

REPRODUCTION AND BODY CONDITION OF CALIFORNIA COYOTES (*CANIS LATRANS*)

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Population dynamics and life-history evolution depend heavily on fecundity, which, in the coyote (*Canis latrans*), can vary substantially according to environmental conditions. Although well studied in the central part of its range, little is known about coyote reproduction in the Mediterranean climates associated with Pacific-coastal North America. I used postmortem examinations of 441 coyotes collected throughout central California to investigate reproduction, including age-specific fecundity, breeding synchrony and seasonality, and relationship to nutritional condition. Reproductive parameters did not vary significantly among sampling locations. Overall, numbers of corpora lutea averaged 6.9 (range = 4–11) and litter size (based on fetuses or placental scars) averaged 6.6 (range = 1–12) among postpartum females. The number of corpora lutea increased with maternal age, and litter size also increased with age to 6 years but decreased in older females. Most (77%) adult females became pregnant and 13% of 1st-year females became pregnant. During January–March, 96% of adult males and 68% of 1st-year males had reproductive testes. Reproductive signs in both sexes occurred 3–4 weeks later in 1st-year coyotes than in adults. Parturition dates, which decreased with increasing maternal age, ranged from 9 March to 7 May, indicating that estrus occurred from early January to late March. Of 1st-year coyotes, reproductive individuals were larger during the breeding season and had higher marrow fat indexes than nonreproductive ones (both sexes). After the breeding season, 1st-year females that did not breed (become pregnant) had similar body mass to 1st-year and adult coyotes that did breed, and adult females that did not breed were larger than the others but similar to the weight of breeders during the breeding season. Thus, whether yearlings attained breeding condition apparently depended on their nutritional condition. Adult fecundity estimates were among the highest reported for coyotes.

Key words: breeding, *Canis latrans*, coyote, fecundity, litter size, reproduction, synchrony

Population dynamics and life-history evolution depend heavily on fecundity. Fecundity of coyotes (*Canis latrans*) is highly variable, even relative to most other canids, depending on exploitation (Knowlton 1972), food resources (Clark 1972; Todd and Keith 1983; Todd et al. 1981; Windberg 1995), and possibly ambient stress levels (Hartley et al. 1994). The ability to compensate via reproduction for increased mortality is a widely recognized implication for population dynamics (Connolly and Longhurst 1975; Knowlton 1972). The high variability in fecundity also results in an unusually wide range of life-history strategies for coyotes, which resemble r-strategists (high productivity and short life span) in some situations and K-strategists (low productivity and long life span) in others (Pianka 1970).

Although numerous studies have recorded reproductive data on coyotes from the central part of their range (e.g., Clark 1972; Todd and Keith 1983; Todd et al. 1981; Windberg 1995), there is a paucity of such information from coyotes in the Mediterranean climate zone associated with Pacific-coastal North America. Examination of available data suggests that, relative to inland regions of North America, coyotes in Pacific-coastal regions breed earlier in the year and less synchronously (Atkinson and Shackleton 1991; Hamlett 1938; Sacks 1996). These geographic differences likely are environmentally mediated (e.g., by seasonal temperature differences). Because Pacific-coastal North America is itself an environmentally diverse area, regional differences in the timing of coyote reproduction might be expected to occur within this area as well.

For this study, I took advantage of the relatively long breeding period of coyotes in California to investigate age-specific differences in seasonal reproduction of females and males and fecundity as well as regional variation of such patterns. I also investigated relationships between reproduction and body condition to explore trade-offs between these parameters.

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MATERIALS AND METHODS

Study area.—Although California as a whole is broadly characterized by a Mediterranean climate, with hot, dry summers and cool, wet winters, bioregions of the state vary considerably with respect to rainfall, temperature, and biotic communities, which may affect coyote reproduction. Indeed, although the coyote population is continuous throughout central California, discrete genetic subdivisions divide this population into subpopulations corresponding to 4 major bioregions: The Northwestern, Central Western, Sierra Nevada, and Great Valley (Sacks et al. 2004). In this study, coyotes were obtained from these California bioregions. The Northwestern and Central Western bioregions are dominated by the Coast Range foothills and are separated from the Sierra Nevada mountain bioregion by the Great Valley bioregion, a flat low-elevation region, composed primarily of annual grasslands and agricultural lands (Hickman 1993).

