G. Torres provided useful comments on the manuscript.

STUDY AREA

The winter range of the Mount Baxter population encompasses the base of the eastern escarpment of the Sierra Nevada from Thibaut Creek to Sawmill Canyon, northwest of Independence, California. Sheep occupied elevations as low as 1,450 m (4,800 ft) but rarely exceeded 2,075 m (6,800 ft) while on this winter range. Their alternate range encompasses alpine and subalpine habitats at considerably higher elevations. Winter range use by this population has varied considerably among years. Peak numbers of sheep have consistently occurred in March, coincident with ewes entering their third trimester of pregnancy and rapid increase in winter range diet quality. While most ewes have usually left the winter range in

April prior to the onset of lambing, in years of heavy snow, rams have remained there into the second half of May. Only in the the heaviest snow years has there been much winter range use prior to February, potentially beginning as early as late November. During the recent series of consecutive drought years beginning in 1987, winter range use, even in March, has dropped to almost nothing.

The vegetation on this winter range is a sagebrush scrub community dominated by shrubs, but includes a substantial cover of perennial grass, primarily Stipa speciosa. Young et al. (1977) classified this vegetation as a southern Great Basin community separate from the more northern sagebrush steppe, which begins north of Owens Valley; milder winters in the south were considered the important discriminating factor. More detailed description of this community, and of the food habits of the sheep occupying it, can be found in Wehausen (1980).

METHODS

Fresh fecal samples were collected from mountain sheep on the winter range every year from 1976 to 1990 except 1980. An attempt was made to obtain samples at least once every month while sheep were on the winter range. Because winter range use varied considerably among years, the number of samples collected in any year has varied from 2 to 6. The earliest samplings were in December, but typically began in late January or early February. Sampling occurred on a single day and represented that point in time, rather than the month as a whole. At each sampling, pellets were collected from numerous sheep, from which a composited sample was submitted for Kjeldahl crude protein analysis.

Temperature data were from the town of Independence at 1,200 m (3,925 ft). Precipitation data were from Independence, as well as from Onion Valley at 2,700 m (8,850 ft), which lies in the Sierra Nevada due west of Independence. Because the rain shadow on the east side of the Sierra Nevada causes a steep precipitation gradient with elevation, precipitation data from Independence substantially underestimated rainfall on the sheep winter range, while those from Onion Valley represented an overestimate. Consequently, an average of the precipitation from the 2 sites was used as an approximation of what occurred on the sheep winter range.

Sixteen variables were developed for use as independent variables in regression models (Table 1). Three were time variables: (1) the sampling date measured as the number of days after 30 November; (2) the sampling date measured as the number of days after the storm that initiated winter range forage growth; and (3) the date of the initiating storm, measured as the number of days after 31 October. To qualify as the initiating storm, it had to produce enough rain or snow to soak the soil deep enough to initiate perennial grass growth. This usually was based on direct observations of soil moisture and plant response on the winter range. In most cases, this date was obvious on the basis of such observations or precipitation data; in the few cases in which it was not, the first storm to exceed 13 mm (0.5 in.) of rain was chosen. There was considerable variation in the date of this initiating storm, ranging from 5 November to 13 February. For the 14 years of data, this storm occurred 5 times in November, 6 times in December, once in January, and twice in February.

Table 1. Independent variables and their abbreviations used to build regression models of winter range diet quality for mountain sheep from the Mount Baxter herd in the Sierra Nevada.

Variable	Abbreviation
1. DAYS AFTER NOV 30	DATE
2. DAYS AFTER FIRST STORM	DAYS/STORM
3. 1ST STORM DATE (DAYS AFTER OCT 31)	STORMDATE
4. PPT 7-30 DAYS PRIOR TO SAMPLING	PPT/7-30D
5. PPT 7-60 DAYS PRIOR TO SAMPLING	PPT/7-60D
6. PPT NOV 1 TO 7 DAYS PRIOR TO SAMPLING	PPT/7D-11/1
7. PPT 31-60 DAYS PRIOR TO SAMPLING	PPT/31-60D
8. PPT NOV 1 TO 61 DAYS PRIOR TO SAMPLING	PPT/61D-11/1
9. PPT FIRST MONTH AFTER INITIATING STORM	PPT/1STMO
10. AVERAGE HIGH TEMP. PREVIOUS 15 DAYS	TEMP/15D
11. AVERAGE HIGH TEMP. PREVIOUS 30 DAYS	TEMP/30D
12. AVERAGE HIGH TEMP. PREVIOUS 45 DAYS	TEMP/45D
13. DEGREE-DAYS ABOVE 40 F	D-D>40
14. DEGREE-DAYS ABOVE 48 F	D-D>48
15. SQUARE ROOT OF DEGREE-DAYS ABOVE 40 F	SQRT D-D>40
16. SQUARE ROOT OF DEGREE-DAYS ABOVE 48 F	SQRT D-D>48

