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REPRODUCTION IN CAPTIVE WILD-CAUGHT COYOTES (*CANIS LATRANS*)

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We assessed reproductive patterns of coyotes (*Canis latrans*) from a 12-year data set involving 24 pairs of captive animals acquired from Latah County, Idaho. None of the females had placental scars (fetal implantation sites) at 1 year of age, but over 80% had placental scars by 2 years of age. The fraction with placental scars remained at 80–90% through age 9 years and then declined to <40% by age 12 years. Similarly, mean number of placental scars per female rose rapidly through 2–3 years of age, remained stable until age 8 years, and then progressively declined to a very low level by age 12 years. Numbers of pups observed were typically smaller than numbers of placental scars, with fewer placental scars represented by pups among younger females than older females.

Key words: *Canis latrans,* captive, coyote, placental scars, reproduction, senescence, serial productivity

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Knowledge of reproductive patterns among coyotes (*Canis latrans*) is essential for understanding coyote population dynamics as well as developing realistic coyote population models. Details of specific physiological aspects of coyote reproductive functions have been reported for captive coyotes (Hodges 1990; Kennelly 1978; Kennelly and Johns 1976; Stellflug et al. 1981), whereas other studies have gleaned reproductive data from the field (Crabtree 1988; Gese et al. 1989; Gier 1968; Hallett 1977; Hamlett 1938; Knowlton 1972; Knudsen 1976; Windberg 1995; Windberg et al. 1997). The latter typically use data derived from field-collected coyote carcasses or from observations around dens. Examinations of carcasses yield only a single data point per animal, whereas observations around dens usually involve small sample sizes and frequently omit important reproductive parameters. Usually, neither situation provides longitudinal information about serial reproductive patterns over coyote life spans.

A study of reproduction among a cohort of captive coyotes was initiated by D. A. Barnum et al. (in litt.) at the United States Sheep Experiment Station at Dubois, Idaho. Herein we report, via additional data, analyses, and interpretations, a unique set of reproductive data from captive coyotes. Our specific objectives are to document age-related reproductive efforts of these coyotes in terms of the fraction of females breeding and the mean litter sizes.

MATERIALS AND METHODS

This study involved a total of 24 pairs of coyotes acquired as pups from dens in and around

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TABLE 1.—Summary of reproductive performance among a cohort of 24 pairs of captive coyotes at the United States Sheep Experiment Station, Dubois, Idaho, 1977–1988.

Age (years)	Implantation sites			Observed number of pups			Ratio of pups per implant
	n	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	
1	18	0		18	0		
2	18	3.89	0.63	18	2.22	0.65	0.44
3	20	4.85	0.60	20	3.50	0.61	0.72
4	22	4.41	0.53	22	4.00	0.58	0.83
5	16	4.44	0.53	18	3.61	0.51	0.79
6	12	5.42	0.74	14	4.00	0.66	0.81
7	10	5.10	0.84	11	3.55	0.91	0.78
8	12	5.33	0.86	12	4.17	0.77	0.84
9	9	3.89	1.06	9	2.89	0.68	0.85
10	9	2.44	0.84	9	2.33	0.87	0.83
11	9	1.44	0.53	9	1.22	0.52	0.75
12	8	0.63	0.38	8	0.38	0.26	0.56

Latah County, Idaho, in spring, 1976. They were transferred to the United States Sheep Experiment Station at Dubois, Idaho, where they were placed in kennels and hand reared. The pups were initially part of a growth rate study (Barnum et al. 1979) and were subsequently incorporated into a 5-year study attempting to manipulate reproductive performance via extraneous exposure to the urine and vocalizations of other coyotes (D. A. Barnum et al., in litt.). Because no reproductive effects were detected as a result of those treatments (D. A. Barnum et al., in litt.), we used data from all animals during those 5 years and extended the data set for an additional 7 years on all surviving pairs. We started with 18 pairs of coyotes and added 3 other pairs (from the same cohort) each in years 3 and 4, with a total of 24 pairs eventually incorporated into the study. Throughout the study, individual pairs were lost as a result of natural mortality or human intervention until only 8 remained by year 12 (Table 1). During individual years, the number of coyote pairs ranged from 8 to 22 ($\bar{X} = 14 \pm 1.43$ *SE*).

After completion of the study on pup growth rate, coyotes were maintained as male–female pairs in individual pens (6 by 1.8 by 1.8 m) equipped with self-watering and self-feeding devices as well as shelters. Pens were located so that some were within visual and vocal communication of one another, whereas others were visually and vocally isolated from other captive coyotes. Coyotes were maintained on a diet of dry commercial dog food and water ad lib., although during year 3, 1 group was fed commercial mink food.

