

Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep

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Abstract. Behavioural and ecological consequences of pregnancy in a medium-sized herbivore were examined by testing the hypothesis that pregnant females should move to areas that maximize nutrient intake once the demands of gestation are high, even at the risk of increased predation. Observational and experimental data were contrasted for six populations of bighorn sheep, *Ovis canadensis*, living in heterogeneous environments with natural predators at Great Basin ($N=4$), Sonoran Desert ($N=1$) and northern prairie ($N=1$) study sites. Manipulations included the alteration of dietary protein (via alfalfa supplements) in habitats that varied in predation risk when females were at different stages of pregnancy and, hence, protein requirements. Both sexes left the mountainous terrain during late winter to feed on bajadas where emergent new grasses were highest in crude protein. In these areas females were more than twice as likely as males to flee from natural predators. Females also (1) remained closer to mountainous slopes while feeding and (2) incurred greater losses in feeding time when away from slopes than males. These data suggest that predation pressure affects the sexes differently. Results of the experimental manipulations were consistent with the posed hypothesis since protein supplements on bajadas were consumed by both sexes until emergent new grasses became more abundant on mountainous slopes. However, natural variation in female reproductive status allowed a further refinement of the extent to which pregnancy incentives and predation constraints affected habitat use. Ewes not accompanied by lambs or yearlings used areas where they were at risk from predators, such as bajadas, more frequently than those without young, observations that favour the tenet that potential predation pressure overrides increased nutrient demands during late stages of pregnancy. These data suggest that species of mammals with access to heterogeneous environments prior to parturition are ideal subjects in which to examine the extent to which habitat shifts result from balancing increased dietary requirements during late gestation and safety from potential predators.

Pregnancy and lactation have conspicuous and well documented behavioural and ecological effects (Michener 1989). These include increased feeding rates and more selective diets to compensate for heightened energetic requirements (Clutton-Brock et al. 1982a; Carl & Robbins 1988; Iason & Waterman 1988), and increased vigilance and parental care (Altmann 1980; Lipetz & Bekoff 1982). It is less clear whether the stage of parental (prenatal or postnatal) investment affects the vulnerability of females to predation. For instance, egg retention may impede locomotion and increase predation on gravid snakes and lizards (Fitch 1970; Bauwens & Thoen 1981). Among mammals, lactating females may shift to areas that minimize predation on

their neonates (Wehausen 1980; Edwards 1983; Festa-Bianchet 1988a).

Little work has focused on the habitats used by pregnant females. Such areas can be of critical importance because the last trimester of gestation imposes increased energy, mineral, protein and vitamin demands (Robbins 1983; Oftedal 1985). In both wild and domestic mammals, inadequate nutrition during pregnancy can reduce birth weights and postnatal growth and cause poor recruitment (Hight 1967; Robinson & Forbes 1968; Thorne et al. 1976). If other factors are equal, these costs should cause pregnant individuals to move to areas that maximize nutritional benefits for developing fetuses. However, because other factors rarely are

equal, it is unclear how and/or whether habitat shifts are affected by pregnancy and predation.

The study of these phenomena in mammals is difficult for three principal reasons. First, many species are nocturnal, making it difficult to detect or manipulate possible ecological factors. Second, because observations of interactions between predators and prey often go unwitnessed (Pfeifer 1980; Bowyer 1987), predation risk has usually been assumed (Grubb & Greenwald 1982; Kotler 1984). Although this may be an unavoidable problem in working with many species (Anderson 1986; Huntley et al. 1986), it creates a dilemma in evaluating quantitatively how predation shapes habitat use. For instance, in more than 5000 h of observation, only two instances of coyote, *Canis latrans*, predation on marmots, *Marmota flaviventris*, were observed (Armitage 1982). One way to reduce this problem is to select species in which predator-prey interactions can be manipulated (Tait & Krebs 1983) or to use species for which predation in different habitats has been described, allowing derivation of an index of potential risk (Ryan 1985; Longland 1989). Third, habitat trade-offs in relation to pregnancy may be subtle, particularly where habitats appear homogeneous. An additional complication arises in deciding the extent to which observations of populations in reserves may be used to make inferences about the role(s) of the posited processes because much of the world's large mammal fauna now occupy areas where predation by natural predators no longer occurs.

An unusually good opportunity to examine questions about pregnancy, predation risk and habitat use is still afforded by seasonally breeding montane ungulates of temperate regions. Many are diurnal and occur in relatively open habitats where natural predators have not been eliminated. Parturition occurs during spring so that increased gestational stresses are present towards the end of winter, a period when ambient temperatures may still be low but variation in food quality is high because there is a mixture of dormant and emergent new grasses. Most importantly, it is not uncommon for species such as elk, *Cervus elaphus*, mule deer, *Odocoileus hemionus*, and Dall and bighorn sheep, *Ovis dallii* and *O. canadensis*, to depart from the safety of mountainous habitats to feed on protein-rich vegetation at the bottom of valleys and on bajadas (see definition in Methods; Geist 1971; Hebert 1973; Wehausen 1980). Because the track-

ing of plant phenology may involve shifts to habitats where the risk of predation is greater, it is possible to investigate the role(s) played by reproductive condition or stages of pregnancy. Here, using bighorn sheep, I examine the hypothesis that a balance in habitat use results from the interaction between pregnancy and predation risk, with risk-taking being greatest during the last trimester of gestation.

Mountain sheep (*Ovis* spp.) are medium-sized ungulates of western North America ranging from northern Alaska to Baja, California and Sonora, Mexico where they rely on rocky, precipitous and usually non-forested terrain to detect and escape from predators (Geist 1971; Shackleton 1984). The gestation period in bighorns is about 175 days (Shackleton et al. 1984), with the parturition period varying with latitude (Bunnell 1982, but see Festa-Bianchet 1988a). Throughout much of the year the sexes inhabit different areas (Geist & Petocz 1977; Morgantini & Hudson 1981; Shank 1982), with habitats varying from rolling hills and talus slopes to steep cliffs and canyons. Interactions between sheep and terrestrial predators have not been summarized systematically but an extensive literature spanning nearly 50 years is available, enabling me to estimate predation risk in different habitats (see Methods). This is important because, to show that habitat shifts may result from predation pressure, it must be demonstrated that the predation rate varies between habitats.

Sheep in the Great Basin Desert are well suited to address the hypothesis proposed above. They occupy habitats where predation risks, other potential costs (i.e. loss of time spent feeding) and possible benefits can be estimated. They occur in multiple, insular mountains, many possessing almost vertical cliff faces abutted against expansive desert bajadas, sites that can be used both for replication and experimental manipulations. Not only do natural predators including mountain lions, *Felis concolor*, coyotes, and bobcats, *Lynx rufus*, occur, but the loss of wolves, *Canis lupus*, from most of the continental U.S.A. does little to alter Great Basin predator communities because wolves were never common there (Simpson 1876; Hall 1946). Plant growth is predictable, progressing from valley floors (in late winter) to mountain tops (in summer), creating habitats that vary in nutritional quality and predation risk (Wehausen & Hansen 1988). Finally, the stage of pregnancy can be estimated because approximate birth

dates are known in the different mountain ranges.