Precipitation variables were defined by amounts occurring during different time periods prior to each FCP point. The 3 basic periods were: 7-30 days; 31-60 days; and >61 days, but not earlier than 1 November. Combinations of these variables were used to provided 2 more such precipitation time periods: 7-60 days prior; and 7 days to 1 November. A minimum of 7 days prior to the sampling time was chosen on the assumption that it would take at least a week after rain for vegetation to produce a response that might influence sheep diet quality. In the couple of cases where samples were obtained prior to the initiating storm, it took about 1 month for any FCP response to be measured. A sixth precipitation variable was the amount occurring in the first month of the growing season, beginning with the initiating storm.

Three temperature variables investigated were the average high temperatures 15, 30 and 45 days prior to each sampling point. Additionally, 2 composite variables were developed that combined temperature and days since the initiating storm into a single variable. This was done by integrating daily high temperatures in Independence between the initiating storm and the sampling date above 2 baseline temperatures: 4.4 and 8.9 C (40 and 48 F). These 2 baseline values were used to approximate 1.7 and 6.1 C (35 and 43 F) on the sheep winter range, based on elevation differences from Independence and the temperature lapse rate from further north in the Sierra Nevada (Major 1977). The latter temperature is considered the minimum for grass growth (Langvatn and Albon 1986). These composite variables were measured in degree-days, where 1 degree F above the baseline temperature for 1 day was 1 degree-day.

The relationship between digestibility and FCP is curvilinear (Wehausen unpubl.). A log transformation of FCP linearizes this relationship well; consequently, lnFCP was used in all analyses as the measure of diet quality. Analyses consisted of building simple and multiple regression models with an interactive stepwise regression program using lnFCP as the dependent variable. Automated stepwise regression was not used. A correlation matrix also was produced to investigate any possible lack of independence among variables that would cause multicollinearity (Neter and Wasserman 1974).

Subsequent to developing a variety of predictive models from the existing data set, 5 previously unused fecal samples from the years used to derive these models were discovered. FCP values were obtained for these, and they were used to test the predictive abilities of these models. These 5 samples included considerable variation in the variables most influential in the resulting models.

RESULTS

There was a significant ($\underline{P} < .001$) overall increasing seasonal trend in lnFCP values. However, points were widely scattered, with DATE (days after 30 November) accounting for only 56.6% of the variation in lnFCP. Examination of the residual variation by individual years points out the strong influence of the timing of the growth initiating storm (Fig.1). Changing the independent variable to days after this storm substantially tightened the cluster of points and accounted for 78.4% of the variation. Alternatively, adding the date of the first storm as a second independent variable with DATE increased this to 82.3% (Table 2). Again, examination of yearly patterns within the residual variation shows clear patterns. In this case, it can be explained by temperature differences among years. Figure 2 illustrates 3 of these. The 1985 growing season began with an early first storm; but it was followed shortly by a particularly cold early winter period that almost ceased gains in diet quality until warmer weather again prevailed. The 1983 season also had an early first storm; but instead, that year experienced a particularly cool late winter and spring. The result is a lnFCP curve that crosses from the upper side of the data points to the lower side during spring. In contrast, because the first storm did not occur until mid-February in 1987, it was followed immediately by warm weather, causing the diet quality curve to climb completely out of the rest of the data points (Fig. 2).

