

IMPACT OF A SARCOPTIC MANGE EPIZOOTIC ON A COYOTE POPULATION

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Abstract: Although sarcoptic mange is a mite (*Sarcoptes scabiei*) infection that occurs as periodic epizootics in wild canids, the effect of this disease on populations has not been explained. We collected data from 1,489 coyotes (*Canis latrans*) during 1974–91 in southern Texas and examined the effect of a sarcoptic mange epizootic on the coyote population. Mange appeared in 1975, peaked during spring 1980 (69% of coyotes infected), and then decreased until absent among coyotes collected in 1991. The epizootic encompassed 60,000 km² in southern Texas during 1982–89. Adult males were more ($P < 0.001$) frequently infected than other age-sex classes during the stationary phase of peak prevalence. Mange prevalence in juvenile males increased ($P < 0.01$) overwinter during the stationary and decline phases of the epizootic. There were more cases of severe mange among adult males ($P < 0.01$) during the stationary than the decline phase. Reduced ovulation ($P = 0.04$) and pregnancy rates ($P = 0.03$) were associated with greater mange severity in adult females. Usually, coyotes with severe mange had less ($P < 0.05$) internal fat. We suggest that this epizootic was initiated by the appearance of a virulent strain of *S. scabiei* in the host population, spread of the epizootic was enhanced by high host population densities but moderated by the social organization of coyotes, and decline of the epizootic resulted from selection for mange-resistant individuals in the host population. Understanding the effect of diseases on wildlife populations requires long-term analysis of host population dynamics, with attention to other relevant factors such as behavior.

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Pence et al. (1983) documented the effects of a sarcoptic mange epizootic on a coyote population in southern Texas over 7 years (1975–81). Although the mortality rate among mange-infected individuals was greater than among uninfected coyotes during 1979–80, it was compensatory with overall mortality in the population (Pence et al. 1983).

The high-density coyote population (0.9–2.0 coyotes/km² in spring) in southern Texas had a well-developed social organization (Andelt 1985, Windberg and Knowlton 1988) and experienced light exploitation by humans (Windberg et al.

1985). The diverse food base was consistently abundant (Brown 1977, Windberg and Mitchell 1990). In conjunction with other studies, we monitored the prevalence and severity of mange in this population during 1981–91. We present data for the duration of the epizootic to further assess its dynamics and effect on the coyote population. Our objectives were to (1) describe stationary through decline phases of the mange epizootic (1979–91), (2) compare the severity of mange infection across temporal (seasons) and host (age and sex) factors over the latter years of the epizootic, and (3) reassess the effect of

mange on reproduction and body condition of coyotes on the basis of additional data from 1981–91.

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METHODS

The 7,000-km² study area was within a 70-km radius north and east of Laredo, Webb County, Texas (Fig. 1). We collected coyotes on 15 sites (30–90 km² each) of privately owned rangeland during 1976–87 to estimate mange prevalence and demographic variables (Windberg, unpubl. data). We sampled a different site each fall (Oct–Nov) and spring (Mar–Apr), except during 1987, 1989, and 1991 when we collected spring samples during January–February. Additional samples for mange prevalence on the study area were from a study of coyote survival during 1974–76 (Windberg et al. 1985) and other studies during 1987–91 (Linhart et al. 1988, Phillips and Mullis 1991, Radomski and Pence 1993).

Coyotes marked with radio transmitters for other studies (Pence et al. 1983, Knowlton et al. 1986, Windberg and Knowlton 1988) on intervening sites within the study area provided data on the progression of mange infection in individuals and the territorial status of hosts. Habitats on all study sites were similar and representative of the South Texas Plains (Gould 1975, Windberg et al. 1985).

Procedures for capture of coyotes, determination of age, and analysis of reproductive data followed Pence et al. (1983). Age classes of coyotes were juvenile (≤ 1 yr) and adult (> 1 yr) for

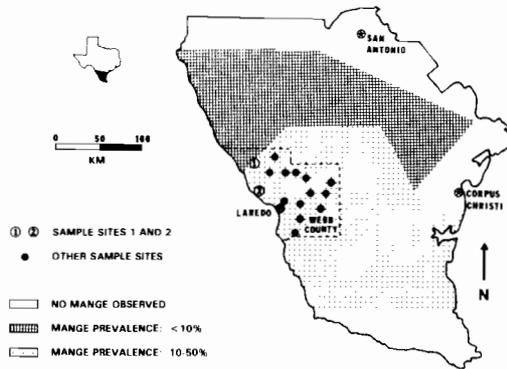


Fig. 1. Location of coyote sample sites in Webb County, Texas, and geographic distribution of sarcoptic mange epizootic in southern Texas derived from personal interviews, 1982–89. There was a distinct demarcation in prevalence of mange between sample sites 1 and 2.

analysis of mange prevalence, and juvenile (< 1 yr), yearling (1–2 yr), and adult (> 2 yr) for analyses of reproductive variables and body condition.

