POPULATION ATTRIBUTES FOR THE BLACK-FOOTED FERRET (*MUSTELA NIGRIPES*) AT MEETEETSE, WYOMING, 1981–1985

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ABSTRACT.—Numbers of adults and juveniles in the single known free-ranging population of the endangered black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming were estimated annually in July from spotlighting as 88 (1983), 129 (1984), and 58 (1985). Population sizes in September, determined from mark-recapture studies, were 128 ± 25 (1984) and 31 ± 8 (1985). Lower population estimates in 1985 reflected, at least in part, an ongoing epizootic of canine distemper in ferrets that decimated the population through November 1985, reducing it to ca. 6 individuals. From 1982 to 1985, adult sex ratio was 1 male : 2.2 females; juvenile sex ratio (1 male : 0.80 females) did not differ significantly from 1:1. The ratio of young to adults averaged 1.95:1 from 1982 to 1984 and 1.2:1 in 1985. At least 224 young were produced in 68 litters from 1982–1985, with a mean litter size at emergence of young of 3.3. Juvenile ferrets reached adult weight by September. Only one female tagged as a juvenile was recaught at 1 year of age, and she reproduced. Intercolony movements were primarily by juvenile males and occurred from September to October. Adults maintained geographic fidelity between years. Disappearance (mortality and emigration) rates ranged from 53 to 86% annually and were highest for juveniles. Observed ferret mortality in the absence of disease was primarily from predation. Reduction of the population during the epizootic suggests persistence of this population in the wild is unlikely.

The black-footed ferret (*Mustela nigripes*), the North American representative of a Holarctic polecat group (subgenus *Putorius*; Youngman, 1982), seemed nearly extinct until the discovery of a population near Meeteetse, Wyoming in September 1981. Formerly ranging from Canada to Texas at the turn of the century (Fig. 1), black-footed ferret numbers and habitat declined greatly through this century (Anderson et al., 1986; Cahalane, 1954). A small population in South Dakota studied from 1964 to 1974 provided the first general life history for this nocturnal and secretive species, but the scope of these studies was limited by the few animals observed (Fortenbery, 1972; Henderson et al., 1969; Hillman, 1968). Additional knowledge of key population attributes, including population status and trend, reproduction, dispersal, survival, and mortality, is essential to develop a conservation strategy for the species.

In November 1985, canine distemper, a fatal disease to ferrets (Carpenter et al., 1976), was diagnosed in the population following discovery of sylvatic plague (*Yersinia pestis*) in the ferret prey base (S. Ubico, pers. comm.). This paper details population attributes of black-footed ferrets observed at Meeteetse from 1981 to 1985 and decline of the population in 1985.

Study Area

The study area (Park Co., Wyoming; Clark et al., 1986*a*; Fig. 1) is vegetated predominantly with junegrass (*Koeleria cristata*) and sagebrush (*Artemesia tridentata*)-junegrass prairie (Collins and Lichvar, 1986). Temperature extremes range from −43 to 40°C. Elevation ranges from 1,980 to 2,290 m.

Prairie dogs (*Cynomys* sp., Sciuridae) are colonial, semifossorial rodents that construct burrows that ferrets use and are the major food of ferrets (Campbell et al., 1987; Sheets et al., 1972).

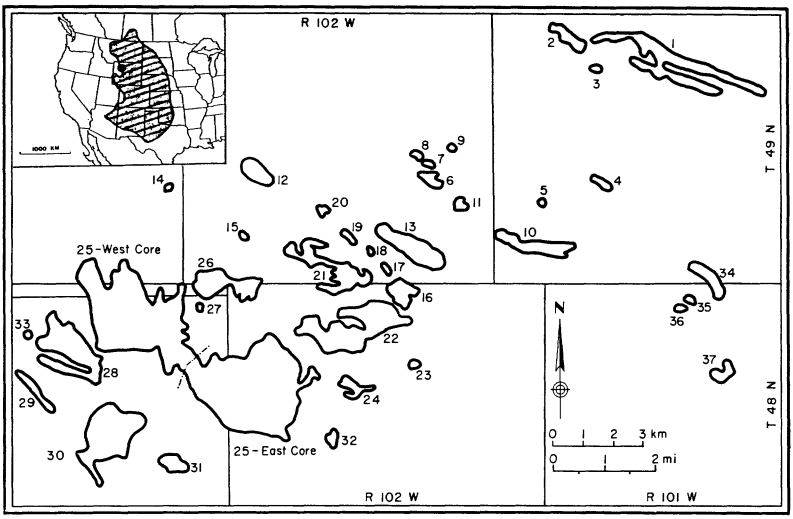

FIG. 1.—Location and distribution of 37 white-tailed prairie dog colonies within the Meeteetse black-footed ferret study site, Park Co., Wyoming, and former black-footed ferret range (inset).

Ferrets commonly move between prairie-dog colonies, but are not known to remain away from them (Biggins et al., 1985; Henderson et al., 1969; Richardson et al., 1987). Ferrets, therefore, are found within sharply defined habitat boundaries easily identified by prairie-dog mounds (Clark et al., 1984; Forrest et al., 1985*a*; Henderson et al., 1969). A total of 3,100 ha of white-tailed prairie-dog (*C. leucurus*) colonies (n = 37, range = 2.5–740 ha) was located in a 200 km^2 area (Fig. 1). Twenty-five colonies showed evidence of ferret occupancy from 1981 to 1985, with ferrets distributed at one ferret/40–60 ha of prairie-dog colony (Forrest et al., 1985*a*). No other black-footed ferrets were found in searches of 43 prairie-dog colonies (most known colonies) from 3 to 200 km from the study area. We concluded that no nearby pool of ferrets for recruitment was available.

