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Movements and survival of black-footed ferrets associated with an experimental translocation in South Dakota

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Black-footed ferrets (*Mustela nigripes*) apparently were extirpated from all native habitats by 1987, and their repatriation requires a combination of captive breeding, reintroductions, and translocations among sites. Improvements in survival rates of released ferrets have resulted from experience in quasi-natural environments during their rearing. Reestablishment of a self-sustaining wild population by 1999 provided the 1st opportunity to initiate new populations by translocating wild-born individuals. Using radiotelemetry, we compared behaviors and survival of 18 translocated wild-born ferrets and 18 pen-experienced captive-born ferrets after their release into a prairie dog colony not occupied previously by ferrets. Translocated wild-born ferrets moved significantly less and had significantly higher short-term survival rates than their captive-born counterparts. Using mark–recapture methods, we also assessed potential impacts to the established donor population of removing 37% of its estimated annual production of kits. Annual survival rates for 30 ferret kits remaining at the donor subcomplex were higher than rates for 54 ferret kits at the control subcomplex (unmanipulated) for males (+82%) and females (+32%). Minimum survival of translocated kits did not differ significantly from survival of those at the control subcomplex. Direct translocation of young, wild-born ferrets from site to site appears to be an efficient method to establish new populations.

Key words: behavior, captive breeding, compensatory mortality, density dependence, dispersal, endangered species, *Mustela nigripes*, reintroduction

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Reintroduction, including translocation, is a common tool used in conservation programs for endangered species and involves attempts to establish populations of animals in unoccupied areas of the species' historical range (Wilson and Stanley Price 1994). In its broadest sense translocation can refer to the general process of intentionally releasing animals into the wild to establish, reestablish, or augment a population (Griffith et al. 1989), allowing for various origins (e.g., captive-born or wild-born) and encompassing various destinations (e.g., within or outside the historic range). We use the term translocation in the more restrictive sense of Wilson and Stanley Price (1994) to describe the process of capturing free-ranging, wild-born animals in one part of the range and moving them to a different part of the range for release. Translocations of wild-born animals are often more successful than releases of captive-born animals (Wolf et al. 1996). Compared to captive-born animals, wild-born animals should have better survival skills, as demonstrated for otters (*Lutra lutra*—Sjoasen 1996, 1997) and other carnivores (Jule et al. 2008). Nevertheless, deleterious impacts on the donor population could result from removal of animals for translocation, a topic of considerable importance to managers responsible for conservation of endangered species.

Black-footed ferrets (*Mustela nigripes*; hereafter, ferret) approached extinction in the mid-1980s when epizootics of plague and canine distemper ravaged the last known wild population and its prairie dog prey in Wyoming (Forrest et al. 1988; Williams et al. 1988). Eighteen ferrets removed from

that population became the nucleus for a captive-breeding program that produced surplus animals for reintroduction since 1991. The advantages of giving ferrets prerelease experience in outdoor pens with quasi-natural prairie dog (*Cynomys*) colonies became apparent in 1992 (Biggins et al. 1999), and several variations of that strategy were tested in subsequent years (Biggins et al. 1998). Methods included breeding and rearing of animals in cages followed by transfers of kits to pens for conditioning. Kits can be transferred to pens at about 60 days of age with their dams (formerly called the PEN60 treatment) or transferred to pens without the dams at >90 days of age (PEN90 animals). Conditioning is accomplished in pens located at ferret-production facilities or at reintroduction sites. Also, ferrets bred and raised in pens or transferred to pens as family groups when kits are young (e.g., 2–4 weeks) have postrelease survival rates up to 10 times higher than survival of ferrets reared in cages (Biggins et al. 1998). Groups with intermediate levels of conditioning (i.e., PEN60 and PEN90) have intermediate survival rates (Biggins et al. 1998). Ferrets with intermediate levels of conditioning, however, have survival rates up to 83% (for 8 months) when they are conditioned in pens located near the release sites rather than at the breeding facilities, then released on suitable habitat in South Dakota (T. M. Livieri, pers. obs.).

By 1999 most ferret kits born at the Conata Basin, South Dakota, habitats were being produced from wild-born stock. Direct translocation of these kits to ferret-unoccupied habitats was hypothesized to be an efficient method for establishing new populations. Nevertheless, we believe new strategies should be tested in a comparative manner before adoption (Biggins et al. 2006e; Miller et al. 1996) to document differences carefully and to reduce the chance that unexpected difficulties will arise. For example, homing (return to place of capture or home range) tendencies could stimulate excessive dispersal of ferrets captured in the wild and translocated short distances from their natal areas. One primary objective of this study was to compare behaviors and survival of translocated wild-born ferrets and released captive-born ferrets that have been conditioned in outdoor pens. We predicted that translocated wild-born ferrets would move less and survive longer than captive-born ferrets.

Territoriality can impose density-dependent constraints on populations of mustelids and other carnivores (Ewer 1973; Kruuk 1978; Lockie 1966). Male ferrets seem territorial, judging from gross movements and spacing patterns (Clark 1989; Fagerstone and Biggins 2011), and ferrets seem to compete for patches of quality habitat (Biggins et al. 2006b, 2006d). Harvesting young ferrets for translocation is similar to harvesting animals for other purposes (e.g., muskrats [*Ondatra zibethicus*] —Clark 1987), improving survival rates of remaining individuals by reducing densities of populations that are near carrying capacity or saturation point (Leopold 1933). Another objective of this study was thus to compare survival of ferrets remaining at the donor subcomplex (from which ferrets were removed) of prairie dog colonies to survival of ferrets at a control subcomplex (unmanipulated), allowing this study to be an initial evaluation of density-dependent survival in ferrets. We predicted that reduction in density of ferrets by removing a portion of the kits produced would increase survival of remaining kits.