We determined presence of sarcoptic mange by visual examination of restrained live coyotes or carcasses of euthanized coyotes and classified its severity (Pence et al. 1983): Class I mange was the initial stage of infection distinguished by active lesions primarily on the lower legs and the ischial protuberance with $< 5\%$ of the body surface infected; Class II mange involved 5–50% of the body; Class III cases had $> 50\%$ of the body surface infected; and Class IV was a category of hosts that appeared to be recovering from mange. For an overview of mange prevalence in the coyote population, we combined sexes and age groups in fall and spring of each annual period into a single class (I, II, III) of active mange. We excluded vehicle-caused mortalities of coyotes included by Pence et al. (1983) from this analysis because of potential biases (Windberg and Knowlton 1990). Because seasonal patterns in prevalence were asynchronous (Fig. 2), we analyzed fall and spring periods separately.

During 1982–89, our assessment of the geographic distribution of the mange epizootic throughout southern Texas was based on continuing annual personal interviews with predator trappers and game wardens initiated in 1979 by Pence et al. (1983). We sought an estimate of mange prevalence among coyotes during winter–spring in each respondent's area of operation. We delineated the geographic bound-

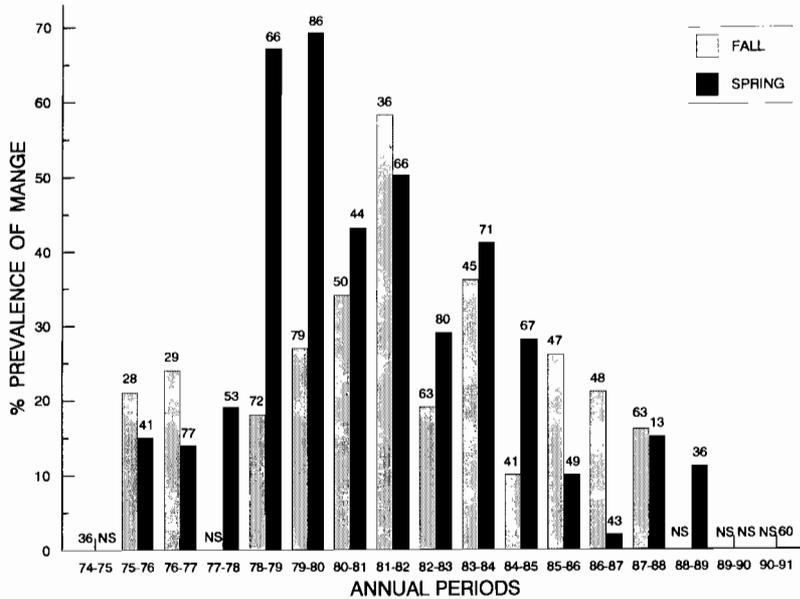


Fig. 2. Prevalence (%) of sarcoptic mange among coyotes (combined sex and age classes) in fall (Oct–Nov) and spring (Mar–Apr) in Webb County, Texas, 1974–91. Samples for spring 1987, 1989, and 1991 were during January–February. Sample sizes above bars; NS = no sample.

ary of the mange epizootic from respondent estimates of percent prevalence of infected coyotes.

We combined prevalence data for all years of the epizootic for analysis; however, data were partitioned by season, age, and sex because of differences associated with those variables. We analyzed relationships of mange severity (Class I, II, III) among coyote sex and age groups in fall and spring for stationary (spring 1979–82) and decline (fall 1982–87) phases of the epizootic.

We assessed effects of mange severity on reproductive variables by combining all data from spring 1979–86. We analyzed adults and yearlings separately because of reproductive differences between those age groups (Pence et al. 1983). Because samples for females with Class I mange were limited, we combined Classes I ($n = 13$) and II ($n = 29$).