METHODS

Snow-tracking (Clark et al., 1984; Richardson et al., 1985) provided estimates of ferret numbers on colony 25-East (Fig. 1, 24% of the total Meeteetse-prairie-dog-colony area) from December to March each year. Complete (origin to terminus) track sequences verified that each individual counted was unique. Three to 10 consecutive tracking days were used to develop an estimate because not all ferrets were active each night (Biggins et al., 1986; Richardson et al., 1987).

Spotlight surveys (Campbell et al., 1985; Clark et al., 1984) were used to count adults and young, and to observe ferret behavior. Total-population counts were produced from spotlight surveys during approximately 30 nights from early July to early August, 1983 through 1985. A total-population count for 1982 was not made; only colonies 25-East, 25-West, 1, 10, and 13 were spotlighted using efforts comparable to other years. Teams of observers were used each night for complete coverage of all colonies searched. Observers used spotlights mounted on vehicles or carried in hand. Each observer searched 100 ha or smaller nonoverlapping areas of prairie-dog colonies each night. Spotlighting effort was concentrated from 2100 to 2400 h and from 0200 to 0600 h when ferrets were expected to be most active (Biggins et al., 1986; Clark et al., 1986*b*; Hillman, 1968). Spotlighting continued in the same location for 3–5 consecutive nights because ferrets were not active every night. Effort between years was standardized by duration (spotlight nights/colony) and intensity (spotlight hours/night). Spotlight hours (and unit-nights) totalled 150 (45) in 1982, 260 (82) in 1983, 554 (93) in 1984, and 647 (78) in 1985. The cumulative count of ferrets (Fig. 2) averaged 82% of the total after 4 nights of search per unit area. The mean minimum number of nights searched per colony ranged from 4.1 to 4.8 annually. This mean exludes three peripheral colonies (1, 16, and 21) that received additional search effort because of incomplete litter counts. Mean unit-hours/night spent spotlighting each year ranged from 2.9 to 6.9. Some ferrets (four in 1983; nine in 1984) were found when the search period was extended

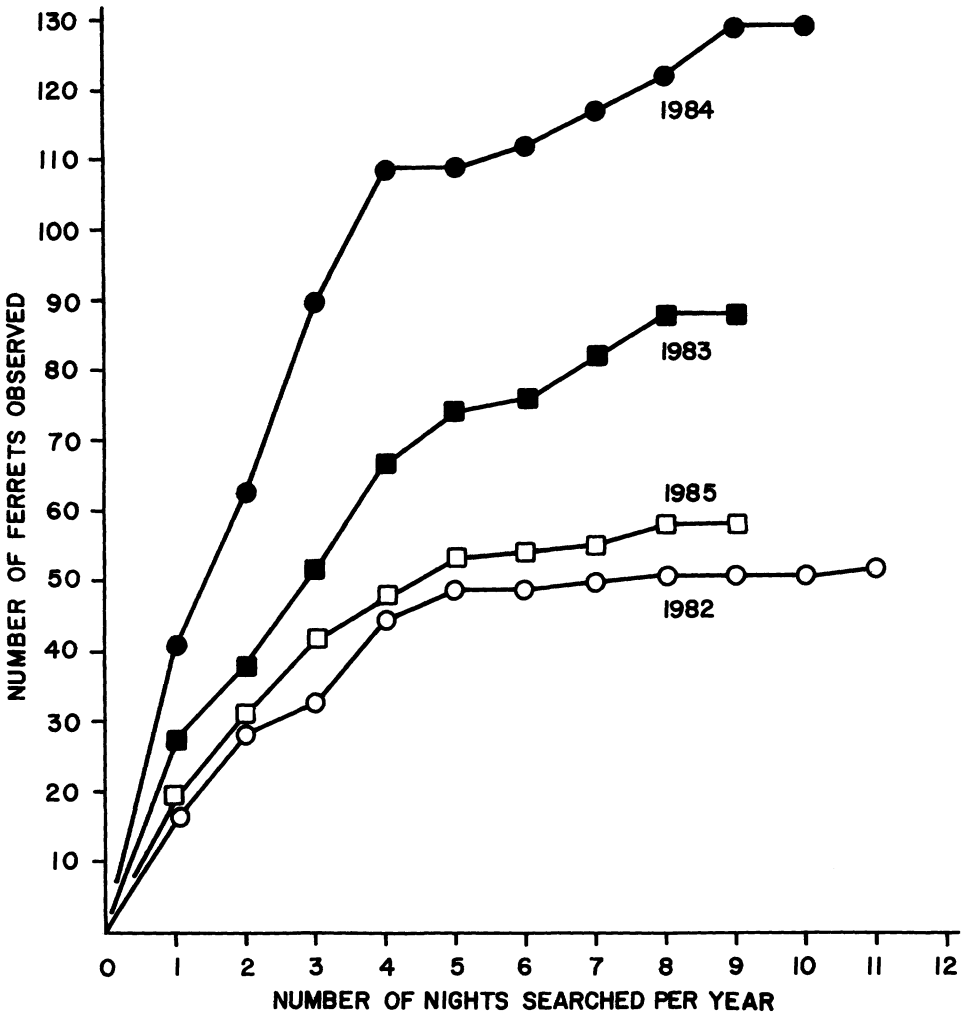

FIG. 2.—Spotlight search effort in unit-nights searched/year and number of ferrets observed in July, 1982–1985, at the Meeteetse study site, Park Co., Wyoming. Data for 1982 represent only those prairie-dog colonies spotlighted using methods similar to those used in subsequent years.