METHODS

Study Sites and Periods

Sheep were studied intensively at three Great Basin sites prior to parturition, at a Sonoran Desert and northern prairie site prior to and after parturition, and sporadically at an additional Great Basin site. The four Great Basin sites were all precipitous, block-faulted mountains, and surrounded by gentle and broad bajadas. Each was at least 2700 m in elevation, had at least 1300 m of elevational relief, and contained perennial streams and springs. Brief descriptions of the six sites and periods of study follow.

Lone Mountain, in the southern Great Basin, contains a native population of about 200 *O. c. nelsoni*. Sheep were studied in January 1986 and from February to August of 1987 and 1988. The Stillwater Range, in the western central Great Basin, contains a translocated population of about 100 *O. c. nelsoni*. They were studied from January or February until August in 1987 and 1988. The Santa Rosa Range, in northern central Nevada, contains about 70 reintroduced *O. c. californiana* and was studied from March and April of 1987 and during February–May 1988. The northern Snake Range, in the eastern Great Basin, is inhabited by a small declining population of about 30 reintroduced *O. c. canadensis* that were studied during March and April of 1987 and 1988. Natural predators, including coyotes, bobcats and mountain lions were present at each site. Moreover, evidence of lion predation on sheep was found at the first three sites while predation on mule deer was noted at the Snake Range.

Because the focus of the study of Great Basin bighorn sheep was on habitat and foraging relationships during different stages of pregnancy, data from two additional sites are also presented; these contrast prenatal and postnatal patterns of habitat use. The first site was in the Santa Rosa Mountains in the western Sonoran Desert, a peninsular range extending from southern California (U.S.A.) into Baja California (Mexico). This area contains several hundred native *O. c. cremnobates* studied from January to April 1977 (see Berger 1979 for details). The second site was Badlands National Park in South Dakota (Berger &

Cunningham 1988) where about 125 reintroduced *O. c. canadensis* occur on deeply eroded sod table-tops, some rising about 100 m above the rolling prairie with a base of about 600 m. Observations at Badlands National Park were made from March to September 1985, in March of 1986, and from May to August of 1986–1988. Although no evidence of lions was available at either of these latter sites, bobcats and coyotes were present.

Observations and Sampling

Sheep were observed with spotting scopes from distances ranging from 300 to 2000 m, with habitats being sampled randomly. Data on group size, altitude, habitat, distance from the base of the mountain or rugged terrain, and slope were noted. A simple measure of foraging efficiency was calculated for centrally located animals in randomly selected groups by noting the percentage of time in a 180-s bout that animals fed or walked with their heads oriented to the ground. The measure is based on the time allocated to different activities (Berger & Cunningham 1988) and is not intended to convey information about assimilation efficiency.

Because habitats occupied by sheep vary geographically and are rarely directly comparable when vegetation components are considered (Morgantini & Hudson 1981; Warrick & Krausman 1987), I grouped observations of where sheep were located as follows: (1) slopes, areas situated on mountains, not less than 15° slope, including cliffs and talus; (2) bajadas, areas between mountain slopes and valley floors, lacking large rocky areas, boulders or other features that could be used to aid in predator avoidance; (3) ravines; (4) tabletops, uplifted areas with steeply eroded edges that drop to a floor (tabletops occurred only in the Badlands and were considered as escape terrain). Only 1.8% of 1627 observations involved uncertainty in classification; these were omitted from analyses.

Habitat use was examined in relation to four time periods, each standardized for stage of pregnancy as follows. Approximate birth dates were known for the Badlands, Santa Rosa Mountains, Stillwater Range and Lone Mountain sites (unpublished data); birth dates were estimated from observations made by Nevada Division of Wildlife personnel at the Snake Range and Santa Rosa Range sites. Except for the Snake Range, where observations of lambs were infrequent, median birth date was determined for all sites and two

6-week periods were assigned both prior to and after median birth date. For simplicity, I designated the periods I to IV, and used them to examine the hypothesis that pre- and postnatal events affect habitat use. For the Snake Range site, I designated median birth date as 1 May, which is similar to that for the Lone Mountain and Santa Rosa Range sites.

In a strict sense, the two prenatal 6-week periods do not correspond directly to trimesters of pregnancy because the gestation period in bighorn sheep is about 175 days (Shackleton et al. 1984). Eight-week periods would be the appropriate measure here, but because of sampling differences at my six study sites, the only way to standardize prenatal development is by adjustment of periods to 6 weeks. The results should remain unaffected because the intent is to examine how pre- and postnatal changes affect habitat use in relation to predation.

Assessment of Food and Experimental Manipulations

Vegetation was sampled by noting the frequency of emergent new grasses at each step along randomly selected 220-step transects (Canfield 1941); data were then converted to the percentage of steps with emergent new grasses on each transect. Data from a total of 168 km of transects were available. The three most intensively studied Great Basin sites, Lone Mountain, the Santa Rosa Range and the Stillwater Range were sampled for emergent new grasses at different altitudes each month a site was visited. Rate of altitudinal 'green-up' for each site was then calculated by linear regression of time against different transect criteria beginning on the bajadas and extending up the mountainous slopes. The criteria for each of four categories were: (1) 10% of the transect contained emergent new grasses in a minimum of 10% of the transects; (2) 20% of the transect contained emergent new grasses in a minimum of 20% of the transects; (3) 30% of the transect contained emergent new grasses in a minimum of 30% of the transects; (4) 50% of the transect contained emergent new grasses in a minimum of 50% of the transects. The regressions indicate green-up rate at the different sites and they reflect the dates at which emergent new grasses first appeared. Grasses were also collected from areas where sheep fed and where they did not. The grasses were air-dried and later analysed for crude protein by the Wild-

life Habitat Laboratory at Washington State University.

Because observational studies may fail to detect the importance of some ecological variables, I manipulated what I believed to be a key nutrition component (protein) of sheep habitat use (Wehausen & Hansen 1988). The experimental manipulations entailed alteration of the distribution and quality of protein available. At both Lone Mountain and the Stillwater sites, a high grade of alfalfa (NSC 31% Grain Supplement, Lovelock, Nevada) that averaged 27% in crude protein and included molasses, whole grains and rice mill was supplemented in 50–100-kg treatments spread evenly over the ground in as large an area as possible. Treatments were deposited both on bajadas, approximately 100 m out from mountains and from 75 to 175 m above the bajada floor on rugged slopes (Fig. 1). The treatments were matched so that approximately similar volumes were deposited at both locations and they were intended to simulate areas where sheep would be exposed to and able to avoid potential predators (the bajadas and slopes, respectively).

To avoid conditioning sheep to the supplements, locations were changed for each treatment. Because the supplements were designed to examine how pregnant sheep respond to differences in food quality and potential predation pressure, they were situated in areas not used by rams. Sites were also selected where there was no evidence of other herbivores, but in one case cattle discovered and consumed the alfalfa. Supplements were checked for evidence of use every second or third day. Approximately 2000 kg of alfalfa was used over the study period.

