

CHAPTER X NUTRIENT PREDICTABILITY, BIRTHING SEASONS, AND LAMB RECRUITMENT FOR DESERT BIGHORN SHEEP

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Introduction

Desert bighorn sheep (*Ovis canadensis*) were once widespread throughout the desert mountain ranges of the southwestern United States and northern Mexico, and persist in many of those ranges (Buechner 1960). As herbivores living in arid environments, their ability to procure nutrients is substantially limited by the phenological patterns of the vegetation they feed on. Nutrient content of diets varies with the amount of green, growing plant tissue available to be eaten. The youngest, most rapidly growing, plant tissue

typically provides the highest digestibility (Van Soest 1982). Sheep maximize their nutrient intake through very selective feeding, eating the most nutritious species and plant parts available. Patterns of nutrient intake determine when the nutrient-expensive process of gestation and lactation will be most successful and how successful it will be relative to lamb survival.

Deserts are characterized by scant precipitation, such that potential evapotranspiration greatly exceeds precipitation overall and soil moisture conditions are not conducive to plant growth for much of the year (Major 1977). Climatic patterns vary across North American deserts in overall temperature (low elevation hot to high elevation cold alpine deserts) and seasons of rainfall (MacMahon 1979). In addition, precipitation is typically quite variable between years (Wagner 1981). Because plant phenology is closely tied to rainfall, nutrient availability for bighorn sheep inhabiting deserts also is quite limited annually. An important question relative to life history and demographic patterns of desert bighorn sheep is the predictability of nutrient availability.

The birthing season for wild sheep in North America varies with latitude. Syntheses of available data have suggested two basic patterns: (1) a short (about 1-2 month) birthing season in late spring and early summer in northern climates that shifts slightly earlier with declining latitude; and (2) a long season (numerous months) in desert ecosystems of southwestern United States and adjacent Mexico (Bunnell 1982, Thompson and Turner 1982). In some desert areas births have been documented throughout the year (Krausman et al. 1999). Bunnell (1982) presented the shift between the two birthing patterns as an abrupt change at a latitude of about 38 degrees.

A related question is what underlies this purported sudden change in birthing patterns. Based on limited data from one bighorn sheep population in New Mexico, Lenarz (1979) hypothesized that the protracted lambing seasons of desert bighorn sheep represented an evolved gambling strategy to an environment that is unpredictable in nutrient availability. That explanation has been widely accepted (Bailey 1980, Bunnell 1982, Thompson and Turner 1982, Krausman et al. 1999), but simulations by Lenarz and Conley (1982) cast some doubt on this characterization of the reproductive strategy of desert bighorn sheep.

Drawing on the work of Beatley (1974) on phenological triggers in Mojave Desert ecosystems, Lenarz (1979) calculated the probability of obtaining 2.5 cm (1 inch) of rain in each month for his study area in New Mexico. From those results Lenarz (1979:671) concluded the following: "in 3 of 10 years plant productivity will not begin until August or will fail altogether. The relationship between precipitation and plant productivity makes forage availability in deserts relatively unpredictable."

Here I examine the question of nutrient predictability using long-term data on diet quality patterns of bighorn sheep from three populations in the Eastern Mojave Desert of California. I analyze patterns of nutrient availability relative to timing of birthing and the survivorship of lambs.

Study Populations

The populations investigated were (SE to NW) the Turtle Mountains, Old Woman Mountains, Marble Mountains, and Old Dad Mountain. They form a transect about 150 km in length that passes through the Granite Mountains. Only 3 years of data are available from the Turtle Mountains, which are used in just one analysis. Of the four mountain ranges studied, the Turtle Mountains is the only one that is decidedly Sonoran Desert, supporting species like Ocotillo (*Fouquieria splendens*) and Ironwood (*Olneya tesota*). The three Mojave Desert ranges form a transect about 100 km long. The Old Woman Mountains are the highest, topping out at about 1600 m and contain sparse pinyon-juniper woodland at the highest elevations. Volcanic and limestone substrates are essentially lacking. The Marble Mountains is the lowest range, peaking out at about 1,150 m. It is primarily a volcanic range with some limestone at the

southern end of the habitat used by sheep. Old Dad Mountain peaks out at about 1300 m and is a combination of a large limestone massive and outlying volcanic ridges, some of which have considerable deposits of blow sand (Bleich et al 1997).

