

REPRODUCTIVE STRATEGIES OF DESERT BIGHORN SHEEP

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We examined temporal breeding patterns of bighorn sheep (*Ovis canadensis*) in the Peninsular Ranges of California to determine the degree of seasonality and identify potential selection for seasonal breeding in this low-latitude desert environment. During a 4-year period, births occurred during 7 months of the year, but 87% of young were born in February–April and 55% were born in March. Peak months of mating and parturition remained relatively constant across years and among different regions of the Peninsular Ranges, and young born in February through April had greater survival than those born later. Female age influenced lamb survival but not timing of parturition. Successful recruitment of young by an adult female had a weak but significant negative effect on the survival of that female's offspring the following year. Previous reproductive history of a female did not influence offspring production or timing of parturition. Months of peak parturition followed annual winter rains and, therefore, were likely to coincide with periods of high plant productivity. Furthermore, most young were born before the hot, arid summer months. We concluded that bighorn sheep in the Peninsular Ranges are seasonal breeders and that climate patterns likely act as ultimate factors in shaping the breeding season.

Key words: bighorn sheep, mountain sheep, *Ovis canadensis*, reproduction, reproductive cost, seasonality, southern California

Reproductive strategies, which evolve through natural selection to maximize reproductive success, are influenced by environmental conditions (Sadleir 1969). Bighorn sheep (*Ovis canadensis*) represent a useful taxon to examine effects of environmental conditions on reproductive strategies because this species inhabits a wide geographic and climatic range in North America, from the cold mountains of Canada to the hot and arid deserts of southwestern United States and Mexico (Berger 1979, 1982; Bunnell 1982; Hass 1997; Thompson and Turner 1982).

In many mammals, timing of parturition

is influenced by temporal patterns of diet quality. Although energy availability during late gestation is important for successful reproduction (e.g., Bowyer 1991), costs of lactation typically outweigh those of other reproductive periods because of the increased demands for nutrients and calories by nursing females (Clutton-Brock et al. 1989; Sadleir 1969). Thus, the breeding season of mammals should be timed so that lactation coincides with optimal climatic and dietary conditions.

Bighorn sheep are seasonal breeders at the northern extent of their range. An important factor regulating breeding season in these environments appears to be seasonal forage availability (Festa-Bianchet 1988b;

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Geist 1971, 1974), which depends on precipitation, temperature, and photoperiod. In northern populations, most births coincide with a short and predictable period of plant productivity (Festa-Bianchet 1988a, 1988b; Geist 1971), and young born during the period of peak parturition have higher survival than those born at other times (Festa-Bianchet 1988a).

In contrast, bighorn sheep in desert environments have been reported to have longer breeding seasons (Hass 1997; Krausman et al. 1989; Lenarz 1979; McQuivey 1978) or to give birth throughout most of the year (Hansen 1965; Witham 1983). It has been hypothesized that a mild climate or unpredictable periods of forage availability in desert environments have relaxed selection for a well-defined breeding season (Hass 1997; Leslie and Douglas 1979; McQuivey 1978). However, the temporal breeding patterns of desert bighorn sheep remain poorly understood. Few studies of desert bighorn sheep have attempted to identify factors influencing periods of peak parturition within the birthing season. For example, survival of lambs relative to month of birth has been only cursorily examined in two studies (Hass 1993; Krausman et al. 1989), and these investigations produced conflicting results.

We examined reproductive patterns of bighorn sheep in the Peninsular Ranges in southern California during a 4-year period. Our primary emphasis was on seasonality of breeding and how environmental conditions act as ultimate factors selecting for seasonal breeding in a desert environment. Baker (1938) defined ultimate factors as those that regulate breeding seasonality in a long-term evolutionary sense, while proximate factors are those that provide the immediate cue for the onset and cessation of breeding. It is the former that we consider in this paper. We tested the null hypothesis that a predictable and well-defined peak period of parturition did not occur. Previous studies on ungulates have suggested that timing of parturition and offspring survival

each may be influenced by female age (Bunnell 1980; Clutton-Brock et al. 1982; Festa-Bianchet 1988a, 1988b, 1988c; Mitchell and Lincoln 1973). We therefore tested the null hypotheses that female age has no effect on offspring production, lamb survival, or time of birth.

Most life-history models assume that reproduction has a cost (Calow 1979; Williams 1966) and that this cost varies with population or environmental conditions (Clutton-Brock et al. 1996; Festa-Bianchet 1989; Festa-Bianchet et al. 1998). Costs of reproduction also can influence timing and success of subsequent reproduction because females must recover body reserves lost during lactation (Clutton-Brock et al. 1989; Guinness et al. 1978; Mitchell et al. 1976). Therefore, we examined effects of reproduction on subsequent offspring production, timing of parturition, and offspring survival and discuss how environmental conditions may influence these costs and resulting reproductive strategies used by bighorn sheep in a desert environment.

STUDY AREA

Our study area was in the Peninsular Ranges, which extend from southern California into Baja California, Mexico. Within the United States, the Peninsular Ranges occupy a portion of the Colorado Desert division of the Sonoran Desert (Jaeger 1957). In these ranges, bighorn sheep typically inhabit arid areas below about 1,400 m elevation (Jorgensen and Turner 1975). A description of habitat of bighorn sheep in these ranges was provided by Ryan (1968). In habitat of bighorn sheep, mean annual rainfall during 1962–1997 was 173.5 mm (range, 35–470 mm). Maximum temperatures often reached 46°C in summer, and winters were mild with temperatures occasionally reaching freezing (National Oceanic and Atmospheric Administration 1962–1997).

All bighorn sheep in the Peninsular Ranges of California have been listed as federally endangered since 1998 (Federal Register, Vol. 63, No. 52, 1998). This study included data collected in 4 regions of the Peninsular Ranges: Santa Rosa Mountains northwest of Highway 74 (Bradley Canyon; 33°45'N, 116°26'W), Santa Rosa

Mountains southeast of Highway 74 (Deep Canyon; 33°38'N, 116°23'W), San Ysidro Mountains (33°14'N, 116°25'W), and Jacumba and In-Ko-Pah Mountains (Carrizo Canyon; 32°45'N, 116°12'W). Those regions were oriented in a north-south line relative to each other, with Bradley Canyon located about 110 km north of Carrizo Canyon. Each of these regions was inhabited by a discrete group of females, or ewe groups, except for the San Ysidro Mountains, which contained 2 ewe groups (Boyce et al. 1999; Rubin et al. 1998). Data from the 2 groups in the San Ysidro Mountains were combined for the current analysis because of small samples.

