SURVIVAL OF COYOTES IN SOUTHERN TEXAS

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Abstract: Survival patterns of coyotes (*Canis latrans*) in southern Texas were studied from 1974 to 1982. Three estimates of annual survival rates of adult (≥1.5-year-old) coyotes ranged from 0.68 to 0.70. A mean annual survival rate of 0.42 for juveniles from 0.5 to 1.5 years of age was estimated by the product-limit method. Juvenile survival was lower ($P < 0.01$) than adults during the cool season (Nov–Feb). Fifty-seven percent of 35 mortalities of radio-collared coyotes were attributed to human-related factors (shooting, trapping, road fatalities). A greater proportion of juvenile females egressed from marking sites than juvenile males or either sex of adults. Comparison of autumn and spring population age ratios implicated an age bias in sampling.

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Management strategies to alleviate depredation by coyotes on livestock or game animals must be developed from knowledge of population processes in different environments. Knudsen (1976), Davison (1980), and Tzilkowski (1980) provided data on survival rates and mortality factors in coyote populations affected by intensive human exploitation. Additional information on coyote survival is available from Knowlton (1972), Nellis and Keith (1976), and Andrews and Boggess (1978).

Coyote abundance has been continuously high in southern Texas since estimates were begun in 1965 (Knowlton 1972, Bean 1981). Human exploitation of coyotes has been light in the region (Knowlton 1972) because control efforts for livestock protection were limited and sport hunting and trapping were sporadic. The objective of our study was to quantify survival rates and patterns and to determine mortality causes in this lightly exploited, high-density coyote population.

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STUDY AREA

All study sites were in Webb County, Texas, within 60 km north and east of Laredo. This region in southern Texas, classified as the South Texas Plains vegetational area (Gould 1975), originally supported a grassland-savannah climax, but present vegetative communities are dominated by dense stands of woody shrubs. Extensive brush control by landowners during the past 40 years (S. A. Nelle, pers. commun.) has resulted in varying stages of secondary plant succession. Topography is level to rolling; drainages flow into the Rio Grande River. Upland sites have variable soils ranging from fine sandy loam to clay, and the vegetative communities, comprised of numerous woody species, are dominated primarily by honey mesquite (*Prosopis glandulosa*), blackbrush acacia (*Acacia rigidula*), and Texas pricklypear (*Opuntia lindheimeri*). Drainage bottoms have predominantly clay loam soils, and the dense woody plant communities have wide species diversity; honey mesquite, blackbrush acacia, Texas pricklypear, whitebrush (*Aloysia lycioides*), and spiny hackberry (*Celtis pallida*) are the most prevalent. Poorly drained level sites with saline clay soils have distinct plant communities characterized by smaller growth forms of honey mesquite and Texas pricklypear associated with Texas varilla (*Varilla texana*), leatherstem (*Jatropha dioica*), and pencil cactus (*O. leptocaulis*). Plant names follow Gould (1975). The climate of the region is semiarid: mean annual

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rainfall at Laredo was 51 cm but was erratic among and within years; mean low and high monthly temperatures were 8 C in January and 38 C in July (U.S. Dep. of Commer. 1982). All study sites were on privately owned rangeland used primarily for cattle grazing.

METHODS

During November of 1974–76, 89 coyotes were trapped on a 25,000-ha study area and marked with radiotelemetry collars. In October 1979, 37 additional coyotes were instrumented on the same site and on a separate area of 12,000 ha. Population age structure data were obtained from coyotes trapped during spring (Mar–Apr) and autumn (Oct–Nov) from additional areas of representative habitat ranging from about 4,000 to 10,000 ha, all of which were separated from each other by at least 8 km. These areas were not resampled during the study period (1975–82).

Coyotes were captured with steel leghold traps equipped with tranquilizer tabs (Balser 1965) containing 500 mg of propiopromazine hydrochloride (Diamond Laboratories, Des Moines, Iowa; identification of commercial products and companies does not constitute endorsement by the U.S. Government) to reduce injury and trauma associated with capture. The location, sex, estimated age, weight, description of foot injury, and general physical condition were recorded for each animal captured, and one premolar or canine tooth was extracted for age determination. Coyotes were categorized as juveniles (0.5 year) or adults ($\geq$1.5 years) by interpretation of cementum annuli examined microscopically from tooth sections (Linhart and Knowlton 1967). Tooth sections were prepared from the first premolar tooth of instrumented coyotes and from canine teeth of animals collected for population samples. Coyotes that were marked and released were fitted with a multiple-use transmitter (Kolz et al. 1973) to facilitate relocation and detection of mortality. Individual transmitters were identified by combinations of operating frequencies (164 MHz band) and pulse rates.