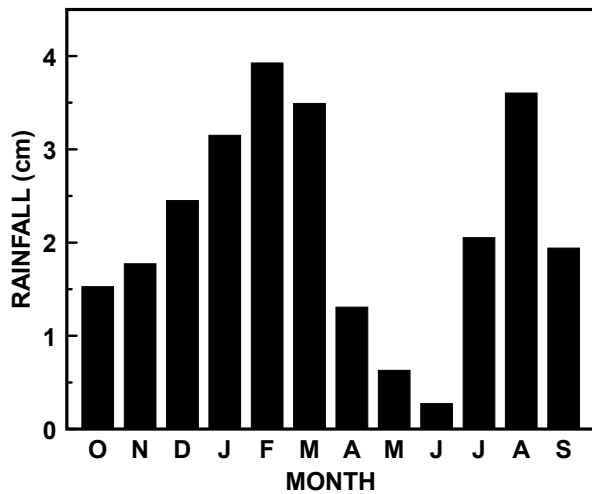


Figure 1. Mean monthly rainfall for Mitchell Caverns in the south Providence Mountains, 1959-2002.

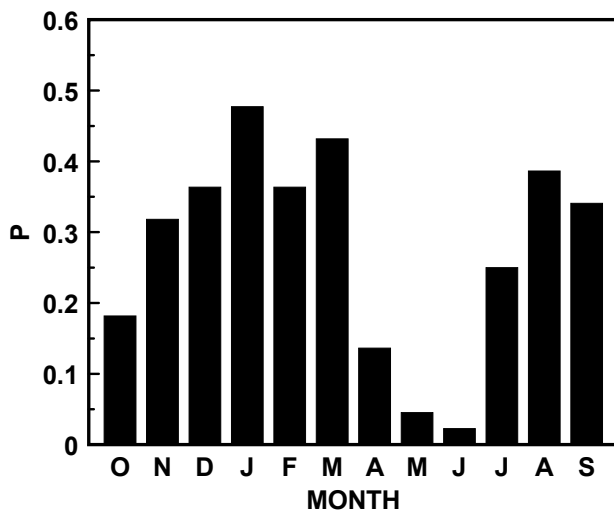


Figure 2. Probability of receiving 2.5 cm of precipitation by month at Mitchell Caverns in the south Providence

The Mojave Desert is something of a hybrid between cold Great Basin and hot Sonoran Desert ecosystems that bound it. Temperatures are intermediate. Precipitation patterns also are intermediate (Figure 1), showing the bimodal pattern of the Sonoran Desert, but with a predominance of winter rainfall that characterizes the Great Basin Desert. For 44 years of data from Mitchell Caverns in the south Providence Mountains, 64 percent of the annual rainfall occurred during the winter-spring season (November-May) and 36% during the hot season (June-October). There is considerable inter-annual variation in rainfall. By the criteria of Lenarz (1979), the eastern Mojave Desert is less predictable than the Chihuahuan Desert ecosystem that he investigated. His peak probabilities of receiving 2.5 cm of rainfall were 0.70 and 0.74 for the months of July and August, respectively, whereas for the eastern Mojave Desert no month even reaches 0.5 (Figure 2). Consequently, unpredictable patterns of diet quality for bighorn sheep in the eastern Mojave Desert would be expected if Lenarz's (1979) criteria are meaningful, while a regular periodicity in diet quality would not be consistent with this expectation.

Methods

Diet quality of sheep was tracked via % nitrogen in feces (FN). FN tracks apparent digestibility of the diet in a curvilinear relationship (Wehausen 1995). The natural log of FN was used to linearize that relationship, and this measure was expressed on an organic matter (ash-free) basis (lnFOMN) because this increases its resolution as an index of diet quality (Wehausen 1995). For the bighorn sheep populations in this study, this index varied from 0.3 to 1.2. For domestic sheep, those values would correspond to a range of about 50-75% apparent digestibility (Wehausen 1995), which also may apply to bighorn sheep; both sheep species have similar

digestive systems, including a very large rumen and reticulum relative to body size (Hanley 1982, Krausman et al. 1993).

Fecal samples mostly were collected fresh from female groups of sheep seen. Where sheep could not be found, very recent tracks were found and followed to find fecal droppings. Those samples were backdated by the estimated age of the tracks. Sampling of feces was approximately monthly. During seasons of rapid phenological change in the vegetation, this interval was somewhat shortened in some years, while during periods of phenological stasis the sampling interval was increased to 2 months in some years. For most samplings, equal amounts of each sample were composited for analysis by commercial labs to produce a single data point. Where separate analyses were made for each sample, the mean was used.

Diet quality over multiple months, rather than single months, is most meaningful relative to many questions, such as lamb recruitment. Consequently, I have measured the area under diet quality curves for the periods of interest (e.g. February through June) using a linear relationship between adjacent points. Because sampling was not on the same day of the month each year, I standardized integrated values by dividing by the number of days between the first and last sampling points.