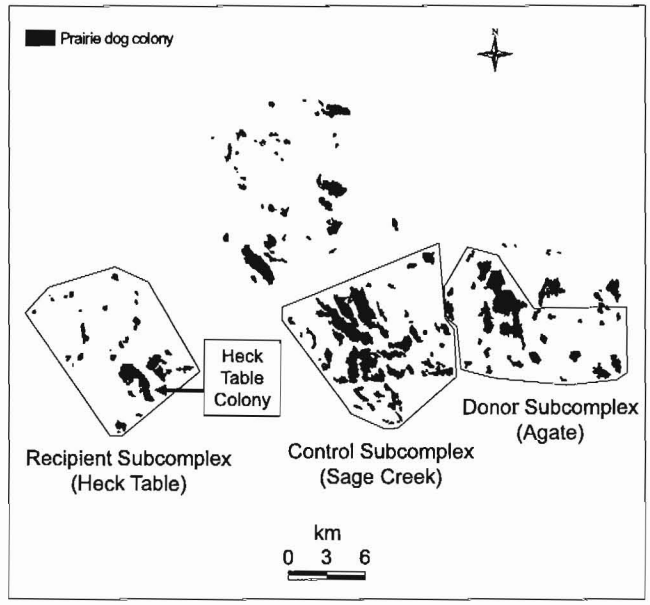

FIG. 1.—Subcomplexes of black-tailed prairie dog (*Cynomys ludovicianus*) colonies within the Conata Basin Complex (on Buffalo Gap National Grasslands), South Dakota, used for experimental translocation of black-footed ferrets (*Mustela nigripres*) in 1999. The Heck Table colony of the recipient subcomplex received equal numbers of young captive-born (i.e., PEN90) ferrets and young wild-born (i.e., WILD) ferrets translocated from the donor subcomplex. No ferrets were removed from the control subcomplex.

MATERIALS AND METHODS

Study sites were black-tailed prairie dog (*Cynomys ludovicianus*) colonies within the Conata Basin Complex on the Wall Ranger District, Buffalo Gap National Grasslands, South Dakota. Colonies occurred in groups referred to as the donor (Agate) subcomplex (43°47′N, 102°11′W), the control (Sage Creek) subcomplex (43°46′N, 102°15′W), and the recipient (Heck Table) subcomplex (43°43′N, 102°31′W) where ferrets were released (Fig. 1). The donor subcomplex has been occupied by reintroduced ferrets since 1996, the 1st release of ferrets in the control subcomplex was in 1997, and ferrets were 1st released at the Heck Table subcomplex in 1999 during this study (Fig. 1). The subcomplexes used in this study represent high-quality habitats for ferrets, with prairie dog densities of 27.9, 37.1, and 42.0 prairie dogs/ha at recipient, donor, and control subcomplexes, respectively (T. M. Livieri, pers. obs.). Densities of ferrets that inhabited the control and donor subcomplexes were 0.022 and 0.015 ferrets/ha, respectively (T. M. Livieri, pers. obs.).

For the purpose of this study any ferret born in 1999 was included in the cohort called kits, even though some analyses herein considered their survival to ages beyond 1.5 years. One

of our treatment groups of released ferrets (PEN90) consisted of ferret kits born in zoos, maintained in cages (Biggins et al. 1998), and transferred to outdoor conditioning pens in the Conata Basin when the kits were about 90 days of age. Outdoor pens were 213.2 m^2 (14.6 × 14.6 m) and constructed on an existing prairie dog colony with an average of 5.9 (SE = 0.4; range = 2–9) prairie dog burrows per pen. PEN90 kits were maintained in family litter groups until they were anesthetized with isoflurane (Gaynor et al. 1997), implanted with passive integrated transponder chips (Fagerstone and Johns 1987), radiocollared, held 1 night in nest boxes, and released at the Heck Table prairie dog colony during 29 September–13 November 1999. The PEN90 group was composed of 9 males and 9 females. Research was done humanely and in accordance with guidelines of the American Society of Mammalogists that were published later (Gannon et al. 2007). Procedures were approved by the Institutional Animal Care and Use Committee of the Fort Collins Science Center (United States Geological Survey).

Wild-born kits (9 males and 9 females) from the donor supcomplex comprised the WILD treatment group. We used a split-litter design, leaving about half of the WILD kits in each sampled litter at the donor subcomplex. The WILD kits were located with spotlights (Biggins et al. 1998; Campbell et al. 1985), captured, chipped, and radiocollared, and held in nest boxes for the remainder of the night before their release at Heck Table. We released 5 males and 5 females in each of the WILD and PEN90 categories on 29 September 1999, spacing animals uniformly throughout the prairie dog colony and placing them directly into prairie dog burrows. We released a 2nd group of 4 males and 4 females in each of the WILD and PEN90 categories on 13 October 1999 and attempted to place those ferrets into habitat not occupied by animals from the 1st group.

Radiotelemetry.—We affixed 6-g radiotransmitters to ferrets destined for release at Heck Table (Biggins et al. 2006c) and implanted chips to allow individual identification (Biggins et al. 2006a) after animals lost their collars due to wear on their degradable wool neckbands. Ferrets were recaptured to replace prematurely lost collars and to remove collars after radiotracking ended.