We monitored instrumented coyotes using a Model LA12 AVM radio receiver (AVM Inst. Co., Champaign, Ill.) from a fixed-wing aircraft during the 12-month period after each successive year's marking. Monitoring intervals were 1–2 weeks except on six occasions during 1976–77 and 1979–80 when intervals were 4–6 weeks because an aircraft was not available. Cause of death was determined by examination of remains, necropsy of fresh carcasses, and assessment of any additional evidence at the mortality site. If the exact date of death could not be determined, the date midway between the time an animal was last confirmed alive and recovery of the carcass was arbitrarily designated as date of death for survival analyses.

Estimates of annual survival rates were computed for the 1-year periods between successive releases of marked coyotes (autumn-to-autumn annual period). The survival estimates derived from telemetry data were based on the assumptions that: (1) the marked sample of coyotes was representative of the population on the study area and (2) all subsequent mortality was documented and unbiased by the marking instrument or process. We attempted to satisfy the first assumption by marking each individual captured during an intensive trapping effort over time intervals ranging from 2 to 4 weeks. To meet the second assumption, we eliminated from the marked sample four adult and six juvenile coyotes that died within 21 days after release. Their deaths were attributed to the effects of capture or handling and were not considered representative mortality.

Seasonal and annual survival rates for instrumented adult and juvenile coyotes were estimated by the product-limit life table method (Kaplan and Meier 1958). This method permitted data from censored individuals to be incorporated in the analyses. A censored individual is statistically defined as one for which the time of death was not observed. Coyotes in this study were censored either by transmitter failure prior to the end of the study period or termination of the study period with the animal still alive. During the 1-year monitoring periods, 12% of 126 transmitters ceased to function in the first half and an additional 32% expired in the second half of the year. We assumed that the fate of instrumented coyotes after the loss of radio reception was comparable to animals with functional transmitters. Hence data for the censored individuals were included in survival rate calculations up to the day of last reception. Data from animals that had been initially withdrawn from the sample groups because of premature transmitter failure, but that were subsequently identified by human recoveries (shooting and trapping) during and after the monitoring pe-

riod, were also incorporated in the survival rate calculations.

For comparison with the product-limit estimate, we calculated estimates of adult survival using two additional types of data and estimation procedures. We computed an estimate of adult survival from the marking data by using Model 3 of program ESTIMATE for tag recoveries (Brownie et al. 1978). This estimator is based on the assumption that tag recovery rates and survival rates are constant from year to year and independent of age or capture history.

We also used the Chapman-Robson model (Seber 1973) to estimate adult survival from population age distribution data ($N = 156$). Validity of the Chapman-Robson estimator is dependent upon the assumptions that: (1) the age distribution is representative of the population sampled; (2) the survival rate is similar for each age-class and remains constant among years; and (3) population size and age distribution are stationary and stable. To check these assumptions, we used Heincke's estimate to test for differences in survival between age-classes (Seber 1973). Population size was estimated each spring by indices to relative coyote abundance from scent-station procedures (Roughton and Sweeny 1982).

The effects of age-class, seasons, and years on the survival rates estimated by the product-limit method were analyzed by three-factor analysis of variance (ANOVA). Annual survival curves of adult and juvenile coyotes from the product-limit method were compared by Breslow's (1970) nonparametric test. We tested differences in seasonal survival rates among age-classes using a normal approximation z test. Chi-square analyses of contingency tables were used to test for distributional differences in sex- and age-specific mortality, population age distributions, and sex and age-related egress. Mean movement distances among sex and age-groups were compared by two-way ANOVA. Friedman's test for a two-way layout was used to compare population abundance indices among years.

RESULTS AND DISCUSSION

Survival Patterns

Annual (autumn-to-autumn) survival rates of adult coyotes, derived by the product-limit method, ranged from 0.54 to 0.84 during the 4 years of study (Table 1). Annual survival rates of juveniles from 0.5 to 1.5 years ranged from 0.37 to 0.60, excluding the small sample of three individuals in 1974–75. A difference in survival rates among years could not be detected for either adult or juvenile (excluding 1974–75) age-classes. Data from all 4 years were therefore pooled for an overall analysis of survival rates (Table 1). The annual survival curve (over all 4 years) of juveniles was lower than adults (Breslow test, $P < 0.01$). The annual survival rates for adult (0.70) and juvenile (0.42) coyotes were slightly higher than estimates derived by Davison (1980) from marking data in northern Utah (adults: 0.47; juveniles: 0.23) and southern Idaho (adults: 0.51; juveniles: 0.45).

