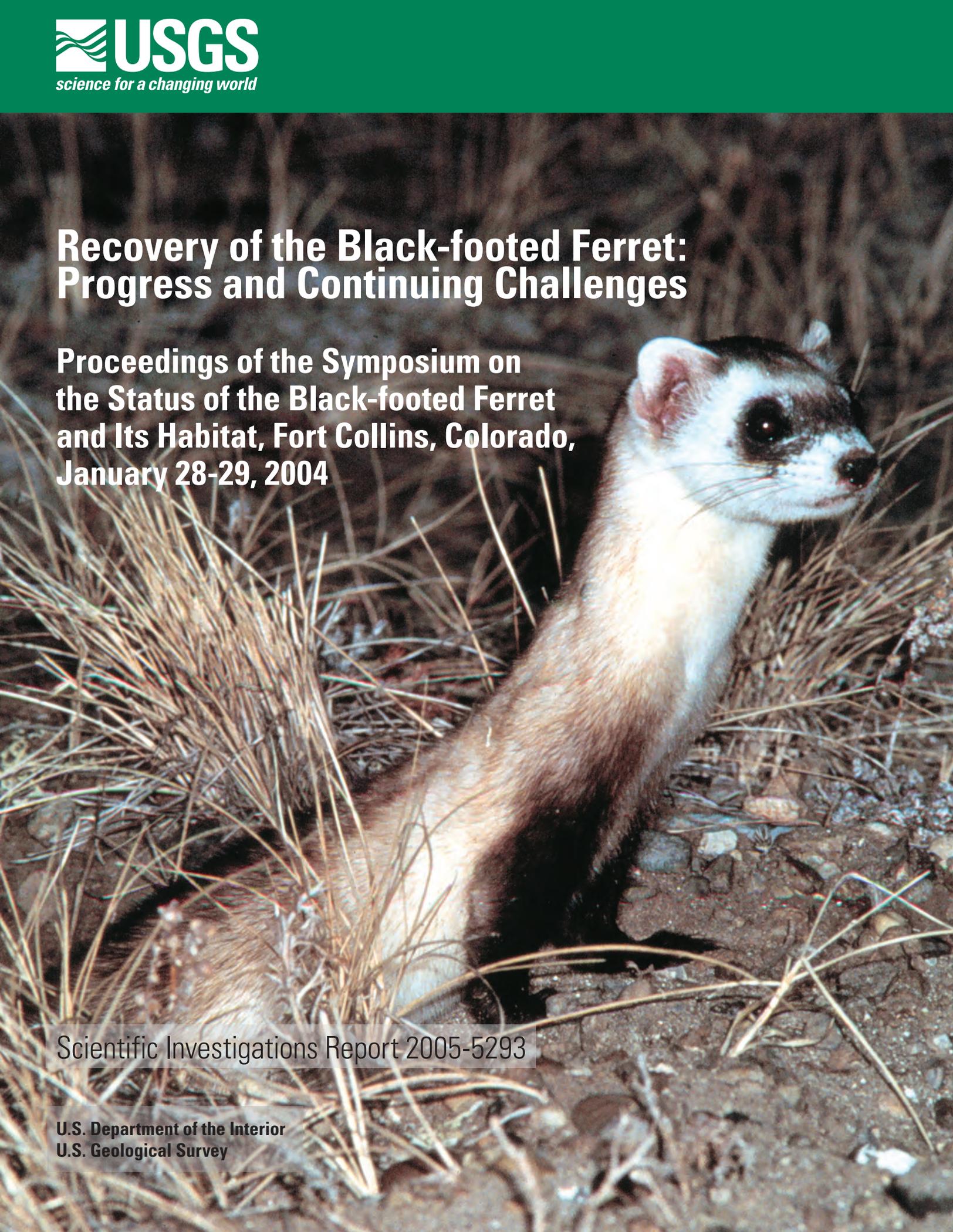# Recovery of the Black-footed Ferret: Progress and Continuing Challenges

Proceedings of the Symposium on the Status of the Black-footed Ferret and Its Habitat, Fort Collins, Colorado, January 28-29, 2004

U.S. Department of the Interior
DIRK KEMPTHORNE, Secretary

U.S. Geological Survey
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U.S. Geological Survey, Reston, Virginia: 2006

Postrelease Movements and Survival of Adult and Young Black-footed Ferrets

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Abstract

A successful captive breeding program for highly endangered black-footed ferrets (*Mustela nigripes*) has resulted in surplus animals that have been released at multiple sites since 1991. Because reproductive output of captive ferrets declines after several years, many adult ferrets must be removed from captive breeding facilities annually to keep total production high. Adults are routinely released, with young-of-the-year, on prairie dog (*Cynomys* spp.) colonies. We evaluated postrelease movements and survival rates for 94 radio-tagged young and adult ferrets. Radio-tagged adult ferrets made longer movements than young ferrets during the night of release and had significantly lower survival rates for the first 14 days. Coyotes (*Canis latrans*) caused the largest number of ferret losses. A larger data set of 623 ferrets represented adults and young that were individually marked with passive integrated transponders but were not radio tagged. Minimum survival rates, calculated primarily from ferrets detected during spotlight searches and identified with tag readers, again were significantly lower for adults than for young ferrets at 30 days postrelease (10.1 percent and 45.5 percent survival, respectively) and at 150 days postrelease (5.7 percent and 25.9 percent). Assessment of known survival time by using linear modeling demonstrated a significant interaction between age and sex, with greater disparity between adults and kits for females than for males. Postrelease survival of adult ferrets might be increased if animals were given earlier and longer exposure to the quasi-natural environments of preconditioning pens.