beyond the systematic-survey period. Litters (females with young) and adult males were considered unique only if they were observed in separate geographic locations within a time frame that precluded movement between their two locations. For example, litters within 100 m of each other would have to be seen nearly simultaneously, whereas litters farther apart could be seen minutes or hours apart depending on the distance separating them. Ferret litters moved infrequently during the July–August period and were readily relocated, allowing repeated counts of litter size. A minimum count of adult females was made from the number of litters observed; nonlactating females captured later suggested the total number of females was higher. Because males weigh 30% more than females (Anderson et al., 1986), sex could be estimated for some animals seen at close range; for others sex was not recorded.

Ferrets were live captured and marked to develop independent population estimates. Ear tattoos (1983–1984) and monel fingerling fish tags (1983–1985) in one or both ears (Fagerstone et al., 1985; Thorne et al., 1985) and transponders (1985) (Fagerstone and Johns, 1987) were used as marks. In 1983, ferrets were marked in three colonies (25-East, 25-West, and 22) during August and September, but no within-year mark-recapture estimate was made because the marks were primarily for telemetry purposes. In 1984 and 1985,

a sample of the population was marked in mid-September and recaptured during the 1st week in October. In 1985, two additional estimates were produced for 3–7 October and 1 November that included trapping from 11 October to 1 November.

We used a Peterson estimate with Chapman's correction for population size,

$$N = [(n_1 + 1)(n_2 + 1)/(m_2 + 1)] - 1,$$

where n_1 = number of animals initially captured and marked, n_2 = total number of animals in the recapture sample, and m_2 = number of marked animals in the recapture sample (Seber, 1982). Ninety percent confidence intervals were calculated by 1.645 ($\sqrt{v}$), where:

$$v = (n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)/(m_2 + 1)^2(m_2 + 2).$$

Individual ferrets were assumed to have equal probability of capture. Ferrets were caught in unbaited live traps (Sheets, 1972) after they were first located with spotlights. Searchers covered equal-sized units of habitat simultaneously, so that all ferrets had an equal probability of being seen if they were above ground. We assumed that rates of emigration, mortality, and intercolony movement between capture periods were the same for marked and unmarked animals. No source for ferret immigration was known, and intercolony movements did not bias the estimate because trapping was conducted over the entire area where ferrets were known to occur. Marked individuals removed from the population between mark and recapture periods in 1985 were not used to calculate the estimate, but were added to N to produce a grand total.

Trapped ferrets were assigned to juvenile or adult age classes by palpation of the sagittal crest, tooth wear, and reproductive status (Thorne et al., 1985). Sex of skulls without carcasses was determined by use of discriminant formulas for black-footed ferrets (Anderson et al., 1986).

Radiotelemetry provided data on ferret dispersal and mortality from August through December 1981–1984 (Biggins et al., 1985, 1986; Fagerstone et al., 1985). We estimated the daily survival rate using:

$$\hat{S}_i = \frac{x_i - y_i}{x_i} \qquad \text{(Heisey and Fuller, 1985),}$$

where x_i was the total number of transmitter-days and y_i was the total number of deaths in interval i. Survival rate for interval i was estimated using

$$\hat{S}_i = \hat{s}_i L_i \qquad \text{(Mayfield, 1961),}$$

where L_i is the length of interval i (in days). We accumulated 894 transmitter-days on 19 juvenile ferrets and 341 transmitter-days on seven adults. Individual radio-tagged ferrets were monitored for periods ranging from several days to several months, thus contributing unequally to the transmitter-day total.

We applied a "bracketing" approach to the data, combining animals that disappeared with known deaths to provide an upper estimate of mortality (Heisey and Fuller, 1985).

Results

Population enumeration.—Snow-tracking provided winter counts of ferrets in colony 25-East in all years. Nine ferrets (including young and adults) were counted in 1982 (March), 6 in 1983 (March), 14, 12, 10, and 10 in monthly counts for the winter of 1983–1984 (December through March), and 5 in 1985 (March). We have no evidence that ferrets left or entered the colony during any census period. Spatial distribution of ferrets appeared stable from December to March (Forrest et al., 1985*a*; Richardson et al., 1987).

Summer spotlighting accounted for 88 individuals in 1983 (60 young, 28 adults), 129 in 1984 (86 young, 43 adults), and 58 in 1985 (38 young, 20 adults; Table 1). Forty young and 21 adults were observed in the 60% of the study area surveyed in 1982. Extrapolation from the proportion of ferrets/colony comparably spotlighted in 1983 (59/88) and 1984 (69/129) gives a range of 79 to 99 ferrets for the total area in 1982.