Table 1. Seasonal and annual survival rates[a] of adult and juvenile coyotes instrumented in Webb County, Texas, November 1974–76 and October 1979.

Year and age at marking	N	Seasonal periods: Cool season (Nov–Feb)	Seasonal periods: Warm season (Mar–Oct)	Annual period[b]
1974–75				
Adult	33	0.97	0.87	0.84 (0.69–0.99)
Juvenile	3	0.33	0[c]	0[c]
1975–76				
Adult	17	0.76	0.71	0.54 (0.27–0.81)
Juvenile	7	0.57	1.00	0.57 (0.20–0.94)
1976–77				
Adult	19	0.89	0.80	0.71 (0.49–0.93)
Juvenile	10	0.60	1.00	0.60 (0.29–0.91)
1979–80				
Adult	19	0.75	0.80	0.60 (0.28–0.92)
Juvenile	18	0.44	0.84	0.37 (0.12–0.62)
Overall				
Adult	88	0.87	0.80	0.70 (0.58–0.82)
Juvenile	38	0.50	0.84	0.42 (0.24–0.60)

[a] Estimated by product-limit method (Kaplan and Meier 1958).
[b] 95% CL (2 SE) in parentheses.
[c] No survivors.

Estimated survival of juveniles was numerically lower than for adults in the cool season (Nov–Feb) of each year (Table 1), and the overall estimate was lower (z test, $P < 0.01$). Survival rates were similar between adult and juvenile coyotes during the warm season (Mar–Oct). Adult survival was similar between seasons. Although data were not separated by age-class, other studies with marked coyotes also indicated highest mortality (74–94%) of coyotes during winter in Idaho (Davison 1980), Utah (Knudsen 1976, Davison 1980), and Wyoming (Tzilkowski 1980).

Table 2. Mortality causes among 35 coyotes instrumented in Webb County, Texas, 1974–76 and 1979.

		Human			Other	
Age at marking	*N*	Shot	Trap	Road	Malnutrition	Undetermined
Adult (≥1.5 years)	18	6	2	0	0	10
Juvenile (0.5 year)	17	7	2	1	2	5
Total	35	13	4	1	2	15

There were no differences (χ^2 test, $P > 0.05$) in survival between sexes in each age-group based on the proportion of the total number of marked coyotes that died within 1 year after marking. Known mortalities among adults included 25% of 53 males and 20% of 35 females. Among juveniles, 47% of 15 males and 61% of 23 females were confirmed dead.

Adult Survival Estimates

The annual adult survival rate from the product-limit life table method was compared with estimates derived by two different methods. The product-limit and tag-recovery estimates (Brownie et al. 1978) used adults ≥1.5 years old from an autumn-to-autumn period. The Chapman-Robson estimate represented adults >2 years of age during a spring-to-spring annual interval. A Chapman-Robson estimator of autumn-to-autumn adult survival was not used because the autumn age distribution of the population differed (χ^2 test, $P < 0.01$) among years. We believe that the assumptions of the Chapman-Robson model were satisfied by using data from the spring-to-spring period of 1977–80 because the population age distribution was relatively stable (χ^2 test, $P = 0.10$), and indices of relative population abundance were stationary (Friedman's test, $P = 0.44$). Because Heincke's estimate (Seber 1973) indicated a lower rate of survival ($P < 0.01$) from 1 to 2 years of age compared with older adults, this first adult age-class was truncated from the population age distribution to fit the model.

The tag-recovery estimate of annual adult survival, which encompassed 3 (1974–76) of the same 4 years used for the product-limit estimate (Table 1), was 0.68 (95% CL = 0.53–0.83). The Chapman-Robson estimate for the 1977–80 period was 0.69 (95% CL = 0.64–0.74). Although our estimators of adult survival did not represent comparable time periods, they yielded similar annual survival rates ranging from 0.68 to 0.70. Davison (1980) also reported similar rates of adult survival using the Chapman-Robson and tag-recovery estimators for two coyote populations in Utah (0.44 vs. 0.47) and Idaho (0.62 vs. 0.51).

Mortality Causes

Assessment of mortality factors was restricted to the 35 coyotes that had operational radio transmitters at time of death during the 1-year interval after marking. Shooting, trapping, and road fatalities accounted for 51% (18) of the mortality of instrumented coyotes (Table 2). The percentage of human-caused mortality between adults and juveniles did not differ (χ^2 test). Cause of death was undetermined for 43% (15) of the marked animals because carcasses had deteriorated. Because 17% of the 18 human-killed coyotes were not reported, we estimated that a similar percentage of the undetermined deaths were also unreported human-caused mortalities. From this assumption, we revised the human-caused mortality to 57%. Additionally, the carcasses of two coyotes (6%) were recovered in emaciated condition and the immediate cause of death was considered malnutrition.