We classified fat deposits in coyotes according to Windberg et al. (1991). We compared indices of intraperitoneal fat (IPF) across mange classes for the respective age groups in fall and spring to assess the effect of mange on coyote body condition. This analysis was restricted to fat deposits because previous studies (Pence et al. 1983, Windberg et al. 1991) showed that IPF was a more sensitive indicator of body condition than was body mass. We excluded Class I mange

because data were insufficient ($n < 10$) across most categories. We combined data for sexes but segregated by season and age group according to Windberg et al. (1991).

We analyzed frequency distributions of mange prevalence across years, seasons, age, sex, and severity classes with Chi-square contingency tables. Similarly, we compared categorical reproductive data (percent with ova, viable fetuses, and resorbed litters) and indices of internal fat deposits among mange-severity classes by Chi-square analyses. We examined mean numbers of ova and fetuses in relation to class of mange severity with 1-way analysis of variance.

RESULTS

Seasonal Prevalence

During fall 1974–spring 1991, we examined 1,489 coyotes for sarcoptic mange. None of 36 coyotes examined in fall 1974 had mange (Fig. 2). Only occasional cases of mange were observed among coyotes captured by trappers throughout southern Texas during the preceding 10 years (F. F. Knowlton, U.S. Dep. Agric., Denver Wildl. Res. Cent., Colo., pers. commun.). We first observed coyotes with sarcoptic mange (21%) in fall 1975 (Fig. 2). Mange prevalence was 14–24% from fall 1975 to fall 1978 ($\chi^2 = 2.0$, 5 df, $P = 0.84$), which we considered

as the initial (inductive) phase of the epizootic. By spring 1979, prevalence had increased ($\chi^2 = 33.6$, 1 df, $P < 0.001$) to 67% of coyotes collected. Mange prevalence was high (69%) in spring 1980 but was only 27% among coyotes examined in fall 1979. During the 2 subsequent annual periods (1980–81 and 1981–82), mange prevalence was higher ($\chi^2 = 11.0$, 2 df, $P < 0.01$) each fall but did not differ ($\chi^2 = 0.7$ – 0.8 , 1 df, $P = 0.39$ – 0.44) from the corresponding spring. Overall, mange prevalence was relatively high during both spring and fall, from spring 1979 to spring 1982 (Fig. 2), although it was lower ($\chi^2 = 7.8$, 1 df, $P < 0.01$) in spring 1981 than spring 1980. Mange prevalence declined in fall ($\chi^2 = 15.9$, 1 df, $P < 0.001$) and spring ($\chi^2 = 6.9$, 1 df, $P < 0.01$) between 1981–82 and 1982–83 (Fig. 2). Hence, we regard spring 1979–spring 1982 as the stationary phase of peak prevalence during the epizootic because of sharply lower prevalences in the preceding and following years (Fig. 2).

We consider fall 1982 as the beginning of the decline phase of the epizootic. Although the trend in mange prevalence was up from 1982–83 to 1983–84 (Fig. 2), it did not differ between years in either fall ($\chi^2 = 3.7$, 1 df, $P = 0.06$) or spring ($\chi^2 = 2.4$, 1 df, $P = 0.13$). Prevalence declined in subsequent years to 11% in spring 1989. Data for mange prevalence were not available from fall 1989 to fall 1990. However, none of 60 coyotes had mange in spring 1991. Moreover, in winter 1993–94 only sporadic cases (<5%) of mange appeared among coyotes from Webb County (K. S. Gruver, U.S. Dep. Agric., Denver Wildl. Res. Cen., Colo., pers. commun.) and throughout southern Texas (R. L. Sramek, U.S. Dep. Agric., Anim. Damage Control, Kingsville, Tex., pers. commun.). Thus, we assumed that the epizootic ended between fall 1989 and spring 1991.

Geographic Distribution

Reports from 40 respondents indicated that mange prevalence increased in most localities within the epizootic area during 1982–89 (Fig. 1) compared with 1980–81 (Pence et al. 1983). Annual prevalence was 10–50%, but 2 local coyote subpopulations within the epizootic area had mange prevalence reported at 70% in 1986 (S. T. Lemish, Lyford, Tex., pers. commun.) and 1987–88 (G. Serbesku, Three Rivers, Tex., pers. commun.). Within the epizootic area, the focal point of the epizootic described by Pence et al.

Table 1. Prevalence of sarcoptic mange among coyotes in 2 sites and the main study area during comparable sample periods, Webb County, Texas, 1982–85.