MATERIALS AND METHODS

We included 68 bighorn females in this study. We captured females in 2 regions (Carrizo Canyon, $n = 19$; San Ysidro Mountains, $n = 19$) in autumn 1992 and in Deep Canyon ($n = 12$) in autumn 1993. We captured animals via net gun from a helicopter, fitted each with a radiocollar and identifying ear tag(s), and estimated minimum age of each animal by counting horn annuli (Geist 1966) and examining patterns of tooth replacement (Hansen and Deming 1980). Bighorn sheep in Bradley Canyon had been radiocollared as part of ongoing studies by the California Department of Fish and Game and the Bighorn Institute (Palm Desert, California), and 18 of those females were added to our study in early 1994. Our study was conducted through October 1996, yielding data from 4 consecutive birthing seasons (1993–1996) in 2 regions (Carrizo Canyon and San Ysidro Mountains) and 3 consecutive seasons (1994–1996) in 2 regions (Deep Canyon and Bradley Canyon).

We attempted to observe each female once monthly at about 30-day intervals. All observations were made from the ground, and age class and sex of each animal in every observed group were recorded. Males were classified according to horn size as Class I–IV (Geist 1971). Each marked female was observed until it could be determined whether she was accompanied by a lamb. Presence of a lamb with a given female was used as an index of lamb production. Lambs were assumed to have been born at the beginning of the month in which they were first observed. If a female was not seen during a month and then was observed with a lamb in the next month, we assigned the lamb a birth month based on its physical development (Bleich 1982)

or comparison with known-age young. Although it was possible to determine ages of some lambs to within 1–2 weeks, some of our observations were made at distances of >500 m, making this level of accuracy impossible. We therefore chose months as the unit of age for lambs and restricted our analysis of survival to 3 and 6 months of age. Young were included in survival analyses only if their dams were alive during the entire 3- or 6-month period.

We defined the peak birthing months as the minimum number of months when $\geq 75\%$ of young were born. We examined data from individual years and regions to determine whether those months remained constant across time and throughout the range. To assess synchrony in mating activity among regions and across years, we calculated, for each region, the proportion of observed groups containing females that also included ≥ 1 Class III male and ≥ 1 Class IV male during each month of the study. Only months when ≥ 6 groups containing females were observed were included. We examined whether the peak months of sexual aggregation (Bleich et al. 1997) remained the same across years and regions and used Spearman correlation analyses (r_s —Sokal and Rohlf 1995) to test whether monthly proportions of groups including males were correlated among pairs of regions. Using an estimated gestation of 174 days (Shackleton et al. 1984), we calculated r_s between the percentage of groups observed each month that included Class III or Class IV males and number of young born 6 months later. That allowed us to assess how accurately the months when sexes were aggregated reflected the actual mating period. All tests were 2-tailed at $P = 0.05$. Analyses were completed using the program StatMost (DataMost Corporation, Sandy, Utah).

We compared survival of young born during peak months with those born outside of the peak months using G -tests (Sokal and Rohlf 1995). Statistical analyses were performed using each lamb as a separate datum; thus, some females were represented up to 4 times (or 3% of total young born). However, we also repeated analyses using data from individual years. We applied the Williams's correction to all G -values (G_{adj}) and used a Fisher exact test when samples were small (i.e., when an expected value was < 5 —Sokal and Rohlf 1995). We applied Bonferroni adjustments to significance levels in tests in-

volving multiple comparisons (Sokal and Rohlf 1995).

To examine relationships between female age and reproductive patterns, we assigned females to 3 age categories: young = 2- to 3-year-old females, prime = 4- to 9-year-old females, and older = females ≥ 10 years old. We used *G*-tests to compare offspring production, lamb survival, and time of parturition (during-peak months versus after-peak months) among age categories. We also assigned sequential numbers to months of parturition (1–7 for February through August) and used Kruskal–Wallis tests (Sokal and Rohlf 1995) to evaluate differences in month of parturition among the 3 age categories. When samples were adequate, we compared reproductive success of 2- and 3-year-old females.

To assess short-term costs of reproduction, we used sign tests (Sokal and Rohlf 1995) to compare reproductive patterns (offspring production, lamb survival, and timing of parturition) of individual females after years of contrasting reproductive success (e.g., following a year of offspring production versus a year of no offspring production). For example, for every year following either lamb production or no lamb production, a female received a score of 1 if her lamb survived and a 0 if the lamb died. When multiple scores existed for an individual (e.g., following years of successful offspring production), the average score was used for analyses. That is, if a female's offspring died in 1 year (after a year of successful reproduction) and another of her offspring survived (after a year of successful reproduction), she was assigned a score of 0.5 for lamb survival after a year of successful reproduction. Those within-individual comparisons allowed us to assess costs of reproduction while accounting for individual differences in reproductive capabilities (Festa-Bianchet 1989). When small samples did not allow use of the sign test (when number of matched pairs whose difference equaled zero was < 6), we assessed effect of previous reproduction at the level of the population, using *G*-tests or Fisher exact tests. We also used a Mann–Whitney *U*-test (Sokal and Rohlf 1995) to examine effect of previous reproductive success on time of parturition by assigning sequential numbers to the months of parturition (1–7 for February–August) and testing for differences among females with different reproductive histories. Location was a possible confounding variable in

our analyses of lamb survival and time of birth. Therefore, we used *G*-tests to compare lamb survival to 3 and 6 months and test for differences in proportion of young born outside the peak months among the 4 regions.

To differentiate between relative effects of individual variables on lamb survival, we used multiple logistic regression analysis (Hosmer and Lemeshow 1989). We coded the dependent variables, lamb survival to 3 or 6 months of age, as binary outcomes. Independent variables included previous year offspring production (PREVPROD), previous year offspring survival to 6 months of age (PREVREC), birth during peak versus late months (BIRTHTIME), female age category (AGE), region (REGION), and year (YEAR; Table 1). We conducted logistic regression analyses with SPSS 8.0 (SPSS Inc., Chicago, Illinois). We first assessed the effect of independent variables by univariate analyses. We used the likelihood ratio test (Hosmer and Lemeshow 1989) to assess significance of each variable using $P < 0.25$ as the criterion for selection and further consideration of the independent variable as part of the multivariate model (Mickey and Greenland 1989). In the multivariate model, we first used a univariate Wald statistic (Hosmer and Lemeshow 1989) value of ≥ 2.0 and an examination of estimated coefficients to identify potentially important individual variables. Following Hosmer and Lemeshow (1989), we then identified variables to retain in the model by comparing 1 multivariate model to another using the likelihood ratio test with a significance level of 0.05. We used the Hosmer–Lemeshow statistic, *C*, to assess the fit of the final model and considered a nonsignificant ($P > 0.05$) result to indicate a satisfactory fit (Hosmer and Lemeshow 1989). Using the same approach, we used logistic regression analysis to examine effects of the previous individual variables (excluding BIRTHTIME) on time of parturition (parturition during peak versus later months; Table 1).

To determine whether months of peak parturition coincided with or closely preceded climate conditions most likely to be associated with optimal dietary quality, we inspected patterns of precipitation and temperature during 36 years (1962–1997). Climatic data were collected in Palm Desert, Borrego Springs, and Ocotillo, locations that represented the northern, central, and southern parts of the study area, respectively

TABLE 1.—Names and codes of independent variables used in logistic regression analysis of lamb survival and time of birth in bighorn sheep (*Ovis canadensis*) in the Peninsular Ranges, California, 1993–1996.

