Effect of Family Support on the Success of Translocated Black-Tailed Prairie Dogs

D. M. SHIER*

Animal Behavior Graduate Group, University of California, One Shields Avenue, Davis, CA 95616, U.S.A.

Abstract: *Translocation has become a widely used conservation tool but remains only marginally successful. High mortality is often attributed to predation, but for highly social species, founder group composition may also play a critical role in postrelease survival. I compared the fitness of black-tailed prairie dogs translocated with or without their family groups. Animals in the family translocated groups were individually marked and observed until coterie membership was determined. Nonfamily translocated animals were trapped without regard to family membership. I measured fitness by retrapping all marked animals remaining at release sites in the summer following release. Family translocated animals were five times more likely to survive and had significantly higher reproductive success than those translocated without families. Predation was an important impediment of translocation success, but family translocation significantly reduced the success of predators on newly established prairie dog colonies. Postrelease survival was also affected by the timing of release, but appeared to be more important for juveniles than adults. These results demonstrate the importance of considering familiarity when translocations are required. More broadly, these results illustrate the value of applying animal behavior to conservation efforts and suggest that other species dependent on social interactions for survival and reproduction may benefit substantially from the maintenance of social groups during translocations.*

Keywords: behavior, familiarity, founder group, prairie dog, translocation

Efecto del Soporte Familiar sobre el Éxito de Perros de la Pradera Translocados

Resumen: *La translocación se ha convertido en una herramienta de conservación ampliamente utilizada pero solo es marginalmente exitosa. La alta mortalidad a menudo es atribuida a la depredación, pero para especies altamente sociables, la composición del grupo fundador también puede jugar un papel crítico en la supervivencia post liberación. Comparé la adaptabilidad de perros de la pradera translocados con o sin sus grupos familiares. Los animales en los grupos familiares translocados fueron marcados individualmente y observados hasta que se determinó una asociación de camarilla. Los animales translocados sin su grupo familiar fueron capturados sin tomar en cuenta su asociación familiar. Medí la adaptabilidad mediante la recaptura de todos lo animales marcados que permanecían en los sitios de liberación el verano siguiente a la liberación. Los animales translocados con familia tuvieron una probabilidad de supervivencia cinco veces mayor y su éxito reproductivo fue significativamente mayor que la de los translocados sin familia. La depredación fue un impedimento importante para el éxito de la translocación, pero la translocación con familia redujo significativamente el éxito de los depredadores sobre colonias de perros de la pradera establecidas recientemente. La supervivencia post liberación también fue afectada por el tiempo de liberación, pero pareció ser más importante para juveniles que para adultos. Estos resultados demuestran la importancia de considerar la familiaridad cuando se requieren translocaciones. Más ampliamente, estos resultados ilustran el valor de aplicar el comportamiento animal a los esfuerzos de conservación y sugieren que otras especies*

dependientes de interacciones sociales para su supervivencia y reproducción pueden beneficiarse sustancial-mente del mantenimiento de grupos sociales durante las translocaciones.

Palabras Clave: comportamiento, familiaridad, grupo fundador, perro de la pradera, translocación

Introduction

The primary goal of translocation is to increase the viability of a species by releasing individuals into new sites within the species' historic range (Griffith et al. 1989). Although this conservation tool is increasingly popular, most translocations fail because of high postrelease mortality (Fischer & Lindenmayer 2000). Blame has long been placed on the behavioral responses of the translocated animals (Kleiman 1989), but tests of this hypothesis await controlled experimentation.

Translocated animals must immediately find shelter and may have to modify the new site (e.g., by digging burrows). Until these modifications are complete, predation rates can be high (Truett et al. 2001). Vulnerability to predation may also be elevated by dispersal from a release site, a common response to translocation (Kleiman 1989). In social species, dispersal may occur in part because translocated animals typically lack familiarity with individuals at the release site (Kleiman 1989).