Sample period	Prevalence (%)		
	Site 1 ^a (n)	Site 2 ^a (n)	Main area ^a (n)
Jan–Apr 1982	13 (46)	74 (46)	60 (20)
Feb–Mar 1983	7 (27)		29 (80)
Feb–Oct 1984	11 (38)	25 (64)	30 (111)
Feb–Mar 1985	3 (36)	27 (49)	28 (67)

^a See Fig. 1.

(1983) remained distinguishable from the outlying epizootic area because mange prevalence remained higher (30–50%) there than elsewhere during 1982–85. The peripheral area where only isolated cases of mange were reported by Pence et al. (1983) also had increased prevalence during 1982–89, but it was <10% (Fig. 1). The area of the mange epizootic in southern Texas during 1982–89 encompassed approximately 60,000 km².

We noted a distinct demarcation in prevalence of mange between 2 sample sites (Sites 1 and 2) on the west side of the study area (Fig. 1), which were separated by 20 km of contiguous habitat. Coyote density (Knowlton et al. 1986), age distribution, and social composition (Windberg and Knowlton 1988) did not differ between the 2 sites in spring 1985. Mange prevalence was less on Site 1 than Site 2 in 1982 ($\chi^2 = 37.4$, 1 df, $P < 0.001$), 1984 ($\chi^2 = 3.2$, 1 df, $P = 0.08$), and 1985 ($\chi^2 = 8.5$, 1 df, $P < 0.01$) (Table 1). Prevalence also was less on Site 1 than on the main study area during 1982–85 ($\chi^2 = 17.6$ – 5.1 , 1 df, $P < 0.001$ – 0.02) (Table 1). Interview results indicated that mange prevalence was relatively low in the coyote population north of the 2 sites (Fig. 1).

Mange Severity

There were no differences in mange severity (i.e., distribution of coyotes among mange classes) between yearling (1–2 yr) and adult (>2 yr) coyotes ($\chi^2 = 0.4$ – 5.8 , 3 df, $P \geq 0.13$). Therefore, data were combined and designated as the adult (>1 yr) age class.

Sex.—Mange severity was greater among adult male than adult female coyotes in fall ($\chi^2 = 11.5$, 3 df, $P < 0.01$) and spring ($\chi^2 = 8.5$, 3 df, $P = 0.04$) during the stationary phase of the epizootic, but not during the decline phase ($\chi^2 = 0.7$ – 1.9 , 3 df, $P = 0.67$ – 0.87) (Table 2). Mange severity in juveniles was greater among males

Table 2. Age- and sex-specific prevalence of mange severity classes of coyotes in fall and spring during the stationary and decline phases of sarcoptic mange epizootic, Webb County, Texas, 1979–87.

Phase of epizootic	Age and sex	Prevalence (%)									
		Mange class ^a (fall) ^b					Mange class ^a (spring) ^c				
		n	0	I	II	III	n	0	I	II	III
Stationary	Ad M	55	42	9	33	16	84	28	12	29	31
	Ad F	55	73	7	15	5	76	50	12	17	21
	Juv M	28	82	4	7	7	42	33	19	36	12
	Juv F	27	74	4	18	4	60	52	18	20	10
Decline	Ad M	102	75	3	17	5	93	69	6	22	3
	Ad F	104	79	3	15	3	99	73	4	17	6
	Juv M	48	88	2	6	4	31	61	0	36	3
	Juv F	53	79	6	13	2	44	82	5	9	5

^a 0 = uninfected, I = initial (<5%) infection, II = intermediate (5–50%) infection, III = severe (>50%) infection.

^b Included 1979–81 during stationary phase, 1982–87 during decline phase.

^c Included 1979–82 during stationary phase, 1983–86 during decline phase.

than females in spring of the decline phase ($\chi^2 = 8.9$, 3 df, $P = 0.03$). There were no differences between sexes of adults or juveniles among the 3 classes of mange severity ($\chi^2 = 0.3$ – 5.0 , 2 df, $P = 0.09$ – 0.86) (Table 2).

Age.—A greater ($\chi^2 = 4.8$, 1 df, $P = 0.03$) percentage of adult (58%) than juvenile (18%) male coyotes were infected in fall of the stationary phase (Table 2). There were no other age-related differences in overall prevalence, or differences across mange severity classes, among same-sex comparisons in fall or spring during either the stationary or decline phases ($\chi^2 = 0.5$ – 5.8 , 1–3 df, $P = 0.08$ – 0.78).