We radiotracked the translocated ferrets at the recipient subcomplex via triangulation from fixed stations fitted with 11-element dual-beam yagi antennas (Biggins et al. 2006c). We used handheld tracking equipment to find shed collars and predator-killed ferrets. We tested accuracy of fixed stations and calculated an error quadrangle for each estimated location (Biggins et al. 2006c; White and Garrott 1990). We compared areas of error quadrangles for PEN90 and WILD ferrets using a 2-sample t-test. We used 3–5 beacons to reference the antennas to grid north and used program TRITEL (Biggins et al. 2006c) to perform referencing calculations, produce estimates of fixes, and estimate error.

Movements.—We estimated an individual movement as the straight-line distance between 2 consecutive fixes for an animal. Because many biologically interesting phenomena involve extremes (Gaines and Denny 1993), we examined 2 types of maxima. Maximum cumulative movement in 12-h periods was sums of individual moves, with no restriction regarding time separation of the consecutive fixes. We defined maximum dispersal for each animal as straight-line displacement between its point of release and its most distant telemetric location.

We characterized more typical (i.e., nonextreme) movements as sums of distances between consecutive fixes for each animal during each night if consecutive fixes were separated by <6 h. We calculated these cumulative nightly movements only for nights with detected movement; an additional analysis was conducted on the proportion of nights with and without detected movement. To examine cumulative movements per night we separated the 30-day postrelease monitoring period into 3 subperiods of 10 days each and analyzed each subperiod separately using a general linear model. An animal-specific mean nightly movement was calculated for each 10-day period. Sample size was thus the number of animals for this and other analyses of movements.

Several variables were incorporated into statistical models to assess variation in movements induced by radiotracking methods. We used the mean area of the error quadrangles for the 2 fixes defining the origin and termination of a move as an index to error associated with that move (Biggins et al. 2006b, 2006c), incorporating that error variable into most multivariate models involving movement. Because error can be a consequence of movement rather than a cause of apparent movement, we did not use a covariate of movement error in analyses of dispersal. Variation in timing of location determination can affect estimates of linear movement. We evaluated influences of time as covariates in several multivariable statistical models. For maximum dispersal the measure was elapsed time from release of each animal until its last telemetric location. For maximum cumulative movements the measure was cumulative time spent monitoring each animal. The cumulative measure did not include time when tracking stations were not operating (e.g., daylight hours and equipment referencing following shift changes), time between an animal's loss of its radiocollar and subsequent recollaring, or time spent by an animal in a location where it could not be radiotracked. Because of the potential for irritation induced by the radiocollar to influence behaviors of the ferrets, we included in the statistical models a variable that identified evidence of abnormalities of the skin on the ferrets' necks, including loss of hair.

Statistical procedures for radiotelemetry data.—Statistical analysis of various attributes of behavior and survival involved multivariable model selection via backward elimination (Kleinbaum et al. 1988). We attempted to reduce the general model to a more parsimonious submodel through stepwise elimination of variables that seemed to offer relatively little explanatory power. Explanatory influence was evaluated using partial F-tests in general linear modeling with continuous response variables (i.e., movements), and using likelihood ratio chi-square (χ^2) tests for analysis of short-term survival

rates (Heisey and Fuller 1985). A more general model was favored over its reduced counterpart when $P \leq 0.10$. Eliminated variables were not considered for reinclusion. We retained movement, time, and neck condition variables regardless of their statistical significance. All general models included rearing history (i.e., the primary treatment), sex, and release period as categorical variables subject to elimination. The general linear models (but not the short-term survival model) also included all possible interactions between these variables. We considered differences between treatment groups to be significant if $P \leq 0.05$.

Two ferrets that disappeared from radiocontact within 3 days after release and were not observed during subsequent searches with mobile radiotracking equipment or spotlights were assumed to be dead and were pooled with the 4 known mortalities for analysis of survival. Modeling of survival did not include a variable for neck condition because of potential bias due to our inability to observe the neck condition of missing ferrets or remains of dead ferrets lacking a neck.

We assessed residual variation of the most general linear models and of the final reduced models. Normality and homoscedasticity of residuals were improved by our use of log-transformed measures of movements and dispersal. We used transformed values for testing but used nontransformed values for summaries presented in figures.

Annual survival.—We evaluated annual survival as the basic reencounter rate for ferrets found during annual searches. Because this measure is the product of the probability of detection (p) and the probability of true survival (Burnham et al. 1987), it tends to underestimate survival (i.e., p is usually <1.0). Also, this measure can be considered apparent survival because we could not distinguish between mortality and permanent dispersal. We henceforth use the term minimum survival (Biggins et al. 1998) to emphasize the underestimation of true survival due to both factors.

We assessed annual minimum survival for ferrets at the donor subcomplex (i.e., Agate), the control subcomplex (i.e., Sage Creek), and at the recipient subcomplex (i.e., Heck Table) using a mark–recapture strategy. We used spotlights to locate animals (Biggins et al. 2006a) during the postbreeding season (July–November 1999), captured most ferrets detected at donor and control subcomplexes, and marked them with chips (if they were not already implanted with a chip). During July–November 2000 and 2001 we conducted additional spotlight surveys to locate and identify ferrets. To identify individual ferrets we used automated transponder readers with ring antennas that were left at ferret-occupied burrows. We searched all known ferret habitat in the Conata Basin Complex, and dispersing animals that reached other suitable habitat were classified as alive. If animals were not relocated, we assume that their probability of death was high, and more important, that they were not alive for the purpose of contributing to the populations of interest. Thus, our failure to distinguish between permanent emigration and actual mortality should not have compromised our ability to interpret the survival data.