Recent efforts to enhance the effectiveness of translocation have focused on questions about the composition of the founding population, such as age distribution, sex ratio, group size, and genetic diversity (e.g., Bodkin et al. 1999). Yet, translocation research has essentially ignored the relationships between individuals (e.g., parent and offspring, siblings). The benefits of group living have been documented for many taxa (e.g., Dugatkin 1997). Experienced kin help shape the development of survival skills in juveniles, from food finding to predator defense to mate selection (Galef & Laland 2005). Social relationships are especially likely to influence post-translocation survival in colonial species (Kleiman 1989) but have only been examined in a controlled way in territorial birds (Armstrong 1995).

I examined the impact of preserving family groups in a large-scale translocation of black-tailed prairie dogs (*Cynomys ludovicianus*). Prairie dogs are obligately social and live in territorial harem-polygynous family groups (coteries) within larger colonies (Hoogland 1995). Females are philopatric; thus, coteries contain closely related females (Hoogland 1995). Genetic differentiation between coteries within a colony can be as high as between colonies (Dobson et al. 1997).

Black-tailed prairie dogs are considered keystone species because they play an integral role in the grassland ecosystem (Kotliar et al. 2006). They have declined an estimated 98% from the number that occupied between 0.4 and 1 million km^2 of the Great Plains before European settlement (Proctor et al. 2006). Most remaining colonies are small (<40 ha) and isolated. Until 2004 the U.S. Fish and Wildlife Service (USFWS) had designated the black-tailed prairie dog as a candidate species for listing under the Endangered Species Act (USFWS 2000). That designation stimulated conservation efforts by private organizations and by 11 states in the species' original range. Current conservation methods include translocations to supplement small populations or to restore extirpated ones.

Prairie dog translocation methodology has been far from effective. Until recently, survival rates rarely exceeded 40% and were frequently much lower (Truett et al. 2001). Since then extensive numbers of translocations have been conducted, the success of which has been mixed (Long et al. 2006). Predation is a major cause of death following release in translocated prairie dogs (Truett et al. 2001). Current methods are not sensitive to the importance of social factors; prairie dogs are trapped and translocated without regard to family membership and before newly emergent young are likely to have developed appropriate survival skills.

Keeping family groups together during translocation is not trivial because it requires exhaustive trapping of individual coteries. Therefore, the main goal of this study was to determine whether maintaining family groups could be significantly more effective and economical than translocating animals without regard for family membership.

Methods

Study Site and Subjects

I studied prairie dogs on the Vermejo Park Ranch in Colfax County, New Mexico (36°N, 104°W, elevation 1850 m). *C. ludovicianus* inhabit the short-grass prairies in the southeastern portion of the ranch.

During the springs of 2001 and 2002, the wildlife manager on the property and I selected 10 uninhabited sites within the historical range of black-tailed prairie dogs, based on soil quality (deep, well-drained soils of sandy loam clay texture), vegetation cover, slope (<6%), and location on the ranch. Pairs of family translocated (FT) and nonfamily translocated (NFT) sites were matched for soil, vegetation cover, slope, proximity on the ranch, and sex and age-class ratios to control for these factors. To limit dispersal and allow prairie dogs to acclimate to the new site, sites were prepared for "soft release" by installing 20 acclimation cages at each site (for general translocation methods see Long et al. 2006).

Subjects were 973 wild-caught black-tailed prairie dogs (232 juvenile males, 212 adult males, 269 juvenile females, 260 adult females) divided into two treatment groups: FT (moved in intact coteries; $n = 484$ adults [≥ 1 year old] and juveniles into five sites, 87–100/site) and NFT (moved without consideration of coterie membership; $n = 489$ into five sites, 88–103/site). I refer to areas where animals were to be released as *sites* but changed this terminology to *colonies* once prairie dogs established burrow systems in these sites.

Determining Coterie Membership; Capturing and Holding Animals for Release

I determined coterie (family) membership during March and April by trapping, sexing, aging, dye marking, ear tagging, releasing, and then observing interactions and sleeping patterns of adult prairie dogs from 44 coteries in five distinct source colonies. I chose coteries randomly from the edge and center of colonies to maximize variability in predator–vigilance behavior and genotype. From mid-June to August, all animals from the designated coteries were trapped again, including previously marked adults and emergent young. Age from emergence was assigned to each FT juvenile through observations of first emergence from the natal burrow (in days). The ratio of adults to juveniles and males to females was determined by the natural variation in the field.