Keywords: age, behavior, mortality, *Mustela nigripes*, predation, radio telemetry

Introduction

Black-footed ferrets (*Mustela nigripes*) nearly became extinct when diseases invaded the last known free-ranging population near Meeteetse, Wyo., in 1985 (Lockhart and others, this volume). A rescue effort resulted in a captive population that has provided ferrets for reintroduction since 1991. The mean life expectancy of free-ranging black-footed ferrets in the ancestral Meeteetse population was about 0.9 years (calculated by using the negative reciprocal of the natural log of 0.34, an annual survival rate estimated by Forrest and others, 1988). With such a short average life expectancy, natural selection may have applied little pressure for sustained productivity in older age classes of ferrets. In captivity, productivity declines rapidly after ferrets are only a few years old (Williams and others, 1991). Efficient management of the captive breeding program thus involves relatively rapid rotation of animals (Marinari and Kreeger, this volume). Older animals are placed in zoos for exhibit and used for research, but the supply of such animals exceeds the demand. Adult ferrets are routinely released at reintroduction sites, a practice that has been criticized. Although both young and adult ferrets have been released at several sites, their postrelease movements and survival have not been compared. Marking of animals, spotlight searches, and identification of surviving ferrets are tools routinely used for monitoring at release sites (Biggins, Godbey, Matchett, and others, this volume), providing useful multiyear data sets. In certain years, more intensive radio-telemetry studies (Biggins, Godbey, Miller, and Hanebury, this volume) were directed at testing hypotheses regarding prerelease experience and rearing methods. Cumulative data from these former efforts provide the opportunity to contrast the movements and survival of released adult and young ferrets.

Methods

Stratification Based on Rearing and Prerelease Experience

Rearing conditions and prerelease experience have profound effects on behaviors of young ferrets (Miller and

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others, 1990a,b; Vargas, 1994; Biggins and others, 1999; Biggins, 2000), ultimately influencing postrelease survival rates (Biggins and others, 1998). Released adult (age at release >1 year) black-footed ferrets reported herein were given experience in outdoor pens, including living in natural burrows and killing prairie dogs, for 1–4 months prior to release. Former experimental designs that focused on testing effects of rearing on young ferrets (kits), however, involved more categories of preconditioning and more carefully controlled environments (Biggins and others, 1998). Those experimental designs encompassed most of the radio-tagged kits used in the following analyses but only a portion of the released kits that were not telemetrically monitored. Because early experiments indicated that cage-reared kits were dramatically different in several respects from their counterparts with experience in pens (Biggins and others, 1998, 1999), we did not include cage-reared kits in any of our analyses (telemetry or recapture). We also excluded kits that were born in pens or transferred into pens at the natal facility at an early age (<60 days) with their dams (the PENRES category of Biggins and others, 1998) from the telemetric data set. For a large number of kits that were not part of the early experiments, preconditioning was much more variable. Thus, our capture-recapture analyses encompassed a more broadly defined "preconditioned" group of kits that ranged from those placed in pens prior to 60 days of age with dams to those shipped after 90 days of age, without accompanying adults, from their original breeding facility to pens at other facilities or to remote pens near reintroduction sites.

In summary, we used two types of data to examine the influence of age of ferrets on their movements and survival. Radio telemetry provided information on cumulative movements, dispersal, minimum survival rates, and causes of mortality. A larger sample of ferrets that were individually marked (including those that were radio tagged) allowed additional estimates of survival via mark-recapture methods.

Radio Telemetry

We radio collared 137 black-footed ferrets with 5-g transmitter packages attached to 100 percent wool collars with Teflon® (DuPont, Wilmington, Del.) heat-shrink tubing (the latter to resist mud accumulation). Radio-tagged ferrets were released on Gunnison's prairie dog (*Cynomys gunnisoni*) habitat in the Aubrey Valley of northern Arizona and on black-tailed prairie dog (*C. ludovicianus*) habitat at UL Bend National Wildlife Refuge in Montana and the Burns Basin portion of Badlands National Park, S. Dak.

Transmitters, with their 20-cm whip antennas, provided a pulsed signal (pulse interval = 1.5 seconds; pulse width = 20 milliseconds) of about -14 dB, with battery life of about 45 days. Radio location was accomplished via triangulation from fixed stations fitted with paired, 11-element Yagi antennas on rotating masts (Biggins and others, 1999; Biggins, Godbey, Miller, and Hanebury, this volume). We tested accuracy of stations by comparing station-derived azimuths with true

azimuths to beacon transmitters. We used standard deviations of the differences between such pairs in confidence intervals to predict the accuracy of future azimuths and the areas and diagonals of error quadrangles associated with positional "fixes" (White and Garrot, 1990). An initial test for each station provided data for evaluating bias patterns and developing formulas for adjustment, and a second set of readings was used to calculate residual variation after bearings were adjusted (Biggins and others, 1999). We referenced stations prior to each tracking session (Biggins, Godbey, Miller, and Hanebury, this volume) using from 2 to 5 beacon transmitters. For these analyses, we used radio-telemetry data for the first 14 days postrelease (although tracking extended over a longer period at some sites). We used the computer program TRITEL to process azimuth data (Biggins, Godbey, Miller, and Hanebury, this volume); processing included adjustments for referencing and bias and calculation of coordinates and error estimates for each fix. Hand-held tracking equipment assisted us in recovery of lost collars and dead ferrets.