Although we did not use a true Cormack–Jolly–Seber framework for the analysis of survival (because we effectively had only 2 occasions of capture), many of the 12 assumptions listed by Burnham et al. (1987) are germane. Several of these assumptions are relaxed, however, because our goal was to compare survival among treatment groups rather than to estimate absolute survival rates (Burnham et al. 1987). We regarded the assumption that probability of detection was equal among the donor, control, WILD, and PEN90 groups as important and plausible. Survival was conditioned on those ferrets individually identified during 1999 (i.e., the 1st occasion), namely the WILD and PEN90 ferrets at the recipient subcomplex, ferrets captured and marked at the control subcomplex, and marked ferrets remaining at the donor subcomplex after WILD ferrets were removed for translocation. We considered a ferret to have survived the 1999–2000 period if it was found during the 2000 or 2001 surveys (the cumulative 2nd occasion). We used a logistic regression model to compare annual survival rates of ferrets at donor and control subcomplexes, a 2nd model to compare released ferrets in WILD and PEN90 categories, and a 3rd model to compare released ferrets with those at the control subcomplex. Initial general models included the variables sex, age (i.e., adult or kit), subcomplex or rearing group, and their interactions; likelihood ratio tests aided in the quest for the most parsimonious submodel accounting for significant variation (Lebreton et al. 1992).

Results

We accumulated 868.2 ferret-days (ferret-day = 1 ferret monitored for 1 day) of telemetric monitoring on the 36 radiotagged ferrets, of which 469.8 ferret-days were intensive monitoring during hours of darkness (used for assessing movements of animals). Telemetric signals were received from ferrets during 18% of the intensive monitoring time (85.2 cumulative ferret-days per 469.8 ferret-days), allowing us to produce 4,901 fixes. The 4 fixed tracking stations produced bearings varying $\pm$ 0.68° to $\pm$ 1.00° with 90% confidence, resulting in an average error quadrangle area of 1,221 m^2. Mean error quadrangle areas of WILD (1,050 m^2) and PEN90 (1,429 m^2) did not differ significantly ($t_{29} = -0.756$, $P = 0.456$).

Movements.—WILD ferrets made no measurable movements on 43.6% ($SE = 3.9\%$) of the nights monitored, which was significantly different from the 16.7% ($SE = 3.7\%$) overall rate for their PEN90 counterparts ($F_{1,30} = 24.89$, $P < 0.001$). The proportion of nights with no movement decreased with increasing monitor time ($F_{1,30} = 14.50$, $P = 0.001$). During nights when ferrets moved cumulative nightly movements of PEN90 ferrets generally were greater than those of WILD ferrets. In separate analyses of each subperiod (Fig. 2) cumulative nightly moves by PEN90 ferrets were about double those of WILD ferrets in the first 10 days postrelease ($F_{1,22} = 13.35$, $P = 0.001$) and during postrelease days 11–20 ($F_{1,21} = 10.80$, $P = 0.004$), but cumulative

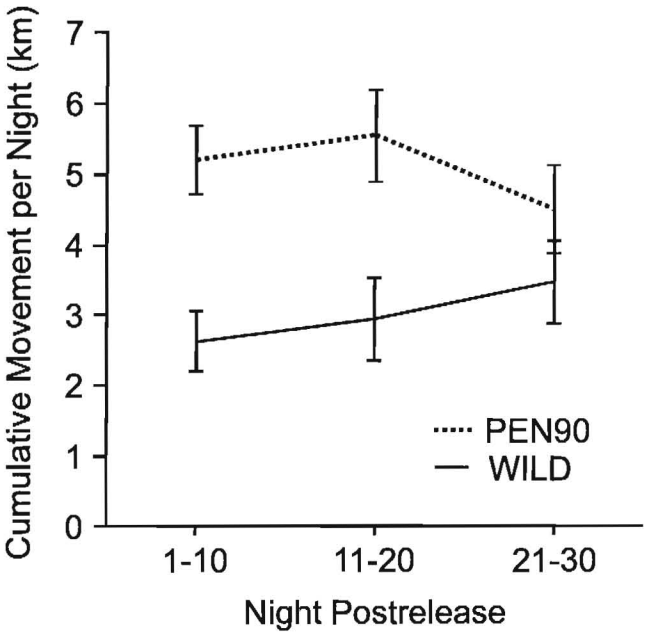

FIG. 2.—Mean cumulative movement per night for radiotagged wild-born (i.e., WILD) and captive-born (i.e., PEN90) black-footed ferrets (*Mustela nigripres*) during the first, second, and third 10-day periods after release on the recipient subcomplex of black-tailed prairie dogs (*Cynomys ludovicianus*). An observation was a nightly mean for each 10-day period and animal. Observations were summarized as least-squares means (± *SE*) for each treatment adjusted for effects of sex,[b,c] neck condition,[a,b,c] telemetry error,[a,b,c] release period,[b,c] sex * rearing group interaction,[c] and sex * release * rearing group interaction[b] in multivariable linear models. [a] = model for days 1–10, [b] = model for days 11–20, and [c] = model for days 21–30.