Coyote collection and aging.—I obtained coyote carcasses from United States Department of Agriculture–Wildlife Services and the Santa Clara County Vector Control District. Coyotes were killed as part of livestock depredation control and public health programs. Each coyote was aged by enumeration of root cementum annuli of a lower canine or premolar (Matsons Laboratory, Milltown, Montana—Linhart and Knowlton 1967). Only coyotes killed after 15 September of their 1st year (approximately 6 months old) were used in the study.

Reproductive parameters.—Carcasses of female coyotes were examined for signs of proestrus (thickening of the vaginal and uterine wall, ovarian enlargement, and follicular activity), pregnancy (corpora lutea, localized uterine swelling but no placental scars, embryos, and fetuses), and parturition (placental scars—Kennelly 1978). To avoid biasing detection of pregnancy in seasonal analyses, females with corpora lutea present but without signs of implantation in January and February ($n = 3$ adults) were considered pregnant (i.e., postfertilization and preimplantation). Corpora lutea were counted after fixing ovaries in 10% buffered formalin for 36 h and slicing them into 1-mm-thick sections (Harder and Kirkpatrick 1994). Placental scars were counted at necropsy and differentiated from resorption scars and scars from previous years based on internal darkness (Lindström 1981) and texture. The number of corpora lutea represents the minimum number of ova shed and the number of fetuses and placental scars represented the maximum (e.g., late abortions would reduce litter size) litter size (hereafter, litter size). Because testes and epididymides enlarge substantially during sperm production (Kennelly 1978), I used testis mass (average of the 2, including epididymides) as an index of male reproductive capability. The presence of spermatozoa in the epididymides of enlarged testes was confirmed via microscopic examination in a subset of individuals.

To assess proportions of females breeding (i.e., becoming pregnant) in a particular location or age class, I used only those killed during March–October. Females were considered breeders (i.e., pregnant or postpartum) if they had localized uterine swellings, embryos (fetuses), or placental scars, all of which indicated fertilized ova. To assess proportions of males with reproductively active testes in a particular location or age class, I used only those killed during January–March. Based on testis mass during May–September (range = 1.5–4.0 g), when males were assumed to be nonreproductive, I considered testes >4.5 g to be reproductive, which also was consistent with observations of testis mass associated with sperm production in captive coyotes (Kennelly 1978).

Parturition dates were estimated from pregnant females based on a 60-day gestation period and the presence or size (mass and crown–rump length) of embryos or fetuses (Cavallini and Santini 1996; Kennelly 1978). When embryos or fetuses were present, their masses

and crown–rump lengths were averaged over the litter and used with regression equations from Kennelly (1978) to estimate time to parturition. Because coyotes were frozen before necropsy and physical condition was variable, fallopian tubes were not examined. When corpora lutea were present in the ovaries but no localized uterine swelling, embryos, or fetuses were visible in the uterus, I assumed that parturition would have occurred 50 days later. If localized uterine swellings (without associated placental scars) were present, but embryos were not found, I assumed that parturition would have occurred 40 days later. These approximations were based on the observation that embryos (fetuses) grow, approximately linearly, from 10 mm during midpregnancy (30 days preparturition) to 175 mm at parturition (Kennelly 1978). An additional 7 parturition dates of radio-collared coyotes determined in an earlier study (Sacks 1996) were included in the analysis.