The three long-term data sets analyzed consisted of continuous diet quality curves for 15-18 years depending on the population. To investigate the question of temporal predictability of diet quality, I calculated for each month the proportion of the years in which the diet quality index reached 0.6 and 0.7. Those values represent modest increases in diet quality relative to the minimum of 0.3. For domestic sheep, these respective values correspond to increases in apparent digestibility of about 8 and 10.5%.

As a test of Lenarz's (1979) approach to using precipitation data, I investigated actual influences of precipitation in individual months on diet quality for the longest data set (Marble Mountains) via simple and multiple linear

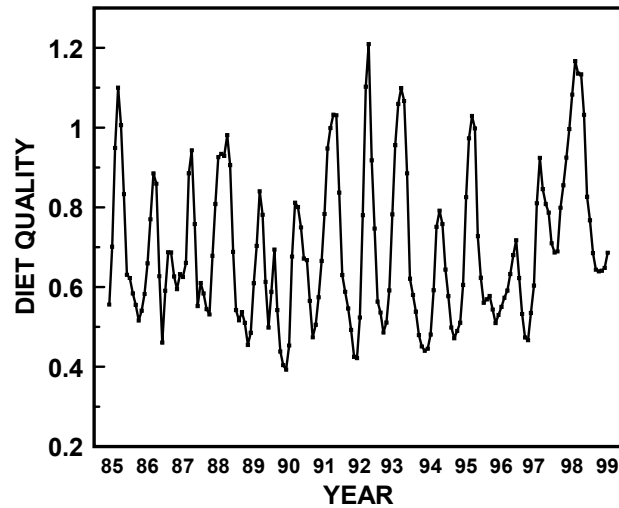


Figure 3. Diet quality (% fecal organic matter nitrogen) for bighorn sheep in the Old Woman Mountains, 1984-1999.

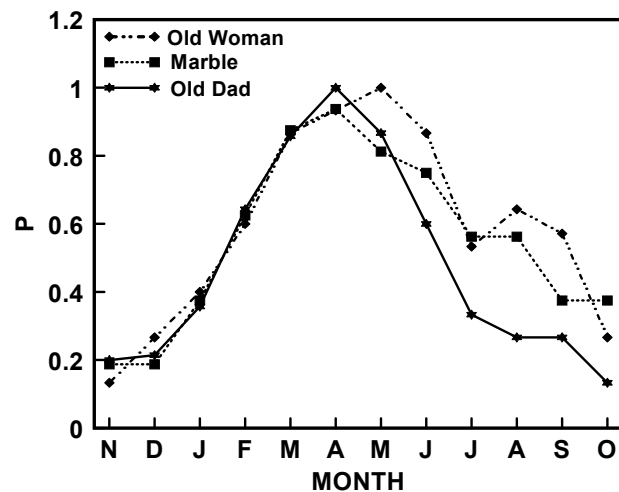


Figure 4. Probability by month that the natural log of fecal organic matter nitrogen equals or exceeds 0.6 for bighorn sheep at Old Dad Mountain and the Marble and Old Woman Mountains, California.

regression, and the use of logged variables to investigate curvilinear relationships.

I investigated the influence of February-June diet quality on recruitment of lambs to the beginning of summer via regression analysis. Lamb recruitment was measured as the ratio of lambs per 100 ewes from direct samplings in late spring and analysis of automated cameras placed at water sources at the beginning of the hot season.

Results and Discussion

Diet Quality Patterns and Predictability

Contrary to predictions from Lenarz's (1979) hypothesis and analytic methods, diet quality curves from the study area show a clear periodicity (Figure 3) and temporal predictability (Figure 4). What is unpredictable is not when peak diet quality will occur, but the amplitude of that peak. Figure 4 depicts the probabilities of only a modest increase in diet quality ($\ln\text{FOMN} = 0.6$). Increasing that threshold level of diet quality narrows the time period in which it is likely to be reached and lowers the peak probability of actually reaching that level. The lowest threshold tested was reached in every year sampled for each population (Figure 4). Increasing that threshold to 0.7 already lowered the probability of reaching it to less than 1 (Figure 5). Further increases in that threshold will further lower that peak probability, while also narrowing the time period.