Variable	Lamb survival ^a	Time of birth ^b
AGE (female age category)	2–3 years ^c 4–9 years ≥10 years	2–3 years ^c 4–9 years ≥10 years
REGION (region)	Bradley Canyon ^c Deep Canyon San Ysidro Mountains Carrizo Canyon	Bradley Canyon ^c Deep Canyon San Ysidro Mountains Carrizo Canyon
PREVPROD (previous year lamb production)	0 = had no lamb 1 = had lamb	0 = had no lamb 1 = had lamb
PREVREC (previous year lamb recruitment) ^d	0 = did not recruit lamb 1 = recruited lamb	0 = did not recruit lamb 1 = recruited lamb
YEAR	1996 ^c 1995 1994 1993	1996 ^c 1995 1994 1993
BIRTHTIME (peak versus late months)	0 = birth in late months 1 = birth in peak months	

^a Dependent variable: 0 = lamb did not survive (to 3 or 6 months of age), 1 = lamb survived (to 3 or 6 months of age).

^b Dependent variable: 0 = born outside of peak birthing months, 1 = born during peak birthing months.

^c Reference group.

^d Produced and raised a lamb to 6 months of age in the previous year.

(National Oceanic and Atmospheric Administration 1962–1997). To determine how closely totals for monthly precipitation were correlated among these 3 sites, we calculated product moment correlation coefficients (r —Sokal and Rohlf 1995) for pairwise comparisons. To compare the amount of yearly variation in winter (November–February) versus summer (July–October) rainfall, we calculated coefficients of variation (CV —Fowler et al. 1998) based on data collected in Borrego Springs and compared this relative variability using the method described by Lewontin (1966). We also reviewed results of previous research on temporal patterns of plant productivity in the Peninsular Ranges and neighboring mountain ranges. Although we were interested primarily in breeding season relative to long-term climate patterns, we examined diet quality of females in Deep Canyon for 1 year to determine whether short-term patterns of diet quality were consistent with the hypothesis that births were timed so that lactation occurred during the period of highest diet quality. From October 1994 through September 1995, we collected monthly fecal samples from 5 to 13 individually identified females. Samples were analyzed for percentage fecal nitrogen using

standard Kjeldahl procedures and used as an index of diet quality (Leslie and Starkey 1985).

RESULTS

During 1993–1996, we recorded 133 young born to 68 females. Lambs were born in each month from February through August; however, the timing of births was skewed. Eighty-seven percent of young were born during February–April, and 55% were born in March (Fig. 1). Most births occurred during March in every year except 1995, when an equal percentage of births occurred in March and April. Seventy-eight to 100% of young were born during February–April each year. We therefore refer to these months as the peak lambing months. In each of the 4 regions, most lambs were born during those peak months (Table 2).

Based on female–male associations, the months of peak mating also remained relatively consistent across years and among regions. When data from years and regions were considered individually, 38–71% (\bar{X} = 57%, n = 6 years for which complete data

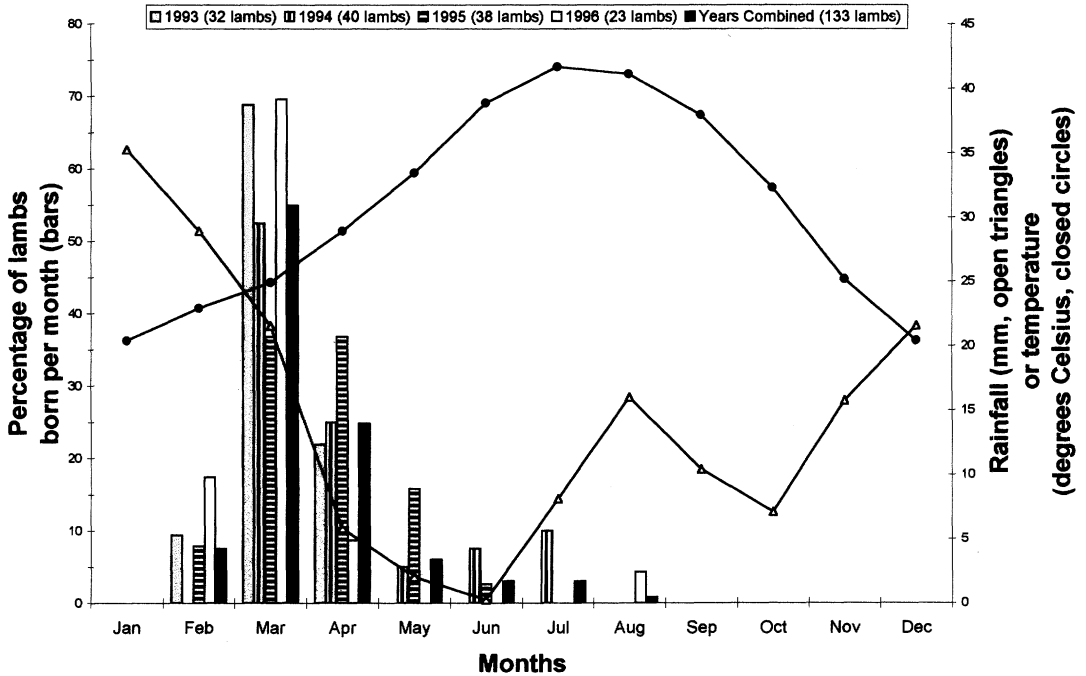


FIG. 1.—Percentage of bighorn lambs born per month in the Peninsular Ranges, California, 1993–1996. Mean monthly rainfall (mm, open triangles) and mean monthly high temperature ($^{\circ}\text{C}$, closed circles) based on 36 years (1962–1997) of climatic data collected in Borrego Springs (National Oceanic and Atmospheric Administration 1962–1997).

were available) of groups of females including ≥ 1 Class IV male were observed during September–October, whereas 62–100% ($\bar{X} = 83\%$) of groups including ≥ 1 Class IV male were observed during August–November (Fig. 2). Class III males were present in groups during more months than Class IV males. Monthly proportions of groups including ≥ 1 Class IV male were correlated among pairs of regions ($r_s \geq$

0.53, $P \leq 0.02$, $n = 17$ –32 months depending on the pair of regions being compared), with 1 exception (San Ysidro–Bradley comparison). Presence of Class III males exhibited less correlation among regions, with only the Carrizo–San Ysidro and San Ysidro–Deep Canyon comparisons revealing significant correlations ($r_s = 0.49$, $P = 0.004$, $n = 32$ months and $r_s = 0.51$, $P = 0.03$, $n = 18$ months, respectively). In all

TABLE 2.—Reproductive patterns of bighorn sheep (*Ovis canadensis*) in 4 regions of the Peninsular Ranges, California, 1993–1996.

Region	% lambs surviving to 3 months of age ^a (total lambs)	% lambs surviving to 6 months of age ^a (total lambs)	% lambs born after peak months ^b (total lambs)
Bradley Canyon	43.5 (23)	26.1 (23)	26.9 (26)
Deep Canyon	86.9 (23)	73.9 (23)	16.0 (25)
San Ysidro Mountains	85.7 (42)	57.1 (42)	10.6 (47)
Carrizo Canyon	80.7 (31)	67.7 (31)	2.9 (35)

^a $P < 0.005$ when all regions were compared but not significant when Bradley Canyon was excluded.