For comparisons of age groups, we used the subset of the 137 instrumented animals (excluding 20 PENRES kits and 23 cage-reared kits as defined above) that included 38 adults and 56 "preconditioned" kits (table 1). We screened data for gross radio-tracking and data entry errors by using the systematic approach of Breck and Biggins (1997). We then summarized cumulative movements between consecutive fixes and dispersal from the release site for each ferret and night. We analyzed cumulative movements by using a repeated measures multivariate general linear model (MGLM) with average area of error quadrangle, sex, and site as covariates. We used square root transformations of the response variables to improve normality and homoscedasticity of residual variation. We assumed that the area of an error quadrangle would account for a portion of the variation in the cumulative movement of a ferret and retained this measure of tracking error as a control variable in statistical models regardless of its significance. Because dispersal is defined as movement away from the release site and increased distance from tracking stations causes larger error quadrangles, tracking error was not considered in statistical evaluations of dispersal, but sex and site were included as covariates.

Causes of mortality were determined by evidence at recovery sites (e.g., tracks, scat, fur, feathers, digging), condition of carcass (e.g., hemorrhage, bite wounds, saliva), and radio-tracking data (patterns of fixes and activity, timing of death). We assessed risk-adjusted survival rates by relating deaths (table 1) to days of telemetric monitoring (Heisey and Fuller, 1985). An estimate of maximum survival resulted from considering only known deaths. Counts of animals known dead underestimate mortality rates because not all dead animals are detectable (underground deaths due to badgers, for example, may be underestimated) and because some proportion of loss of telemetric contact with animals is due to transmitter damage inflicted during predation. (We have recovered a few badly damaged transmitters that were barely functional and assume that others became nonfunctional.) We thus

Table 1. Numbers of preconditioned adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) released in Arizona, South Dakota, and Montana during 1994–96.

	Arizona (1996)	South Dakota (1995–96)	Montana (1994)	Montana (1995)	Total
Ferrets					
Adult	15	14	5	4	38
Kit	8	11	10	27	56
Total	23	25	15	31	94
Ferret-days of monitoring					
Adult	90.7	21.3	25.0	29.7	166.7
Kit	43.0	93.2	54.0	291.0	481.2
Total	133.7	114.5	79.0	320.7	647.9
Deaths					
Adult	4	11	3	1	19
Kit	0	5	5	1	11
Total	4	16	8	2	30

estimated a minimum survival rate by summing the number of ferrets that were lost from telemetric contact and the number known to be dead. If an animal was found alive at a later date during spotlight surveys, it was considered alive for the first 14 days (even if telemetric contact was lost and it would have been listed as missing). If an animal died or became missing after 14 days, it was treated as alive for the first 14 days. Our multivariate general model had eight parameters (two ages, four site/year combinations). In this survival analysis, we compared models and their nested submodels using likelihood ratio tests.

Mark-recapture

The data set for this portion of the study (table 2) included all black-footed ferrets released during 1994–2000 at Badlands National Park and Conata Basin in South Dakota, ferrets released during 1994–97 at UL Bend in Montana (including the radio-tagged individuals mentioned above), and ferrets released at the Coyote Basin site of Utah and adjacent Colorado. Of the 623 ferrets released (table 2), 325 were males and 298 were females. All released ferrets were individually marked, mostly with passive integrated transponder (PIT) tags subcutaneously implanted over the shoulder. A second PIT tag often was implanted over the hip (Biggins, Godbey, Matchett, and others, this volume). "Recapture" (in this case, mostly reading the transponder) was accomplished via spotlight surveys to locate the ferrets (Campbell and others, 1985; Biggins and others, 1998) followed by placement of a transponder reader at the occupied burrow to automatically read and retain the chip number (Biggins, Godbey, Matchett, and others, this volume). The first survey at each site usually

Table 2. Numbers of preconditioned adult and young black-footed ferrets (*Mustela nigripes*) marked and released at sites in Montana, South Dakota, and Utah-Colorado during 1994–2001.

	South Dakota (1994–2000)	Montana (1994–97)	Utah-Colorado (1999–2001)	Total
Adult	49	13	60	122
Kit	261	80	160	501
Total	310	93	220	623

was conducted about 1 month postrelease, with additional surveys conducted prior to the breeding season (in some cases) and postwhelping (most sites). Intensity of these survey efforts varied among sites and years due to availability of resources.

Counts of surviving animals at 30 and 150 days postrelease were based on the same released ferrets and thus cannot be considered statistically independent. Also, the 71 radio-tagged ferrets in South Dakota and Montana are a subset of the 623 animals considered in the capture-recapture analyses. We chose to maintain separate 30-day and 150-day mark-recapture analyses (rather than a more complex single model) because of sample size differences and unequal time intervals between surveys and because survival estimates for these time periods can be compared with similar estimates reported elsewhere for ferrets. Survival was considered cumulatively; ferrets found alive at 150 days (or later) were counted as alive on day 30 even if they were not found in the earlier period. Because spotlight sessions of equal intensity were

not replicated systematically at all sites (or even among days within sites), we did not attempt traditional capture-recapture modeling where capture rates and survival rates could be estimated separately. Our rates, therefore, must be considered as minimum survival (the products of capture rate and survival rate), recognizing that not all ferrets were likely to have been located at any site. Interpretation of the comparisons between adults and kits thus requires the assumption that each age class (within each site) was equally detectable by spotlighting, an assumption that we believe is reasonable. We estimated survival rates from spotlight searches by using an iterative numerical optimization procedure (program SURVIV; White, 1983). The general model included 12 parameters (3 sites, 2 sexes, 2 ages).