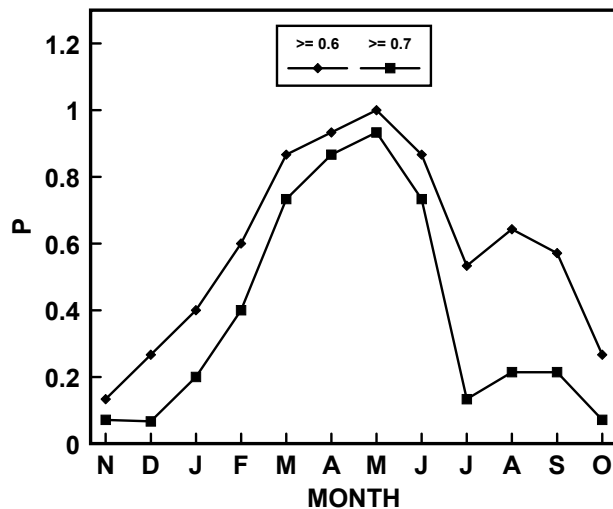


Figure 5. Probability by month that the natural log of fecal organic matter nitrogen equal or exceeds 0.6 and 0.7 for bighorn sheep in the Old Woman Mountains, California

The pattern that emerges in Figure 4 is the important result, rather than the threshold chosen. That pattern demonstrates that there is a predictable timing of the winter-spring growing season that determines diet quality for the sheep. In contrast, forage growth from summer rainfall yields minimal nutritional gains for these sheep (Figs. 4 & 5). The winter-spring rising pattern in Figure 4 is remarkably coincident among the 3 study populations, suggesting that this growing season is regional in nature. This also is indicated by the pattern of diet quality for the February-June period for 1985 - 2002; the patterns for the 4 populations sampled correlate closely (Figure 6A). The variance among years represents the

unpredictable aspect of nutrient availability to these sheep in the primary growing season. This variance can be termed amplitude predictability, to be distinguished from the high temporal predictability for the populations sampled. Lenarz (1979) failed to distinguish these two separate aspects of resource predictability.

Variables Driving Diet Quality Patterns

The interannual variance in winter-spring diet quality (Figure 6A) is driven by rainfall patterns. The single month with the greatest rainfall effect on spring diet quality in the Marble Mountains is February, followed by October. When those two months are combined in a multiple linear regression, together they explain 64% of the variation. In that multiple regression, the slope associated with October rainfall is 67% greater than February (Table 1); thus a unit of rainfall in October generates considerably more nutrition for sheep than an equivalent amount in February. Rainfall in October and February has different effects on vegetation growth. Fall rainfall is important for initiating the growth of cold-tolerant species: annuals, herbaceous perennials, and perennial grasses (Beatley 1974, Turner and Randall 1989). February rainfall is important for continuance of growth of those cold-tolerant species that might have been initiated earlier, but also is important for growth of cold-intolerant perennial species during spring (Beatley 1974). When October rainfall is expressed as logged values along with February rainfall, the model improves slightly, suggesting some curvilinearity in the effect of October rainfall (Table 1).

The forage species initiated by fall rains provide the first new green growth eaten by sheep. Those species determine diet quality for sheep in winter and account for the initial rise in the growing season curve in Figure 4. As the growing season progresses with warming temperatures, numerous cold-intolerant perennial species initiate growth and flowering. The peak in digestibility of sheep diets (Figure 4) coincides with the peak in growth and flowering of perennial species. However, the greater influence of early precipitation on February-June diet quality speaks to the critical importance of the earliest rise in diet quality in winter. Because the dependent variable analyzed begins with the February sampling, early precipitation determines the diet quality level at that first sampling, from which the curve rises to the spring peak. Also, in the years of high peak diet qualities, species whose growth was initiated by the early rains are still available and eaten at the time of that peak.

When rainfall is combined for adjacent pairs of months, the best 2 independent variables are October + November, and January + February, which together explain 75% of the variation in February - June diet quality. For those longer time periods, the distinction between the role of precipitation in initiating early plant growth and contributing to later growth begins to blur; the slope of the earlier rainfall variable is only 17% larger than the later one (Table 1). A single independent variable of total rainfall for October through April explains yet 6% more of the variation in winter-spring diet quality in a curvilinear relationship (Figure 7, Table 1). Eliminating December and March rainfall from that cumulative rainfall explains yet another 4% of the variation. However, there is no clear biological explanation why December and March

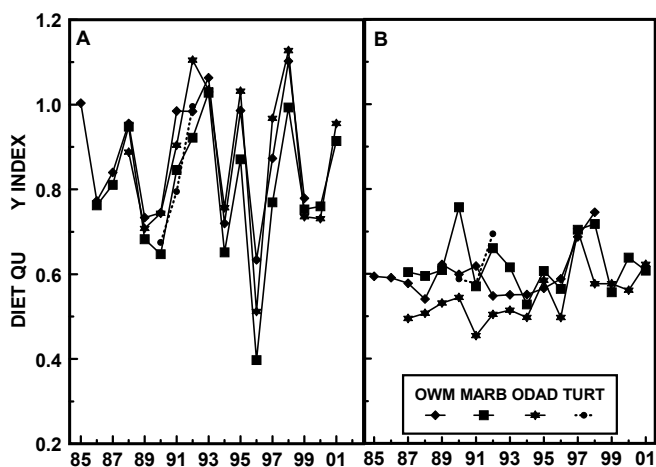


Figure 6. February-June (A) and July-October (B) diet quality by year for bighorn sheep at Old Dad Mountain, and the Marble, Old Woman, and Turtle Mountains, California.