Body condition indexes.—I used 3 indexes of body condition: body mass (kg), an indicator of protein content; femur marrow fat, a reduction of which indicates depleted fat reserves; and visceral fat, a measure of body fat (Huot et al. 1995; Sacks and Blejwas 2000; Windberg et al. 1991). Femur marrow fat was evaluated for each coyote in terms of its color (red = 1, pink = 2, and white = 3) and consistency (runny = 1, intermediate = 2, and buttery = 3) and the 2 scores were averaged (Anderson 1981; Sacks and Blejwas 2000). Visceral fat was evaluated by averaging 2 standardized scores, 1 for organ or omentum fat (1 = none, 2 = very little, 3 = intermediate, and 4 = much) and 1 for the thickness of sternum fat (mm). The femur marrow fat index and the visceral fat index were expressed in terms of standard deviations from the mean. Body condition was compared among coyote age and reproductive groups relative to early (proestrus and early gestation; November–February), late (late gestation and lactation; March–June), and post- (July–October) reproductive periods.

Statistical analyses.—I used the general linear model (GLM) procedure in SYSTAT (version 9.0, SPSS Incorporated, Chicago, Illinois) to examine bioregional differences in corpora lutea counts and litter size, including body mass and age as covariates in the model. The GLM also was used for body condition analyses. To avoid unnecessary text, interactions terms are only reported when significant. I used chi-square tests of independence to compare proportions of breeding females and reproductive males among bioregions. I calculated 95% confidence intervals for age-specific proportions of females breeding based on Student's *t*-distribution (Zar 1984:378). Relationship between age and parturition date was tested via linear regression, with age log-transformed for linearity. For all parametric statistics, model residuals were examined with normal probability plots and confirmed to be approximately normal.

RESULTS

Litter size, ovulation, and age-specific fecundity.—I examined 441 coyotes from the Central Western ($n = 30$), Northwestern ($n = 257$), Great Valley ($n = 82$), and Sierra Nevada ($n = 72$) bioregions. Because the Central Western bioregion and the Northwestern bioregion were ecologically similar (Hickman 1993) and because the sample size was small in the former, these bioregions were pooled for analyses. Numbers of corpora lutea were similar among bioregions ($F = 1.21$, $d.f. = 2, 26$, $P = 0.32$), averaging 6.9 ($n = 30$, $SD = 1.8$, range = 4–11). Litter sizes also were similar among bioregions ($F = 1.35$, $d.f. = 2, 51$, $P = 0.27$), averaging 6.6 ($n = 55$, $SD = 2.2$, range = 1–12). Age was a significantly positive covariate affecting both corpus luteum counts and litter sizes ($F = 29.64$,

$df = 1, 26, F = 8.56, df = 1, 51, P \leq 0.005$). Specifically, average numbers of corpora lutea increased steadily with coyote age, ranging from 5.6 in yearlings to 10 in 8- and 9-year-olds (Fig. 1A). Average litter size also increased with age from 1 to 6 years, but declined in 8- and 9-year-olds. Discrepancies between corpora lutea counts and litter sizes were apparent only in the youngest and oldest age classes. Based on 25 coyotes for which both corpora lutea and litter sizes were assessed, litter size was on average 1.1 less than the number of corpora lutea (range = 0–5). Based on postpartum females, 10 of 31 had resorption scars; the average portion of litters resorbed was 5.7% (range = 0–27%).

Of females killed during March–October, a much higher proportion of adult (77%, $n = 57$) than 1st-year (13%, $n = 47$) females became pregnant, which was similar among bioregions ($\chi^2 \leq 0.97, df = 2, P \geq 0.62$). Of 51 females with corpora lutea present during this period, only 1 did not also have evidence of pregnancy, indicating that nearly all females that ovulated became pregnant. Among adults, the proportion of females breeding increased with coyote age from 13% of 1st-year coyotes to 100% of 4th- through 9th-year females (Fig. 1B). By multiplying age-specific estimates of litter size and proportion breeding, the expected number of offspring (i.e., fecundity) was calculated and appeared to be a humped relationship peaking at ages 5 or 6 years (Fig. 1C).