Elapsed time from release until the last detection for each ferret also was calculated. Time intervals between releases and the first spotlight survey and between subsequent spotlight surveys varied considerably among sites and years, from a single survey per year to nearly continuous surveys. Variability in survey timing tended to distribute this measure of survival in a continuous (but skewed) form, and square root transformation improved its suitability for use as a continuous response variable in a MGLM analysis, allowing additional assessment of the potential interaction between age and sex.

We recognize that detectability of ferrets via spotlight searches is likely to differ among sites due to differences in access, vegetative cover, topography, intensity of effort, and other variables. Thus, we consider multivariate modeling, with a site variable included, as critically important. Potential differences in search efficiency also preclude any conclusions regarding differences in survival among sites.

An important consideration in our experimental design, for both telemetric and capture-recapture data, was to maintain a reasonable balance of treatments within sites (and within years, with one exception). Other priorities always affected allocations of animals, but, to avoid serious confounding during interpretation of results, we did not allow any cell of the design to be empty. Thus, groups of released ferrets that did not contain adults and kits of both sexes were excluded from analyses. The exception to this general rule occurred within the telemetry data set, where adult ferrets were released in Badlands National Park in spring, and kits were released at that site during fall of the following year.

We followed the principle of parsimony in evaluating competing statistical models (Lebreton and others, 1992), attempting to reduce general models to simpler submodels by eliminating variables that appeared to have low explanatory power. For capture-recapture analysis within program SURVIV, reduced models were evaluated by likelihood ratio tests and Akaike's Information Criterion (AIC) (Anderson and Burnham, 1994). For MGLM evaluations and likelihood ratio testing, P values >0.10 were deemed sufficient for eliminating variables from models.

Results

Radio Telemetry

Of the 137 radio-tagged ferrets that were released, 59 were considered lost to the population, mostly as a result of predation (fig. 1). Coyotes (*Canis latrans*) caused the most losses, but prior to its removal a great horned owl (*Bubo virginianus*) had a substantial impact at one site in South Dakota. American badgers (*Taxidea taxus*) were common on prairie dog colonies where ferrets were released, but they killed ferrets only occasionally. The species of predator responsible for ferret deaths could not always be determined, however, resulting in some classifications of "unknown predator" or "unknown raptor" (fig. 1).

Multivariate repeated measures analysis of square root transformed cumulative movements for ferrets that were monitored for at least three nights yielded a significant interaction between night postrelease and age group ($F_{2,59} = 7.407$, $P = 0.001$) with a model that included age, site, and mean area of error quadrangle (per animal over three nights). Thus, the pattern of change in nightly movements of kits and adults was significantly different over the first three nights postrelease (fig. 2; nontransformed data). Tracking error (area of error quadrangle) contributed significantly to the variation in movements ($F_{1,60} = 5.620$, $P = 0.021$), underscoring the importance of a variable to account for this source of "nuisance" variation
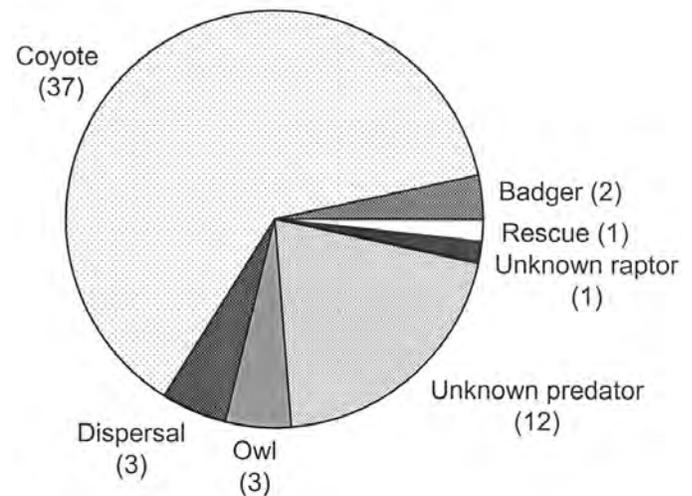

Figure 1. Causes of loss for 59 of 137 radio-tagged black-footed ferrets (*Mustela nigripes*) released in Montana, South Dakota, and Arizona during 1994–96. "Rescued" ferrets are those that we assume would have been lost without our intervention (translocation or treatment for injuries). "Unknown predator" and "Unknown raptor" are general categories for which the species of predator could not be identified.
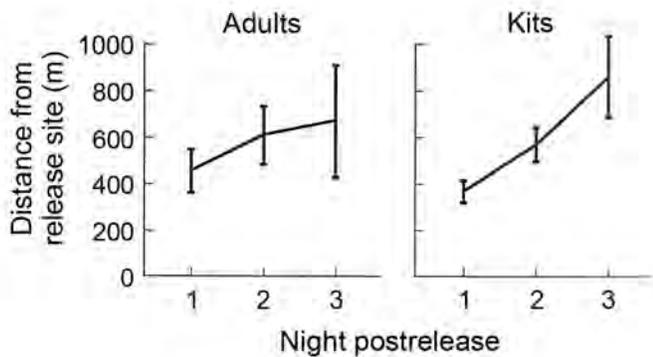
in models of movement. Nightly movements also appeared to be different at different sites ($F_{3,60}$ = 3.693, P = 0.017).