Table 1. Results (independent variables, slopes, coefficients of determination, and total model probabilities) of regression analyses of February-June diet quality of bighorn sheep in the Marble Mountains on precipitation in different time periods.

X ₁	X ₂	B ₁	B ₂	R ²	P
Feb		0.020		0.401	0.006
Feb	Oct	0.021	0.035	0.636	0.001
Feb	lnOct	0.020	0.043	0.674	<0.001
Jan-Feb		0.017		0.554	0.001
Jan-Feb	Oct-Nov	0.018	0.021	0.752	<0.001
lnOct-Apr		0.198		0.808	<0.001

rainfall would not contribute to sheep diet quality. Consequently, that finding is treated here as a statistical artifact.

While the left side of the rising curve in Figure 4 is essentially identical for the 3 populations sampled, the declining pattern in late spring and summer is notably different among them. That variation reflects important habitat differences between the mountain ranges sampled. Temperature exhibits a classic inverse relationship with elevation (Major 1977), and strongly affects plant growth (Hoefs and Cowan 1979, Wehausen 1980). In high mountain ranges, sheep and other large herbivores typically use altitudinal migration to increase their nutrient intake by following the growing season as it progresses up mountain slopes (Hebert 1973; Hoefs 1979; Wehausen 1980, 1983). Sheep in desert mountain ranges also can do this to a limited extent. The extended peak in the Old Woman Mountains (Figure 4) is an example that reflects the higher elevation there.

The diet quality curve for Old Dad Mountain declines more rapidly than the other two populations and remains lower through the hot season (Figure 4). This reflects differences in the availability of 1 forage species, catclaw acacia (*Acacia greggii*), which is readily available to the sheep in the Old Woman and Marble Mountains, but is lacking for the Old Dad sheep. Catclaw acacia is a very deep-rooted deciduous member of the pea family that leafs out about mid April and carries green leaves throughout the hot season until November or later. It elevates the diet quality of sheep throughout the hot season where available (Figure 6B).

The curves for all 3 mountain ranges in Figure 4 show a changing pattern beginning in August that represents the diet quality response to summer rains. Summer rains clearly produce much less nutrient availability for sheep than cold season rains. Indeed, summer diet quality in the best years barely overlaps diet quality in the worst years for the winter-spring period (Figure 6A, B). There are a number of reasons for this, of which temperature is fundamental. Cold season precipitation mostly occurs as soaking rains that persist for long periods as soil moisture because of subsequent cool temperatures. In contrast, much of summer rainfall runs out of the mountain ranges as flash floods to habitats not used by sheep. What moisture makes it into the soil in sheep habitat evaporates rapidly due to hot temperatures. Just as rainfall in different periods of the cool season cannot be equated in terms of effects on nutrient availability, cool

season rain is very different from that in the hot season relative to effects on diet quality of sheep.

Lenarz's (1979) simplistic analysis of rainfall data relative to nutrient predictability for bighorn sheep failed to predict diet quality patterns in part because it failed to account for the important influence of temperature and season on vegetation response to rainfall. Among those influences are important cumulative effects of rainfall in the cool season (Figure 7) that cannot be accounted for by analyses that treat months independently.

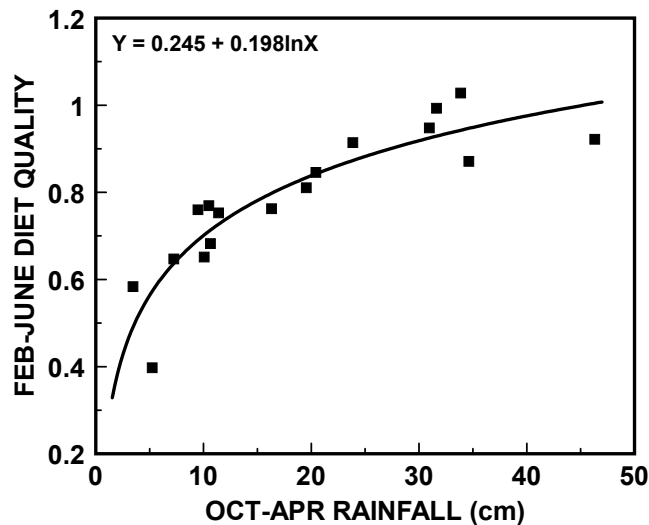


Figure 7. The relationship between February-June diet quality for bighorn sheep in the Marble Mountains and October-April rainfall at Mitchell Caverns in the south Providence Mountains, California.

patchy in distribution compared with winter rains. The other is that mountain ranges closer to the Colorado River and Sonoran Desert are more likely to receive summer rainfall. This influence can be seen in Figure 4 in the differences among populations in the amount of rise in the predictability of August and September diet quality.