All prairie dogs were transferred to and maintained in an indoor, temperature-controlled facility and held until 100 animals were captured (<2 weeks). The NFT animals were trapped following standard methods (removing animals from large source colonies and mixing them in holding cages; Long et al. 2006) and were weighed, ear tagged, aged, sexed, and held in the holding facility under the same conditions. All transfers occurred between the end of June and August of 2001 and 2002.

Release to New Site

Once approximately 100 animals were captured, they were transported to acclimation-cages at one of the new sites. I placed four to seven animals in an acclimation-cage, depending on number and sex ratio of animals in a coterie. If a coterie contained fewer than seven members, all animals were placed into the same acclimation cage. Otherwise. I split the coterie among adjacent acclimation cages. To verify that the number of individuals in an acclimation cage did not affect postrelease survival, I used logistic regression, clustered by family. Survival was not related to number of individuals in an acclimation cage (logistic regression: Wald $\chi^2 = 2.39$, OR $= 1.29$, $p = 0.122$). For the NFT animals, one male, two females, and two pups were placed in each acclimation cage at a new site. The ratio of adult males to adult females in acclimation cages varied slightly depending on the number of each released on a site. The FT and NFT colonies in a

matched pair were released within 2 weeks of each other to control for possible seasonal effects. Family members were transferred to acclimation cages at five sites. Non-family members from three source colonies were transferred into acclimation cages at five other sites (five individuals per burrow). At the end of the acclimation period, the aboveground portions of the acclimation cages were removed. I attempted to minimize predation by driving by and chasing potential predators (coyotes and badgers) off each pair of sites at least three times per week for the first month following release.

Postrelease Behavior

My field assistants and I observed the prairie dogs during the first 2 hours following release from the acclimation cages and documented the presence or absence of the following behaviors: alarm calling, allogrooming, foraging, ranging outside mowed areas, tactile greeting, and play. Two weeks following release, I drove a vehicle to within 150 m of each 2001 release site and used instantaneous scan sampling to quantify the number of individuals: vigilant (bipedal stance, oriented toward vehicle), foraging (placing vegetation in mouth with forefeet), or digging (movement of dirt with forefeet, hindfeet, or both). One year after release, we observed each of the 10 new sites for a minimum of 25 hours. I drove to within 100 m of the edge of a colony, selected a focal "coterie" at random, and observed all coterie members aboveground with binoculars for 1 hour. Three to seven coteries were observed per day, and all coteries were observed one to three times over the course of the summer for a total of 386 hours of focal coterie observation.

Burrow Establishment and Habitat Features

I counted burrows and used a GPS receiver to document the position of each burrow established on each new site at seven different points following the 2001 release. I used the same procedure for the 2002 release, but I assessed burrows only once, 1 year after release.

Although I paired colonies by vegetation cover, soil quality, and slope, I assessed differences in these variables to confirm that no significant differences existed between sites within a pair. I conducted vegetation analysis of sample plots at each new colony and each source colony to determine percent vegetation cover. I placed a 1×1 m square quadrat (with 10-cm tic marks) randomly at 10 locations within each colony. I took digital photographs of each quadrat under cloudy skies or low sun angles with a Canon 10D camera through a 20–35 mm lens (Canon USA, Lake Success, New York). Images were transferred to Adobe Photoshop (Adobe Systems, San Jose, California) and overlayed with a 10×10 cell grid to obtain estimates of mean total percentage of vegetation cover and mean percentage of open soil (Causton 1988) for each quadrat. Cells (10×10 cm) with <25%

cover were coded as 0, cells with 25–75% cover were coded as 0.5, and cells with >75% cover were coded as 1. On the basis of a U.S. Department of Agriculture map of Colfax County, New Mexico (Anderson et al. 1982), I determined soil associations within the study site. To determine soil quality, permeability, rooting depth, and vegetation type supported, I manually overlaid latitude and longitude coordinates of new prairie dog colonies on soil-association maps. Slope of sites was calculated with a clinometer.