^b Lambs born after April; $P = 0.008$ when Bradley and Carrizo canyons were compared.

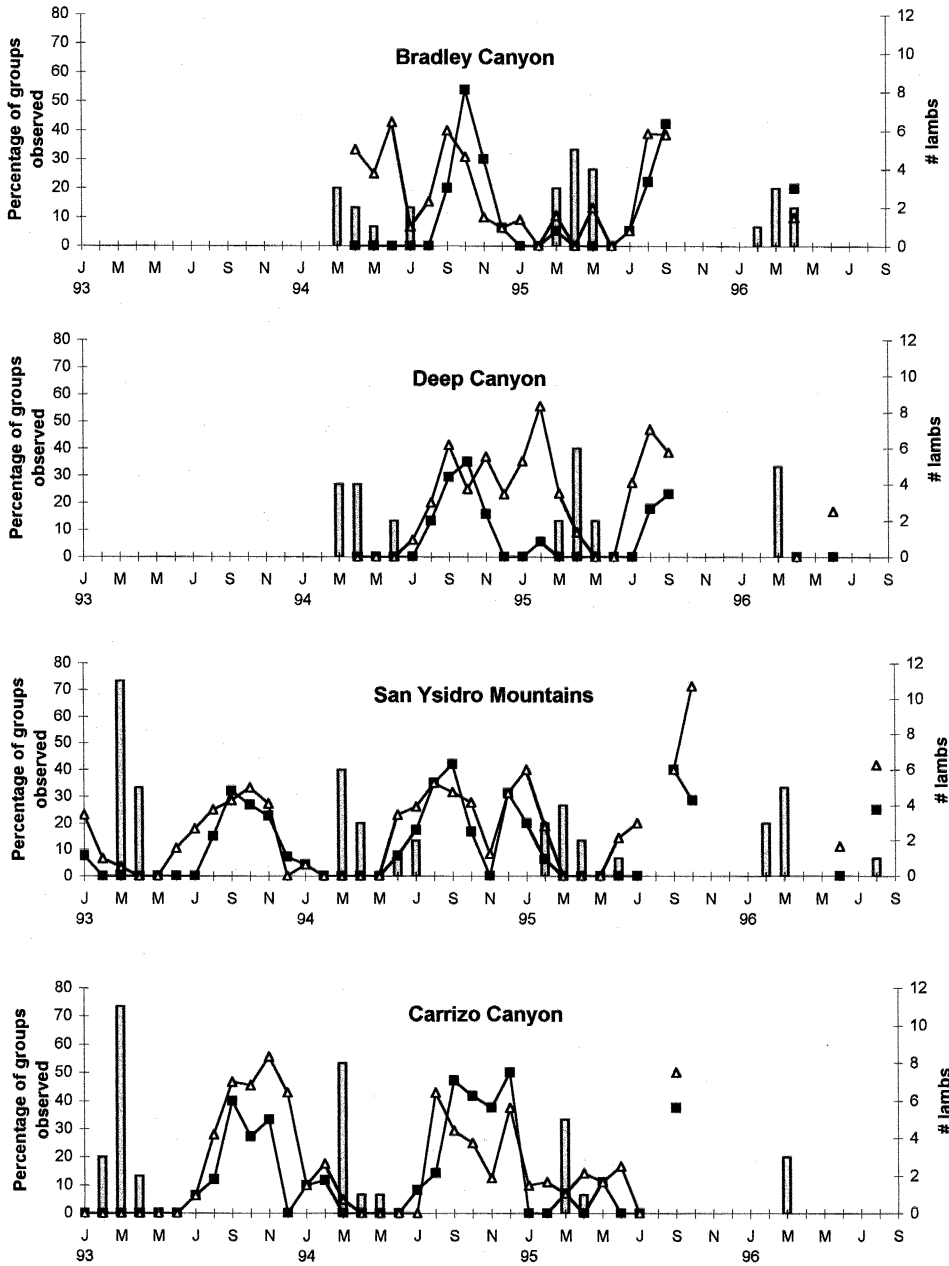


FIG. 2.—Temporal relationship between group composition and birth of bighorn lambs in 4 regions of the Peninsular Ranges, California, 1993–1996. Percentage of observed groups containing females that also included ≥ 1 Class IV male (closed squares) and ≥ 1 Class III male (open triangles); shaded bars indicate number of lambs born each month.

regions, number of young born per month was correlated with the percentage of groups observed 6 months earlier that included Class IV males ($r_s \geq 0.65$, $P <$

0.001 , $n \geq 18$; Fig. 2). A weaker correlation occurred when the presence of Class III males was considered, and that relationship was significant in only 3 of the regions

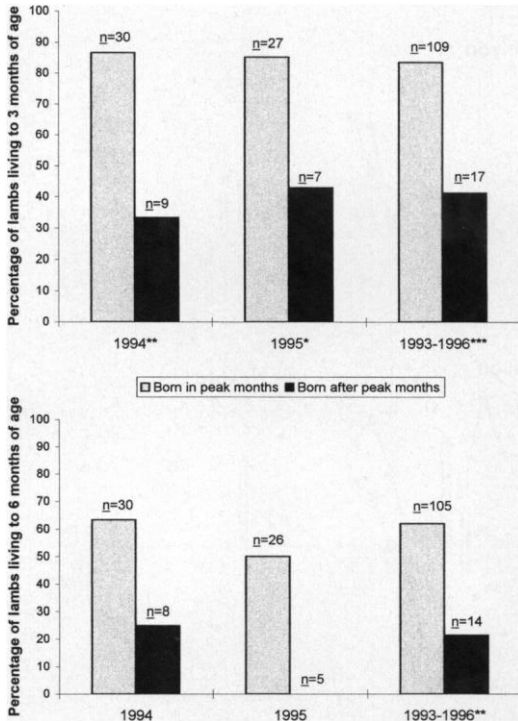


FIG. 3.—Survival of bighorn lambs to 3 months (top) and 6 months of age (bottom) relative to time of birth (peak months versus late months) in the Peninsular Ranges, California, 1993–1996. Sample (n) equals number of lambs born in peak months (February–April) or during late months (May–August). No late births occurred in 1993, and only 1 late birth occurred in 1996. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

(Bradley Canyon, San Ysidro Mountains, and Carrizo Canyon; $r_s \geq 0.49$, $P \leq 0.04$).