Predation Risk

Because observations of predator–sheep interactions are rare, it was not possible to determine the actual risk of predation experienced by sheep when using different habitats on a site-specific basis. However, the combination of observations from the literature (see below) and my own observations at several sites (Berger 1978a, 1979) yielded data on 79 interactions between sheep and potential terrestrial predators. Undoubtedly the sample from the literature is biased because observations in which either a possible predator or sheep responded to the other would be more likely to be reported than those in which a response was not elicited. None the

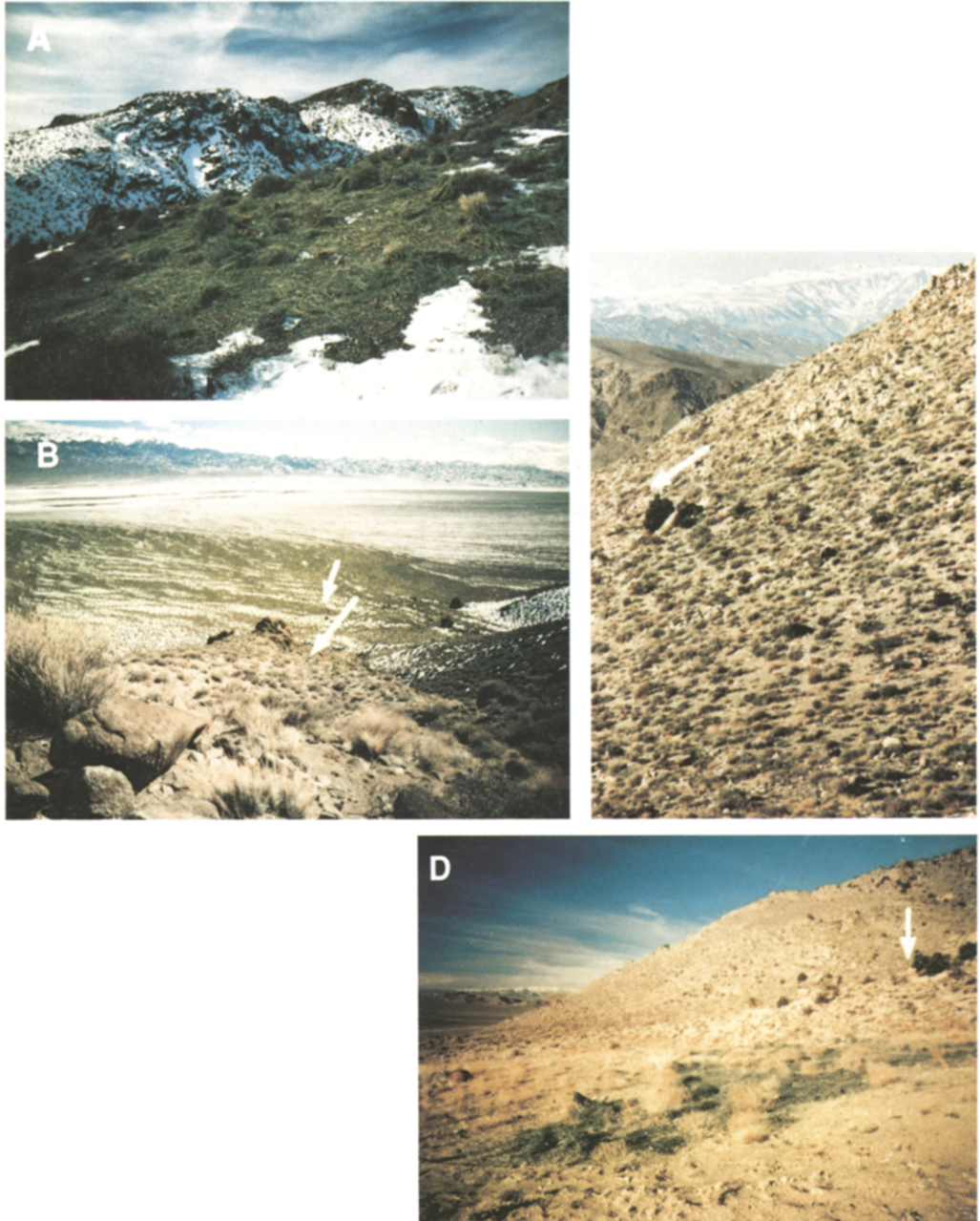


Figure 1. Overview of experimental treatments on slopes and bajadas at the Stillwater Range (A, B) and Lone Mountain (C, D) sites in the Great Basin. (A) Alfalfa (darkened areas in foreground) on slopes during January; (B) approximate locations of treatments on bajada (smaller arrow) and on slope (larger arrow), which is also the same location as in (A); (C) location of treatment on slopes; (D) location of treatment on bajada (the arrow indicates treatment on slopes, which is also the same location as indicated by arrow in C).

less, rather than just accepting assumptions about predation risk, it is important to ask whether such assumptions are justified, and the literature reports can serve as a useful gauge of the frequency and context of response in different habitats. In searching the literature for interactions, I tallied all cases in which either a response or lack of one was reported, although descriptions often lacked information on distances between the potential predator and the sheep, or the habitats in which the interactions occurred. In trying to evaluate the responsiveness of sheep to potential predators, I used only instances in which information on habitats, distances or the responses of sheep were available. I also noted whether sheep fled or stayed and whether they were killed or escaped.

Statistical Analyses and Interpretations

The data on foraging efficiency were skewed with the mean and variance being positively correlated. Hence, data were arcsine transformed before regression, ANOVA and *t*-tests were carried out. The effects of group size and distance on bajada (or distance to mountain mass) on foraging efficiency were evaluated by multiple regression after the data had been normalized. Partial correlation was used to hold constant the effects of one variable when examining the effects of another. The potential for resource-related differences among sites was investigated with ANOVA and then with the Student–Newman–Keuls multiple range test. The *G*-test, with and without an adjustment for small sample sizes (Sokal & Rohlf 1981), was used to evaluate possible differences in predation risk between habitats and to determine the effect, if any, of stage of pregnancy on habitat use.

Like many ungulates, sheep live in groups (Geist 1971; Jarman 1974), and statistical problems may arise because activities of individuals may be affected by those of other group members (see Machlis et al. 1985). This is especially true where the gregarious nature of some species affects decisions about habitat use, thus violating assumptions about independence (Sokal & Rohlf 1981; Festa-Bianchet 1988a). Nevertheless, the results reported here appear conservative and must underestimate the use of slopes because (1) it is much easier to detect sheep on bajadas than on slopes, in canyons or on mountaintops, and (2) only observations of sheep seen (rather than their inferred presence) were used in analyses of habitat use.