Measuring Translocation Success and Population Viability

I measured translocation success by retrapping all ear-tagged animals present at the release site and counting emergent young in the spring or summer following release (May–July 2002 for the six colonies translocated in 2001 and May–June 2003 for four colonies translocated in 2002). Colonies in a matched pair were trapped at the same time to avoid effects of time of trapping on survival estimates. I used dye marking and observation to verify that all prairie dogs remaining at a colony had been trapped. I walked the area in grids to determine whether there were any active burrows within a 1.5-km radius, placing traps and bait at those burrows and observing until I had trapped any animals on the outskirts. To further ensure that no individuals were living outside of new colonies, I took aerial photographs from an airplane at 90–150 m altitude and examined them for active burrows within a 4-km radius of each colony. I did not distinguish between dispersal and mortality because dispersing animals do not contribute to the population viability of a release site. Nevertheless, successful dispersal >3 km is extremely rare in the wild (Garrett & Franklin 1988), probably because long-distance (>1 km) dispersers are prone to heavy mortality because of predation and injurious interactions with residents of colonies into which they are attempting to immigrate (Garrett & Franklin 1988). Therefore, I considered a prairie dog deceased if it was not trapped at the colony in which it was released or at another new colony located within 3 km of the release site. To determine whether viable populations were established at the colonies, I estimated colony size during the summer of 2003 for all colonies established in 2001. Survival was estimated by observing and trapping all animals at a random subset of five burrow clusters (presumed coteries; a set of active burrows separated from other burrows by ≥10 m representing 25–80% of existing "coteries") on a new colony and multiplying the average number of animals of each age class in the focal burrow clusters by the total number of burrow clusters on a colony. I tested the accuracy of this technique by estimating the number of animals on the four 2002 release sites prior to exhaustive trapping. The estimates were within 8% of the actual numbers present for both juveniles and adults (number estimated vs. number present).

Data Analysis

Because half of the animals were statistically nested within families, I used multilevel analytic techniques and regression with a cluster function to take into account the potential for correlated data within families. Standard regression techniques could result in biased results because they assume independence of the data from each individual. I conducted multilevel analyses with hierarchical general linear modeling (HGLM) with survival (0, not surviving at release colony; 1, surviving at release colony) as the outcome variable. I used a Bernoulli model among the nonlinear multilevel model options. Analysis of the best-fit model was conducted with likelihood ratio tests. Possible predictor variables included (1) age class of the individual before translocation (0, juvenile; 1, adult); (2) sex of the individual (0, male; 1, female); and (3) weight prior to translocation. Possible family level predictors included (1) translocation method (0, nonfamily; 1, family); (2) time of release (day of release counted from June 1); (3) predation pressure (scaled from 1 to 10 on the basis of the number of acclimation cages and underground retention baskets dug out by predators by the following spring, total amount of coyote scat present on a colony, and total number of predators observed on a site); (4) vegetation cover on site at release; (5) difference in vegetation cover between source and release site; (6) soil type (on a scale of 1–10 based on soil quality, water permeability, rooting depth, and vegetation type supported); (7) terrain (slope of the release site); and (8) pair designation (pair was included in the model to control for any differences among sites in a pair that were not included in the model, e.g., rainfall). The model yielding the best fit to the data was as follows:

$$\text{prob}(Y = 1/\beta) = P$$

$$\log[P/(1 - P)]$$
$$= \gamma_{00} + \gamma_{01} * (\text{pair1})$$
$$+ \gamma_{02} * (\text{pair2}) + \gamma_{03} * (\text{pair3})$$
$$+ \gamma_{04} * (\text{pair4}) + \gamma_{05} * (\text{translocation method})$$
$$+ \gamma_{06} * (\text{predation pressure}) + \gamma_{07} * (\text{time of release})$$
$$+ (\text{sex})[\gamma_{10} + \gamma_{11} * (\text{translocation method})]$$
$$+ (\text{age class})[\gamma_{20} + \gamma_{21} * (\text{time of release})] + \mu_0.$$