Birthing Seasons of Desert Bighorn

The high temporal predictability of diet quality found here leads to the expectation that the birthing season should occur in the late winter and spring. Contrary to suggestions by Lenarz (1979) and others, the birthing seasons of desert bighorn sheep typically show a clear winter-spring peak that is aligned well with diet quality patterns. Two studies have produced excellent data on birthing dates for telemetered female bighorn sheep. In the Sonoran Desert of southwestern Arizona, Witham (1983) found a January - February birthing peak, with about 76% of 215 lambs born during January-March over a 4-year period. In the Sonoran Desert Peninsular Ranges of California, Rubin et al. (2000) recorded a consistent birthing peak in March for 133 lambs born over a 4-year period. This latter pattern is representative of the eastern Mojave Desert of California (Wehausen 1991), where the birthing peak occurs in March and April.

Peak diet quality mostly occurs in April in the region of this study. Consequently, there is a tendency for the peak of birthing to occur somewhat earlier than the peak in nutrient

There are also differences in plant species responses to cool and hot season rains that influence diet quality differences between those two periods. Relatively few species respond to hot season rains compared with cool season rains. Also, tropical grasses have different biochemical pathways (C4) and structural chemistry that typically make their peak digestibilities for ungulates lower than temperate (C3) grasses (Van Soest 1982). The same probably holds for hot season versus cold season grasses in the Mojave Desert.

In contrast to winter-spring diet quality patterns, there is little correlation in summer diet quality patterns among the populations sampled (Figure 6B). One reason for this is that summer rains are very

availability. There is a good reason for this. The survival of lambs to summer is strongly influenced by the amount of body growth they put on in spring (see below). The earlier they are



born, the more body mass they can accumulate during the spring growing season before diet quality plummets in late spring. However, the earlier the births, the higher the probability that diet quality will be insufficient for females at the end of gestation and early lactation. What mediates these opposing forces is the body condition of females. Females in better condition can ovulate earlier and potentially use their body reserves to get through a period of insufficient nutrient intake (Wehausen 1984). Cook et al. (2004) documented this relationship

between body condition and ovulation date for elk. Witham (1983) found birthing peaks to shift between January and February in different years. I have observed similar shifts of a month in the eastern Mojave Desert of California. Those year-to-year shifts probably reflect differences in body condition of females the previous year.

Witham (1983) and Rubin et al. (2000) both documented tails of the birthing curve that extend into summer. This also occurs in the eastern Mojave Desert. However, this distribution tail amounts to a small proportion of lambs produced. July-September births accounted for less than 2% of the births in Arizona (Witham 1983) and less than 5% in the Peninsular Ranges (Rubin et al. 2000). Using total length of the birthing season as the basis of hypotheses on reproductive strategies of desert bighorn sheep is therefore inappropriate given this lack of uniformity in the distribution of births within those periods.

The characterization of protracted birthing seasons of desert bighorn sheep as an abrupt latitudinal change from the northern pattern (Bunnell 1982) does not accurately represent the geography of this phenomenon. The timing of the beginning of the birthing season is a parameter of considerable importance in that it largely sets the length of the birthing season. The beginning of the birthing season shows clinal change from hot to cold desert ecosystems. For monthly categories, this initiation varies from November in the hot Sonoran Desert to (late) April in the southern Great Basin Desert (Table 2). Data are mostly lacking from further north in the heart of the cold desert, where native sheep appear not to begin birthing until May (Wehausen 1991). Thus, the more northern desert regions exhibit relatively short birthing seasons that are northern in character. However, the change in the initiation of lambing seasons is not strictly latitudinal (Table 2); instead, it simply reflects habitat differences such as elevation. The San Gabriel Mountains on the north side of the Los Angeles Basin is a prime example of this (Table 2).

Results of translocations of bighorn sheep suggest that different birthing seasons across the desert region may have a strong genetic basis. The Nevada Department of Wildlife has moved sheep from the southern warm-desert end of that state to northern cold desert ecosystems, where the early (February) initiation of birthing has persisted, but is about 3 month earlier than would be appropriate for the ecosystem to which they were moved (Wehausen 1991). Similarly, sheep moved from the Corn Creek pens at the Desert Game Range in Nevada to the Los Angeles Zoo maintained an intermediate timing of birthing initiation (Hass 1993).