We captured 135 individual ferrets from 1981–1985. Mark-recapture estimates of the total

TABLE 1.—*Size of the black-footed ferret population at Meeteetse, Wyoming based on spotlight counts and mark-recapture estimates.*

	1982	1983	1984	1985	
Spotlighting (July)					
Population size	†	88	129	58	
Adults	21	28	43	20	
Males	7	6	13	4	
Females	12	18	25	13	
Unknowns	2	4	5	3	
Juveniles	40	60	86	38	
Colony 25-East					
Adults	6	5	9	4	
Males	2	1	3	1	
Females	4	4	6	2	
Unknowns	0	0	0	1	
Juveniles	13	13	20	5	
				September	October
Mark-recapture (September)					
Population size (±90% C.I.)		95 (45)*	128 (25)	31 (8)	16 (4)
Adults			45	13	
Juveniles			87	16	

† No estimate by total population size.
* Back estimated from mark returns of 1983 animals in 1984.

population with 90% confidence intervals were 128 ± 25 ($n_1 = 56$, $n_2 = 51$, $m_2 = 22$) in September 1984, 31 ± 8 ($n_1 = 18$ (+2 removed), $n_2 = 10$, $m_2 = 6$) in September 1985, and 16 ± 4 ($n_1 = 7$) (+3 removed), $n_2 = 8$, $m_2 = 4$) in October 1985 (Table 1). Mark-recapture trapping was not conducted in 1983, but a population estimate was calculated from the hypergeometric model (Seber, 1982) based on the 1983 sample ($n_1 = 18$) and the four (m_2) marked animals found among the 1984 adult cohort ($n_2 = 24$) present on the colonies sampled in 1983. Although minor violations of the model assumptions occurred, including possible recruitment from adjacent nonsampled colonies and variation in mortality between sampled age cohorts (partially accounted for by the distribution of marks among adult and juvenile classes), the estimate produced, 95 ± 45, closely approximated the spotlight estimate for 1983, given the large bounds of the confidence interval.

Spotlight counts and mark-recapture estimates were nearly identical in 1984 (Table 1) and also were comparable for the largest colonies (25-East, 39 and 34; 25-West, 36 and 37; 22, 24 and 21) as were estimates calculated for age class (86 and 87 young, and 43 and 45 adults). The difference between population estimates by spotlighting and mark-recapture in 1985 was most likely a result of ferret mortality between the estimation periods.

Age and sex ratios.—A minimum of 224 young was observed above ground from 1982 to 1985. The ratio of young : adults based on spotlighting was 2.0:1 (combined years). The mark-recapture ratio was 1.9:1 in 1984, but 1.2:1 in September 1985. The adult sex ratio (males : females) for all years from spotlight data was 1:2.3 (Table 1). Sample sizes were too small to produce meaningful mark-recapture estimates of adult sex ratio, but of 42 adults caught from 1982 to 1985, 13 were males and 29 were females, a sex ratio of 1:2.2. Juvenile male ($n = 46$) : female ($n = 37$) sex ratio based on ferrets caught in August and September for all years was 1: 0.80. This ratio does not differ significantly from 1:1 ($G = 0.77$, $d.f. = 1$, $P = 0.44$), but differs significantly from the sex ratio of captured adults ($\chi^2 = 6.754$, $P < 0.01$).

Population trends.—Spotlight counts and mark-recapture estimates increased (by 32 and 8%, respectively) from 1983 to 1984 and declined (by 55 and 76%) from 1984 to 1985 (Table 1). Spotlight counts for colony 25-East were identical from 1982 to 1983 and increased 34% from 1983 to 1984. However, spotlight counts from 1984 to 1985 declined 69% on colony 25-East and 89% on 25-West. These were substantially larger declines than observed on other colonies.