Seasonal patterns: females.—Proestrus was 1st evident in November and peaked in December and January (Fig. 2). The seasonal pattern of pregnant adult females and then of postpartum adult females closely paralleled that for proestrus, lagging by approximately 2 and 4 months, respectively. Trends in all of these parameters indicated that each breeding phase occurred in the population over a 3- to 4-month period. The greatest increase in proestrus occurred between November and December; that in pregnancies occurred between January and February; and that in postpartum females occurred between March and April. Relative to adults, 1st-year females showed signs of proestrus, pregnancy, and parturition later in the season and less frequently. Parturition dates also were inversely related to age ($r = -0.47, F = 4.96, df = 1, 18, P = 0.04$; Fig. 3).

Relationship between reproduction and body condition: females.—Seasonal variability in body mass differed for reproductive and nonreproductive females, as indicated by an interaction between season and reproductive status of females ($F = 3.95, df = 2, 151, P = 0.02$; Fig. 4). Nonreproductive females were progressively heavier from one reproductive period to the next, whereas reproductive females decreased in body mass during the postreproductive period. Age was a significant covariate in the model ($F = 16.7, df = 1, 151,$

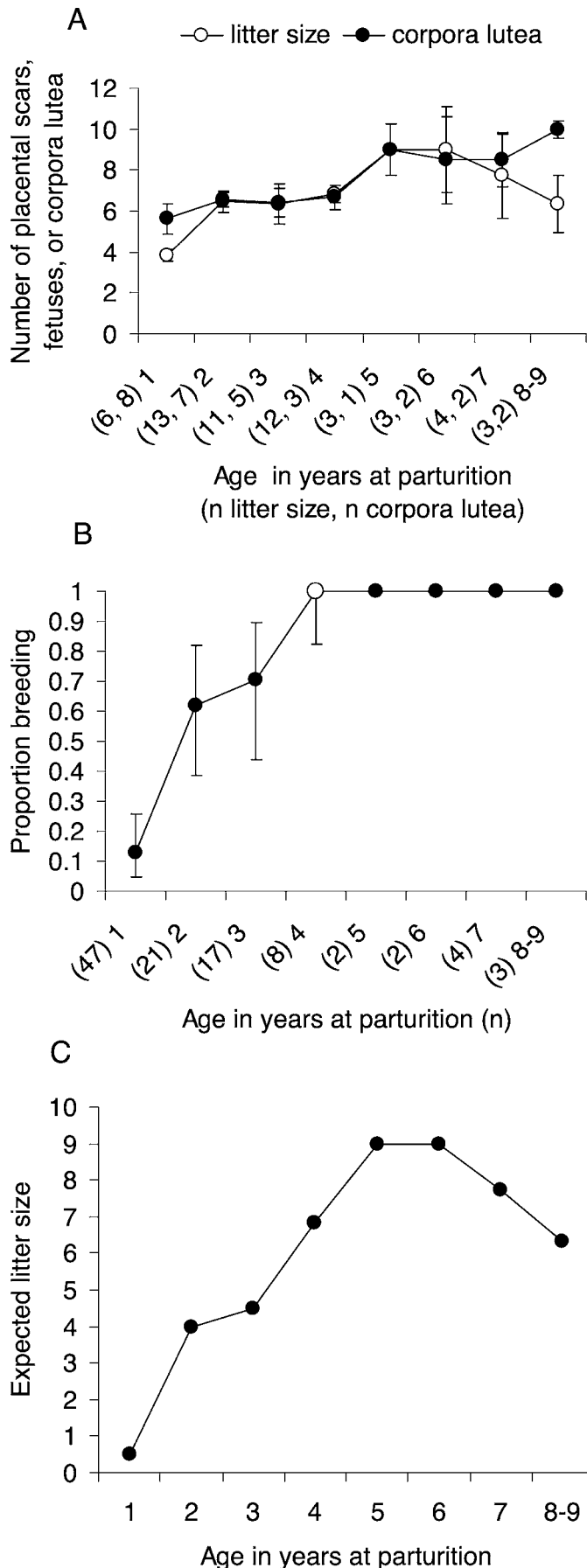


FIG. 1.—Age-specific estimates of reproductive parameters for coyotes in California. A) Average ($\pm SE$) litter size and numbers of corpora lutea (ovulation); B) proportion (and 95% confidence interval) of individuals killed during March–October that became pregnant; and C) expected litter size (fecundity), calculated as the product of litter size and proportion of individuals breeding. Confidence interval associated with the open circle in B) was based on ages 4–9, pooled.