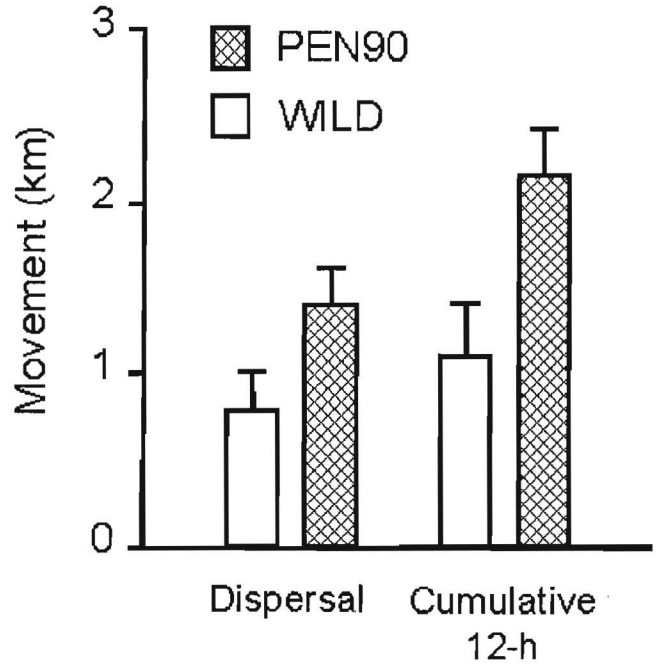

FIG. 3.—Maximum dispersal and maximum cumulative movement in any 12-h period for radiotagged wild-born (i.e., WILD) and captive-born (i.e., PEN90) black-footed ferrets (*Mustela nigripres*) during the 1st month postrelease at the recipient complex. Maxima for each animal were summarized as least-squares means (± *SE*) for each treatment adjusted for effects of neck abrasion,[a,b] telemetry error,[b] and monitor time[a,b] in multivariable linear models. [a] = dispersal model and [b] = 12-h cumulative movement model.

movements for the 2 groups tended to converge during days 21–30 ($F_{1,19}$ = 1.61, P = 0.220).

Overall maximum cumulative movements in any 12-h period (Fig. 3) were greater ($F_{1,29}$ = 13.25, P = 0.001) for PEN90 ferrets (2,158 m) than for WILD ferrets (1,110 m). This measure of cumulative movement showed a significant increase with increasing error quadrangle ($F_{1,29}$ = 7.83, P = 0.009) and increasing monitor time ($F_{1,29}$ = 14.80, P = 0.001). Maximum dispersal (Fig. 3) also was significantly greater ($F_{1,30}$ = 5.15, P = 0.031) for PEN90 ferrets (1,412 m) than for WILD ferrets (778 m), and monitor time again was influential ($F_{1,30}$ = 5.94, P = 0.021). Differences between sexes were not significant in any model of movements and were eliminated during stepwise evaluations. The WILD ferrets showed no tendency for homing at a large scale.

Short-term survival.—WILD ferrets were more likely to survive than PEN90 ferrets over the short-term postrelease period. Minimum daily survival rates for WILD ferrets (0.9981; 95% confidence interval [95% *CI*] = 0.9943–1.0000) and for PEN90 ferrets (0.9861; 95% *CI* = 0.9740–0.9982) were extrapolated to 30-day rates of 0.9434 (95% *CI* = 0.8415–1.0000) and 0.6566 (95% *CI* = 0.4541–0.9494), respectively. Examination of telemetry data suggests that short-term survival rates differed between rearing categories but that survival did not differ between sexes. The short-term survival modeling process did not support pooling of rearing categories (likelihood ratio χ^2_1 = 4.58, P = 0.032) in the final step but did suggest pooling of sexes in the 1st step (likelihood ratio χ^2_8 = 5.36, P = 0.718). Six ferrets (including the 2 missing animals) died during the 868.2 ferret-days of telemetric monitoring (5 deaths in 354.1 ferret-days for the PEN90 group and 1 death in 514.1 ferret-days for the WILD group). Four deaths were caused by coyotes (*Canis latrans*).

Annual survival.—During July–November 1999 we identified 169 ferrets at the donor (n = 70) and control (n = 99) subcomplexes. These kits (n = 95, excluding the 18 kits translocated) and adults (n = 56) provided the basis for estimates of survival. In the general statistical model of annual minimum survival rates for ferrets at the donor and control subcomplexes we found evidence for 3-way interaction (sex * age * treatment; likelihood ratio χ^2_1 = 4.37, P = 0.037). We thus conducted separate analyses for kits and adults, including sex and treatment (and their interaction) in the general models for each.

Estimated annual minimum survival rates differed for kits remaining at the donor subcomplex and those at the control subcomplex where no ferrets were removed (likelihood ratio χ^2_1 = 4.15, P = 0.042; Fig. 4), and survival rates differed between male and female kits (likelihood ratio χ^2_1 = 8.69, P = 0.003; Fig. 4). Male kit survival was 82% higher and