The relatively long movements of adult ferrets on the night of release suggested that they might have "bolted" from the release site (i.e., dispersed rapidly away from the point of release), but a repeated measures analysis of dispersal during the first three nights did not support that contention (fig. 3). Although there was a significant tendency for ferrets to drift away from their release sites over the first several nights ($F_{2,58}$ = 8.860, P < 0.001), the pattern of dispersal was not significantly different for kits and adults ($F_{2,58}$ = 1.107, P = 0.337). Thus, "bolting" is not an appropriate description of the behaviors of adults. They simply moved more than kits during their first night but did not tend to leave the area of release any differently than did kits. In this analysis of dispersal, there was no evidence of differences among sites ($F_{3,59}$ = 1.209, P = 0.315).

Survival of radio-tagged adults appeared to differ significantly from survival of radio-tagged kits. For the estimates of maximum survival, generated by considering only known
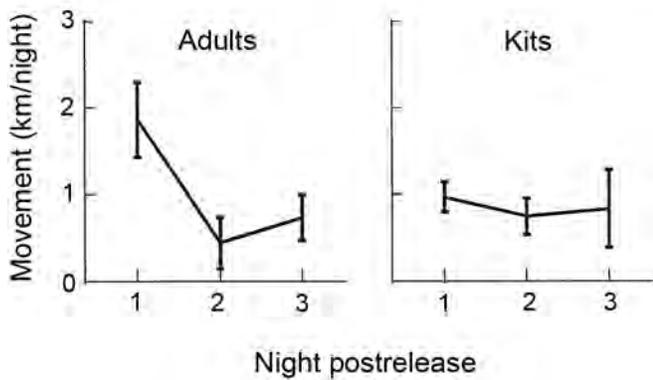
deaths (fig. 4), likelihood ratio testing did not support reduction in number of parameters by pooling sites (X^2 = 45.4, df = 6, P < 0.001) or ages (X^2 = 29.3, df = 4, P < 0.001). The same was true for the estimates of minimum survival, using ferrets known to be dead plus those with whom radio contact was lost during the 14-day tracking period (sites, X^2 = 38.6, df = 6, P < 0.001; ages, X^2 = 38.7, df = 4, P < 0.001). There was thus a similar overall pattern of differences between survival rates of adults and kits, regardless of the method of categorizing mortalities (fig. 5). If about one-third of the missing animals actually died when their signals were lost, the overall projected survival rates for 30 days postrelease would have been 42 percent for kits and 11 percent for adults. The curves vary among sites and with methods, but kit survival was higher than adult survival within each comparison.

Mark-recapture

The preferred model of minimum survival from the spotlight search data was the general model for both the short-term (30-day) (table 3) and the long-term (150-day) assessment (table 4), although the evidence for distinction between the sexes was strongest in the long-term evaluation. Minimum survival rates were higher for kits than for adults in 11 of the 12 pairs of estimates for the two time periods, averaging 45.5 percent (kits) and 9.8 percent (adults) at 30 days (fig. 6) and 25.9 percent (kits) and 5.7 percent (adults) at 150 days (fig. 7). Minimum survival rates tended to be higher for females

Figure 2. Mean cumulative nightly movements for adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) during the first three nights postrelease (mean ± SE).
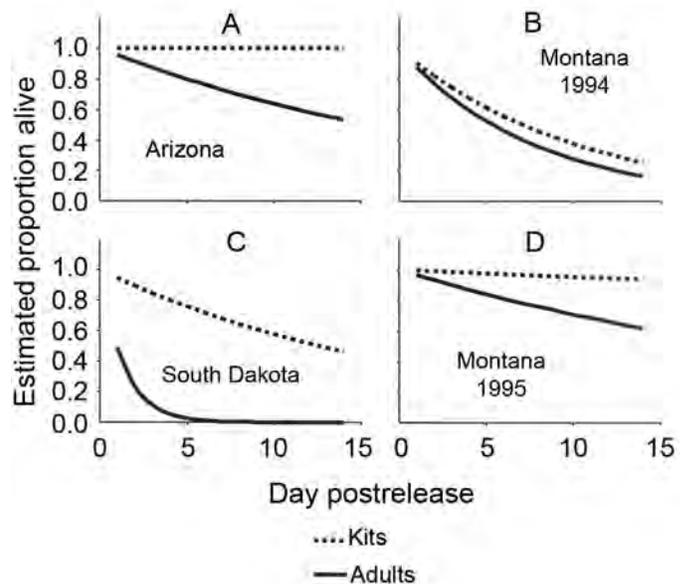