The maximum number of offspring (pups) observed with each coyote pair for each year of the study was recorded. This was determined by inspection of the den (shelter) in the first 3 days after whelping. Laparotomies were performed on each female at 1–8 weeks after whelping to assess the number of placental scars (fetal implantation sites) within the uterus (Green et al. 1979).

RESULTS

We detected no placental scars during the coyote's 1st reproductive season (Table 1; Fig. 1a). During years 2–9, 80–90% of the females were reproductively active, as determined by presence of placental scars. Subsequently, the percentage of females with placental scars progressively declined through age 12 years (Fig. 1a). Coincident with the change in incidence of placental scars, the mean number of placental scars among all females increased from 3.9 at age 2 years to more than 5 at ages 6–8 years, followed by a systematic decline through age 12 years (Table 1). When only data from reproductively active females are considered, this pattern is emphasized (Fig. 1b). We were able to determine age of 1st reproductive activity, as evidenced by placental scars, among 17 females. Most (15) 1st showed placental scars in year 2, with placental scars 1st detected for 1 coyote each in years 3 and 6.

We did not see any pups during the 1st reproductive season. In the 2nd year, we saw pups with 8 of 18 (44%) females (Fig. 1a). Pups were seen with 70–90% of females 3–9 years of age (Fig. 1a). Thereafter, the percentage of females we observed with pups declined successively until pups were only seen with 25% of 12-year-old females (Fig. 1a). The mean number of pups detected among all females followed a similar pattern as observed for placental scars (Ta-

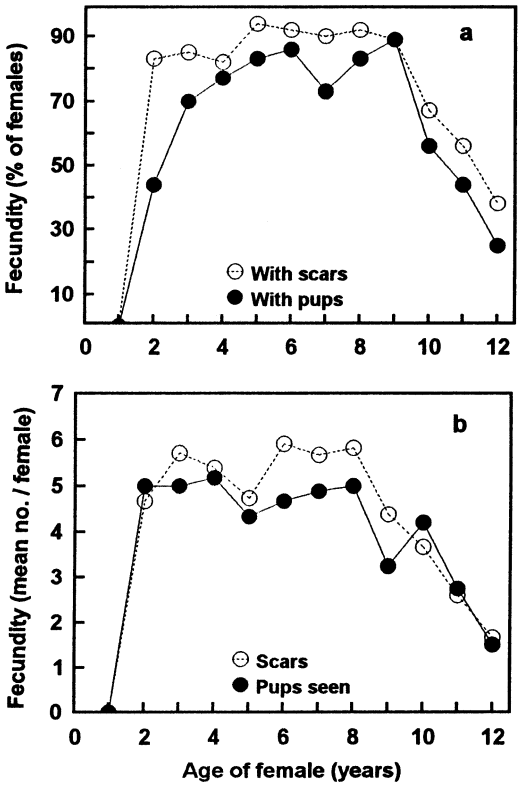

FIG. 1.—Age-related fecundity of a cohort of 8–22 captive female coyotes (*Canis latrans*) based upon a) relative frequency with which placental scars and live pups were observed and b) mean number of placental scars and live pups seen per producing female.

ble 1; Fig. 1). Our index of fetal viability, assessed by the ratio of live pups seen to the numbers of placental scars detected, followed a similar pattern, with 75–85% of the placental scars represented by live pups in most years, although lower percentages were observed among younger and very old females (Table 1).

In 6 of 118 laparotomies, the number of placental scars identified was less than the number of pups observed in that litter; in 4 cases, it was 1 less, and in 2 cases, it was 2 less. These may result from oversights or from scheduling laparotomies too soon after whelping without allowing adequate time for the uterus to atrophy to the point placental scars are obvious and distinct.

DISCUSSION

We document an age-related rise and fall in fecundity among a cohort of captive coyotes that was maintained under reasonably constant conditions. Similar reproductive patterns among wild coyotes have been inferred from field studies, but those data are typically meager and inconclusive. Lower reproductive performance among yearlings (1 year of age) than adult coyotes is documented from pen studies (Kennelly 1978; Kennelly and Johns 1976) and field research (Gier 1968; Knowlton 1972; Knudsen 1976; Windberg 1995). Kennelly and Johns (1976) noted that among 22 captive yearling coyotes, 3 were sexually inactive, 8 probably experienced false heat, 7 had ovulated and could have become pregnant, and 4 others may have ovulated but were not adequately examined. Gier (1968) reported 10–70% pregnancy rates among yearling coyotes in Kansas, and Knudsen (1976) reported pregnancy rates of 29–100% for small samples of 1-year-old coyotes from a highly exploited population in northern Utah. Similarly, Nellis and Keith (1976) recorded low pregnancy rates of yearlings (14%) in Alberta when snowshoe hares (*Lepus americana*) were scarce. Windberg (1995) also noted that only 10 of 186 (5.2%) 1-year-old females from dense populations in southern Texas had ovulated, and of these, only 4 carried fetuses. He also reported that, among 106 females 2 years of age, pregnancy rates ranged from 13% to 100% ($\bar{X}$ = 37%) among years, whereas among 217 adult coyotes, pregnancies ranged from 38% to 81% ($\bar{X}$ = 65%). Studying an unexploited coyote population in eastern Washington, Crabtree (1988) reported no yearlings, and only 29% of 2-year-old females produced pups.