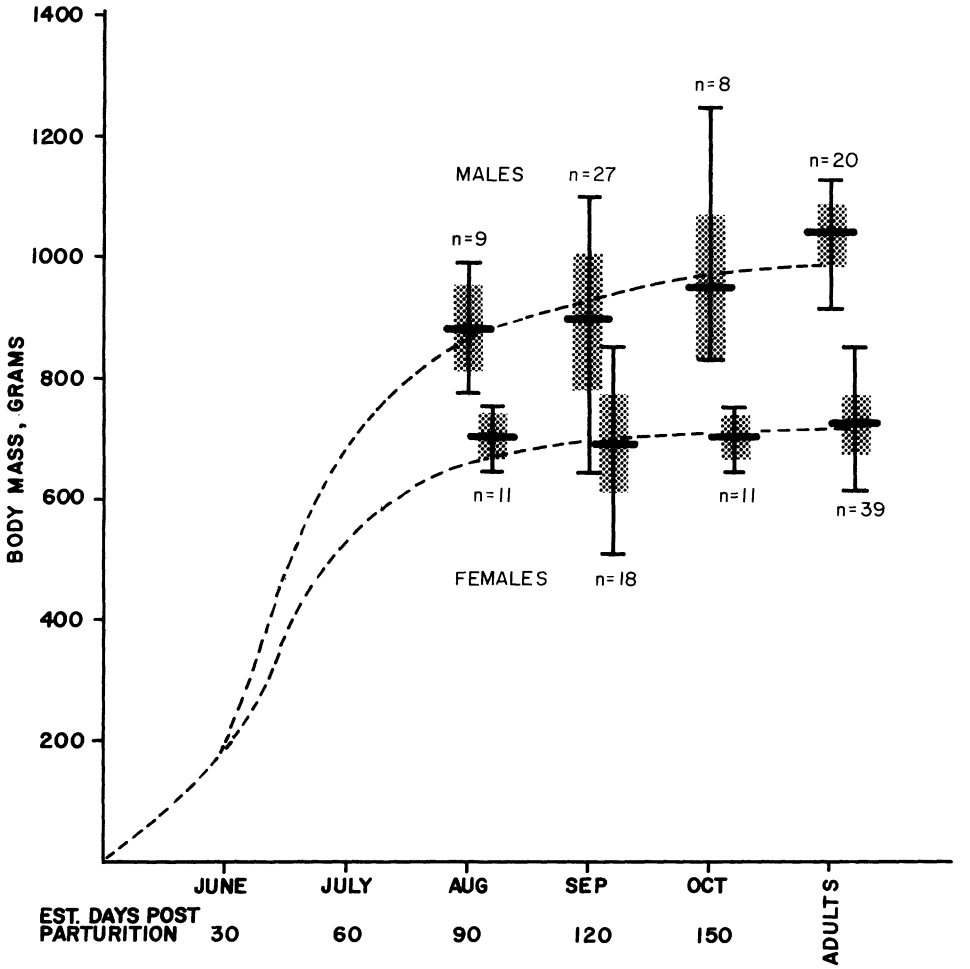

FIG. 3.—Means (horizontal lines), *SD* (bars), and ranges (capped vertical lines) of weights of juvenile male and female black-footed ferrets by month (August–October) compared with those of adult males and females. A hypothetical growth curve is superimposed (after Stromberg et al., 1983).

In 1985, unlike previous years when ferret numbers remained constant between the spotlight period and the trapping period, geographically localized disappearance occurred from 27 July to 9 September. Sixteen ferrets (three litters, including mothers, and three other adults) located within colonies 25-East and 25-West in July could not be relocated later. By September, only one ferret (a juvenile male) could be found on 25-East. In contrast, September mark-recapture estimates on colony 22 (N = 15 ± 4) were similar to numbers (n = 20) observed during spotlighting in July. The overall population estimate for September was 47% lower than the spotlight count in July. Most of this decline (60%) was observed on colonies 25-East, 25-West, and 19.

Two male ferrets were removed from the population on 13 September 1985 and one male and two females were removed from 5 to 7 October 1985. A third female was removed on 12 October. On 21 October, two of these animals (a male taken on 7 October and the female taken on 12 October) were diagnosed as having canine distemper contracted in the wild. Ferrets caught during trapping from 10 to 12 October and a rescue effort to remove additional animals from the wild from 26 October to 2 November provided a second opportunity for mark-recapture estimation. The estimate derived from this effort (16 ± 4; 4–7 October) was 48% lower than the

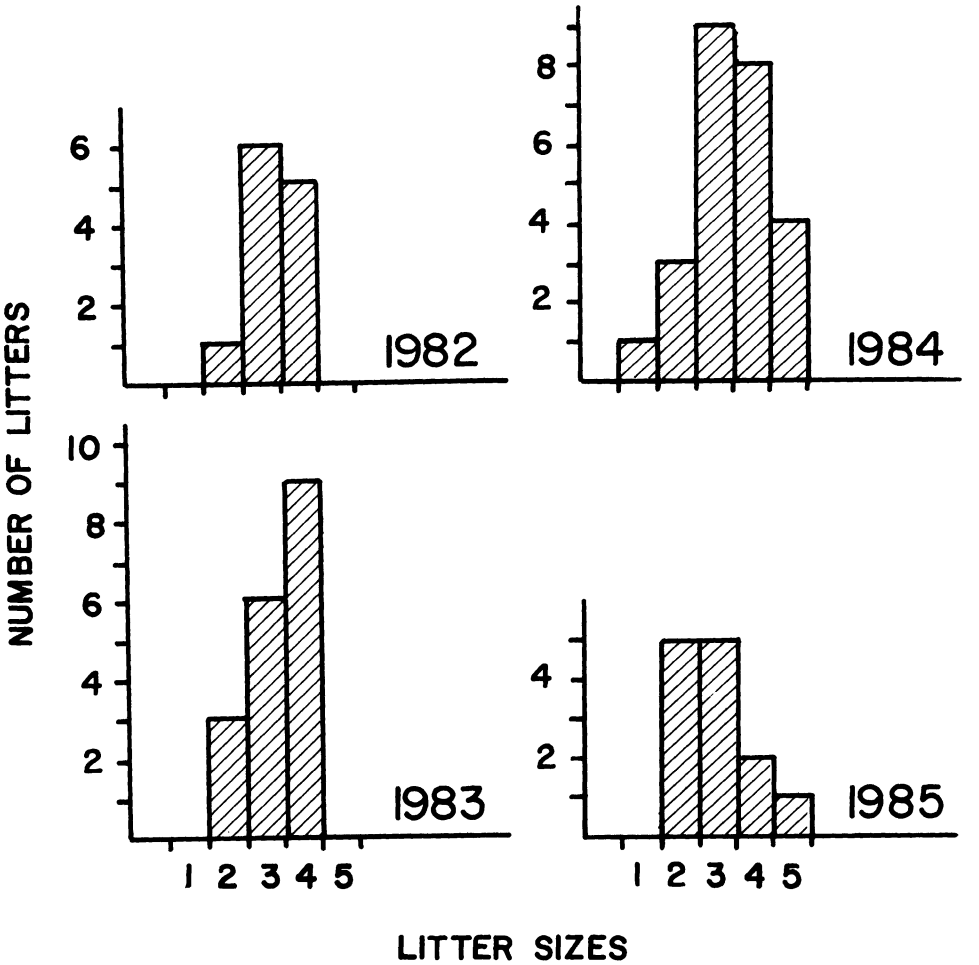

FIG. 4.—Distribution of litter size for black-footed ferrets at Meeteetse, Wyoming, 1982–1985 (n = 68).