When data from all years were combined, young born during the peak months had greater survival to 3 months of age ($G_{adj} = 12.18$, $d.f. = 1$, $P < 0.001$) and 6 months of age ($G_{adj} = 8.13$, $d.f. = 1$, $P < 0.01$; Fig. 3) than those born later. When individual months within the peak birthing period (February, March, and April) were compared, no difference in survival to 3 or 6 months occurred ($G_{adj} = 1.59$, $d.f. = 2$, $P > 0.2$ and $G_{adj} = 4.15$, $d.f. = 2$, $P > 0.1$, respectively). When data from 1994 and 1995 were examined individually, young born in peak months had higher survival to

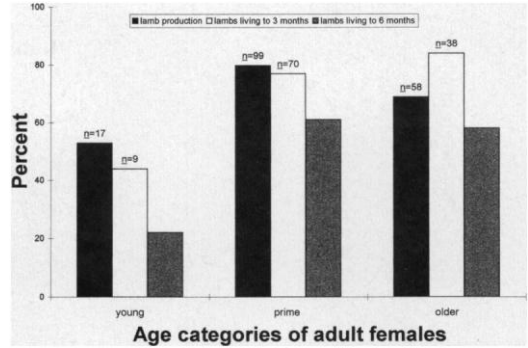


FIG. 4.—Percent lamb production among big-horn females in different age categories and survival to 3 and 6 months of age of their lambs, Peninsular Ranges, California, 1993–1996. Young = 2- to 3-year-old females, prime = 4- to 9-year-old females, and older = females ≥ 10 years of age. Samples on tops of bars indicate number of females and number of lambs included in the analyses.

3 months than those born later (Fisher exact test $P = 0.004$ and 0.037 , respectively; Fig. 3). Although more lambs born during the peak months lived to 6 months of age, survival of those lambs did not differ from those born later (Fisher exact test $P = 0.107$ and 0.058 in 1994 and 1995, respectively; Fig. 3). It is likely that small samples reduced the power of that test.

Lambs were produced by females estimated to be 2–16 years of age. Although production of offspring tended to be lowest among young females (Fig. 4) and a significant difference existed between young and prime females (Fisher exact $P = 0.029$), there was no significant difference in offspring production when the 3 categories of female age were compared ($G_{adj} = 5.85$, $d.f. = 2$, $P > 0.05$). Among young females, offspring production by 3-year-old females was greater (86%, or 6 of 7 gave birth) than production by 2-year-old females (30%, or 3 of 10 gave birth; Fisher exact $P = 0.049$). No difference existed between 3- and 4-year-old females, the youngest females in the next age category (Fisher exact $P = 1.0$).

Survival to 3 months of age tended to be

lowest among offspring of young females (Fig. 4) and was lower than among older females (Fisher exact $P = 0.023$). No difference existed when the 3 categories of female age were compared ($G_{adj} = 5.34$, $d.f. = 2$, $P > 0.05$). Although pairwise comparisons revealed that offspring of prime females had greater 6-month survival than offspring of young females (Fisher exact $P = 0.034$; Fig. 4), we detected no difference in 6-month lamb survival when the 3 female age categories were compared. Among young females, we were unable to detect a difference between 6-month survival of lambs of 2-year-old females (33%, or 1 of 3) and 3-year-old females (17%, or 1 of 6), but small samples likely reduced the power of that test. Six-month survival of offspring of 4-year-old females (75%, or 6 of 8) tended to be greater than for lambs of 2- or 3-year-old females combined (22%, or 2 of 9), but the difference was marginally nonsignificant (Fisher exact $P = 0.057$).

The 3 age categories did not differ ($G_{adj} = 0.609$, $d.f. = 2$, $P > 0.5$) in proportion of females giving birth during peak parturition months (young females, 89%; prime females, 90%; older females, 85%), and young and older females were not more likely to give birth outside of the peak birthing months than prime females (Fisher exact $P \geq 0.546$). There was no difference (Kruskal–Wallis $H = 4.986$, $d.f. = 2$, $P = 0.083$) in the month of parturition among the 3 female age-groups. When data from 1994 and 1995 were examined separately, young and older females were not more likely to give birth outside of the peak months than prime females (Fisher exact test $P \geq 0.47$ for 1994; $P = 1.00$ for 1995).

Neither offspring production (sign test $P = 0.344$) nor lamb survival to 3 or 6 months of age ($P = 1.00$ for both) influenced production of offspring by a female in the following year. However, recruitment of a lamb to 6 months of age in 1 year had a negative effect on lamb survival (to 6 months of age) in the following year (sign test $P = 0.031$). Sample sizes were too

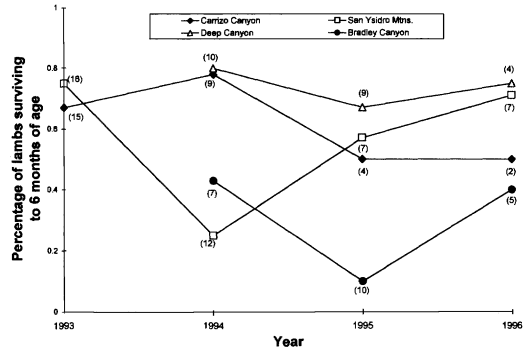


FIG. 5.—Percent of bighorn lambs living to 6 months of age in 4 regions of the Peninsular Ranges, California, 1993–1996. Number of lambs born to radiocollared females each year in each region given in parentheses.

small to evaluate effects of offspring production or survival to 3 months on lamb survival in the subsequent year using within-individual comparisons. At the population level, however, a female's success in raising a lamb to 6 months of age was not influenced by offspring production (Fisher exact $P = 0.287$) or lamb survival to 3 months of age ($P = 0.104$) in the previous year.

Recruitment of young (to 3 and 6 months of age) did not influence month of birth in the subsequent year (sign test $P = 1.00$ in both instances). That is, females did not give birth later in years after they raised young (to 3 or 6 months of age) than they did in years after they had no lamb or their lamb died before reaching these ages. Samples were too small to evaluate the effect of offspring production on month of parturition in the subsequent year using within-individual data; however, at the population level there was no difference in month of parturition (Mann–Whitney U , $P = 0.305$) or time of parturition (peak versus late months; Fisher exact $P = 1.00$) between females that had and had not produced offspring in the previous year.

Within a region, offspring survival varied across years, but that pattern was not synchronized among regions (Fig. 5). Across years, lamb survival to 3 and 6 months of

age differed among the 4 regions ($G_{adj} = 15.12$, $d.f. = 3$, $P < 0.005$ and $G_{adj} = 13.08$, $d.f. = 3$, $P < 0.005$, respectively; Table 2). When data from Bradley Canyon (where survival was the lowest) were removed from these analyses, however, no differences existed among the 3 remaining regions. Only Carrizo Canyon and Bradley Canyon differed (Fisher exact $P = 0.008$) in the number of young born after the peak months (Table 2). There did not appear to be a simple relationship between number of young born after the peak months and lamb survival in a particular region because Deep Canyon had the 2nd greatest proportion of young born late, and it also had the greatest lamb survival each year (Table 2, Fig. 5).