The pooling of individuals sighted on different days presents a problem in that the magnitude of the contributions made by different individuals entering the data set more than once is unknown. Unfortunately, there is no easy way to circumvent this sampling problem. Indeed, in most studies of habitat use, especially those in which the populations are composed of only a few individuals sampled intensively for short time periods, it is virtually impossible to achieve true independence (Schoener 1981; Swihart & Slade 1985). Powell (1986) suggested that, because some large wide-ranging vertebrates, such as bears, do not move randomly, statistical independence may be biologically unrealistic. For the bighorn sheep that I studied, it is possible to offer some idea of the minimum number of different individuals (e.g. the maximum number of different animals observed at any one time) in a given habitat and the percentage this represents of the largest number observed in a different habitat. The largest groups I observed on bajadas were 22 (Lone Mountain), 18 (Santa Rosa Range), 16 (Stillwater Range), 16 (Badlands National Park), 12 (Santa Rosa Mountains) and 3 (Snake Range). Expressed as a percentage of the maximum number of sheep seen on slopes on a given day, the values for each area (respectively) are 65, 113, 107, 52, 63 and 60. While pooling the data may affect statistical interpretation of habitat use to an unknown degree, the above figures indicate that resource exploitation on bajadas is a regular, independent biological feature of sheep at multiple study areas.

Assumptions

I made three assumptions prior to interpreting the data. First, regardless of sex, sheep are in poorer body condition at the end of winter than when it began. Second, most ewes are pregnant. Third, energy and protein requirements increase most rapidly during the last trimester of pregnancy. These assumptions are evaluated below.

RESULTS

Indirect Tests of Assumptions

Body condition over the winter

While no direct evidence exists for bighorns, data for other temperate ungulates, including mule, red,

C. elaphus, and white-tailed, *O. virginianus*, deer, bison, *Bison bison*, and wild horses, *Equus caballus*, indicate losses in body condition over the winter (Clutton-Brock et al. 1982b; Torbit et al. 1985; Berger 1986; Miura & Maruyama 1986; Berger & Peacock 1988). It seems reasonable to expect that bighorn sheep would be no different.

Pregnancy

Four methods have been used to evaluate pregnancy in wild bighorns: examination of dead animals, observations of lambs soon after birth, hormone assays and ultrasound. Based on data reported from a combination of 13 different sites or years and employing these methods (eight are lamb production data, five direct assessments), pregnancy can be estimated (Murie 1940; Spalding 1966; Ramsey & Sadler 1979; McCutchen 1982; Harper 1984; Bunch et al. 1986; Berbach 1987; Brundige et al. 1988; Festa-Bianchet 1988b; Stockwell 1989). These studies reveal that, on average (\pm SE), $85.1 \pm 2.5\%$ of the ewes produced lambs and that $94.3 \pm 2.0\%$ were pregnant. To be conservative, I adopt for my estimation of pregnancy rate the minimum reported value, which was 83.3% for *O. c. nelsoni* in southern Utah (McCutchen 1982).

Protein needs during late pregnancy

Daily nitrogen requirements of a 45-kg domestic ewe increase by about 44% during the last 6 weeks of pregnancy (Klosterman et al. 1953; Robinson & Forbes 1968). Sheep that fail to meet nutritional requirements during this period may experience pregnancy toxemia, which is associated with reduced blood glucose and elevated blood ketones, give birth to lambs of low weight, and produce lambs that experience greater mortality (National Academy of Sciences 1975).

Predation Risk in Different Habitats

While it is sometimes assumed that sheep are more vulnerable to predation when away from mountainous terrain (Berger 1978b; Risenhoover & Bailey 1985), there are few data on predation risk in different habitats. Therefore, estimates of predation risk were generated by combining my observations ($N=13$) of interactions between potential

terrestrial predators and sheep with those found in the literature ($N=66$; Table I).

Because sheep are dimorphic, with males being larger (Geist 1971; Shackleton 1984), females may be more vulnerable to predation. If this were the case, females should be more likely to flee from predators than males, a prediction complicated by potential sex differences in habitat use and exposure to type of predator. To evaluate the prediction, the success of different predators in capturing sheep was examined (Table I), and then the flight response of each sex by habitat and potential terrestrial predator; coyotes, wolves, black and grizzly bears, *Ursus americanus* and *U. arctos*, mountain lions, and small carnivores (badgers, *Taxidea taxus*; wolverines, *Gulo gulo*; and bobcats).

In contrasting kills per encounter between the sexes, I excluded data on two male yearlings because males of this age usually associate with ewe groups (Geist 1971; Festa-Bianchet 1986), but included data on lambs since they are found exclusively with ewe groups. If adult males and females respond differently to potential predators, it makes biological sense to look for a possible difference in the effectiveness of predators when encountering groups that vary in sex composition. Irrespective of which categories were included, the results (Table I) remain unchanged. A higher proportion of deaths occurred in female than in male groups when interactions with all possible predators (20.4% versus 12.5%, $N=49$ and 16, respectively) are considered or when only those with coyotes and wolves (23.3% versus 8.3% $N=43$ and 12, respectively) are considered. However, in neither case were the differences significant ($G_{\text{adj}}=0.50, 1.16$, respectively).

Nevertheless, the sexes varied in their responses to potential predators when in different habitats. In open environments (defined simply as non-escape terrain because more precise details were not available in the literature) females fled more than twice as often as males (89 versus 44%, $N=19, 9$ respectively; $G_{\text{adj}}=5.80, P<0.025$) whereas no sex difference occurred when the animals were on cliffs or steep slopes ($G_{\text{adj}}=0.36, \text{NS}$). Females were more likely to flee in open areas than when they were on cliffs ($G=16.16, P<0.001$), but for males flight did not vary by habitat ($G=0.08, \text{NS}$). The habitat-related difference in flight among females is undoubtedly a consequence of the distance to rugged, rocky terrain, especially since mortality was almost three times as great for ewes and lambs when they

Table I. Summary of frequency of observed interactions between mountain sheep and potential terrestrial predators in different habitats based on literature (below)

	Coyotes		Wolves		Bears		Small carnivores		Lions		Total killed
	Open	Slopes	Open	Slopes	Open	Slopes	Open	Slopes	Open	Slopes	
Adult females											
Fled	15 ^a	0	1	4 ^b	0	2	1 ^c	0	1	4 ^d	7
Stayed	1 ^e	7	0	3	1	0	0	0	0	0	0
Adult males											
Fled	2 ^f	0	1	1 ^g	1	0	0	1 ^h	0	5 ^d	8
Stayed	4	3	0	2	1	0	0	1	0	0	0
Lambs											
Fled	3 ⁱ	7 ⁱ	3 ^b	0	1 ^j	2 ^k	0	1	0	0	7
Stayed	0	0	0	0	0	0	0	0	0	0	0
Total killed	4	2	3	4	0	0	0	0	0	9	22

Bears: black and grizzly; small carnivores: badgers, bobcats and wolverines; slopes: cliffs and canyons; open: bajadas and non-sloping, non-rocky areas. References are: Ashcroft (1986); Berger (1978a, unpublished data); Buechner (1960); Bunch et al. (1986); Burger (1985); Creden & Schmidt (1983); Dekker (1986); Demarchi & Mitchell (1973); Elliot (1978); Festa-Bianchet (1987, 1988b); Groves (1957); Haas (1989, personal communication); Hoefs & Cowan (1979); Hornocker (1969); Kelly (1980); McCutchen (1982); Murie (1940, 1944, 1981); Pitzman (1970); Shank (1977); Simmons (1969); Weaver & Mensch (1970); Welles (1965) and Welles & Welles (1961, personal communication).