September estimate. Subtracting the 10 ferrets removed following the 4–7 October estimate, and without considering other losses after 7 October, the number of ferrets remaining in the wild as of 2 November 1985 was ca. 6.

Reproduction.—Mating in captive black-footed ferrets occurs from late February to April (Carpenter and Hillman, 1979). Mating, pregnancy, and parturition were not detected in the field. However, changes in space use by Meeteetse ferrets during February and March suggested breeding at that time (Richardson et al., 1987), and experience during the spring of 1986 with two captive ferrets suggested breeding behavior in February (DonCarlos et al., in press). The known gestation period for captive ferrets was 42 and 45 days (Carpenter and Hillman, 1979), meaning birth occurred in spring. Young were observed above ground by the 1st week of July in all years. One female was seen carrying four young with unopened eyes on 26 June (Clark et al., 1986*b*). Juveniles attained adult weight by late September (Fig. 3).

Sixty-eight litters were observed from 1982 to 1985. Average ± *SD* litter sizes were 3.3 ± 0.65 (n = 12) in 1982, 3.3 ± 0.77 (n = 18) in 1983, 3.4 ± 1.04 (n = 25) in 1984, and 2.9 ± 0.95 (n = 13) in 1985 (Fig. 4), with an overall mean of 3.3 ± 0.89 (n = 68). No statistically significant differences in litter size were observed among years (F = 0.98, $d.f.$ = 3, 64, P = 0.44).

Only one female tagged as a juvenile was recaught at 1 year, and she reproduced. Litter size

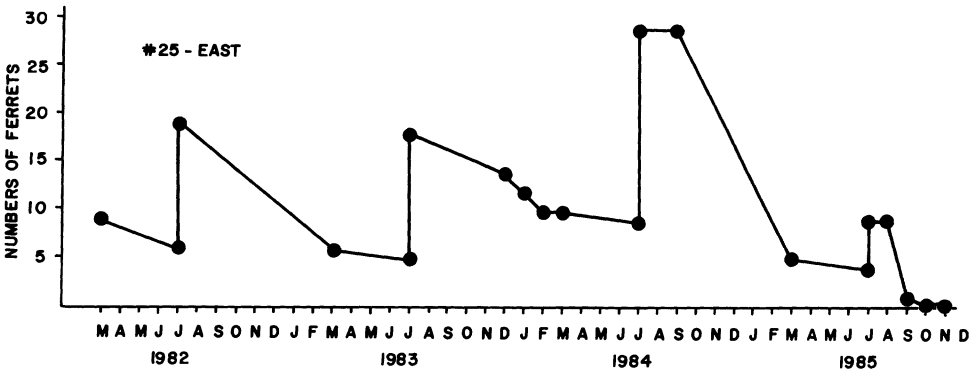

FIG. 5.—Changes in black-footed ferret numbers on colony 25-East from March 1982 to November 1985 using all enumeration methods. Changes include all immigration, emigration, and mortality with natality shown by the vertical lines.

was not significantly different between years in six females followed for 2 consecutive years ($P > 0.10$, $U = 25.5$, Mann Whitney U). Two adult females trapped in 1984 were not lactating, indicating they had not reared litters. One of these had reared a litter of four in 1983.

Dispersal.—Sibling juveniles remained together until late August, when litters fragmented. We observed two types of movement following litter breakup: 1) long (1–7 km) movements to adjacent prairie-dog colonies, usually with no return and 2) short movements (<300 m) from the natal area, with young remaining within or near their mother's activity area. Long-dispersal movements were observed for 9 male (6 with radios) and 3 female (2 with radios) juveniles between 4 September and 1 November (1981–1985). During this same period, four radio-tagged juvenile females exhibited only short movements and remained on their natal prairie-dog colonies until the radios were removed (mid-December for two of the animals). One juvenile female remained on her mother's range and reared a litter there the following year in her mother's absence. No radio-tagged juvenile male remained in its natal colony.

Adult ferrets exhibited geographic fidelity. Eight of 10 marked adults (two males, six females) caught 1 year later were ≤200 m from their original capture locations. Two adult females made intercolony movements. One radio-tagged female left the activity area she used from July through September on colony 25-West and moved 2.5 km to colony 26; she disappeared shortly afterward. The second female reared a litter on colony 22 in 1983, but moved 1.8 km to colony 25-East in 1984 and did not rear a litter.

Disappearance and survival.—Limited cohort data prevented us from developing a life table for ferrets. A male known to be at least 2 years old in 1983 and caught again in 1984 was the longest lived animal we observed. One of nine juveniles and three of nine adults marked in 1983 were found in 1984, but no ferret marked in 1983 was found in 1985. None of 49 marked young from 1984 was recaptured in 1985. Of 20 adults observed during the spotlight survey in 1985, 10 were captured in September or October and three others were observed closely enough to read marks or verify they were unmarked. Seven were unmarked (three males and four females) and six were marked adult females. All six marked females reared litters in 1984. Seven of 24 marked adult females (29%) were reobserved the year after marking, compared with two of 10 adult males (20%).