Univariate logistic regression analyses revealed that BIRTHTIME, REGION, AGE, and PREVPROD should be considered in a multivariate model for 3-month lamb survival, whereas BIRTHTIME, REGION, AGE, and YEAR should be considered in a model of 6-month lamb survival (Table 3). A preliminary multivariate model for 3-month lamb survival resulted in values of the Wald statistic that suggested that all individual variables except PREVPROD were significant in the model. This model contained classification table cells with values of zero, possibly making the model numerically unstable. We therefore proceeded with a reduced model that excluded PREVPROD. Likelihood ratio tests indicated that a model containing the 3 remaining variables (BIRTHTIME, REGION, and AGE) showed an improved fit compared with models containing any 1 or 2 of these variables ($G \geq 6.767$ and $P \leq 0.05$ in all cases). No interactions occurred between the 3 variables. The final model had a satisfactory fit ($C = 7.031$, $d.f. = 5$, $P = 0.218$; Table 4) and correctly classified 84.9% of observations.

The multivariate model for 6-month survival, including BIRTHTIME, REGION, AGE, and YEAR, resulted in values of the Wald statistic that suggested each of those variables was significant in the model.

However, a likelihood ratio comparison of that model with one in which YEAR was excluded indicated that it did not contribute significantly to the model ($G = 5.354$, $d.f. = 3$, $P > 0.5$); we therefore proceeded with the reduced model. Further likelihood ratio comparisons indicated that AGE did not contribute to a model containing only BIRTHTIME and REGION ($G = 4.243$, $d.f. = 2$, $P > 0.1$). A model containing those 2 variables showed an improved fit compared with models containing only REGION ($G = 5.851$, $d.f. = 1$, $P < 0.025$) or only BIRTHTIME ($G = 10.795$, $d.f. = 3$, $P = 0.025$), suggesting that both those variables were important in determining survival to 6 months of age. No interaction existed between these variables. The resulting model fit well ($C = 0.368$, $d.f. = 4$, $P = 0.985$; Table 4) and correctly classified 68.1% of observations.

The purpose of the 3rd model was to determine which variables influenced timing of parturition (birth during peak months versus later months). Univariate logistic analysis indicated that REGION and YEAR should be considered for inclusion in this model (Table 3). A model including both variables showed an improved fit compared with a model including only REGION ($G = 9.014$, $d.f. = 3$, $P < 0.05$) but not a model including only YEAR ($G = 3.779$, $d.f. = 3$, $P > 0.1$), indicating that YEAR was more important in determining time of birth. The model including YEAR resulted in classification table cells containing values of zero, potentially making that model numerically unstable (Hosmer and Lemeshow 1989). Results agreed, however, with our observation that number of young born after the peak birth months differed among years. There were differences in number of late births between 1993 and 1994 (Fisher exact $P = 0.004$) and between 1993 and 1995 (Fisher exact $P = 0.013$).

Based on 36 years of data, mean monthly precipitation exhibited a bimodal pattern, with most rain falling in winter (with a peak in January) and a lesser amount of rain fall-

TABLE 3.—Results of univariate logistic regression analysis of bighorn sheep (*Ovis canadensis*) reproductive patterns in the Peninsular Ranges, California 1993–1996, relative to lamb survival to 3 months, lamb survival to 6 months, and time of birth (peak versus late months); see Table 1 for description and coding of variables and reference group designation.

Variable	Estimated coefficient	SE	Odds ratio	95% CI odds ratio	Log-likelihood	G	P	n
Lamb survival to 3 months								
BIRTHTIME	2.492	0.646	12.082	3.41–42.84	–56.48	16.89	<0.001	119
REGION					–57.11	15.64	0.001	119
Deep Canyon	2.159	0.749	8.667	1.99–37.58				
San Ysidro Mountains	2.054	0.609	7.800	2.36–25.75				
Carrizo Canyon	1.689	0.619	5.417	1.61–18.24				
AGE					–62.01	5.84	0.054	119
4–9 years old	1.379	0.726	3.971	0.96–16.48				
≥10 years old	1.928	0.804	6.873	1.42–33.25				
YEAR					–64.58	0.69	0.875	119
1995	–0.197	0.699	0.821	0.21–3.24				
1994	–0.223	0.676	0.800	0.21–3.01				
1993	0.214	0.726	1.238	0.29–5.13				
PREVPROD	1.269	0.692	3.560	0.92–13.82	–35.75	3.23	0.072	69
PREVREC	0.444	0.589	1.558	0.49–4.94	–35.34	0.57	0.450	67
Lamb survival to 6 months								
BIRTHTIME	1.785	0.682	5.958	1.56–22.66	–77.05	8.43	0.004	119
REGION					–74.58	13.38	0.004	119
Deep Canyon	2.083	0.672	8.028	2.15–29.94				
San Ysidro Mountains	1.329	0.568	3.778	1.24–11.50				
Carrizo Canyon	1.783	0.611	5.950	1.79–19.69				
AGE					–78.79	4.96	0.084	119
4–9 years old	1.682	0.838	5.375	1.04–27.76				
≥10 years old	1.616	0.865	5.031	0.92–27.43				
YEAR					–78.25	6.03	0.110	119
1995	–0.777	0.605	0.459	0.14–1.51				
1994	–0.241	0.583	0.786	0.25–2.47				
1993	0.486	0.623	1.626	0.48–5.52				
PREVPROD	0.629	0.679	1.875	0.49–7.10	–47.38	0.88	0.347	69
PREVREC	0.431	0.495	1.539	0.58–4.06	–46.05	0.76	0.382	67
Time of birth								
REGION					–39.73	6.74	0.081	119
Deep Canyon	0.856	0.780	2.353	0.51–10.86				
San Ysidro Mountains	1.209	0.708	3.353	0.84–13.44				
Carrizo Canyon	2.359	1.121	10.588	1.17–95.46				
AGE					–42.74	0.72	0.698	119
4–9 years old	0.134	1.133	1.143	0.12–10.53				
≥10 years old	–0.375	1.149	0.688	0.07–6.55				
YEAR					–37.12	11.97	0.008	119
1995	–1.185	1.139	0.306	0.03–2.85				
1994	–1.512	1.103	0.221	0.03–1.92				
1993	7.369	29.056	1,587.0	0–8.57 × 10 ²⁷				
PREVPROD	0.329	0.869	1.389	0.25–7.64	–28.49	0.14	0.712	69
PREVREC	–0.555	0.755	0.574	0.13–2.52	–26.15	0.56	0.453	67

TABLE 4.—Final model of logistic regression analysis of lamb survival of bighorn sheep (*Ovis canadensis*) in the Peninsular Ranges, California, 1993–1996, relative to lamb survival to 3 months and lamb survival to 6 months; see Table 1 for description and coding of variables and reference group designation.