Season.—During the stationary phase of the epizootic, mange severity increased from fall to spring in adult female ($\chi^2 = 8.9$, 3 df, $P = 0.03$) and in juvenile male ($\chi^2 = 16.7$, 3 df, $P < 0.001$) coyotes (Table 2), but did not increase overwinter in adult males ($\chi^2 = 5.0$, 3 df, $P = 0.19$) or juvenile females ($\chi^2 = 5.4$, 3 df, $P = 0.16$). There were no overwinter changes ($\chi^2 = 1.3$ – 2.5 , 2 df, $P = 0.30$ – 0.53) in the percentage of coyotes in the 3 mange classes for any sex-age group during the stationary phase; however, the percentages

of adult males ($\chi^2 = 3.8$, 1 df, $P = 0.05$) and females ($\chi^2 = 6.3$, 1 df, $P = 0.01$) with Class III mange increased overwinter during this phase. The only seasonal difference in mange severity during the decline phase was an increase ($\chi^2 = 11.5$, 3 df, $P < 0.01$) from fall to spring in juvenile males.

Phase of Epizootic.—In the stationary, but not decline, phase of the epizootic, mange severity was greater ($\chi^2 = 10.4$ – 37.4 , 3 df, $P \leq 0.02$) in spring than fall among all coyote sex-age groups (Table 2). Adult males were the only sex-age cohort with greater prevalence ($\chi^2 = 16.4$ – 28.6 , 1 df, $P < 0.001$) during the stationary (fall and spring) than the decline phase. Also, there was greater prevalence ($\chi^2 = 10.0$, 2 df, $P < 0.01$) of Class III mange in adult male coyotes during the stationary than decline phase (Table 2). A similar trend may have occurred ($\chi^2 = 5.3$, 1 df, $P = 0.07$) in adult females.

Recovery from Mange

In adult coyotes, only 1% ($n = 270$) had Class IV mange (indicative of recovery from infec-

Table 3. Reproductive variables of adult and yearling coyotes in relation to mange severity classes, Webb County, Texas, 1979–86.

Reproductive variables	Adults (≥ 3 yr)			Yearlings (2 yr)		
	0 ^a (n)	I–II ^a (n)	III ^a (n)	0 ^a (n)	I–II ^a (n)	III ^a (n)
% with ova	95 (61)	90 (31)	70 (10)	67 (48)	64 (11)	50 (12)
% with viable fetuses	69 (61)	48 (31)	30 (10)	33 (48)	27 (11)	9 (12)
% with resorption ^b	18 (51)	40 (25)	40 (5)			
\bar{x} no. ova	6.3 (58)	5.5 (28)	6.8 (6)	4.5 (31)	4.6 (7)	4.2 (6)
\bar{x} no. viable fetuses	6.3 (42)	5.6 (15)	7.0 (3)	4.4 (16)	4.7 (3)	

^a 0 = uninfected, I–II = initial (<5%) and intermediate (5–50%) infections, III = severe (>50%) infection.

^b Refers to resorption of all fetuses.

Table 4. Age-specific frequency (%) of indices of intraperitoneal fat (IPF) for mange severity classes of coyotes (sexes combined) in fall and spring, Webb County, Texas, 1979–86.

Season	Mange class ^a	Juvenile					Yearling					Adult				
		n	IPF index ^b (%)				n	IPF index ^b (%)				n	IPF index ^b (%)			
			0	1	2	3		0	1	2	3		0	1	2	3
Fall	0	126	28	48	21	4	63	8	49	29	14	139	6	34	40	20
	II	18	67	33	0	0	11	18	36	36	9	43	16	35	35	14
	III	5	80	20	0	0	4	0	100	0	0	15	73	27	0	0
Spring	0	81	25	38	28	9	58	31	43	14	12	82	13	56	21	10
	II	41	24	46	17	12	11	45	45	9	0	40	20	43	25	13
	III	10	70	30	0	0	9	100	0	0	0	26	81	15	0	4

^a 0 = uninfected, II = intermediate (5–50%) infection, III = severe (>50%) infection.

^b Rating of relative quantity of IPF using scale of zero (none) to 3 (abundant) (Windberg et al. 1991).

tion) during the stationary phase of the epizootic. Also, 1% (*n* = 398) had Class IV mange during the decline phase. No juveniles (*n* = 333) had Class IV mange.