An attempt to account for these temperature differences with the composite degree-days variables was only partly successful. First, the variable with the lower baseline temperature (4.4 C/40 F) provided the better fit of the two (Table 2), but the relationship was somewhat curvilinear. A square-root transformation straightened this and improved the fit; but it still accounted for only an additional 3.7% of the variation in lnFCP compared with DAYS/STORM, and essentially nothing additional when compared with the multiple regression of DATE and STORMDATE (Table 2). Second, there remained yearly temperature differences apparent in the residuals (Fig. 3). The 1978 and 1983 growing seasons were particularly wet years (Fig. 4), the former of which was a warm winter, while the latter was cooler, especially in spring, as noted above. This temperature difference is very apparent in the parallel curves.

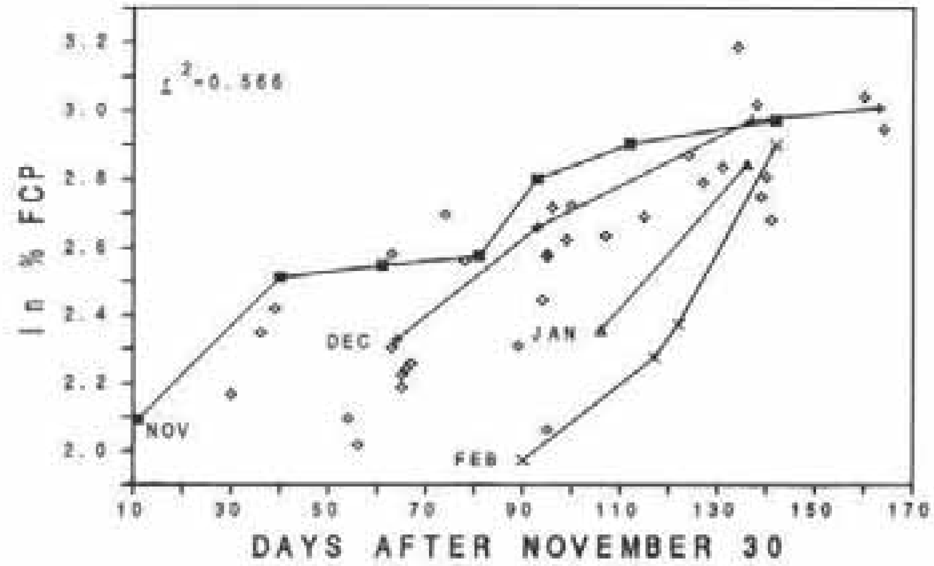

Fig. 1. Winter range fecal crude protein as a function of date for mountain sheep in the Mount Baxter herd, Sierra Nevada. Four years are plotted separately from the rest to illustrate the influence of the timing (by month) of the first major storm.

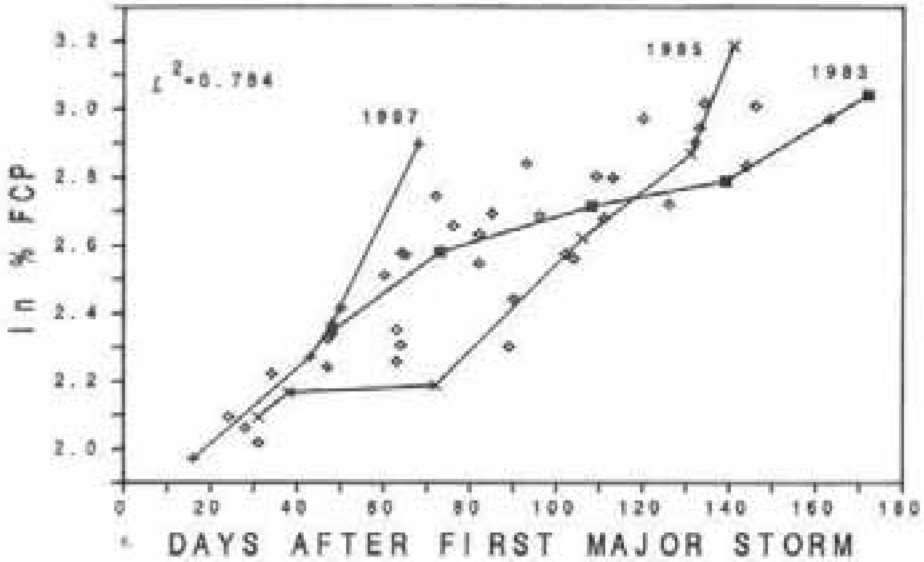

Fig. 2. Winter range fecal crude protein as a function of days since the first major storm for mountain sheep in the Mount Baxter herd, Sierra Nevada. The years 1983, 1985, and 1987 are labeled to illustrate the effects of temperature differences: a very cold period following growth initiation for 1985; very warm temperatures following very late growth initiation in 1987, and a cold late winter and spring in 1983.