Andelt (1982) reported similar mortality factors for coyotes on a wildlife refuge about 200 km east of our study area. He had 6 (38%) human-caused mortalities and 9 (56%) deaths in which the cause could not be verified among 16 mortalities of instrumented coyotes. The proportion of human-caused mortality among coyotes in southern Texas was markedly lower than reported elsewhere: (1) Knudsen (1976) found that 92% of 52 mortalities were human-caused in northern Utah (Curlew Valley); (2) Tzilkowski (1980) had 93% human-caused deaths of 41 mortalities in northwestern Wyoming; (3) Davison (1980) reported 89% human-caused mortality among 46 juveniles and 93% for 29 adults in Curlew Valley; and (4) in southern Idaho, he recorded 78% human-related mortalities for 51 juveniles and 83% for 35

adults. Other mortality factors in all of these studies were either malnutrition or unknown. There was no evidence offered in any of these investigations that the proportion of human-caused mortality differed between adults and juveniles. Greater human exploitation of coyote populations may contribute to lower adult survival. In the three studies in Utah and Idaho, human-related coyote mortality ranged from 78 to 93% and annual adult survival rates ranged from 0.44 to 0.62. In comparison, human-caused mortality was lower (57%) and adult survival slightly higher (0.69) for our study in southern Texas.

Table 3. Percent juveniles (≤1 year) among coyotes trapped in Webb County, Texas, during autumn (Oct–Nov) and spring (Mar–Apr).

	Oct–Nov		Mar–Apr	
Year	% Juveniles	*N*	% Juveniles	*N*
1975–76	32	28	15	41
1976–77	35	34	36	77
1977–78	54	52	58	53
1978–79	31	72	41	68
1979–80	42	79	48	86
1980–81	10	50	7	44
1981–82	44	36	45	66
Mean	36	351	38	435

Movement Patterns

We analyzed movements of instrumented coyotes by comparing the mean distances between sites of capture and death: adult males, $\bar{x} = 6.4$ km ($N = 23$); adult females, $\bar{x} = 3.4$ km ($N = 13$); juvenile males, $\bar{x} = 3.7$ km ($N = 6$); and juvenile females, $\bar{x} = 15.3$ ($N = 16$). Because the mean home-range size reported for coyotes in southern Texas (Andelt 1982, Harris 1983) was <5 km², we classed movements of >15 km from marking site to mortality site as egression. Seven of 16 juvenile females were recovered dead >15 km from their marking location (range 20–80 km) compared with 3 of 23 adult males and none of 13 adult females and 6 juvenile males. The greater (ANOVA, $P = 0.04$) mean movement distance for juvenile females was associated with a greater ($P < 0.01$) proportion of individuals that egressed between the time of marking and death. Hibler (1977) and Davison (1980) reported trends for greater emigration by instrumented juvenile females from a heavily exploited coyote population in Curlew Valley, Utah. Recoveries of ear-tagged or instrumented coyotes from studies in Wyoming (Robinson and Grand 1958), California (Hawthorne 1971), Iowa (Andrews and Boggess 1978), and southern Idaho (Davison 1980) did not show significant differences in movements among sex and age-classes.

The product-limit method for analyzing survival allows data for instrumented coyotes that moved from their marking site to be included in the computations. Knowlton (1972) reported that immigration occurred in the coyote population in southern Texas primarily during November–March. Davison (1980) documented emigration of instrumented juvenile coyotes in Utah and Idaho from September through early April. In six of seven instances where timing of egress was documented in our study, movements occurred during October–December (the other was in Apr). We recorded loss of transmitter signals for 8% of 88 instrumented adults and 13% of 38 juveniles during the October–March periods. Although some of these presumed equipment failures probably represented undocumented egress, they included less than 10% of the marked sample. We believe that the fate of most instrumented coyotes that egressed was documented and that our survival estimates approximated actual survival rates.

Age Bias in Survival Assessment

Lower survival ($P < 0.01$) of juveniles during the cool season (Table 1) should have been reflected by a lower proportion of that age-class in the spring population (1.0 year) compared with the preceding autumn (0.5 year). However, population age ratios in each of 7 consecutive years did not differ (χ^2 test, $P > 0.05$) between autumn and spring (Table 3). Our seasonal samples of the population age ratio may have been insufficient to detect a difference. Comparison of the age distributions over all years (Table 3) also indicated that the percentage of juveniles did not differ (χ^2 test, $P > 0.05$) between autumn (36%) and the following spring (38%).