Figure 3. Nightly maximum displacement from release sites for young and adult radio-tagged black-footed ferrets (*Mustela nigripes*) during the first three nights postrelease (mean ± SE).
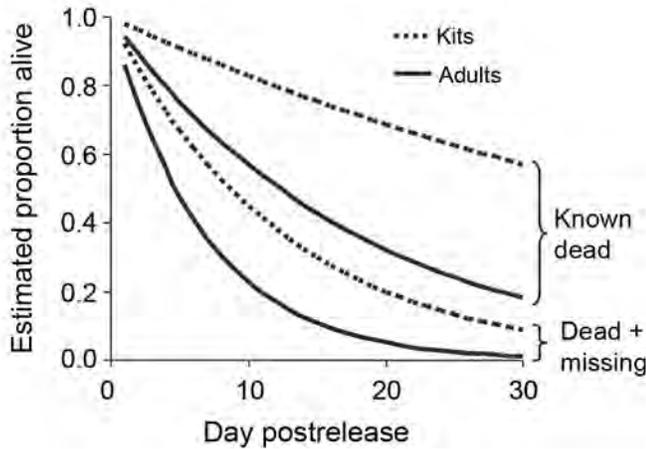

Figure 4. Postrelease survival curves for preconditioned adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) extrapolated from daily survival rates (assuming a constant hazard rate for the 14-day period of the experiment and using only known deaths).

Figure 5. Bracketed high and low survival of adult and young radio-tagged black-footed ferrets (*Mustela nigripes*) for the first 30 days postrelease, generated by using only ferrets known to be dead (high) and known deaths plus ferrets lost to radio contact (low). Curves were extrapolated from daily survival rate estimates assuming a constant hazard rate for the period.

Discussion

Radio Telemetry

There is a potential bias built into assessments of ferret movements. Repeated measures analyses, particularly, require complete sets of multiple measures on single animals; any ferret that lacked a measure of movement for any of the first three nights postrelease (fig. 2), for example, was excluded from our analysis. Thus, ferrets that tend to engage in risky behaviors tend to be removed (by death) at higher rates from the sample, likely causing movements to be generally under-estimated, and (more seriously for this kind of experiment) the effect may be greater on some treatment groups than on others. If we assume that there is a positive correlation between movement and mortality rate (Biggins and others, 1998), we likely underestimate movement differences between groups. We have been able to detect such differences, but more subtle disparities between treatment groups may remain unnoticed. Statistical models that are not based on repeated measures also would be affected, but more flexible rules for handling those data should result in a less dramatic influence. Although early deaths of individuals having presumably lower fitness may cause a shift in representation of animals, their movements before they were killed remain in data sets used for statistical analyses other than repeated measures.

Survival of radio-tagged kits differed more dramatically from adults at the Burns Basin, S. Dak., release site than at any other site (fig. 4). Although the same release site was used for both kits and adults, and they were radio tracked from the same system, Burns Basin was the only site where adults and kits were not released at the same time. It is possible that the differences there were due to year or season.

The different appearance of survival curves among sites generated from telemetric data (fig. 4) should not be construed as being linked to the species of prairie dog or other site-specific conditions. Efficiency of radio tracking is likely responsible for much of the variation. The Aubrey Valley site

than for males (figs. 6 and 7). For kits, the disparity between sex-specific survival rates was proportionately greater for the long-term estimates (males, 18.9 percent; females, 35.7 percent) than for the short-term estimates (males, 39.9 percent; females, 53.4 percent). Moreover, there seemed to be different patterns for adults and kits within the two genders for both the short-term and long-term data sets. That potential interaction warranted closer examination.

General linear modeling of elapsed time between release and the last detection demonstrated a significant interaction between sex and age ($F_{1,617} = 5.522$, $P = 0.011$); known survival times tended to be shorter for adults than for kits (fig. 8). We retested the sexes separately because of the interaction. As implied by the pairs of graphs, female kits survived significantly longer than did adult females ($F_{1,294} = 40.250$, $P < 0.001$), but the difference between the age groups was only marginally significant for males ($F_{1,294} = 3.387$, $P = 0.067$).

Table 3. Modeling of short-term (30-day) return rates for preconditioned black-footed ferrets (*Mustela nigripes*) released at three sites, with parameter estimates for sites, sexes, and ages.

Model	ln(L)[a]	np[b]	AIC[c]	Versus model[d]	X^2	P
1. General	-19.842	12	63.685			
2. Sites same	-65.391	4	138.783	1	91.10	<0.001
3. Ages same	-53.722	6	119.443	1	67.76	<0.001
4. Sexes same	-28.060	6	68.120	1	16.44	0.012

[a]ln(L) = log-likelihood.

[b]np = number of parameters.

[c]AIC = Akaike's Information Criterion.

[d]The model identified in this column was compared via a likelihood ratio test to the model in the first column (same row), resulting in the Chi-square value and corresponding probability given in the last columns.

Table 4. Modeling of long-term (150-day) return rates for preconditioned black-footed ferrets (*Mustela nigripes*) released at three sites, with parameter estimates for sites, sexes, and ages.

Model	ln(L)[a]	np[b]	AIC[c]	Versus model[d]	X^2	P
1. General	-16.687	12	57.374			
2. Sites same	-34.662	4	77.324	1	35.95	<0.001
3. Ages same	-35.060	6	82.121	1	36.75	<0.001
4. Sexes same	-28.609	6	69.219	1	23.84	0.001

[a]ln(L) = log-likelihood.

[b]np = number of parameters.

[c]AIC = Akaike's Information Criterion.