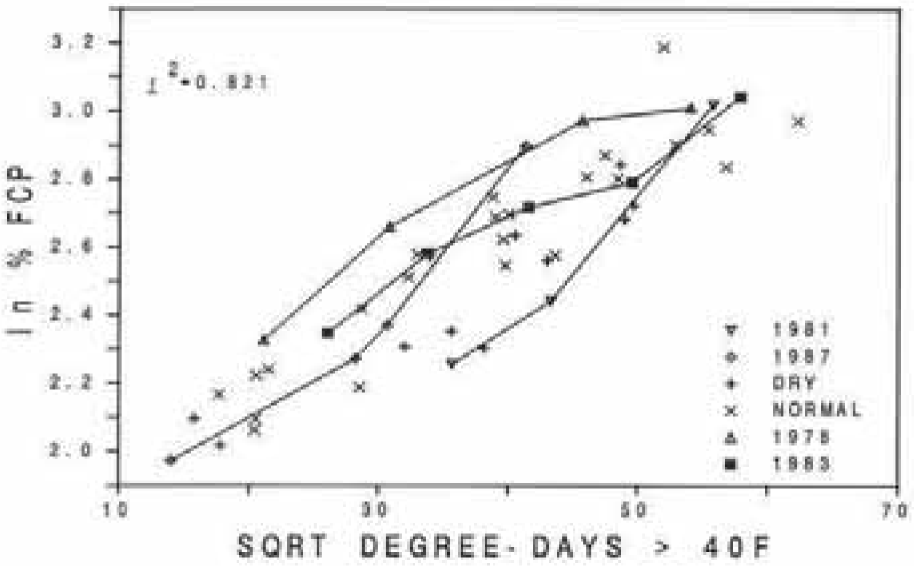

Fig. 3. Winter range fecal crude protein as a function of the square root of degree-days above 40 F since the first major storm for the Mount Baxter herd in the Sierra Nevada. 1981 and 1987 were both dry years, while 1978 and 1983 were particularly wet years, the former of which was notably warmer than the latter. 1981 experienced two months without rain following the growth initiating storm. This first storm did not occur until mid February in 1987.

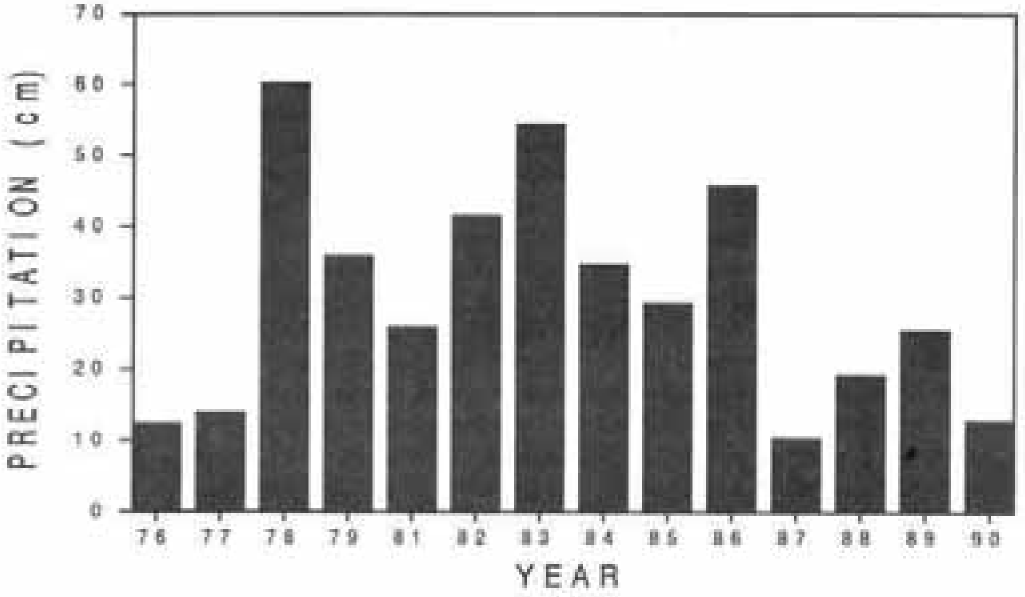

Fig. 4. November-March precipitation at Onion Valley (2700 m/8550 ft) in the Sierra Nevada for the years of study.