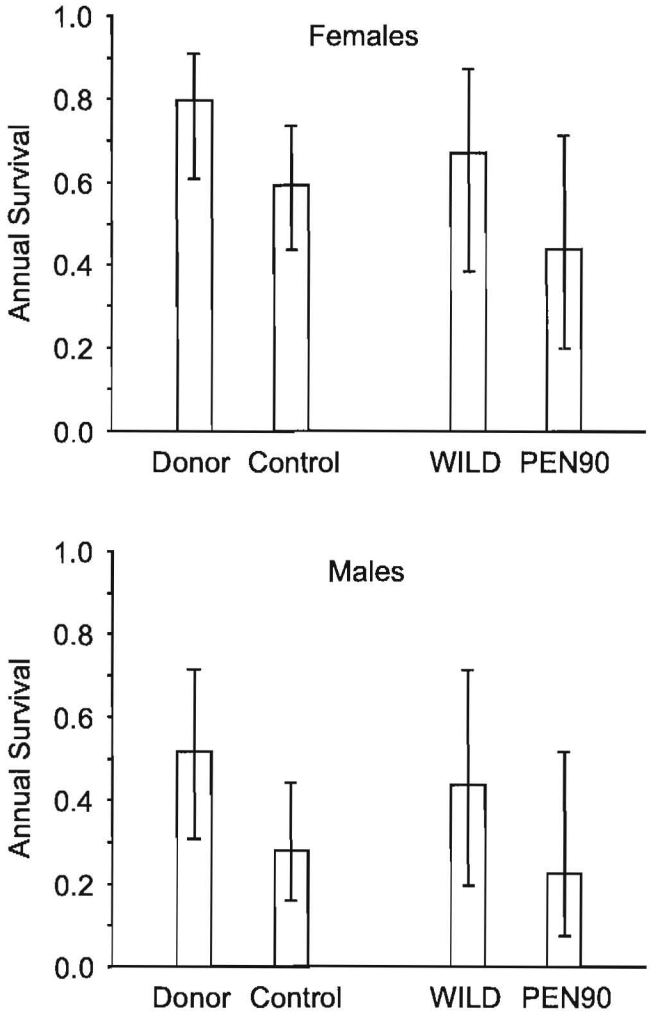

Fig. 4.—Estimated minimum rates of annual survival (and 95% confidence interval) for female and male black-footed ferrets (*Mustela nigripres*) in the Conata Basin Complex, South Dakota. Estimates for donor and control ferrets and estimates for wild-born (i.e., WILD) and captive-born (i.e., PEN90) ferrets were derived from kits detected during spotlight surveys.

female kit survival was 32% higher at the donor subcomplex than at the control subcomplex. Our models failed to detect differences between survival rates of adults at donor and control subcomplexes (likelihood ratio $\chi^2_1 = 0.33$, $P = 0.564$) or differences between survival rates of adult males and females (likelihood ratio $\chi^2_1 = 0.31$, $P = 0.578$).

Annual survival rates of WILD and PEN90 kits released at the recipient subcomplex (likelihood ratio $\chi^2_1 = 1.85$, $P = 0.174$; Fig. 4) did not differ statistically, and survival rates of male and female kits at the recipient subcomplex were similar (likelihood ratio $\chi^2_1 = 1.85$, $P = 0.174$; Fig. 4). Also, we did not detect differences in survival between ferret kits released at the recipient subcomplex and those at the control subcomplex (likelihood ratio $\chi^2_1 = 0.82$, $P = 0.366$; Fig. 4).

Numbers of radiocollars initially dropped by PEN90 ferrets ($n = 8$) and by WILD ferrets ($n = 4$) did not differ significantly (Fisher exact test, $P = 0.343$). Efforts to recapture ferrets that had lost their collars resulted in replacement of all 8 collars for PEN90 ferrets and 3 of the 4 collars for WILD ferrets. Neck condition did not significantly impact several metrics of radiocollared ferret movement, including frequency of nights without movement ($F_{1,30} = 0.41$, $P = 0.525$), cumulative movements in the first, second, or third 10-day periods (respectively: $F_{1,22} = 1.82$, $P = 0.192$; $F_{1,21} = 0.39$, $P = 0.537$; $F_{1,19} = 1.34$, $P = 0.262$), or maximum 12-h cumulative movements ($F_{1,21} = 1.62$, $P = 0.217$), but coding for neck condition was retained as a controlling covariate in all multivariable models.

Discussion

Compared to captive-born ferrets, WILD ferrets moved on fewer nights and moved shorter distances on the nights that they moved. Although quasi-natural rearing environments have produced dramatic changes in behaviors of captive-reared ferrets (Biggins et al. 1999), the findings of this study support the contention that captive breeding and rearing strategies tend to produce ferrets that are relatively bold, make long moves, and spend much time above ground (Biggins 2000). The reduced movement of WILD ferrets should reduce encounter rates with dangerous predators. Thus, the wild animals we translocated seem to offer a useful baseline of behavioral expectations for ferrets released on this type of habitat.

We defined dispersal as movement away from the point of release. Although dispersal can connote abandonment of a former area of activity, we do not suggest this to be the case with released ferrets. Many of the dispersal distances of this study were short, especially compared with distances observed in former studies of ferrets (Biggins et al. 1999), and dispersal of some animals might be entirely within what later becomes their activity areas. Nevertheless, the maximum measures of displacement from the point of release and maximum cumulative movements, considered with the patterns of nightly movements, suggested a consistent trend for reduced activity in the WILD ferrets compared to the PEN90 animals.

Failure to document movements by ferrets during some nights could have been due to the relatively low intensity of tracking on individual animals. Two fixes are required to define a movement, and some animals might be active above ground for short periods. When large numbers of animals were simultaneously active (which was not uncommon, especially shortly after release), intervals between fixes became long as technicians sequentially tracked them, and these intervals could have been longer than the total durations of activity bouts in some cases. This phenomenon could be an alternative explanation for the negative correlation between monitor time and proportion of nights with no moves. As the number of nights of radiotracking increased, technicians presumably became more efficient at finding and tracking active animals, and trackable subjects became less numerous, combining to increase the chance of obtaining multiple fixes on those that remained. Regardless, this artifact of tracking should have

influenced all treatment groups, and controlling for monitor time in the analyses should have reduced the probability of bias during comparisons among those groups.

The pattern of change in cumulative nightly movements (Fig. 2) could have been influenced similarly by temporal changes in tracking. The generally longer movements during the second 10-day period postrelease compared to the first 10 days, for example, could have been due to greater accumulation of fixes on those animals for the reasons cited above. Again, the differences between treatment groups should have been unaffected. We might expect convergences among treatment groups as animals with poorer survival skills succumb and those that survive presumably increase their skills and knowledge of their environment. Supporting this contention was the apparent difference between survival during the initial month and annual survival. For example, the daily survival rate for the WILD group calculated during the 1st month postrelease expands to an annual rate of only 1%, in contrast to the documented minimum survival rates of 29% for males and 76% for females of that group.