^aIncludes two cases where sheep moved slowly to cliffs and resumed feeding.

^bThree killed.

^cBadger.

^dAll killed.

^eSheep approached to within 30 m of coyote.

^fBoth killed (one a yearling).

^gOne killed.

^hWolverine.

ⁱTwo killed.

^jDraw at bottom of creek' (Murie 1981).

^k'Sharp slope' (Murie 1981).

were more than 100 m to cover (67%, $N=6$) than when closer to or on slopes (23%, $N=23$); the differences are not quite significant ($G_{adj}=3.01$, $P<0.10$). Nevertheless, such mortality may also result because ewes attempted to minimize predation on their lambs rather than to ensure their own safety. In contrast, the lack of a difference in flight for males suggests that ram vulnerability does not vary by habitat.

Because location affected how females responded to potential predators, it seems reasonable to expect that such behaviour is associated with different levels of predation risk. Data on predation (Table I) and habitat use (Fig. 2) for females and young permit some rough calculations to examine this idea. Lambs in open or on flat areas were killed more often than those on rocky or steep mountainous slopes (71 and 22%, respectively) but, again, the differences were not quite significant ($G_{adj}=3.72$, $P<0.10$). This relationship remains unaltered when only coursing predators such as coyotes or wolves are included in the analysis ($G_{adj}=3.72$, $P<0.10$). Overall, the relative risk of predation can be calcu-

lated with regard to coursing predators; on bajadas it was 3.22 (0.714/0.222) times as great as it was when on slopes or cliffs. For stalking predators like mountain lions, the relative predation risk experienced by sheep could not be evaluated; despite nine of 10 mortalities situated on slopes or in brush-covered areas (Table I), none were observed, preventing assessment of sheep responses to lions when in different habitats.

Differential Use of Habitats

As reported for other sheep populations (Geist 1971; Shank 1982; Krausman & Leopold 1986), both sexes used rugged slopes more than bajadas or other areas away from escape terrain; at my six study sites (data pooled), females and young used slopes 84.4% of the time ($N=1081$) whereas ram use was 63.9% ($N=374$; Fig. 2). Prenatal habitat use was consistent among sites. At each of the four sites where sufficient data or sampling periods were available, females increased use of bajadas during the last period of pregnancy (Fig. 2; $P<0.05$, G -test). Over the same time frame no increase

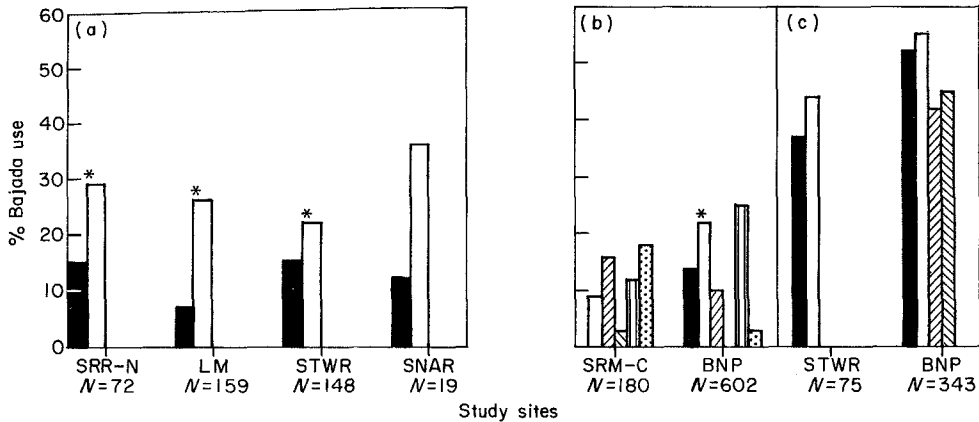


Figure 2. Comparison of prenatal (a) and postnatal (b) habitat use in females at six sites and males (c) at two sites. Sample sizes shown below; asterisks indicate that differences between period I and II are significant ($P < 0.05$; G -test). Study site abbreviations as follows: Santa Rosa Range, Nevada: SRR-N; Lone Mountain: LM; Stillwater range: STWR; Snake Range: SNAR; Santa Rosa Mountains, California: SSM-C; Badlands National Park: BNP. See Methods for standardization of time periods. ■: period I; □: period II; ▨: period III (without lambs); ▩: period III (with lambs); ▧: period IV (without lambs); ▨: period IV (with lambs).

occurred for males, although compared to females rams used bajadas 266% more often ($t = 6.91$; $df = 11$, $P < 0.01$).

Compared with prenatal patterns, those after parturition should be more varied because females with young may rely on steeper areas than those without young (Geist 1971; Geist & Petocz 1977; Wehausen 1980; Festa-Bianchet 1988a). Twenty-five per cent ($N = 223$) of ewes without lambs at Badlands National Park were away from tabletops during period IV whereas less than 3% ($N = 86$) of those with lambs used these areas (Fig. 2). Overall, the presence of neonates and time period both affected the frequency that areas away from slopes were used at Badlands National Park and the Santa Rosa Mountains (multi-dimensional contingency analysis $\chi^2 = 34.76$, $df = 4$, $P < 0.001$). Each factor exerted independent effects but lamb presence had a stronger influence ($\chi^2 = 26.39$, $df = 3$, $P < 0.001$) on habitat use than time period ($\chi^2 = 12.62$, $df = 3$, $P < 0.025$), presumably because neonates 6–12 weeks old (time period IV in Fig. 2) are nearly as vulnerable to predation as are younger lambs (time period III; Geist 1971; Carl & Robbins 1988).

If females with young restricted themselves chiefly to areas where predation pressure was less, did they sacrifice access to high-quality food? While few data are available on locations for mothers with newborns, at three Stillwater Range sites (each with

10 grass samples collected) ewes with 1–3-day-old lambs fed on cliffs where crude protein averaged $5.99 \pm 1.03\%$ whereas three sites where ewes without lambs fed (matched by time period and each with at least eight samples/site) averaged $11.05 \pm 2.39\%$ crude protein ($t = 3.17$, $df = 4$, $P < 0.05$). Thus, ewes with very young lambs were secluded in areas where crude protein levels were lower than areas where non-mothers foraged.