Table 2. Month in which the birthing season begins for some native bighorn sheep populations in the southwestern United States.

Population	Latitude	Beginning Month	Source
SW Arizona	33	November	Witham 1983
Old Woman Mts., CA	34.5	December	pers. obs.
Marble Mts., CA	34.5	January	Wehausen 1991
Peninsular Ranges, CA	33	February	Rubin et al. 2000
Old Dad Mt., CA	35	February	pers. obs.
River Mts., NV	36	February	Hass 1993
Inyo Mts., CA	37	March	pers. obs.
Corn Cr., NV	37	March	Hass 1993
Canyonlands, UT	38.5	March	Douglas 1991
San Gabriel Mts., CA	34.5	April	Holl and Bleich 1983
White Mts., CA	37.5	April	Wehausen 1991
Sierra Nevada, CA	37	April	Wehausen 1991

Rather than a gambling strategy, the protracted birthing season of bighorn sheep in warm and hot desert regions is probably due to relaxed selection. I suggest that the operative variable is temperature. While annual temperature regimes underlie patterns of plant phenology and nutrition (Figure 4), temperature also affects the risk of losing a newborn to hypothermia (Bunnell 1980). This latter selective constraint on the birthing season declines from cold northern and high mountain ecosystems to hot deserts, effectively disappearing in the hot Sonoran Desert. A related phenomenon is that in warmer environments adult females in poorer body condition can more readily survive the winter cold season because less fat will be needed to maintain body temperature. This also means that the acceptable ratio of allocation of resources between body maintenance and current reproductive effort can shift in favor of reproduction. This would allow females to successfully give birth earlier and still meet overall nutrient needs even when conditions are not optimal.

The probability of a lamb surviving to adulthood is greatly influenced by the timing of its birth; thus, natural selection can be expected to closely tailor lambing seasons. Relaxed selection relative to birthing seasons means that lambs born over long time periods in warm desert environments all have a high enough probability of surviving and reproducing that natural selection has not censored any part of those time periods, as it has in colder climates. The lack

of uniformity in the distribution of births across those time periods, however, points to variation in the probability of lambs born at different times surviving to adulthood.

The advantage of longer birthing seasons lies with flexibility. There appears to be a threshold body condition that females must reach for ovulation to occur. In northern environments with short birthing seasons, there is a short time window in which that can occur. If conception fails after the first ovulation, there is unlikely to be more than a second opportunity for a female to conceive where birthing seasons are short (Bunnell 1980). If conception does not occur during the breeding season, a female must wait nearly a year until the next one. In contrast, the long breeding season of sheep in warmer desert environments provides considerably more opportunity for females to gain the necessary body condition to ovulate and to ovulate numerous times until conception occurs if necessary. Long breeding seasons mean that the period between consecutive births can vary considerably in both directions from 1 year, as mediated by prior nutrient intake and expenditures. For bighorn sheep in the Sonoran Desert of Arizona, Witham (1983) reported the period between consecutive births to vary from 279 to 446 days. In short, the flexibility afforded by longer birthing periods gives females the opportunity to produce more offspring in a lifetime.

Nutrient Availability and Lamb Survival

The variance among years in diet quality for bighorn sheep in the Mojave Desert has important implications for lamb survival. The primary loss of lambs occurs prior to summer. Unless a water source dries up during the hot season, there is almost no loss of lambs between late spring and fall (unpubl. data). However, depending on diet quality, there can be a large loss of lambs prior to the hot season. That loss exhibits an interesting relationship with diet quality that indicates 2 opposing factors are operating on lamb mortality. Up to a February-June diet quality value of almost 1, spring lamb recruitment increases linearly with increasing diet quality, as expected. However, this relationship reverses sharply with higher diet qualities (Figure 8). The point of change corresponds to 23.4 cm of October-April rainfall at Mitchell Caverns. The year 1990 is a notable outlier in this relationship (Figure 8) and is treated as such. That year was the second of 2 consecutive years of low rainfall in the growing season, which likely accounts for its outlier status.

The pattern in Figure 8 is consistent with similar patterns previously elucidated (unpubl. data). In the initial years of this research, bighorn sheep in the Old Woman and Marble Mountains suffered from a disease syndrome that killed most lambs during spring. During those disease episodes, the relationship between lamb recruitment and February-June diet quality for both populations was the same pattern as Figure 8, except that the meeting of the two curves was shifted greatly to the left to where the peak lamb recruitment was only 30 lambs:100 ewes, compared with 61:100 in Figure 8.