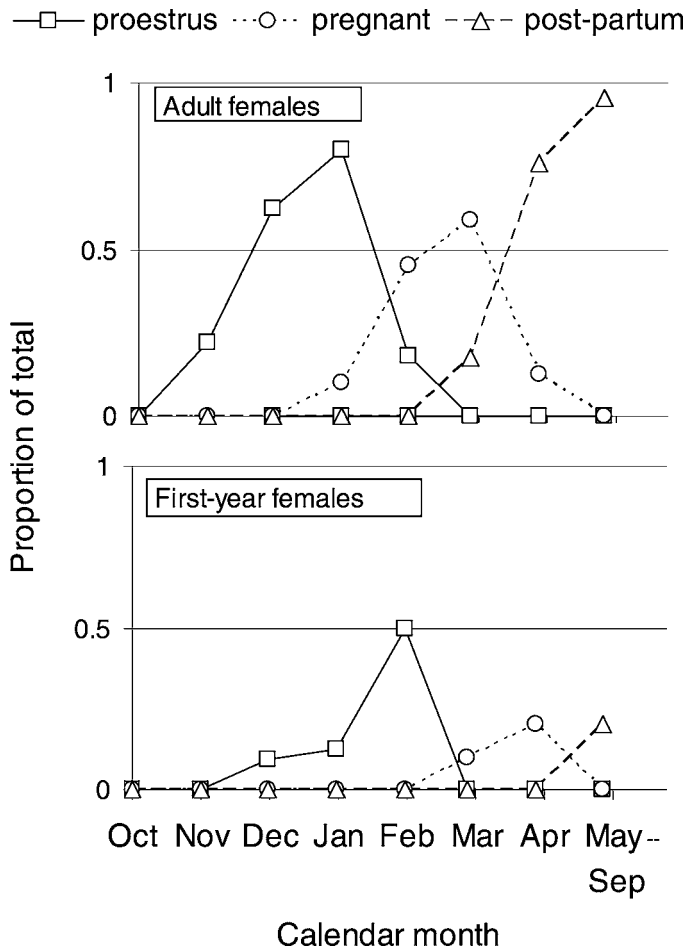


FIG. 2.—Monthly proportions of top) adult and bottom) 1st-year female coyotes in California showing signs of proestrus (square), pregnancy (circle), or parturition (triangle).

$P < 0.001$). First-year nonreproductive females were smaller on average than other female coyotes during early and late reproductive periods (Fig. 4).

Reproduction-related differences in marrow fat index differed for 1st-year and adult females, as indicated by an interaction between age and reproductive status ($F = 5.9, df = 1, 125, P = 0.017$). When analyzed separately for adults and 1st-year females, marrow fat index was higher for nonreproductive (marrow fat index = $0.42 SDs$) than reproductive (marrow fat index = $-0.21 SDs$) adults ($F = 6.4, df = 1, 58, P = 0.014$) and the trend was opposite between nonreproductive (marrow fat index = $-0.11 SDs$) and reproductive (marrow fat index = $0.23 SDs$) 1st-year females, although the difference was not significant in this age class ($F = 0.62, df = 1, 67, P = 0.43$). No significant seasonal trend was found in marrow fat index for adults or 1st-year females ($P \geq 0.11$). No age- or reproduction-related differences were found in visceral fat index ($P \geq 0.17$), but significant seasonal variability was found in visceral fat index ($F = 10.9, df = 2, 128, P < 0.001$; Fig. 4).