Table 2. Results of simple and multiple regression analyses of winter range diet quality (lnFCP) on time, temperature, and precipitation variables for mountain sheep from the Mount Baxter herd in the Sierra Nevada. Abbreviations are explained in Table 1.

X_1	X_2	X_3	X_4	S.E.(Y)	R^2
DATE				.206	.566 [1]
DAYS/STORM				.145	.784
DATE	STORMDATE			.133	.823
PPT/7-30D				.308	.027 (NS)
PPT/7-60D				.312	.000 (NS)
PPT/7D-11/1				.247	.376
PPT/31-60D				.310	.014 (NS)
PPT/61D-11/1				.219	.508
PPT/1STMO				.301	.068 (NS)
TEMP/15D				.204	.570
TEMP/30D				.170	.703
TEMP/45D				.170	.704
D-D>40				.144	.786
D-D>48				.153	.760
SQRTD-D>40				.132	.821
SQRTD-D>48				.140	.800
SQRTD-D>40	PPT/7D-11/1			.124	.845
SQRTD-D>40	PPT/1STMO			.120	.856
SQRTD-D>40	PPT/7D-11/1	TEMP/30D		.110	.882
SQRTD-D>40	PPT/1STMO	TEMP/30D		.110	.880
DAYS/STORM	TEMP/45D			.118	.861
DAYS/STORM	TEMP/30D			.117	.863
DAYS/STORM	TEMP/30D	PPT/7D-11/1		.108	.886
DAYS/STORM	TEMP/30D	PPT/7-60D		.108	.886
DAYS/STORM	TEMP/30D	PPT/1STMO		.107	.887
TEMP/45D	PPT/7D-11/1			.122	.850
TEMP/30D	PPT/7D-11/1			.122	.850
TEMP/30D	PPT/7D-11/1	DATE	STORMDATE	.108	.888

[1] For simple regressions, all variables are significant ($P \le .05$) except where noted otherwise; for multiple regressions, all variables are significant at $P \le .01$.

Also, 1987, warm because of its late first storm, still exhibited a curve that increased upward through the other points, although no longer exceeding them.

Precipitation effects are also apparent in Figure 3. First, the 2 wettest years, 1978 and 1983, fall along the top of the points. Second, the drier years, which include 1981 and 1987, fall largely along the lower side. The 1981 season is illustrated because it was an extreme year due to a hiatus of 2 months with no precipitation that followed the storm which initiated growth. The effect on diet quality is clearly apparent (Fig 3).

The variance in total winter precipitation was great during the study period (Fig. 4). Using 25 and 50 cm (10 and 20 in.) of November-March precipitation in Onion Valley as separation points, years were partitioned into 3 categories: dry, normal, and wet. Covariance analysis of lnFCP for these categories, using SQRT D-D>40 as a covariate, produced a very significant precipitation effect ($\underline{P}$ = .006), but this rainfall factor accounted for only 2.3% of the variation explained by the overall model.

When multiple regression models were built on SQRTD-D>40, precipitation and temperature variables could be entered significantly as second and third variables, respectively; however, these 2 added variables accounted for only an additional 6% of the variation in lnFCP. Further, using the same second and third variables with DAYS/STORM produced somewhat better models (Table 2). Clearly, the composite degree-day variables did not functioned as expected.