Effects on Reproduction

With increasing severity of mange, there were fewer adult female coyotes with ova ($\chi^2 = 6.8$, 2 df, *P* = 0.04) and viable fetuses ($\chi^2 = 7.4$, 2 df, *P* = 0.03) (Table 3). This relationship was attributed mainly to females with Class III mange because a lower percentage had ova ($\chi^2 = 7.0$, 1 df, *P* < 0.01) and viable fetuses ($\chi^2 = 5.6$, 1 df, *P* = 0.02) than did uninfected females. Adult females with Classes I–II mange had greater ($\chi^2 = 4.5$, 1 df, *P* = 0.04) resorption of all their fetuses than did uninfected females (Table 3); equal resorption (40%) among Class III females was not significant ($\chi^2 = 1.4$, 1 df, *P* = 0.24), possibly due to the small sample size (*n* = 5). Although yearlings and adults had similar numerical trends associated with mange severity (Table 3), there were no differences for percent yearlings with ova ($\chi^2 = 1.2$, 2 df, *P* = 0.57) or with viable fetuses ($\chi^2 = 3.0$, 2 df, *P* = 0.23). Mean numbers of ova and viable fetuses per female did not differ across mange severity classes in adults or yearlings (*F* = 0.1–2.0; 2, 17–19 df; *P* > 0.10).

Mange and Body Condition

Intraperitoneal fat indices did not differ between uninfected adult coyotes and those with Class II mange in fall ($\chi^2 = 4.5$, 3 df, *P* = 0.22) or spring ($\chi^2 = 2.1$, 3 df, *P* = 0.56) (Table 4). During each season, a greater percentage of adults with Class III mange had less IPF than did uninfected adults ($\chi^2 = 43.5–55.8$, 3 df, *P* < 0.001) and those with Class II ($\chi^2 = 19.2–$

24.7, 3 df, *P* < 0.001) mange. The frequency of IPF indices was similar ($\chi^2 = 1.7$, 3 df, *P* = 0.65) between uninfected and Class II yearlings in fall (Table 4), whereas juveniles with Class II mange had less ($\chi^2 = 12.4$, 3 df, *P* < 0.01) IPF than uninfected individuals. The numbers of yearlings and juveniles with Class III mange in fall were insufficient for analysis (Table 4). There were no differences in IPF indices between uninfected and Class II hosts ($\chi^2 = 2.1–2.2$, 3 df, *P* = 0.54–0.56), but juvenile ($\chi^2 = 10.0$, 3 df, *P* = 0.03) and yearling ($\chi^2 = 15.4$, 3 df, *P* < 0.01) coyotes with Class III mange had less IPF than did uninfected individuals. Thus, relationships between mange severity and IPF among juveniles and yearlings in spring were similar to adults.

Mange in Individual Coyotes

During 1979–80 (stationary phase), 3 of 8 radio-transmitted adult coyotes progressed (time of marking to retrieval) from Class II to Class III mange in 7, 8, and 11 months, respectively, but 2 other adults with Class II mange had no change in 2 months. During 1979–80, mange infection in 2 juveniles progressed from Class II to Class III in 3 and 4 months, respectively. However, during 1984–85 (decline phase), severity in 2 radio-transmitted adult coyotes with Class II infections was unchanged after 8 and 12 months. Two additional adults with Class II mange had recovered from infection 12 and 16 months later; 1 was classified as Class IV and the other had no evidence of mange. One adult coyote with Class III mange was unchanged 8 months later. During 1984–85, 1 juvenile with Class I mange progressed to Class II in 4 months, but another juvenile with Class I mange had no evidence of mange 3 months later.

DISCUSSION

Pattern of Mange Prevalence

The sarcoptic mange epizootic among coyotes on our study area in southern Texas transpired over approximately 14 years. We identified initial (3–4 yr), stationary (3 yr), and decline (7–8 yr) phases of the epizootic according to the pattern of prevalence in the coyote population.

We suspect that estimates of mange prevalence for the coyote population were biased high as an artifact of the sampling procedures. Sampling populations by capturing coyotes on relatively small areas resulted in overrepresentation of transient (nonterritorial) individuals (Windberg and Knowlton 1988, 1990). Among 8 mange-infected coyotes of known territorial status (Windberg, unpubl. data), transients were disproportionately high (6 of 8) compared with the estimate of 34% for the population in 1984–85 (Windberg and Knowlton 1988). Further, we speculate that some coyotes in poor condition because of chronic mange may have been disproportionately attracted to fetid lures used as attractants for capture while seeking food (i.e., carrion).