Reproductive condition: males.—As with female reproduction, the proportion of 1st-year males with reproductive testes were similar among bioregions ($\chi^2 = 2.19, df = 2, P = 0.33$), which totaled 68% ($n = 47$). Ninety-six percent ($n = 52$) of

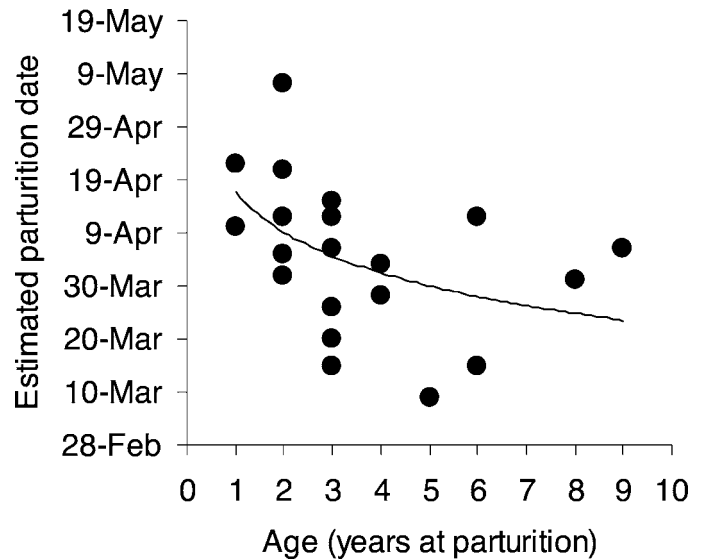


FIG. 3.—Relationship between estimated parturition date and maternal age of coyotes in California, indicating a negative relationship. Note: age was log-transformed for linearity in the corresponding statistical analysis.

adult males killed during January–March had reproductive testes. All but 2 adult males (both from the Sierra Nevada in late March) had reproductive testes, which precluded statistical comparison among bioregions.

Seasonal patterns: males.—Seasonal patterns of testis mass in males paralleled those of proestrus in females (Fig. 5). First-year males showed a peak in testis mass lower than that of adult males and occurring approximately 3 weeks later.

Relationship between reproduction and body condition: males.—Because there were only 2 nonreproductive adult males, body condition parameters were compared among adult reproductive males, 1st-year reproductive males, and 1st-year nonreproductive males. Body mass was significantly lower in 1st-year nonreproductive males ($\bar{X} \pm SE = 10.1 \pm 0.4$) than in 1st-year (11.5 ± 0.2) or adult (12.5 ± 0.3) reproductive males ($F = 11.5, df = 2, 94, P < 0.001$; Tukey $P \leq 0.02$), and the greater body mass of adult relative to 1st-year reproductive males was marginally significant as well (Tukey $P = 0.051$). The marrow fat index was higher in 1st-year reproductive ($0.18 SDs \pm 0.17$) than 1st-year nonreproductive ($-0.73 SDs \pm 0.22$) males ($F = 4.5, df = 2, 92, P = 0.014$; Tukey $P = 0.012$), but neither of these groups of 1st-year males differed significantly from adult reproductive males ($-0.20 SDs \pm 0.13$; Tukey $P \geq 0.18$). No difference was found among the 3 groups in visceral fat index ($F = 0.87, df = 2, 92, P = 0.42$), although significant seasonal variability was found in visceral fat index for males that was similar to that for females ($F = 8.4, df = 2, 213, P < 0.001$; Fig 4).