The dramatic loss of fecundity noted among females over 8 years of age in our study is of particular interest. A reduced likelihood of females producing pups, coupled with a drop in mean litter size, between ages of 8 and 12 years indicates a

10-fold drop in productivity, from about 4 pups/year to less than 0.4 pups/year. This interpretation is supported by Crabtree's (1988) observation that none of his subjects over 6 years of age successfully produced offspring and Windberg's (1995) indication that pregnancy rates among females 10 to 12 years old were only a half to a third that of females 4 to 9 years old. Loss in fecundity appears to coincide with the timing at which older coyotes may become transient (Windberg and Knowlton 1988), although Crabtree (1988) suggests that some coyotes maintain territorial status 3–4 years into reproductive senescence. However, occasionally 12- to 14-year-old coyotes produce litters in the wild (Gese 1990, pers. comm.).

We do not suggest that reproductive values presented here are directly applicable to any specific set of field conditions because reproductive rates vary among sites (Crabtree 1988; Davison 1980; Hamlett 1938; Knowlton 1972; Windberg 1995) as well as among years on any specific site (Knowlton and Stoddart 1983; Nellis and Keith 1976; Windberg 1995). An extreme example of the latter is a change in mean litter sizes among producing females, based upon placental scars, from 4.9 to 8.5 pups per litter associated with changes in jackrabbit abundance in Curlew Valley, Utah (Knowlton and Gese 1995; Knowlton and Stoddart 1983).

Demographically, coyote populations appear to function similar to those of gray wolves (*C. lupus*), with territorial social groups partitioning the suitable habitat (Mech 1970) and using a primary reproductive strategy of producing 1 litter per territory each year. Both species are seasonally monestrous, with usually only the alpha female in each social group breeding and rearing young; behaviorally induced reproductive inhibition is common among subordinate canid females (Crabtree and Sheldon 1999; Knowlton and Gese 1995; Knowlton et al. 1999; Mech 1970). Coyotes may exhibit slightly greater reproductive latitude by becoming reproductively mature at somewhat younger ages than wolves and perhaps by having a capacity for slightly larger litters.

From a demographic perspective, maintaining a stable breeding population requires only that each breeding component replace itself during its reproductive life. If female coyotes acquire and maintain alpha status between 3 and 8 years of age, they could be expected to produce 6 litters of 5 pups each. Hypothetically, only 2 of the 30 pups produced ($<7\%$) need to be recruited into the breeding population to maintain breeding stability. Reproduction among younger, older, or subordinate members (or both) of territorial groups adds to the reproductive potential of the population but under normal circumstances is of little demographic consequence. However, the capacity for additional members of a population to assume reproductive functions contributes to the resilience of the population. The apparent reproductive senescence among older coyotes is interesting but generally of little demographic significance.

These data may be useful with regard to developing and implementing strategies for managing coyote depredations and for generating population models to assess the impact of various management strategies. Coyote predation on lambs of domestic sheep can occur whenever lambs are present and is attributable primarily to territorial coyotes of breeding age (Sacks et al. 1999). However, throughout much of the western United States, the presence of coyote pups and young lambs coincides, and provisioning pups appears to be an important motivation for coyote depredations on livestock. Depredations end, or are markedly reduced, when pups are removed or absent (Bromley 2000; Bromley and Gese 2001; Till and Knowlton 1983). The decreased productivity reported by Crabtree (1988) among older coyotes in an unexploited population has led to speculation that unexploited coyote populations might pose lower risks to sheep enterprises than those in which coyote removal is practiced

(Crabtree 2000; Finkel 1999; Wilkinson 1996). Their rationale suggests that older coyotes predominate in unexploited populations, have fewer and smaller litters, and hence have reduced motivations to attack livestock. Our data suggest that higher productivity among younger animals may not be realistic, and those that become pregnant may be less competent at nurturing offspring because only 44% of placental scars among 2-year-old coyotes were represented by viable young compared with 72–85% among older coyotes (Table 1). More importantly, normal patterns of senility among coyotes are unlikely to provide significant relief from depredations because even among unexploited populations, coyotes over 8 years of age usually comprise only about 5% of the population (Crabtree 1988; Knowlton 1972; Knowlton et al. 1999).

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