Habitat Effects on Group Size and Foraging Efficiency

As in numerous taxa, sheep in larger groups fed more efficiently than those in smaller groups (Hoogland 1979; Bertram 1980; Berger et al. 1983), although other factors also modify foraging responses (Jenkins 1979; Stacey 1986; Lima et al. 1987). At the Lone Mountain, Stillwater and Santa Rosa Range sites, mean foraging time/180-s bout increased with group size (two-way ANOVA $F_{4,76} = 74.36$, $P < 0.001$) but neither a study site nor interaction effect was detectable ($F = 0.19$, NS). Possible habitat effects were investigated by contrasting sheep foraging efficiency among three areas, mountainous slopes, bajadas within 100 m of slopes and those more than 100 m away from slopes. Because differences between the first two habitat categories were not found ($F = 0.33$, NS), data were pooled and contrasted between sheep

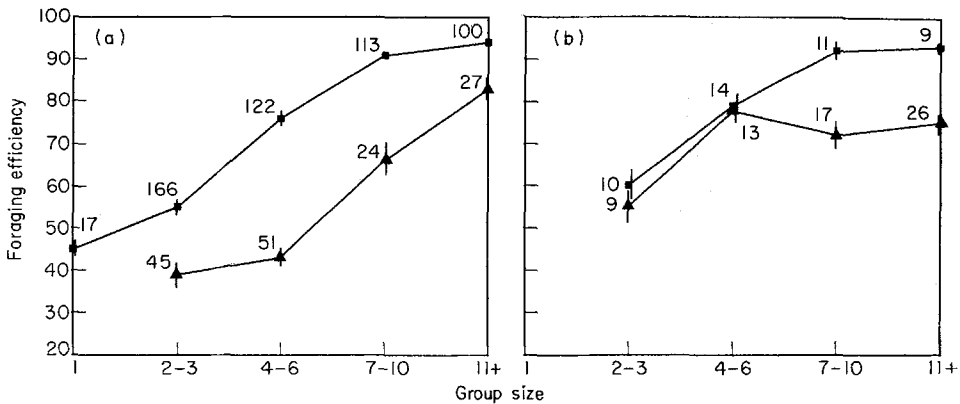


Figure 3. Effects of group size and habitat on foraging efficiency in four Great Basin bighorn sheep populations (a) females; (b) males. Contrasts were between groups of sheep that were more than 100 m from slopes and cliffs (■) and those less than 100 m or on slopes and cliffs (▲). Numbers refer to sample sizes.

foraging on or within 100 m of slopes and sheep on bajadas (or flat areas) more than 100 m from slopes or escape terrain (Fig. 3). Habitat effects were striking, with foraging losses of males and females averaging (by group size): 2-3 = 31% (females), 7% (males); 4-6 = 45% (females), 2% (males); 7-10 = 26% (females), 24% (males); 11+ = 12% (females), 23% (males, Fig. 3). Distance from escape terrain had a stronger negative influence on foraging efficiency in females than males (ANCOVA $F_{1,35} = 10.76$, $P < 0.005$), an effect consistent with the idea that females should be more sensitive to potential predators while feeding on bajadas than males since they or their lambs were at greater predation risk (Table I).

The percentage of total variance in feeding efficiency explained by group size and distance to escape terrain was high for the primary Great Basin sites (females: Lone Mountain = 79, Stillwater Range = 81, Santa Rosa Range = 79; males: Stillwater Range = 71) but more variable when contrasted for each factor among sites. Group size accounted for 26, 73, 44 and 70% of the variance at the above sites (respectively) whereas distance to escape terrain contributed 71, 8, 45 and 19%. Nevertheless, significant positive relationships between group size and distance from escape terrain existed in three of the four cases (for females, Lone Mountain: $r_s = 0.34$, $Z = 2.96$, $P < 0.003$; Santa Rosa Range: $r_s = 0.73$, $Z = 4.54$, $P < 0.0001$; Stillwater Range: $r_s = 0.20$, $Z = 1.32$, $P = 0.19$; for males, Stillwater Range: $r_s = 0.48$, $Z = 2.75$, $P < 0.006$). Because larger groups foraged more

efficiently than smaller ones (Fig. 3), it seems that sheep were buffered against foraging losses or predation (or both) by associating with more individuals as distance from slopes increased.

Not only did males use bajadas more frequently than females (Fig. 2), but males moved further from slopes and apparently remained there longer than females. At the Stillwater site, where the largest data set exists, mean distance from slopes when a group was first observed was 0.84 km (range = 0.06-2.50) for males and 0.07 km (0.01-0.24) for females (Mann-Whitney U -test $Z = 2.37$; $P < 0.02$). One group of five males remained more than 0.80 km from slopes for at least 36 h whereas the longest period that females were on bajadas was 145 min.

Variation in Food Quality and Experimental Manipulations

If, as the data seem to indicate, females experienced higher costs and undertook greater risks than males, then the question arises why did they use bajadas in the first place?

Two explanations for bajada use by females are possible. First, females did not really suffer greater costs. The above evidence suggests otherwise even though their magnitude in relation to potential fitness remain unknown. Second, protein needs were increased. To evaluate this possibility requires information on the distribution and quality of available food.

The amount of emergent new grasses varied within and between sites (Fig. 4). Emergent new

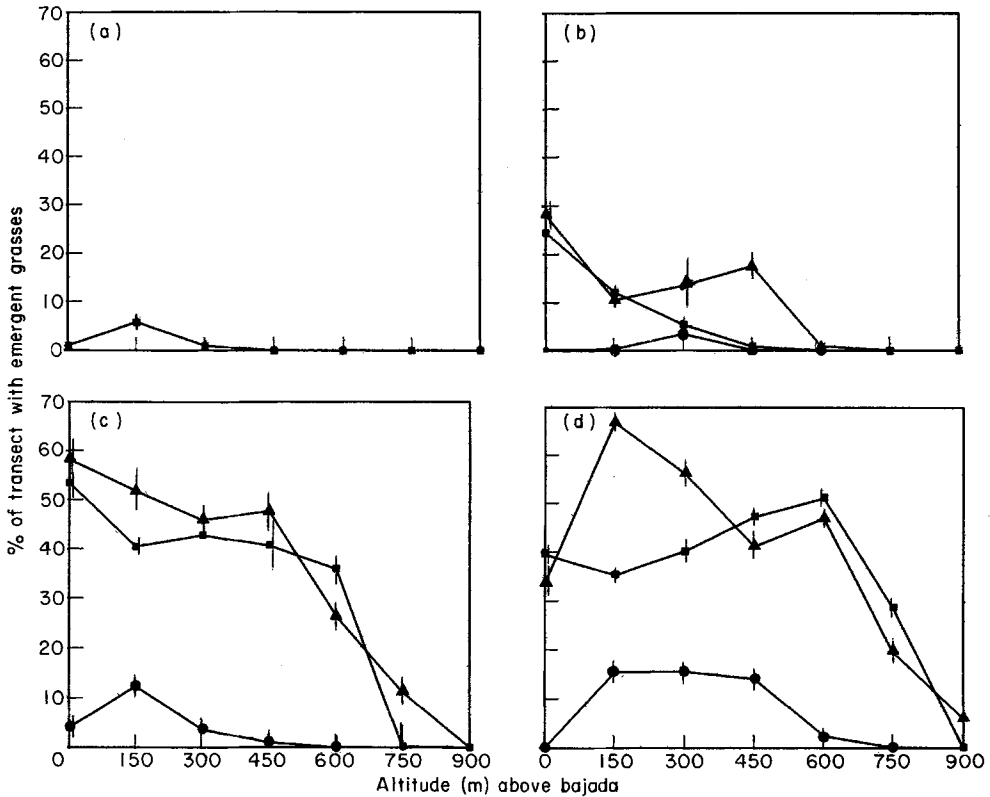


Figure 4. Relationships between plant phenology (mean percentage of transect having emergent new grasses), month, and altitude at three Great Basin study sites. Zero altitude above bajadas indicates emergent new grasses occur on bajadas. Stillwater Range (■), Santa Rosa Range (▲) and Lone Mountain (●). (a) January; (b) February; (c) March; (d) April.

grasses generally appeared first on south-facing slopes, usually because of greater insolation when compared to bajadas, and crude protein averaged (\pm SE) $13.7 \pm 1.3\%$ ($N=25$) of dry matter. Greater quantities of emergent new grasses occurred on bajadas in late winter, and a progressive altitudinal increase in emergent new grasses followed (Fig. 4). Because the rate of green-up was predictable (Table II) and because emergent new grasses were higher in protein than dormant grasses (Hebert 1973; Wehausen 1980; Wehausen & Hansen 1988), opportunities to exploit the more nutritive portions of home ranges existed simply by adjusting altitudinal distribution in accordance with emergent new grasses.