Short-term survival rate estimates from telemetry data suggested higher survival for WILD than for PEN90 ferrets (42% higher survival for 30 days). The longer term mark–recapture–based estimates of annual survival suggested 68% better survival for the WILD than for the PEN90 groups, but the proportionately greater difference was not statistically significant. For male ferrets the trend for lower annual minimum survival of PEN90 compared to WILD groups released at the recipient subcomplex suggests that captive-born males might be at a competitive disadvantage as they approach maturity.

Because only those ferrets radiotracked or found were classified as living, estimates of survival from both telemetric and spotlighting data were minimums. Ferrets that left the complex are not represented but could be alive elsewhere. Thus, any difference in long-distance dispersal by PEN90 and WILD ferrets would tend to reduce disproportionately the survival rate (as we define it) of the group with the most dispersing animals. Considering that dispersing ferrets likely have high mortality rates, however, the phenomenon is not likely to influence dynamics of resident populations of ferrets significantly.

Reducing the density of kits at the donor subcomplex appeared to improve survival of those kits that remained, consistent with the themes of density dependence and compensatory mortality that are important principles of wildlife ecology and management (Burnham and Anderson 1984; Clark 1987; Errington 1946). We considered several alternative explanations for comparative survival rates at the donor and control subcomplexes but found none of them to be plausible. For example, predation is an important cause of ferret mortality (Biggins 2000), and predation rates were not necessarily uniform across donor and control subcomplexes. A study conducted on these subcomplexes during 1996–1997 demonstrated higher predation rates for ferrets released on the donor subcomplex than for those released on the control subcomplex (Poessel et al. 2011), mostly due to habitat features at the donor subcomplex that disproportionately favored use by great horned owls (*Bubo virginianus*). If this trend continued through 1999, it should have caused underestimation of the benefit of removing ferrets from the donor subcomplex to reduce their density. The initially higher overall density of ferrets at the control subcomplex than at the donor subcomplex should also have resulted in underestimation of the effect of our manipulation of density. Density of prey likely influences ferret behavior and survival (Biggins et al. 2006b), but prairie dog densities were only marginally lower at the donor subcomplex than at the control subcomplex. At both subcomplexes prairie dog densities were well above the threshold (18 prairie dogs/ha) at which territorial behavior of ferrets is thought to increasingly supplant prey density with regard to influence on female ferret spacing (Biggins et al. 2006d). Moreover, donor and control subcomplexes were near the threshold (42 prairie dogs/ha) above which prey density might not influence ferret spacing (Biggins et al. 2006d).

Survival rates of young male and female ferrets seem to become increasingly disparate during their 1st year of life, presumably as a result of increased intraspecific (and intrasexual) competition. Our results are similar to those of previous studies that failed to detect effects of sex during initial releases of ferrets (Biggins et al. 1998, 1999). Trends toward increasing disparity between survival of males and females begin to appear during analyses of annual survival (Biggins et al. 1998), which would be expected given the skewed sex ratios in populations of adult ferrets (Forrest et al. 1988).

Relative movements and survival rates of the wild-born ferrets in our study supported the contention that their translocation is an efficient strategy for establishing new populations; however, we do not suggest that the generally greater movements and lower survival of the captive-born and conditioned ferrets we released, compared to their wild-born counterparts, make the captive-born ferrets poor candidates for reintroduction. The survival rates of captive-born ferrets in our study compare favorably with survival of released ferrets that have served to establish populations at other reintroduction sites (Biggins et al. 1998).

Translocation of wild-born ferrets to establish or augment populations elsewhere can be considered as assisted dispersal. The distribution of prairie dog colonies is now fragmented, and distances between patches of suitable ferret habitat can be long. Assisted dispersal should increase the probability of successful colonization by young ferrets if the stresses of transfer do not increase rates of mortality of transported kits. The tendency for higher survival of WILD translocated kits compared to kits at the control subcomplex (Fig. 4) provides evidence that any adverse effects of the translocation process were countered by the advantages of colonizing vacant habitat. The seemingly improved survival of kits left at the donor subcomplex, and the evidence for lack of impact on the resident adults, provide additional incentives to pursue active translocation of ferrets as a management practice. Nevertheless, attributes of the donor population must be considered

carefully (e.g., size, carrying capacity, presence of disease, predation rates, and quality of habitat) to manage risk. For example, uncertainties caused by demographic stochasticity might preclude removing ferrets from small populations, and large populations that show chronically low or negative population growth rates would be equally problematic as donors. The role of density dependence in rates of survival and fecundity of ferret populations is thus an important topic that deserves further study.

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Literature Cited

Biggins, D. E. 2000. Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*Mustela eversmannii*): conservation and evolutionary implications. Ph.D. dissertation, Colorado State University, Fort Collins.

Biggins, D. E., J. L. Godbey, L. R. Hanebury, B. Luce, M. R. Matchett, and A. Vargas. 1998. The effect of rearing methods on survival of reintroduced black-footed ferrets. Journal of Wildlife Management 62:643–653.

Biggins, D. E., J. L. Godbey, M. R. Matchett, L. R. Hanebury, T. M. Livieri, and P. E. Marinari. 2006a. Monitoring black-footed ferrets during reestablishment of free-ranging populations: discussion of alternative methods and prescription of minimum standards. Pp. 155–174 in Recovery of the black-footed ferret—progress and continuing challenges (J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, eds.). United States Geological Survey Scientific Investigations Report 2005—5293.