[d]The model identified in this column was compared via a likelihood ratio test to the model in the first column (same row), resulting in the Chi-square value and corresponding probability given in the last columns.
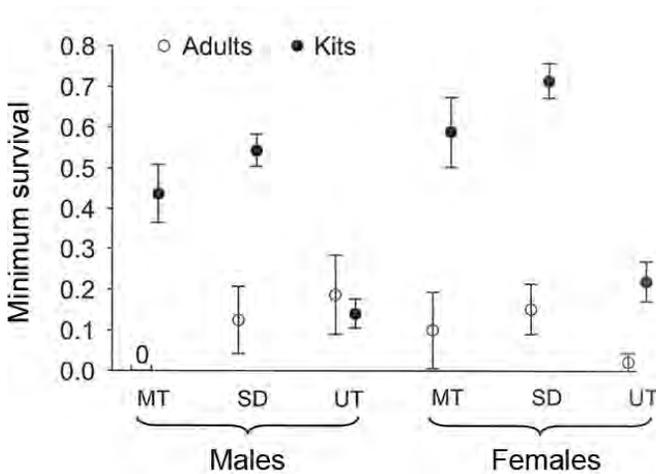
Figure 6. Minimum short-term (30-day) survival of adult and young preconditioned black-footed ferrets (*Mustela nigripes*) released onto prairie dog colonies (*Cynomys* spp.) in Montana (MT), South Dakota (SD), and Utah (UT) during 1994-2001 (mean ± SE).
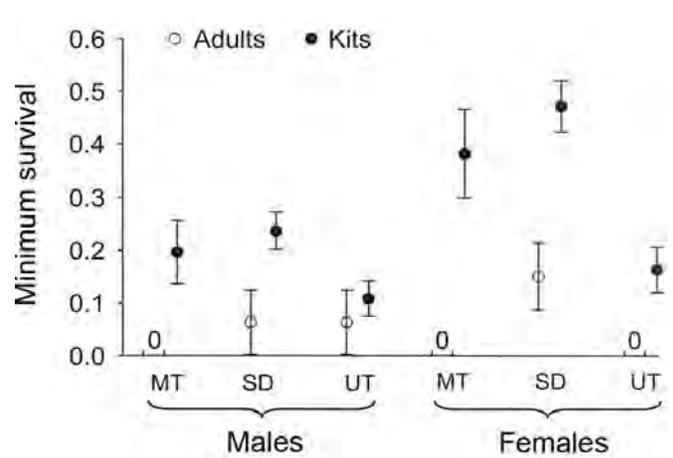

Figure 7. Minimum long-term (150-day) survival of adult and young preconditioned black-footed ferrets (*Mustela nigripes*) released onto prairie dog (*Cynomys* spp.) colonies in Montana (MT), South Dakota (SD), and Utah (UT) during 1994–2001 (mean ± SE).

in Arizona, in particular, presented a challenge. Wide spacing between stations was necessary to achieve appropriate coverage of the site, but contact was lost with many animals because of the long distances over which they were tracked. The result may have been a reduced probability of finding dead ferrets, and such known mortalities were the basis for the curves generated. In contrast, Burns Basin in South Dakota provided much better radio-tracking conditions that favored finding cases of mortality (stations were on high points). Overall, highest rates of survival for kits have been in South Dakota as exemplified by our mark-recapture data set. Site characteristics have influenced the efficiency of both spotlight searches and radio telemetry, causing us to adopt experimental designs that compare two or more treatments within sites, to replicate the design over multiple years and sites to achieve adequate sample sizes, and to exercise caution in interpreting results from multiple sites. We might have remained more suspicious about the possible ramifications of our design and

potential for confounding without the corroborating results produced by the much larger sample sizes of released ferrets in the mark-recapture portion of the study.

Mark-recapture

Differences between survival rates of males and females were not detected previously (Biggins and others, 1998) in a much smaller data set of 262 ferrets (64 of those animals were included in our present data), although there was speculation that the expected trend toward lower male survival in longer-term data was developing and would be validated with larger sample sizes. Failure to detect such a difference in our data would indeed have been troubling given the male bias in the numbers of animals released (325 males:298 females) and the female-biased composition of free-ranging ferret populations (Forrest and others, 1988). For kits only (comparable to the analysis of Biggins and others, 1998), a gender effect
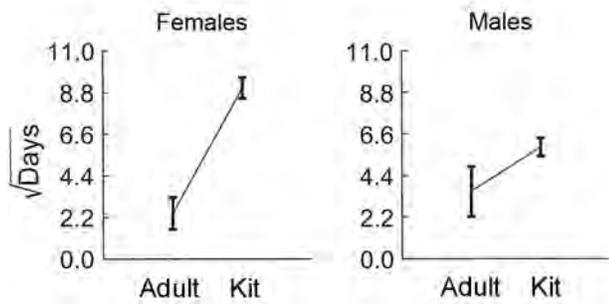
Figure 8. Number of days of known survival for marked adult and young black-footed ferrets (*Mustela nigripes*) calculated using detections from spotlight searches, snow-track searches, and radio telemetry (mean ± SE).

in our data was detectable for both the short-term and long-term evaluations, but the effect became more dramatic over time. Perhaps males became increasingly territorial during the approach of breeding season.