Some variation in seasonal prevalence of mange in our samples probably was related to different levels of susceptibility and transmission in local subpopulations, as reported for red foxes (*Vulpes vulpes*) in Sweden (Lindström and Mörner 1985, Lindström 1992). A decrease in mange prevalence in spring 1981 during the stationary phase of the epizootic may have been attributable to a lower proportion of juveniles in the population that year (Windberg, unpubl. data) because overwinter increases in mange were 1.5–2.0 times greater in juveniles than adults.

Geographic Extent of the Epizootic

Pence et al. (1983) reported that the mange epizootic began expanding from the focal area (18,000 km²) 5 years after its onset and doubled in area within the following year. During the subsequent 4-year period, mange prevalence remained high in the focal area and increased in the peripheral area. The epizootic also expanded northward to include an area that had only isolated cases of mange previously (Pence et al. 1983), but prevalence there remained low (<10%). The mange epizootic extended south into Mexico (Pence et al. 1983).

Although mange prevalence increased throughout the peripheral area of the epizootic

during 1982–89, the epizootic remained confined to the region of highest coyote densities (Pence et al. 1983). Presumably, coyote densities that were below the threshold required for maintaining the transmission potential halted progression of the mange epizootic and defined its boundaries. However, we documented a distinct demarcation in mange prevalence between 2 sample sites at the western boundary of the epizootic area where coyote densities and other host factors were similar, which suggested a subpopulation that was less susceptible to mange. This could be related to various unknown immunologic, genetic, behavioral, or other factors.

Effect of Mange on Hosts

The best defined relationship across host factors was greater mange prevalence in adult male coyotes during the stationary phase of the epizootic. Todd et al. (1981) noted a greater prevalence of mange among adult males in Alberta. Pence et al. (1983) suggested that adult males may have greater contact with other coyotes, thus affording greater potential for transmission.

In southern Texas, mange prevalence seldom decreased in the coyote population from fall to spring during annual periods. Hence, there apparently was no differential loss of mange-infected coyotes from the population overwinter, as suggested for populations with mange in northern latitudes (Gier et al. 1978, Todd et al. 1981). Also, the proportion of adults with Class III mange increased from fall to spring during the stationary phase of the epizootic, indicating overwinter survival of some individuals that had infections the preceding year. Pence et al. (1983) described mange in coyotes in southern Texas as a chronic debilitating disease with some decline in physiological condition as infection progressed. Our study substantiated reduced body condition (less fat) among adults and juveniles with advanced (Class III) mange. Relatively less fat among juveniles than adults with Class II mange in fall suggested that their condition was affected at an earlier stage of infection.

Our few observations of radio-transmitted coyotes suggested that mange progressed more rapidly in juveniles than adults. Mortality rate of radio-transmitted juveniles with mange also was greater than that of infected adults (Pence et al. 1983). The occurrence of coyotes with Class IV mange indicated that some individuals recovered from infection, which was supported by 3 radio-transmitted coyotes that recovered

from mange during our study. Although only 1% of coyotes examined appeared to be recovering from mange, the proportion of the population that had recovered was unknown. Two radio-transmitted coyotes that recovered from mange had no lesions upon reexamination. Complete recovery of infected coyotes can occur within a few weeks after treatment with an acaricide (Stone et al. 1972).

Mange Epizootic and Coyote Demography

Our analysis of additional data on coyote natality in relation to severity of mange revealed greater effects than reported by Pence et al. (1983). In adult females with severe mange (Class III), reduced frequency of ovulation combined with greater resorption of fetuses resulted in a lower proportion that produced viable fetuses. Apparently, natality of some females with Class II mange also was adversely affected by greater resorption of fetuses. In southern Texas, reproductive females are primarily dominant territorial adults (Andelt 1985, Knowlton et al. 1986). We speculate that females with severe mange were relegated to transient (nonterritorial) status in the population and hence failed to reproduce.

Pence et al. (1983) showed a greater mortality rate among infected than uninfected coyotes during the stationary phase of the epizootic. However, mange apparently was not a direct cause of death and the greater mortality associated with mange was compensatory with other mortality factors operating in this population. Annual estimates of adult survival rates varied little (0.64–0.73) during 1976–86 (Windberg, unpubl. data), indicating that mange caused no additive mortality among adults during the epizootic. Decreased coyote abundance in 1980–81 during the stationary phase of the mange epizootic was attributed to high juvenile losses associated with introduction of canine parvovirus into a naive population (Pence et al. 1983, Thomas et al. 1984). Thus, the effects of mange on natality and survival resulted in no effect at the population level.