The ability to build statistically and biologically meaningful multiple regression models for lnFCP was somewhat limited by the lack of independence among some of the important variables. The greatest difficulties lay in correlations with time. Of the precipitation variables, only the long term ones that extended to the beginning of November correlated with time variables, especially with DAYS/STORM (Table 3). This pattern of correlations is to be expected, since later dates provide greater opportunities for increased cumulative precipitation. Because of the normal temperature rise from winter to spring, the temperature variables are strongly correlated with time variables (Table 3). Because of this lack of independence, when temperature variables were entered as second variables with DATE, the latter no longer contributed significantly to the overall regression. This result suggests that the time variables are significant by themselves largely because of this correlation with temperature. Of these 2 variable classes, temperature is biologically the more meaningful one. When temperature variables were used as the starting point of multiple regression models, total winter precipitation entered as the most significant second variable, and the total regression accounted for almost as much variation as 2-variable regressions beginning with time variables (Table 2). In these temperature-based models, the precipitation variable accounted for an additional 14.7% of the overall variation in lnFCP, and 17.3% of the variation accounted for. These were the only models in which the amount of precipitation accounted for more than a trivial portion of the variation. While it would be desirable to add STORMDATE alone to this model, it must be added along with DATE as a time reference to be meaningful. Both were

Table 3. Correlation matrix for the more important independent variables used in regression analyses of winter range diet quality for mountain sheep from the Mount Baxter herd in the Sierra Nevada. Abbreviations are explained in Table 1.

	DAYS/ STORM	STORM DATE	SQRT D-D>40	PPT/ 7-30D	PPT/ 7D-11/1	PPT/ 61D-11/1	PPT/ 1STMO	TEMP/ 30D
DATE	.70	.33	.74	.37	.38	.65	-.02	.80
DAYS/STORM	1	-.45	.96	.22	.66	.80	.21	.73
STORMDATE		1	-.33	-.17	-.40	-.25	-.31	.04
SQRTD-D>40			1	-.27	.53	.70	.08	.86
PPT/7-30D				1	.29	-.10	.37	.34
PPT/7D-11/1					1	.86	.64	.29
PPT/61D-11/1						1	.45	.50
PPT/1STMO							1	-.02

highly significant as added variables, but together accounted for only an additional 3.8% of the variation (Table 2), and the model again became fraught with the problem of the lack of independence between temperature and date.

In an attempt to quantify the relative importance of different classes of variables influencing diet quality, they were each investigated as second variables in multiple regressions with DATE by looking at their partial correlation coefficients and additional variance accounted for. The former measures the relative importance of these variables if date were held constant (Draper and Smith 1981). Storm date was clearly the most influential variable, precipitation variables the least influential, and temperature variables intermediate (Table 4).

Sixteen of the models in Table 2 were tested using the 5 additional past data points. The models with more independent variables that accounted for more of the variation in lnFCP did not generally yield smaller average deviations from predictions. In fact, the model with the smallest average deviation was the single-variable model using DAYS/STORM. However, this model also exhibited the highest variance among deviations from predictions (Table 5). With the exception of this model, all models tested overestimated lnFCP. It is possible that this bias reflected the length of time these samples had been stored before analysis. It will be necessary to make a prospective comparison using future samples to test this possibility and adequately test these equations. Because the average deviations from predictions are in units of lnFCP, their magnitudes are not easy to grasp and vary the FCP level. The smallest average deviation in Table 5 represents %FCP deviations of 0.1 and 0.3% for 8% and 20% FCP, respectively., while these values are 0.6 and 1.5% for the largest average deviation. These deviations are quite small compared with the natural seasonal variation.

Table 4. The relative importance of selected variables when entered as a second independent variable with DATE (days after Nov. 30) in regressions of winter range diet quality (dependent variable) for mountain sheep from the Mount Baxter herd in the Sierra Nevada. Abbreviations are explained in Table 1.

Variable	Additional variance accounted for (%)	Partial $\underline{R}$	Partial $\underline{R}^2$
STORMDATE	25.7	.769	.591
TEMP/45D	15.8	.604	.365
TEMP30D	15.5	.597	.356
TEMP15D	7.9	.425	.181
PPT/7-30D	1.5	.186	.034
PPT/31-60D	8.8	.450	.202
PPT/61D-11/1	8.6	.446	.199
PPT/7-60D	8.1	.431	.185
PPT/7D-11/1	12.7	.540	.291
PPT/1STMO	7.5	.414	.172

DISCUSSION

A number of the variables investigated can be discarded due to their relative lack of importance in the analyses. Among the temperature variables, TEMP/15D was consistently less important than the 2 longer periods. For the precipitation variables, PPT/7D-11/1 and PPT/1STMO were the 2 that consistently provided the best fit. PPT/61D-11/1 accounted for the most variation in lnFCP when considered alone (Table 2); however, it also was the precipitation variable most strongly correlated with DATE and DAYS/STORM (Table 3), which probably accounts for its strength alone, but not in conjunction with other variables.