DISCUSSION

To my knowledge, the present study is the 1st to document male reproductive changes in a free-ranging coyote population. As in observations of captive male coyotes, testis mass of coyotes in the present study increased, presumably because of

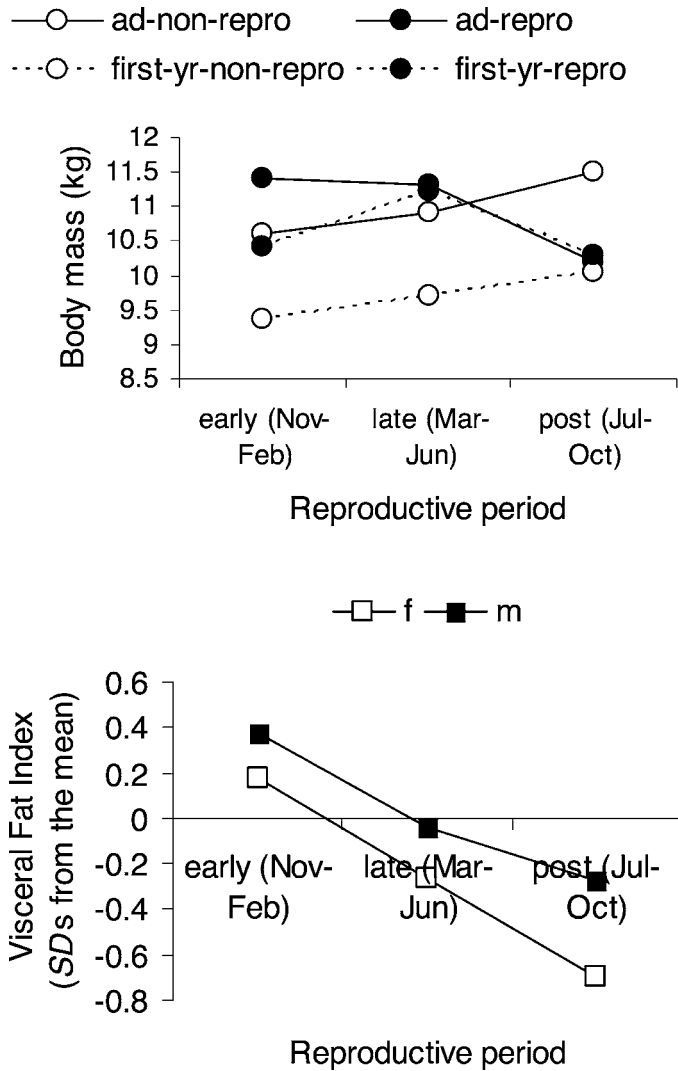


FIG. 4.—Top) Seasonal variability in body mass of female coyotes in California according to reproductive activity and age class. Bottom) Seasonal variability in visceral fat index of female (f) and male (m) coyotes in California (bottom).

sperm production, on a seasonal basis paralleling reproductive changes in females (Kennelly 1978). Although increased testis size in 1st-year males did not imply that these individuals necessarily mated, radiotelemetry and genetic evidence confirmed successful reproduction in at least one 1st-year male in the study population (Sacks 1996; K. M. Blejwas, in litt.). Regarding females, fecundity in this study was lowest in the youngest and oldest age classes because of a combination of reduced ovulation and reduced viability of pregnancies, similar to studies in other parts of the coyote range (Green et al. 2002; Windberg 1995). As is typical of exploited populations, a proportion of 1st-year females in this study became pregnant (Nellis and Keith 1976). Reproductive signs were evident in 1st-year males and females 3–4 weeks after they occurred in adults, which also has been previously observed (Kennelly 1978).

In contrast to previous studies, the present study was conducted in a Mediterranean climate, where seasonal constraints on reproduction are likely less stringent than in the