Dynamics of the Mange Epizootic

Following an epizootic of approximately 10 years during the 1930s (Pence et al. 1983), sarcoptic mange remained enzootic at low prevalence in coyotes in southern Texas until 1975. Recurring mange epizootics in this and other canid populations may result from mutation of

a virulent strain of the mite (Pence et al. 1983). Alternatively, it has been suggested that the onset of a sarcoptic mange epizootic may be associated with increased coyote and reduced prey abundances (Gier et al. 1978, Todd et al. 1981). That hypothesis is not supported by our study because the mange epizootic in southern Texas began during a period of stable high coyote abundance and increasing prey abundance (Brown 1977; Windberg, unpubl. data). Further, it had a focal origin with outward geographic radiation, which supports our hypothesis that it was induced by either mutation of an existing strain or introduction of a new strain of *S. scabiei*.

Although some infected coyotes recovered from mange throughout the epizootic, host resistance appeared greater during the decline than stationary phase because infections progressed more slowly in 5 radio-transmitted adults, and fewer adults advanced to Class III mange. Even during the stationary phase of the epizootic, approximately 50% of the coyotes captured were not infected. This implied a lack of exposure and/or resistance to the infection. Experimental transmission studies (Samuel 1981) illustrated that some individual hosts have natural resistance to infection with particular strains of *S. scabiei*. We found 1 local subpopulation of coyotes that appeared to have differential resistance to the strain(s) of *S. scabiei* causing mange within the epizootic area.

Temporally, the geographic expansion of the mange epizootic in southern Texas probably was related to the dispersal rate of infected coyotes; we attributed its decline to development of resistance in the host population. However, we view the social organization in this coyote population (Andelt 1985, Windberg and Knowlton 1988) as a factor in the expansion and subsequent decline of the epizootic. Long-distance dispersal (20–80 km) of adults and juveniles (Windberg et al. 1985) probably was the mechanism for geographic dispersion of mange. The pattern of dispersion documented during a mange epizootic in red foxes in Sweden involved the occurrence of scattered local populations presumably infected by dispersing individuals, ultimately spreading to intervening populations (Lindström and Mörner 1985, Lindström 1992). Dispersing coyotes are transients (nonterritorial) in the coyote social organization. There was a relatively high proportion of transients (34% in 1984–85) on our study area (Windberg and

Knowlton 1988), which potentially enhanced transmission of mange because transients have larger ranges and greater potential for intra-specific contact.

In a coyote population located outside the northeastern boundary of the mange epizootic area in southern Texas, coyote density was lower than on our area (0.9 vs. 2.0/km²) and only 13% were transients (Andelt 1985). Hence, coyote populations in fragmented habitat, due to agricultural cultivation (Gould 1975) along the northern, eastern, and southern boundaries of the mange epizootic area, probably were characterized by lower densities with fewer transients, which reduced mange prevalence. Further, spacing of coyote social groups (Andelt 1985, Windberg and Knowlton 1988) probably restricted the physical contact necessary for transmission of mange among territorial individuals and potentially slowed dispersion and subsequent decline of the mange epizootic in southern Texas.

MANAGEMENT IMPLICATIONS

We hypothesize that the decline of the mange epizootic among coyotes in southern Texas was an extended process of selection for mange-resistant individuals, mediated by coyote social organization. Susceptible territorial coyotes had low prevalence and transmission of mange because their activities were confined within territories (Windberg and Knowlton 1988), but infected individuals had decreased survival (Pence et al. 1983). Dominant territorial females with mange possibly reproduced, but their offspring were infected and perished. Mange-resistant territorial coyotes had high rates of survival and recruitment. Transient coyotes had no recruitment (Knowlton et al. 1986) and low survival (Gese et al. 1989); susceptible individuals contracted mange and died, while mange-resistant transients were available to reoccupy vacant territories after mortality of social group members. Thus, because susceptible territorial and transient coyotes were replaced by mange-resistant individuals, coyote social organization extended the process of selection for resistant individuals in the population and prolonged the decline phase of the epizootic.

To the casual observer, epizootic diseases with a high visual impact such as mange, which emphasizes morbidity or those that cause episodes of mass mortality, may appear devastating to a species. Our study emphasizes that more critical

examination of host-disease ecological relationships may reveal an insignificant effect at the host population level. We believe that more long-term studies of other major epizootic diseases in important wildlife species are needed to understand their effect on host populations. This should be essential information prior to implementing management plans designed to prevent, control, and/or eradicate specific diseases in natural populations.

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