The significant interaction between age and sex classes has potentially nontrivial management ramifications. The interaction may be explained if older age tends to confer greater social status to males than to females, creating a potential problem if adult males have poor long-term survival skills compared to preconditioned male kits. Some older males may be able to competitively exclude younger males, subjecting the latter to temporarily higher mortality. The competition could result in lower overall survival rates for young males without any compensatory increase in long-term survival rates for adult males. If younger males are lost during transitory social interactions with dominant older males, and the older males tend to be lost before breeding season, a shortage of males could result. This phenomenon could occur with concurrent releases of adult and young males, or during releases to augment populations.

General Considerations

Daily survival rates estimated from the 14-day radio-telemetry data set for 94 radio-tagged ferrets seemed reasonably predictive of the 30-day survival rates derived from mark-recapture data on the larger data set of 623 animals. The telemetrically originated survival rates of 42 percent for kits and 11 percent for adults are similar to the overall capture-recapture survival rates of 46 percent for kits and 10 percent for adults. Such comparisons are speculative, however, because of the differing methods and attendant assumptions. First, it is only a reasonable guess to assume that one-third of cases of lost radio contact were due to death of the ferret. Second, the 14-day survival rates were produced under the assumption of a constant hazard rate, an assumption that

was repeated to produce the 30-day extrapolation. Hazard rates likely decline postrelease as ferrets with lower fitness are culled and as ferrets learn about their new environment. Over short time spans, the flat hazard rate seems reasonable. Applying a rate generated during the first 2 weeks postrelease to long time spans would be ill-advised. Indeed, our spotlight detections at 150 days (25.9 percent of kits released and 5.7 percent of adults released) were much higher than the respective 3.0 percent and 0.0 percent expectations of the extrapolated daily rates from the first 14 days of radio-tracking data. Third, the mark-recapture estimates are for minimum survival; the actual rate must be somewhat higher assuming we do not count all ferrets present. Finally, the average rates discussed here ignore the implications of statistical modeling, which suggested that rates should be separately estimated for sexes and sites.

Postrelease survival of adult black-footed ferrets might be improved if all young were reared in pens whether they were immediately destined for release or for the captive breeding program. A type of phase-specific learning (Davey, 1989) in which an animal may "imprint" on features of its habitat during a critical period of development has not been investigated for ferrets, but differences in postrelease survival and movements of ferrets as a result of rearing history (Vargas, 1994; Biggins and others, 1998, 1999) arouse suspicion. Even if imprinting is not involved, cultural transmission of important behaviors may be enhanced by a natural environment (Biggins, 2000). Ensuring that each generation has early learning experience in a quasi-natural environment has several potential benefits. Whether or not all kits are raised in pens, increasing the amount of time they spend in outdoor pens could be advantageous. Females that have spent three summers rearing young in the burrows of outdoor pens may make better candidates for release than females without such experience. Perhaps males could be kept in the outdoor pens during much of the remainder of the year, a practice that may accrue additional benefits in reproductive performance (D. Kwiatkowski, oral commun., 1991). Additional investigations of these types of variables might lead to enhanced postrelease survival of captive-reared ferrets.

At this point in the recovery program, black-footed ferret kits seem to have short-term and long-term survival rates at least fourfold higher than those of adult ferrets. On the other hand, ferrets released at age 3 or 4 likely have already exceeded the mean life spans of their wild-born counterparts in established populations. Some female ferrets released as adults have produced litters (in South Dakota and Arizona), and a male released at age 5 in South Dakota survived at least 3.5 years longer, becoming the oldest known ferret in the wild at age 8.5. Such anecdotal information representing extreme cases should carry little weight in decisionmaking, but neither do we presume that data on survival rates for hundreds of ferrets can lead to unequivocal recommendations regarding the advisability of releasing adults. Decisions will need to depend

partly on interpreting survival rates of released adults relative to other groups of wild and released ferrets, but philosophical views will continue to exert an influence.

Some conservationists and ethicists may justify extreme means to achieve the goal of preservation and recovery of a species, assuming that the importance of a species is greater than the sum of the rights of its individual constituents (Gunn, 1980). In the words of Rolston (2006, p. 116), "Extinction shuts down the generative processes in a kind of superkilling. It kills forms (species) beyond individuals." Others may set inviolate moral standards regarding the welfare of individuals wherein the "mere size of the relative population of the species to which a given animal belongs makes no moral difference to the grounds for attributing rights to that individual animal or to the basis for determining when that animal's rights may be justifiably overridden or protected" (Regan, 2004, p. 360). Even when thinking is focused on the individual ferret, however, opinions differ. Some emphasize the relative safety of a captive ferret; there is little danger it will miss a meal or, worse yet, become one. This line of ethical reasoning could lead to removing each individual "from its predator-filled natural habitat and providing it with a safe, food-rich environment . . . while exterminating the species" (Agar, 1995, p. 403). The controversy over releasing adult ferrets, however, has a narrower focus and seems to stem mostly from differences of opinion over the relative values of longevity and freedom. Remaining in captivity may allow a zoo animal to avoid an "untimely death" (Regan, 2004, p. 396) but prolongs the "harm" (in the form of "deprivation") that the animal may "suffer as a result of being caged" (Regan, 2004, p. 99). The relative impacts of these "inflictions" and "deprivations" have been contrasted (Regan, 2004, p. 303). Although these philosophical issues may be suitable topics for debate in appropriate forums, extensive discussion of them is beyond the scope of this paper.

Acknowledgments

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