Biggins, D. E., J. L. Godbey, M. R. Matchett, and T. M. Livieri. 2006b. Habitat preferences and intraspecific competition in black-footed ferrets (*Mustela nigripes*). Pp. 129–140 in Recovery of the black-footed ferret—progress and continuing challenges (J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, eds.). United States Geological Survey Scientific Investigations Report 2005—5293.

Biggins, D. E., J. L. Godbey, B. J. Miller, and L. R. Hanebury. 2006c. Radio-telemetry for black-footed ferret research and monitoring. Pp. 175–189 in Recovery of the black-footed ferret—progress and continuing challenges (J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, eds.). United States Geological Survey Scientific Investigations Report 2005—5293.

Biggins, D. E., J. M. Lockhart, and J. L. Godbey. 2006d. Evaluating habitat for black-footed ferrets: revision of a former model. Pp. 143–150 in Recovery of the black-footed ferret—progress and continuing challenges (J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, eds.). United States Geological Survey Scientific Investigations Report 2005—5293.

Biggins, D. E., B. J. Miller, T. W. Clark, and R. P. Reading. 2006e. Restoration of an endangered species: the black-footed ferret. Pp. 581–585 in Principles of conservation biology (M. J. Groom, G. K. Meffe, and C. R. Carroll, eds.). 3rd ed. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

Biggins, D. E., A. Vargas, J. L. Godbey, and S. H. Anderson. 1999. Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*). Biological Conservation 89:121–129.

Burnham, K. P., and D. R. Anderson. 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. Ecology 65:105–112.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph 5, Bethesda, Maryland.

Campbell, T. M., III, D. Biggins, S. Forrest, and T. W. Clark. 1985. Spotlighting as a method to locate and study black-footed ferrets. Pp. 24.1–24.7 in Black-footed ferret workshop proceedings, 18–19 September 1984 (S. H. Anderson and D. B. Inkley, eds.). Wyoming Game and Fish Department, Cheyenne.

Clark, T. W. 1989. Conservation biology of the black-footed ferret (*Mustela nigripes*). Wildlife Preservation Trust Special Scientific Report 3, EcoHealth Alliance, New York.

Clark, W. R. 1987. Effects of harvest on annual survival of muskrats. Journal of Wildlife Management 51:265–272.

Errington, P. L. 1946. Predation and vertebrate populations. Quarterly Review of Biology 21:144–177.

Ewer, R. F. 1973. The carnivores. Cornell University Press, Ithaca, New York.

Fagerstone, K. A., and D. E. Biggins. 2011. Late summer and early fall home range of black-footed ferrets at Meeteetse, Wyoming. Journal of Mammalogy 92:705–709.

Fagerstone, K. A., and B. E. Johns. 1987. Transponders as permanent identification markers for domestic ferrets, black-footed ferrets, and other wildlife. Journal of Wildlife Management 51:294–297.

Forrest, S. C., et al. 1988. Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981–1985. Journal of Mammalogy 69:261–273.

Gaines, S. D., and M. W. Denny. 1993. The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. Ecology 74:1677–1692.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Gaynor, J. S., J. Wimsatt, C. Mallinckrodt, and D. Biggins. 1997. A comparison of sevoflurane and isoflurane for short-term anesthesia in polecats. Journal of Zoo and Wildlife Medicine 28:274–279.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477–480.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Jule, K. R., L. A. Leaver, and E. G. L. Lea. 2008. The effects of captive experience on reintroduction survival in carnivores: a review and analysis. Biological Conservation 141:355–363.

KLEINBAUM, D. G., L. L. KUPPER, AND K. E. MULLER. 1988. Applied regression analysis and other multivariable methods. 2nd ed. PWS-KENT Publishing Company, Boston, Massachusetts.

KRUUK, H. 1978. Spatial organization and territorial behaviour of the European badger *Meles meles*. Journal of Zoology (London) 184:1–19.

LEBRETON, J. D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

LEOPOLD, A. 1933. Game management. Charles Scribner's Sons, New York.

LOCKIE, J. D. 1966. Territory in small carnivores. Symposia of the Zoological Society of London 18:143–165.

MILLER, B., R. READING, AND S. FORREST. 1996. Prairie night black-footed ferrets and the recovery of endangered species. Smithsonian Institution Press, Washington, D.C.

POESSEL, S. A., S. W. BRECK, D. E. BIGGINS, T. M. LIVIERI, K. R. CROOKS, AND L. ANGELONI. 2011. Landscape features influence postrelease predation on endangered black-footed ferrets. Journal of Mammalogy 92:732–741.

SJOASEN, T. 1996. Survivorship of captive-bred and wild-caught reintroduced European otters *Lutra lutra* in Sweden. Biological Conservation 76:161–165.

SJOASEN, T. 1997. Movements and establishment of reintroduced European otters *Lutra lutra*. Journal of Applied Ecology 34:1070–1080.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.

WILLIAMS, E. S., E. T. THORNE, M. J. G. APPEL, AND D. W. BELITSKY. 1988. Canine distemper in black-footed ferrets (*Mustela nigripes*) from Wyoming. Journal of Wildlife Diseases 24:385–398.

WILSON, A. C., AND M. R. STANLEY PRICE. 1994. Reintroduction as a reason for captive breeding. Pp. 244–264 in Creative conservation: interactive management of wild and captive animals (P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, eds.). Chapman and Hall, London, United Kingdom.

WOLF, C. M., B. GRIFFITH, C. REED, AND S. A. TEMPLE. 1996. Avian and mammalian translocations: update and reanalysis of 1987 data. Conservation Biology 10:1142–1154.

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