Interyear recapture rates of marked adults (37% from 1983 to 1984 and 20% from 1984 to 1985) and marked juveniles (11% from 1983 to 1984 and none from 1984 to 1985) differed significantly between adults and juveniles (combined years, $\chi^2 = 11.967$, $P < 0.001$). Recovery rates of adults were 20% higher than for juveniles.

Annual fluctuation in ferret numbers on colony 25-East was evident from combined results of all estimates (Fig. 5). Annual disappearance rates of all ferrets from this colony were 69% (1982–1983), 53% (1983–1984), and 86% (1984–1985). Disappearance between 1983 and 1984

(the most complete data set) appeared logarithmic ($y = -0.0009 \log x + 1.2446$; $r = -0.947$), with highest declines observed in autumn and winter, and few losses between March and July in all years.

We observed three mortalities (all from predation) among 26 radio-tagged ferrets in 1,235 transmitter-days of monitoring. The daily survival rate calculated from these losses was 0.998, or a 0.689 overall survival rate for the period August to December. Interpretation of the rates for colony 25-East are affected by the demonstrated difference in survival rates between age classes, and suspected difference between sexes. Further statistical evaluation of these data sets (e.g., calculation of variances and hypothesis testing) seemed inappropriate because basic assumptions (Heisey and Fuller, 1985; White, 1983) were violated and sample sizes were small. However, the annual loss rate of radio-tagged ferrets (59%) projected from the August–December data compared favorably with the annual loss rates of 53–86% for ferrets on colony 25-East. Sex and age composition of the radio-tagged and samples of ferrets from colony 25-East seemed to approximate the composition of the ferret population in general, further enhancing comparability between data sets.

In addition to the three known mortalities of radio-tagged ferrets, radio contact was lost from three other ferrets (one adult and two juveniles) under circumstances indicating possible mortality. By bracketing the upper and lower bounds of all known and potential mortality, an annual rate for the total population between 83% and 59% was estimated. Using this same approach, upper and lower estimates of juvenile ferret mortality alone were 81% and 56%.

Causes of mortality.—Remains of 30 ferrets were recovered from 1981 to 1985, and six other animals died in captivity from 21 October 1985 to 5 January 1986. Of 17 remains collected in the field for which sex could be determined, 11 (64%) were male; eight of 12 (67%) animals of known age were less than 1 year old.

Nondisease-related sources of mortality in the wild were known or inferred in 12 cases and included four that were human-related and eight from predators. Canine distemper undoubtedly killed many more ferrets in 1985.

An animal killed by a ranch dog led to discovery of the population in 1981. Other human-related mortalities were three ferrets found dead with massive trauma. These may have been struck by vehicles but other evidence suggested they were killed in traps and discarded.

Predation was recorded three times from radio-telemetry and five times from discovery of remains or carcasses. Predation was the only mortality source identified by telemetry. Raptors were responsible for five deaths. One instance each of great-horned-owl (*Bubo virginianus*) and golden-eagle (*Aquila chryseatos*) predation were identified by telemetry, and one complete head that closely resembled the radio-tagged ferret killed by an eagle was found. Eartags and mandibles of one ferret were found in an owl bolus (V. Semonsen, pers. comm.) and one skull was found at an owl roost. A coyote (*Canis latrans*) killed a third radio-tagged ferret. In two cases, the predator could not be determined. On six occasions ferrets were pursued by raptors (prairie falcons [*Falco mexicanus*], ferruginous hawks [*Buteo regalis*], great-horned owls, and golden eagles); ferrets eluded possible capture by diving into nearby burrows. On four occasions, mammalian predators (badgers [*Taxidea taxus*] and coyotes) sniffed and dug at burrows occupied by ferrets.

Canine distemper devastated the population in 1985. Canine distemper occurs in mink (*M. vison*), raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), badgers, and coyotes in Wyoming (Williams, 1982), all of which occur in varying densities throughout the study area. Sylvatic plague, identified in prairie dogs at Meeteetse in June 1985, may have played some role by reducing prairie dogs locally, but no ferrets were known to have died either directly or indirectly of plague. During the period when, in retrospect, the distemper epizootic was assumed to have been active, ferrets disappeared before the period of normal dispersal both from areas affected and unaffected by plague and from at least two disjunct locations. One ferret with distemper caught on 7 October came from an area where a litter of ferrets 200 m distant (the nearest adjacent ferrets) had disappeared within the previous 2 weeks. These observations suggest the importance of both interspecific and intraspecific transmission during the epizootic.

Discussion

The Meeteetse population provided the first information on black-footed ferrets since earlier studies in South Dakota recorded 11 litters (some 90 individuals) over a 10-year period (Linder et al., 1972). Attributes of the two populations are similar despite geographic differences and the use of black-tailed prairie dogs (*C. ludovicianus*) as prey by ferrets in South Dakota. Litter sizes of Meeteetse ferrets ($\bar{X}$ = 3.3, n = 68) were similar to those from South Dakota ($\bar{X}$ = 3.4, n = 11; Linder et al., 1972). Juvenile appearance above ground and time of dispersal were similar (Hillman, 1968; Henderson et al., 1969) and are supported by collection dates of ferrets within the former range (Anderson et al., 1986). Henderson et al. (1969) recognized potential ferret predators such as owls. High mortality in South Dakota ferrets was indicated by the nearly constant adult numbers observed from 1964 to 1972 despite consistent production of young (Hillman and Linder, 1973).