One line of evidence in support of this adjustment would be an association between females and mean percentage of emergent new grasses at different altitudes. Except for January at the Stillwater

Range site ($r_s=0.15$, $N=7$, NS) and February at Lone Mountain ($r_s=0.06$, $N=8$, NS), the relationship was strong for: Lone Mountain in March ($r_s=0.90$, $N=13$, $P<0.01$) and April ($r_s=0.74$, $N=16$, $P<0.01$), for the Stillwater Range in February ($r_s=0.59$, $N=10$, $P<0.05$), March ($r_s=0.86$, $N=13$, $P<0.01$), and April ($r_s=0.97$, $N=15$, $P<0.01$); and the Santa Rosa Range in February ($r_s=0.62$, $N=8$, $P<0.10$), March ($r_s=0.85$, $N=14$, $P<0.01$) and April ($r_s=0.66$, $N=16$, $P<0.01$). These results imply that females maximized access to proteinaceous grasses. However, the lack of significant relationships in mid-winter indicates that sheep were more widely distributed before nutritive grasses were available. Because variance in food quality is low when grasses are dormant (Wehausen 1980), the Great Basin sheep may have reduced their dependency on a single resource by moving altitudinally over wider areas.

Table II. Relationships between emergent new grasses for different transect criteria and elevation in three Great Basin mountain ranges

Transect criteria	Regression	r^2	Earliest date
Stillwater Range (1450 m)			
10% @ 10%	10.52X + 1295.99	0.82	1 January
20% @ 20%	17.78X + 1296.70	0.83	15 February
30% @ 30%	18.33X + 1247.80	0.83	15 February
50% @ 50%	0.06 - 78.19X	0.93	1 March
Santa Rosa Range (1700 m)			
10% @ 10%	0.04 - 64.00X	0.87	1 February
20% @ 20%	0.07 - 98.26X	0.96	1 February
30% @ 30%	0.05 - 64.99X	0.91	15 February
50% @ 50%	0.05 - 66.82X	0.89	1 March
Lone Mountain (1600 m)			
10% @ 10%	0.07 - 114.58X	0.89	1 March
20% @ 20%	0.07 - 126.74X	0.89	1 April
30% @ 30%	Criteria not met		
50% @ 50%	Criteria not met		

Regressions are date (e.g. days at which noted proportion of transects yielded a given proportion of emergent new grasses) on elevation. Earliest date refers to time when the given transect criteria were met. Transect criteria are the proportion of transects given the stated proportion of emergent new grasses. Value after each mountain reflects the difference between its highest point and the bajada.

While sheep used slopes extensively, and moved higher as plant phenology shifted, bajadas were used even in early January. The idea that sheep used bajadas to gain access to protein is bolstered by the (above) correlations between emergent new grasses and altitude, especially because emergent new grasses were more abundant on bajadas than on slopes for at least one site during each month from February to April (Fig. 4). To determine whether protein may have been responsible for the shifts to bajadas during the 6 weeks prior to parturition (Fig. 2), I experimentally altered its availability by distributing alfalfa on slopes and bajadas (Fig. 1). The manipulations occurred at the Lone Mountain and Stillwater sites during late February, mid-March, and early April, periods that corresponded to differential availability of emergent new grasses on slopes and bajadas. Results of the experiment were consistent with observational data on habitat shifts. During the first period all of the protein supplements were consumed on both the bajadas and slopes (Lone Mountain and Stillwater data pooled: Fig. 5). For the second set of provisions emergent new grasses were about 12 and 6 times more abundant at the respective sites (Fig. 4), but the supplements on bajadas were consumed less

than those on slopes ($G_{adj} = 4.07$, $P < 0.05$). During the last provisions, none of the supplements were consumed. Therefore, sheep used bajadas when nutritive grasses were more abundant there than on slopes, but during the second period they favoured treatments on slopes over those on bajadas even though emergent grasses were less abundant on slopes relative to bajadas. Reliance on the experimental sources of protein was inversely related to plant phenology, and it ceased about a month prior to parturition (Fig. 5). The experimental results supported the premise that sheep shifted to slope habitats although emergent grasses and protein supplements were available on both bajadas and slopes.

DISCUSSION

Interaction of Predation Pressure and Nutrition

The results presented here indicate that sheep of both sexes altered their patterns of habitat use by relying on bajadas more during late winter, a period when emergent new grasses first became available and when body condition had presumably declined. This situation is similar to that found in some fish,

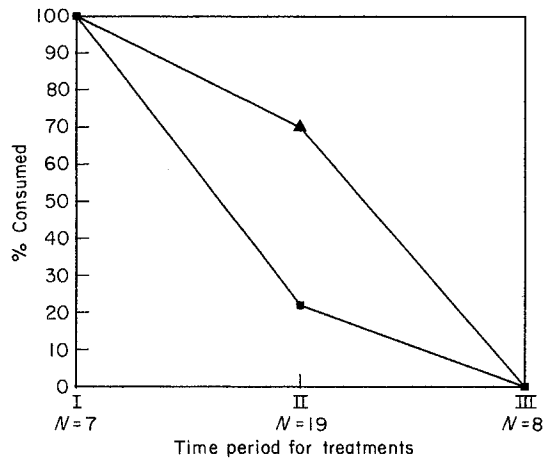


Figure 5. Consumption (%) of experimental treatments by time period and habitat for the Lone Mountain and Stillwater Range sites (data pooled). Habitats as follows: bajadas (■) and slopes (▲).

in that increased nutritional requirements (brought about either experimentally through starvation or by increased growth) resulted in trading access to high-quality food for safety from predators (Milinski & Heller 1978; Werner & Hall 1988; Abrahams & Dill 1989). For sheep, two patterns are noteworthy. First, when away from escape terrain or on bajadas, females and lambs were more than three times more vulnerable to predation than when on slopes. They reacted more vigorously to terrestrial predators in the former environments and experienced reduced feeding rates once the distance to slopes exceeded 100 m. Associated with these changes are increased cardiac responses (MacArthur et al. 1982) and blood cortisol levels (Harlow et al. 1987). Second, compared to females, the costs incurred by males appeared few. Other than a small reduction in foraging (Fig. 3), males were less responsive to coyotes and wolves (see Table I) and they foraged further out on bajadas and remained there longer. Males may have been less sensitive than females to potential predators because of their larger size or because they did not have dependent young (see below). Regardless of sex or habitat, potential losses in feeding efficiency were buffered by the formation of larger groups, as reported in other ungulates (Berger 1978b; Lipetz & Bekoff 1982; Alados 1985); however, increased feeding rates may not overcome predation risk (Fitzgibbon 1989).