The degree-day variables that integrated high temperatures after the first storm were the best single correlates with lnFCP; yet, they failed to improve the models when additional variables were included. This may be because the level of diet digestibility is not entirely a cumulative phenomenon, but is additionally influenced by forage quality differences among species with different temperature requirements for growth initiation. Sheep change their diet composition as these higher quality forages become available (Wehausen 1980). Consequently, temperature variables may be biologically the most meaningful representation of this process, as may be the multiple regression equations built on them.

Table 2 provides a welter of possible predictive models; which is best will be a function of the question being asked. If the goal is simply to predict winter range diet quality for specific dates using available temperature and precipitation data, the regression equation that

Table 5. Retrospective test using 5 data points from 1976 (2), 1978, 1979, and 1984 of selected regression models from Table 2 of winter range diet quality for mountain sheep from the Mount Baxter herd in the Sierra Nevada. Abbreviations are explained in Table 1.

X_1	X_2	X_3	X_4	Average Deviation[1]	SD
DAYS/STORM				-.014	.207
TEMP/45D				.071	.127
SQRTD-D>40				.018	.187
DATE	STORMDATE			.042	.158
DAYS/STORM	TEMP/45D			.043	.173
DAYS/STORM	TEMP/30D			.036	.181
SQRTD-D>40	PPT/7D-11/1			.016	.188
SQRTD-D>40	PPT/1STMO			.046	.189
TEMP/45D	PPT/7D-11/1			.073	.141
TEMP/30D	PPT/7D-11/1			.058	.147
SQRTD-D>40	PPT/7D-11/1	TEMP/30D		.046	.166
SQRTD-D>40	PPT/1STMO	TEMP/30D		.074	.169
DAYS/STORM	TEMP/30D	PPT/7D-11/1		.045	.174
DAYS/STORM	TEMP/30D	PPT/7-60D		.025	.178
DAYS/STORM	TEMP/30D	PPT/1STMO		.065	.176
TEMP/30D	PPT/7D-11/1	DATE	STORMDATE	.047	.170

[1] Deviations were measured as observed minus predicted.

best predicts future values will be the most useful. The ultimate measure of nutrient intake by sheep on this winter range is an integration of diet quality values over the period of occupation. The model that best predicts values by date could be used to produce such an integration; and the value of this integration then could be used as a variable in population models. Alternatively, a less rigorous modeling approach might look for a small set of variables that sufficiently represented the overall inter-annual variation in winter range diet quality. This would best be assessed by looking for correlations with values of the integrations discussed above. In the analyses above, the influence of timing of the first storm and temperature were each very strong and weak depending on how the analysis was built. This is probably because each accounts for different aspects of the overall variation. Temperature accounts for much of temporal variation within each year, and only a small amount of the inter-annual variation. In contrast, the strong influence of the timing of the first storm is entirely a function of inter-annual variation. As such, the date of the first major storm should be the single most important variable to represent inter-annual variation. Second in importance is likely to be a variable that indexes the relative winter-spring temperature regime. The amount of winter precipitation, while easier to obtain, appears least important.

Both integration and simple variable approaches to representing winter range diet quality in demographic models assume that the entire population uses this winter range for the time period in question. In reality, the population is commonly split between animals using the winter range and others wintering much higher, where diet quality is very different. Like the diet quality on the winter range, this split in use of the 2 ranges varies greatly, from years when the entire population uses the winter range to years of essentially no winter range use. Any attempt to model nutrient intake at the population level must take this split into account.

The elucidation of cause-and-effect relations of any ecological system requires observing dynamics in that system through natural or artificial perturbations (Sinclair 1979). The southern Sierra Nevada is clearly an ecosystem with considerable natural dynamics, but the years of this study have had the additional advantage of including a number of years of extreme conditions. Levins (1968) noted that of the attributes generality, precision, and reality, models in ecology and evolution can maximize only 2 at the expense of the third. If models are to represent reality, they will not be both general and precise. The approach taken here was to generate a precise model for a particular system. General models are classically simple, and include few parameters. These can only represent simple systems. The system investigated here clearly is complex, and not likely to be modeled adequately by simplistic models.

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