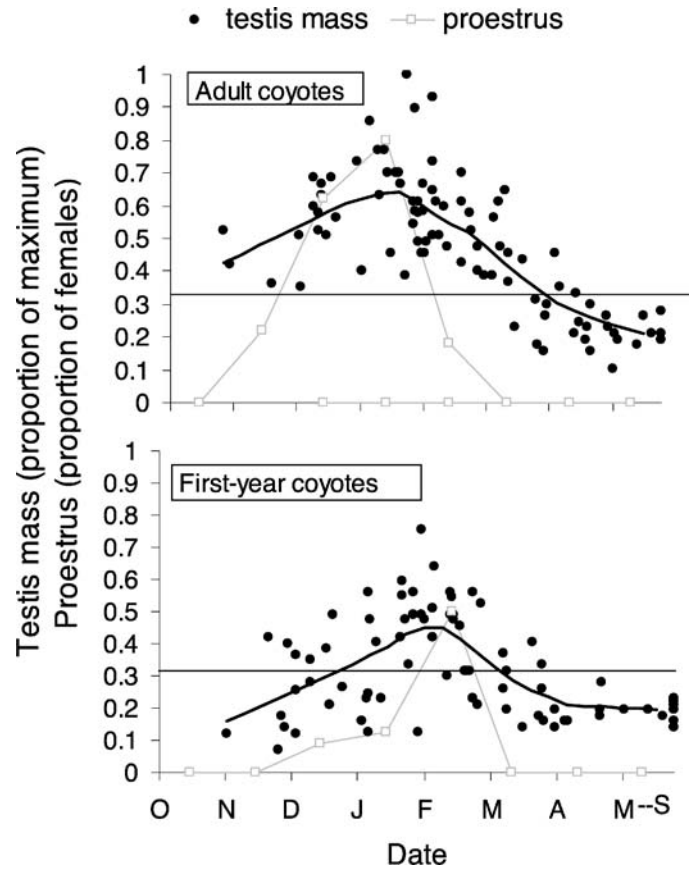


FIG. 5.—Seasonal variability in testis mass of males and proestrus in females of top) adult and bottom) 1st-year coyotes in California. Locally weighted scatterplot smoothing (LOWESS) functions for average testis mass over time are shown (black lines) in each graph for reference to peaks in proestrus.

intermountain region of North America. The mild climate in the present study apparently enabled coyotes to breed earlier in the year, which provided an opportunity to examine the relationship between coyote age and seasonal timing of reproduction. Although it had been previously observed that reproductive signs in 1st-year coyotes lag behind those of yearling and adult coyotes (Kennelly 1978), this study is the 1st I am aware of to find a continuation of age-related differences in the timing of reproduction beyond the 1st year (Fig. 3). This finding suggests that age-related differences in reproductive timing are not solely due to the timing of puberty, a one-time event.

Such an age-associated relationship could have important life-history implications. It seems likely that there is a strong advantage to breeding earlier in the year as long as the climate does not constrain this possibility. In northern California, prey availability is generally highest in the winter and early spring and becomes scarce during the summer drought season. Therefore, energetic costs to the mother of pregnancy and lactation may be easier to compensate for (i.e., nutritionally) earlier in the season. Second, if earlier-borne coyotes tended to be larger than later-borne coyotes (e.g., by virtue of their older age) during the dispersal and breeding season, this could confer a competitive advantage with respect to acquiring mates and territories.

In support of this, both female and male 1st-year coyotes that showed signs of reproductive activity were larger and in better nutritional condition (as indicated by marrow fat reserves) than those that did not show signs of reproductive activity. Although age at 1st breeding (and age when reproduction wanes) varies among populations (e.g., depending in part on level of exploitation—Knowlton et al. 1999), similar trends have been noted elsewhere in early-breeding age classes (Dumond and Villard 2000; Windberg 1995), suggesting that the level of physical maturity necessary for reproduction may only be met by a portion of this age class. The drop in body mass from breeding to postbreeding periods observed here in reproductive female coyotes (1st-year and adult) but not in nonreproductive female coyotes likely reflected energetic costs of reproduction.

However, the evolutionary importance of these observations depends on the causes. For example, if age and timing of ovulation are directly linked (e.g., physiologically), the relationship between age and reproductive value would seem to be straightforward. Alternatively, if older females in this study tended to breed earlier because they were more likely to have been established with a mate in a territory at the earliest opportunity to begin the reproductive process (stimulated in part by social context), the link between age and timing of breeding would be less direct, and possibly contingent on additional factors.

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