The bighorn data also demonstrate that during late winter, when energetic and nutrient demands

are high, females avoided or used infrequently specific habitats. This seems to occur, not because food is unavailable or of low value (i.e. emergent new grasses were approximately equally distributed between slopes and bajadas in March; Fig. 4) but, because of increased vulnerability to predation (Wehausen 1980). In fact, mothers with newborn lambs chose sites on cliffs where crude protein was lower than in areas used by non-mothers, as also found in northern bighorns (Festa-Bianchet 1988b). In other ungulates similar trade-offs may occur, although data on food value and predation risk in different habitats are only available in a single case. Male Asian elephants, *Elephas maximus*, moved seasonally into areas where they experienced higher mortality than females, but in doing so they fed on more nutritious food (Sukumar & Gadgil 1988). Nevertheless, numerous examples imply that nutrient requirements are weighed against predator avoidance. Lactating female moose, *Alces alces*, and caribou, *Rangifer tarandus*, switch to areas where diminished food quality and predation pressure exist (Edwards 1983; Bergerud et al. 1984), whereas lactating bison cows move to open areas even though wolves regularly attack groups with young (Carbyn & Trotter 1987, 1988). The quality of food in these areas remains unknown.

Prenatal Incentives for Postnatal Constraints?

Despite the evidence for habitat shifts, the central issue is whether they were caused by pregnancy.

If so, two predictions follow. (1) Pregnant sheep should be more tolerant of predation risk than non-pregnant ones because their protein requirements are higher (Robbins 1983) and, hence, expectant mothers should be more apt to feed on bajadas. The converse, of course, is that non-pregnant females should be less tolerant of predation risk because they do not incur heightened energy requirements. (2) Lactating females should use bajadas more than pregnant mothers because lactation is energetically more expensive than gestation (Sadler 1969) and more nutritious food appears earlier in the season on bajadas. Unfortunately, stage of lactation (Oftedal 1985) complicates the latter prediction and it cannot be tested with the existing data on Great Basin bighorns. In many mammals, young neonates are energetically more costly than yearlings who may suckle for non-nutritive reasons (Shackleton & Haywood 1985). In several geographical areas lambs are usually weaned by about 6 months of age (Berger 1979) but at the Great Basin sites lambs almost 1 year of age suckle (personal observation). Hence, it is unclear whether the energetic demands on mothers nursing these older lambs would exceed or be less than those experienced by females in late pregnancy.

Some data are available concerning the first prediction. Since pregnancy rates are often higher in ungulate females including desert sheep who have not reproduced in the same year (Clutton-Brock et al. 1982b; Berger 1989; Krausman et al. 1989), ewes without young should be observed more often on bajadas than those with young. This was the case. The frequency of adult females without young on bajadas exceeded that for slopes for time periods I and II in Fig. 2 (I: $G = 8.78$, $P < 0.001$; II: $G = 22.96$, $P < 0.001$). Despite these differences it is likely that not all of the ewes observed on bajadas were pregnant and this bias could affect the above interpretation. To examine this possibility, I performed an additional and conservative test. I multiplied the number of adult ewes using bajadas by 0.833, the minimum proportion of desert sheep expected to be pregnant (see Results) and then determined whether a difference still existed between ewes with and without young on bajadas; the differences persisted for both time periods (I: $G = 6.29$, $P < 0.025$; II: $G = 8.93$; $P < 0.001$). These data are therefore consistent with predictions of the pregnancy incentive hypothesis because those animals using bajadas were also the ones most likely to be pregnant. Additional support for diminished repro-

duction following successful lamb production in desert sheep is available from the Sonoran Desert where less than 20% of the females successfully produced young in the next year (Krausman et al. 1989).

However, my data fail to reject an alternative hypothesis for use of risky areas; mothers with older young (e.g. nearly year-old lambs) refrain from bajada use, not because of pregnancy incentives but because of additional predation risk on their lambs. Under ideal conditions it is possible to discriminate between the two hypotheses. If mothers who nursed older lambs were pregnant and restricted themselves to slopes, then postnatal investment would constrain habitat shifts to a greater extent than pregnancy. This seems to be the most plausible explanation for why variation in habitat shifts exists between female sheep, simply because mothers with young refrain from using non-escape terrain areas where neonates are the cohorts most vulnerable to predation. But, if lactating mothers were not pregnant and still restricted to slopes, then it would be unclear whether postnatal investment (in old lambs or those of any age) or the absence of pregnancy-induced nutritional requirements were responsible for the lack of shifts to areas of higher predation risks. Note that this scenario does not require mothers to be lactating (their older offspring) because investment occurs in many forms, including associations (Green et al. 1989) and the inheritance of home ranges (Clark 1978), the latter of which occurs in some sheep populations (Geist 1971; Festa-Bianchet 1986). This suggests that, after weaning occurs, postnatal care might still constrain mothers from venturing onto bajadas.

Environmental Variation, Pregnancy and Habitat Shifts

The results reported here, from three substantially different environments (northern prairies, Sonoran and Great Basin Deserts), show consistent patterns: ewes were increasingly tolerant of heightened predation risk during late winter (at five of five sites; Fig. 2), pregnant ewes assumed greater risks than those with young (at two of two sites), and pregnant ewes traded safety for access to more nutritive food up to about 1 month before parturition (at five of five sites; Fig. 2). Similar, but apparently more complex, patterns have been reported in the northern Rocky Mountains where movements

to seasonal ranges are complicated by migration of up to 12 km away from escape terrain. At the Sheep River Wildlife Sanctuary, Fester-Bianchet (1988a) found that pregnant ewes migrated earlier than non-pregnant ones, the former moving to lambing areas prior to the onset of most new plant growth. Like the results reported here and for Sierra Nevada animals (Wehausen 1980), Sheep River bighorns with lambs avoided areas of high predation risk and high quality food. However, sheep in late stages of pregnancy at my study sites enhanced access to higher quality food by taking greater risks; whereas pregnant Sheep River bighorns accepted heightened risk during movements to areas where they subsisted on lower food quality for 2–4 weeks.

These findings underscore the importance of comparative and experimental study of factors that promote or restrict habitat shifts in natural populations. I detected habitat shifts in sheep of both sexes during late winter. These could have been caused by increased tolerance to predation risk stemming from a combination of pregnancy and diminished body condition, or because of constraints imposed by postnatal investment. Had the Festa-Bianchet (1988a) data been unavailable, I might have concluded that sheep enhanced their diets during late winter by incurring greater predation risks, but the Sheep River observations suggest otherwise, that predation risks can at times override nutritional benefits. A promising approach to examine further questions about pregnancy and habitat shifts is the selection of species where habitat heterogeneity and predation pressure vary independently (Cerri & Fraser 1983; Stephens & Krebs 1986) so that the role of pre- and postnatal investment can be manipulated by either natural or experimental means.

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