Ferret mortality was high at Meeteetse as well. Loss in fecundity (Nalbandov, 1976) with age was not observed probably because of the brief life span of ferrets we studied, although longer-lived mustelids have been shown to exhibit loss in fecundity with age (Enders, 1952; Hansson, 1947). Rates of disappearance from colony 25-East and telemetry data suggest high mortality rates among all age classes, supporting our contention of brief life spans for ferrets in the wild.

Juvenile male ferrets dispersed long distances whereas juvenile females often settled near their natal areas. This pattern occurs in other mustelids (Erlinge, 1977*a*, 1977*b*; King and McMillan, 1982; Moors and Lavers, 1981; Powell, 1979, 1982; Simms, 1979) and is a common theme in solitary mammals (Waser and Jones, 1983). Therefore, it was not surprising that two juvenile male ferrets dispersed long distances in October 1985 even though ferret densities were low and prairie dogs were available locally.

When juveniles are forced into margins of adult territories or become transients, they spend disproportionate amounts of time exposed to predators and intraspecific and interspecific strife. Predation contributed most to ferret mortality from 1981 to 1984. Based on our estimates of ferret disappearance from colony 25-East and an adult disappearance rate 80% of that for juveniles, 60–80% of all juveniles must have emigrated or died each year when disease was not a factor (1982–1983 and 1983–1984). Because prairie-dog densities decrease rapidly when ferrets leave the available habitat at Meeteetse, emigrants (particularly young males) face loss of prey and exposure to predators, and are even more likely to die, which could explain partially the skewed adult sex ratio of 1 male : 2.2 females.

Mustela sp. that are habitat generalists have high reproductive rates (five to 12 young/litter; Erlinge, 1974; Forrest et al., 1985*b*; King, 1983; King and McMillan, 1982; Lavers, 1973; Simms, 1978). In contrast, black-footed ferrets are habitat specialists and have lower reproductive rates. The Siberian polecat (*M. eversmanni*), the nearest relative of the black-footed ferret (Anderson et al., 1986; Youngman, 1982) is a habitat generalist occurring in diverse environments (Stroganov, 1962) and averages nine young/litter (Stroganov, 1962). Differences between polecat and ferret life-history strategies may reflect the more stable patch dynamics (e.g., longer persistence) of North American *Cynomys* sp. (Clark, 1973), where colonies tend to be more consistent in production of prey biomass than in adjacent grasslands (Agnew, 1983). Smaller litter sizes may be more bioenergetically adaptive where resources are stable (King, 1983; Calder, 1984). Habitat specialists with low reproductive rates (three–five young/litter) in other "stable" environments, such as *M. vison*, *M. lutreola*, and *Martes americana*, became extirpated rapidly when habitat was disrupted (lost) or high artificial mortality (trapping) imposed on them (Linscombe et al., 1982; Strickland et al., 1982; Youngman, 1982), suggesting that the minimum population size for survival may be higher for these species. This could explain the rapid decline of ferrets in this century following fragmentation of their habitat and indicates that depressions in population numbers brought about by habitat reduction or mortality may not have to be large to lead to irrecoverable population decline or extirpation (Soulé, 1983; Terborgh and Winter, 1980; Wilcox, 1980).

The role of infectious diseases in local extinction has major implications for ferrets. Ferret

declines in 1985 far exceeded the proportional loss in ferret habitat (Forrest et al., 1985*a*), although localized ferret decline could be attributed to the loss of area occupied by prairie dogs (estimated at no more than 20%) between 1984 and 1985. Other evidence presented suggests the far more substantial role of distemper, to which ferrets have no apparent natural immunity (Budd, 1981; Carpenter et al., 1976). Given the disappearance dates of at least two of the litters (27 July and 17 August), the epizootic was apparently well established by the end of July. Population estimates from July through October suggested 50% mortality every 30 days during that period.

Whether or how ferrets at Meeteetse survived historic distemper epizootics can only be a matter of conjecture. The historic occurrence of the disease in North America is obscure (Budd, 1981; Gorham, 1966) and provides no explanations. The presence of historically extensive habitat (Anderson et al., 1986) would have provided fewer barriers to transmission (Anderson, 1981) of disease, but numerous opportunities for recolonization of unoccupied patches from other nearby habitat. Severe habitat fragmentation in this century has precluded the opportunity for natural recolonization. Habitat fragmentation also may have played a role in reducing genetic diversity; loss of key alleles has been implicated in loss of disease resistance in other wild mammal populations (O'Brien et al., 1985). However, domestic ferrets (*M. furo*) also exhibit 100% susceptibility to canine distemper (Budd, 1981) yet probably are highly outbred.

Decimation of the population of black-footed ferrets at Meeteetse suggests its persistence in the wild is tenuous. Ferrets will almost certainly require large investments in maintenance to insure persistence of future populations in the wild. The data demonstrate that insular populations are subject to sudden and complete collapse, and suggest the importance of immediate action, including establishment of alternative populations for recovery of insular, endangered species.

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The last known black-footed ferret from this wild population was removed to captivity in February 1987. All survivors and their progeny are currently in a captive propagation program in Wyoming.