The disease syndrome that previously affected the sheep in the Marble and Old Woman Mountains is poorly understood, but is conjectured to have a virus as the ultimate cause, similar to what affected the bighorn sheep in the Peninsular Ranges of California for numerous years (Wehausen et al 1986, DeForge et al. 1995). The lamb recruitment patterns in the Marble and Old Woman Mountains during those disease episodes were consistent with an insect vectored virus, such as bluetongue. While diet quality of sheep benefits from increasing growing season precipitation (Table 1, Figure 7), so do insect populations. It is possible that the declining lamb recruitment phase in Figure 8 is also due to a disease that is adequately spread among sheep by arthropods only during very wet years.

There appears to be a linear increase in spring lamb recruitment relative February-June diet quality up to the inflection point (Figure 8). However, February-June diet quality follows a curvilinear relationship with rainfall (Figure 7). A noteworthy aspect of that curvilinearity is the initial steep increase in diet quality with small gains in rainfall. Thus, small initial increases in rainfall translate to large gains in lamb recruitment.

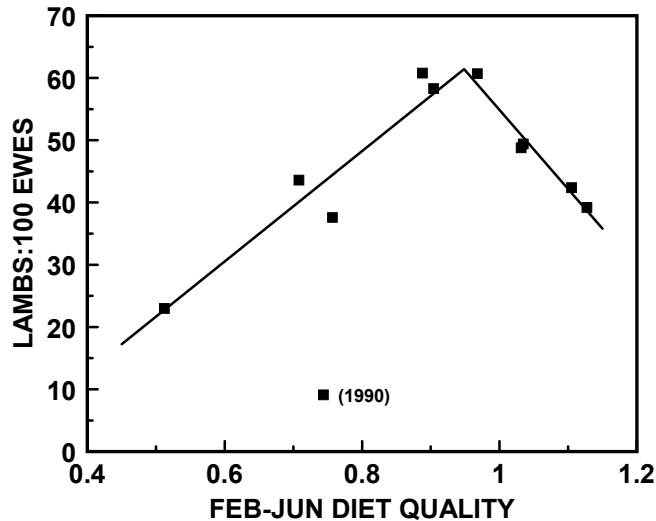


Figure 8. The relationship between lamb recruitment rate in early summer and winter-spring diet quality for bighorn sheep at Old Dad Mountain, California.

birthing seasons of desert bighorn sheep are a gambling strategy response to an unpredictable environment. There is also a lack of support for the idea that there is an abrupt change from northern short birthing periods to long birthing seasons in desert bighorn sheep. Instead, the evidence suggests that the birthing season of desert bighorn sheep varies according to habitat, from long seasons in the southern hot desert to short seasons typical of northern environments in the cold desert of the Great Basin. A key variable in this variation is the timing of the beginning of the birthing season, which varies from November in the hot Sonoran Desert to May in the Great Basin Desert.

The unpredictable aspect of nutrient availability for bighorn sheep in the eastern Mojave Desert is the amplitude of the winter-spring growing season. While geographically consistent, the amplitude of the spring peak varied considerably from year to year. That variation is driven by the amount of rainfall during October-April. Rainfall at different times of year has decidedly different effects on diet quality of sheep. This is even the case within the October-April period, with rainfall in the earlier part of that period having a greater effect on diet quality than later rainfall. Temperature plays a strong role in how rainfall affects subsequent diet quality of sheep.

October-April rainfall probably has a small effect on the timing of the birthing season the following year through its effect on subsequent body condition of females and the effect of body condition on timing of ovulation. In contrast, the amount of rainfall during October-April has a major effect on the survivorship of lambs to summer. That relationship is more complex than expected, with strong gains in survivorship up to about 23 cm of rainfall, but decreasing

Conclusions

Like most scientific questions, it is important to break the concept of resource predictability into its constituent components (Colwell 1974). For nutrient availability to desert bighorn sheep, temporal predictability should be distinguished from amplitude predictability. For the Mojave Desert ecosystems studied here, the temporal predictability of nutrient availability for bighorn sheep is high. The primary growing season occurs consistently in winter and spring, a timing that reflects both temperature and precipitation patterns.

The timing of births matches that pattern of nutrient availability, contrary to the common explanation that the long

survivorship associated with rainfall beyond that amount. This phenomenon deserves further research attention.

The data sets used here allowed analyses of patterns of nutrient availability because of their length (15-18 years). However, because each year represents but a single data point for most analyses, in some ways these data sets allow only the beginning of an understanding of the complexities of this ecosystem. Additional decades of data would allow considerable refinement of that understanding.

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