Variable	Estimat- ed coeffi- cient	SE	Odds ratio	95% CI odds ratio	Log- likelihood	G	P	n
Lamb survival to 3 months					-46.87	36.10	<0.001	119
BIRTHTIME	2.913	0.786	18.415	3.94–85.98				
REGION								
Deep Canyon	2.503	0.881	12.217	2.18–68.63				
San Ysidro Mountains	1.509	0.699	4.524	1.15–17.81				
Carrizo Canyon	1.069	0.701	2.912	0.74–11.49				
AGE								
4–9 years old	1.220	0.859	3.387	0.63–18.24				
≥10 years old	2.522	1.055	12.447	1.58–98.34				
Lamb survival to 6 months					-71.65	19.23	0.001	119
BIRTHTIME	1.633	0.729	5.117	1.23–21.37				
REGION								
Deep Canyon	2.048	0.697	7.753	1.98–30.41				
San Ysidro Mountains	1.176	0.585	3.241	1.03–10.19				
Carrizo Canyon	1.540	0.627	4.666	1.37–15.95				

ing during late summer (National Oceanic and Atmospheric Administration 1962–1997; Fig. 1). Winter (November–February) rainfall totals appeared to fluctuate less among years ($CV = 74.4\%$) than did summer rainfall (July–October; $CV = 93.5\%$), but that difference was not significant.

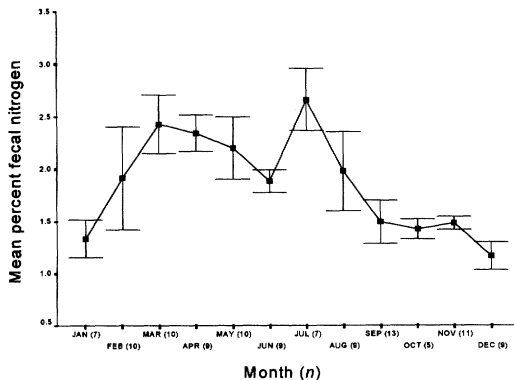


FIG. 6.—Mean (± 1 SE) percent fecal nitrogen from bighorn females in the Peninsular Ranges, California (October 1994–September 1995). Number of individual females that samples were collected from provided in parentheses.

Monthly precipitation totals from the 3 climate data collection sites were correlated during 1992–1996 with a stronger correlation during winter ($r \geq 0.89$, $P < 0.001$, in pairwise comparisons) than during summer ($r \geq 0.43$, $P \leq 0.006$, in pairwise comparisons). Temperatures typically were greatest in July, with a 36-year mean of 41.7°C in Borrego Springs (Fig. 1). In the Peninsular Ranges, therefore, young were born shortly after months of greatest and most widespread precipitation. Most lambs were also born before the driest time of the year (June) and before extreme summer temperatures occurred. Mean percentage fecal nitrogen in Deep Canyon was greatest in July, with the next greatest values found during March–May (Fig. 6).

DISCUSSION

During 1993–1996, bighorn lambs in the Peninsular Ranges were born during 7 months of the year; however, timing of parturition was skewed (Fig. 1). The first 3 months (February–April) represented the peak months of parturition, and most (55%)

births occurred during 1 month (March). The long period of parturition was mirrored by a relatively long period of aggregation of males and females, but the peak birthing period was highly correlated with presence of the largest males 6 months earlier. Both peak months of parturition and peak months when Class IV males were present remained constant across years and regions (Fig. 2). Berger (1992) reported that the gestation period of wild plains bison (*Bison bison*) did not remain constant. Such variation in length of gestation for bighorn sheep might confuse the relationship between the peak periods of sexual aggregation and parturition. However, the magnitude of variation found in bison (about 6 days—Berger 1992) was small relative to the resolution of our analysis, and we concluded that the presence of Class IV males with females best indicated peak months of mating. Based on those collective results, we rejected the null hypothesis that a predictable peak period of parturition does not occur in this population and concluded that bighorn sheep in the Peninsular Ranges of California have a temporally constrained and predictable breeding season.

Young born during peak months of parturition had greater survival than those born later (Fig. 3), and we therefore rejected the null hypothesis that time of birth does not influence lamb survival. It has been suggested that long-term association with a mild or unpredictable climate has relaxed selection for a short breeding season among desert populations of bighorn sheep (Hass 1997; Leslie and Douglas 1979; McQuivey 1978). Although Hass (1993) did not detect a relationship between date of birth and survival in desert bighorn sheep in Nevada, Krausman et al. (1989) suggested that timing of birth may have influenced lamb survival in a desert population in Arizona. Our data provide evidence that there is selection against desert bighorn lambs born outside of the peak months of parturition, a pattern similar to that observed among Rocky Mountain bighorn sheep and other ungu-

lates at northern latitudes (Bunnell 1980; Clutton-Brock et al. 1982, 1989; Festa-Bianchet 1988a).

Female age can influence offspring survival and date of parturition (Bunnell 1980; Clutton-Brock et al. 1982; Festa-Bianchet 1988a, 1988b, 1988c; Mitchell and Lincoln 1973). Reduced survival of late-born lambs may have been related to the age of females that gave birth late in the lambing season. Although young females had the lowest offspring production (Fig. 4), a pattern previously reported in other ungulates (Festa-Bianchet 1988c; Hass 1993; Saether and Haagenrud 1983), females of all ages (estimated 2–16 years) gave birth during our study and could have contributed to births outside of the peak period. Survival was lowest among offspring of young (2- and 3-year-old) females (Fig. 4), but we found no evidence that month of parturition differed among the 3 categories of female age. Young females were not more likely to give birth after the peak lambing months. We therefore concluded that the lower survival of late born offspring was not associated with female age.

Previous reproductive investment may delay parturition and reduce offspring survival (Clutton-Brock et al. 1989; Guinness et al. 1978; Krausman et al. 1989; Mitchell and Lincoln 1973; Mitchell et al. 1976). Therefore, lower survival of late-born lambs observed during our study might be attributed to the cost of reproduction rather than environmental factors selecting against late-born offspring. Although females successfully recruited young to 6 months of age in up to 4 consecutive years during this study, our data suggest that recruitment of a lamb to 6 months of age may reduce probability of survival of an individual's lamb in the following year. Krausman et al. (1989) also proposed that the cost of raising a lamb may have reduced reproductive success in the following year in an Arizona population of desert bighorn sheep; however, that relationship was not evident in a Nevada population (Hass 1993).

We observed no evidence that recent reproductive history influenced timing of parturition. This finding is contrary to studies that showed later parturition among female ungulates that had successfully raised offspring the previous year (Clutton-Brock et al. 1982, 1989; Guinness et al. 1978). Perhaps reproductive success delayed timing of parturition among females in our study, and the resolution of our study design did not allow us to detect these differences. Alternatively, this cost of reproduction may not have been manifested under the existing population or environmental conditions (Clutton-Brock et al. 1982, 1996; Festa-Bianchet 1989; Festa-Bianchet et al. 1998). A 3rd explanation may be that desert bighorn sheep wean their young at an earlier age than northern bighorn sheep (Berger 1979) and thereby may regain condition sooner. Berger (1979) hypothesized that by weaning their lambs early, before the onset of the hot summer, females in the Peninsular Ranges may avoid lactation during an energetically stressful season and begin investing in future offspring. Because body condition in female ungulates can influence both pregnancy rates and the timing of conception (Guinness et al. 1978; Mitchell et al. 1976), it is possible that ample forage (Mitchell et al. 1976) or an extended non-reproductive period following early weaning may have allowed females to recover body reserves adequate for ovulation and conception. If a summer (July) peak in diet quality (Fig. 6) is a typical pattern, it may allow females to recover from the energetic demands of lactation adequately to successfully mate at the same time as females that did not lactate that year. Incomplete recovery may have affected the survival of subsequent offspring of some females, but our observations do not provide evidence that the lower survival of late born lambs was associated with the recent reproductive history of their dams.