Failure of the population age ratio to reflect age-specific mortality overwinter was presumably linked with age bias in our sampling methods. We expected decreased vulnerability to capture among the juvenile cohort in spring compared with the preceding autumn due to: (1) higher overwinter mortality of vulnerable individuals and (2) greater wariness toward our

capture techniques gained from experience by survivors. The combined effect of lower overwinter survival and the expected decrease in capture vulnerability of juveniles failed to result in a lower proportion of juveniles in spring. Apparently other seasonal differences in relative age-related capture vulnerability were operating in the population.

IMPLICATIONS

By telemetrically monitoring a sample of a coyote population, including animals that moved away from the study area, we had opportunity to record mortalities and could estimate survival rates for the adult and juvenile age-classes. The adult survival rates derived from tag recoveries and population age structure were similar to the telemetry estimate. Seasonal population age ratios did not reflect the lower overwinter survival of juveniles we had calculated. Although unable to identify the factors, we believe differential capture vulnerability between juveniles and adults caused an age bias in our age ratio samples. Presumably such a differential vulnerability diminishes with increasing age of juveniles. If true, samples of coyote population age structure for demographic analyses should be timed after winter to reduce age bias.

Human exploitation of the coyote population studied in southern Texas was largely incidental in nature, resulting primarily from fur trapping or shooting by hunters and ranch employees, yet 57% of the overall coyote mortality was attributed to humans. Telemetry studies of coyotes on wildlife refuges also showed that substantial human-related mortality (80% in Idaho, 93% in Wyoming, 38% in Texas) occurred when animals moved out of the protected areas (Davison 1980, Tzilkowski 1980, Andelt 1982). All studies of unexploited coyote populations reported substantial incidental human exploitation of various intensities. Comparing the relationship between survival rates and the percentage of human-caused mortality for the southern Texas area with estimates from two areas in Utah and Idaho (Knudsen 1976, Davison 1980) suggested a trend of lower adult survival associated with greater human exploitation. A causal relationship between human exploitation and coyote survival should not be implied without considering other demographic and environmental variables.

Like the studies in Idaho (Davison 1980), Utah (Knudsen 1976, Davsion 1980), and Wyoming (Tzilkowski 1980), our results indicated that the greatest proportion of coyote mortality on an annual basis occurred during winter. Management schemes directed at general population reduction should recognize that most control measures during winter are probably compensatory with other forms of human exploitation. Our findings support Knowlton's (1972) assessment that post-winter coyote removal clearly offers the most favorable timing to accomplish additive population mortality and hence achieve a more lasting population reduction.

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COYOTE MOVEMENTS, HABITAT USE, AND VULNERABILITY IN CENTRAL ALBERTA

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Abstract: A 2-year radiotelemetry study revealed no migratory movements of coyotes (*Canis latrans*) between agricultural and adjacent boreal forest areas in central Alberta. Resident coyotes were predominantly adults and essentially maintained nonoverlapping home ranges averaging 12.1 km^2 in size. Nonresident coyotes, predominantly subadults, frequented home ranges of resident coyotes but may have avoided contact with them. Mobility of coyotes increased after mid–late February. Dispersal occurred between late January and late March and between July and November. Coyotes preferred forested over open areas and avoided open areas close to travelled roads during daylight hours. Nonresident coyotes were located closer to agricultural carrion than resident coyotes, suggesting a greater vulnerability to hunters and to coyote control using carrion as bait. However, annual survival rates of resident and nonresident coyotes after 1 January were identical ($S_x = 0.38$).

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Todd and Keith (1976) found a positive relationship between coyote densities in mid–late winter and availability of dead livestock on agricultural areas in central Alberta. A seasonal migration of coyotes between forested areas in summer and agricultural areas in winter was hypothesized to explain an apparent coyote population decline on agricultural areas and a concomitant increase on nearby forested areas during late winter. Mobility of coyotes is restricted by deep, soft snow in forested areas (Murie 1940, Ozoga and Harger 1966). In contrast, wind sweeps much of the snow from open fields, and stronger crusts form in open agricultural areas. Greater mobility coupled with an abundance of dead livestock enhance agricultural areas as coyote habitat in winter.

This study was conducted to determine if coyotes migrate seasonally to forested areas in summer and to agricultural areas in winter in central Alberta. We also monitored daily movements and spatial relationship of coyotes in an agricultural area to assess their effect on coyote control during winter months.

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