The geographic location of ewe groups influenced lamb survival. For example, across years, young in Bradley Canyon had

the lowest survival, whereas young in neighboring Deep Canyon (<10 km away) had the greatest survival (Table 2). Bighorn sheep in Bradley Canyon currently face the greatest threat of habitat loss and modification from urban encroachment, and this group has been supplemented with captive-raised animals since 1985 (DeForge et al. 1995). In contrast, most bighorn sheep in Deep Canyon inhabit areas less impacted by urbanization, and this group has not been augmented with captive animals. Although bighorn sheep throughout the Peninsular Ranges experienced similar climatic patterns, annual lamb survival was not synchronized among regions (Fig. 5). This suggests that local conditions or characteristics of individual ewe groups are important in determining regional population dynamics. This observation is consistent with the existence of independent long-term trends in abundance among ewe groups in the Peninsular Ranges (Rubin et al. 1998).

Although months of peak lambing remained constant among regions, proportion of births occurring after these months increased from south to north, with a greater proportion of late births in Bradley Canyon than Carrizo Canyon (Table 2). However, the pattern observed in Bradley Canyon may not represent natural conditions because some females originated from a captive herd that included animals from different ewe groups, and use of urban areas (for feeding) may have altered the behavior of females in this group. There did not appear to be a simple relationship between proportion of births occurring after the peak lambing months and survival of lambs in a particular region. For example, Deep Canyon had the 2nd greatest proportion of late births but had the greatest lamb survival (Table 2). Multivariate logistic regression analyses also indicated that time of birth (peak versus late months) influenced lamb survival even when data were adjusted statistically for the effect of region (and effect of female age in the case of 3-month survival; Table 4).

The relative constancy of peak mating and birthing months across years and regions suggests that the breeding season has been shaped by long-term, rangewide environmental patterns. The breeding period of mammals should be timed so that lactation coincides with periods of high forage quality. In the Peninsular Ranges, rainfall exhibits a bimodal pattern, with most occurring during winter (Fig. 1). Winter rainstorms also are widespread and long-lasting, whereas summer precipitation generally occurs as brief and localized thunderstorms. Plant productivity in desert environments is tied closely to precipitation, and most plant productivity in the Peninsular Ranges and in the nearby Mojave Desert follows the winter rains (Beatley 1974; Burk 1982; Went 1948). In the Peninsular Ranges, growing season of spring annuals typically comes to an end in May (Burk 1982). Summer rains also may trigger growth of desert plants, but number of plant species responding is smaller (Burk 1982), and level and duration of productivity of most plants, including shrubs, are limited because of either high summer temperatures (Went 1948, 1949) or insufficient total rainfall (Beatley 1974). Spring, therefore, is the most predictable period of plant productivity throughout the Peninsular Ranges, and females that give birth during the peak birthing months may have a greater chance of encountering high-quality forage during lactation than females giving birth later. Indeed, a positive relationship between winter (November, January, and February) precipitation and subsequent lamb:ewe ratios in the Santa Rosa Mountains of the Peninsular Ranges was reported by Wehausen et al. (1987).

We evaluated whether lactation coincided with periods of high forage quality by examining an index of diet quality during 1 year. Relatively high fecal nitrogen values occurred during spring (Fig. 6). However, the greater values found in July seemed to contradict the hypothesis that lactation occurred during the period of highest forage

quality. Other researchers also failed to find a consistent relationship between birthing season and indices of plant productivity in desert populations (Lenarz 1979; Thompson and Turner 1982), or they found that the relationship between plant productivity and lambing period was weaker in desert than in high-latitude populations (Bunnell 1982). These researchers used latitude and elevation (Bunnell 1982), temperature (Thompson and Turner 1982), or predictability of precipitation (Lenarz 1979) as indicators of plant productivity. Perhaps none of these indices alone is a satisfactory indicator of forage availability and quality in a desert environment (Witham 1983). This may be true of fecal nitrogen as well, or it may simply be that 1 year of fecal nitrogen data inadequately represented the long-term patterns that most likely shape breeding seasons. However, 2 previous studies conducted in the Sonoran Desert also noted a peak in fecal nitrogen values during summer (May–July—Scott 1986; June—Andrew 1994), tending to corroborate our finding. Although the period of lambing or lactation of some desert populations coincides with periods of high plant productivity or diet quality (Hass 1997; Krausman et al. 1989; Witham 1983), forage availability and quality may not be the sole factors selecting for seasonal breeding in a desert environment.

In northern bighorn sheep, harsh climate conditions and limited forage availability or quality appear to select against late-born lambs (Bunnell 1982; Festa-Bianchet 1988a, 1988b; Geist 1971). Our data also indicate selection against late-born lambs; however, the mechanism of selection may differ in high- and low-latitude populations. For high-latitude bighorn sheep, winter typically is the most stressful season (Festa-Bianchet and Jorgenson 1998), and young that are born late may not survive the winter because they are unable to gain enough weight during the short growing season in summer (Bunnell 1980, 1982; Festa-Bianchet 1988a, 1988b). In the desert, summer

likely represents the most stressful period for bighorn sheep (Blong and Pollard 1968; Turner 1973), and scarcity of water and extremely high temperatures may reduce the ability of a female to produce adequate milk during lactation (Berger 1978, 1979; Russo 1956).

Understanding ultimate factors that regulate breeding seasons will require that we more accurately define birthing seasons of populations of desert bighorn sheep. The overall period between the 1st and last birth may not be an appropriate representation if we are striving to understand the factors that shape breeding seasons (Festa-Bianchet and Geist 1990). Examination of reported birth dates from other desert populations shows that births are not distributed evenly (Hansen 1967; Hass 1997; Krausman et al. 1989; Leslie and Douglas 1979; McQuivey 1978; Witham 1983). Our study clearly showed that offspring born outside of the peak period of parturition had lower survival. Other populations of desert bighorn sheep also should be examined to identify peak periods of parturition and determine whether survival of offspring is influenced by timing of birth. This information, combined with a closer examination of forage availability and quality, climate patterns, and water availability, will be useful in furthering our understanding of selective forces shaping breeding seasons of desert bighorn sheep.

Other issues related to reproductive strategies of desert bighorn sheep also deserve further study. Cost of reproduction in desert bighorn sheep should be examined further, using data with higher resolution than was possible with the monthly observations made during our study. Reproductive patterns of young (2- and 3-year-old) females should be studied with larger samples to discern possible differences in reproductive potential within this age category. Causes of mortality among young also should be identified more specifically. Breeding synchrony may be a strategy to minimize losses of offspring to predation (Estes 1976).

Because causes of lamb mortality are not known in our study area, the role of predation in shaping the breeding season in this population remains unclear.

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