To determine whether translocation method, predation or time of release had a greater influence on survival after release, I used Akaike's information criterion (AIC; $\text{AIC} = \text{deviance} + 2K$, where K is the number of fitted parameters) and calculated Akaike weights ($w_i = \exp[-\Delta_i/2]/\Sigma \exp[-\Delta_i/2]$) to assess the strength of evidence that the selected model was the Kullback–Leibler best model in the set of models considered (Burnham & Anderson 2002). For the best-fitting model and each submodel, I calculated deviance values in HGLM. I considered the model with the smallest AIC to be the best-fitting

model; this was in agreement with the likelihood-ratio tests from the HGLM analysis. I calculated AIC differences between the best model and the other candidate models to determine the relative ranking of the models. Models for which $\Delta_I \leq 2$ had substantial support and were considered for biological importance (Burnham & Anderson 2002). Parameter importance was assessed by summing the Akaike weights for each model in which a parameter was present. The larger this sum of weights, the more important the variable (Burnham & Anderson 2002).

The NFT prairie dogs were coded as having a unique family and consequently their family size was one. Therefore, examination of the relationship between number of individuals in a family and survival was restricted to FT animals and was analyzed with logistic regression clustered by family. The relationship between juvenile weight at translocation and survival was examined with the same analytic technique.

I used a Poisson regression clustered by family to analyze reproductive success. Reproductive success was analyzed only for females that survived at the release site in terms of mean number of emergent pups per number of adult females, mean litter size (for females that weaned a litter) and percentage of females that weaned a litter.

I used one-way analysis of variance (ANOVA) to compare the proportion of individuals that were vigilant, foraging, or digging in the two translocation groups and repeated-measures ANOVA to compare the number of burrows that were established over the six time intervals. Paired *t* tests were applied to analyses of vegetation cover, soil quality, and slope of terrain. No significant differences existed among colonies in a pair in terms of soil quality ($t = -1.43$, df $= 4$, $p = 0.226$), percent vegetation cover ($t = 1.09$, df $= 4$, $p = 0.336$), or slope of terrain ($t = 1.01$, df $= 4$, $p = 0.370$).

Logistic and Poisson regressions were carried out in Stata Version 8.2 for Windows (Stata, College Station, Texas). The HGLM analysis was conducted in HLM (Raudenbush et al. 2003) because it allows modeling of nested data with binomial outcome variables. The remaining statistical analyses were performed in SPSS (SPSS, Chicago, Illinois).

Cost-Effectiveness

To determine how cost-effective FT was in the present study compared with NFT, I calculated the cost of each method in terms of hours invested (including mark, recapture, and observation for the FT treatment). I then used this number to project the total cost of establishing a given number of prairie dogs (defined as number of prairie dogs present on the site) 2 years after translocation. All calculations were based on data from the three colonies established during the 2001 release. For the initial calculation, I used the following equation:

$$c = h/e, \tag{1}$$

where h is the total number of trapping hours invested, e is the total number of prairie dogs (surviving $+$ young of the year) established on all three colonies of each treatment type 2 years after release, and thus c is the cost in terms of number of hours expended per prairie dog.

To estimate the number of prairie dogs needed to establish a given number of animals 2 years after translocation, I used the following equation:

$$n = (i + s)(g/e), \tag{2}$$

where i is the total number of prairie dogs initially trapped to establish the three colonies in each treatment, s is the total additional prairie dogs trapped for supplementation, and g is the goal in terms of number of prairie dogs to be established. For illustration purposes, I set g to 1000, and thus n is the number of prairie dogs needed to establish 1000 prairie dogs 2 years after release.

The total cost in terms of hours invested also includes the number of hours required for postrelease monitoring of new sites (m). Here I assumed two trips/day for 30 days postrelease, where each trip took 0.5 hours. Furthermore, if additional animals are required to reach the goal of 1000 prairie dogs, one must also take into account the additional acclimation cages (a), holding cages (H), and trapping time required for each method. I assumed a mean of 5 individuals/acclimation cage, no more than 15 individuals per holding cage, and that no acclimation or holding cages is needed for the supplement at year 1. Thus, a is given by $[i(g/e)]/5$ and H is given by $[i(g/e)]/15$. Assuming that each colony is established with 100 animals, then (t) total number of trapping hours required to establish 1000 prairie dogs 2 years after release is

$$t = (n/100) * h. \tag{3}$$

I determined the cost of establishing 1000 prairie dogs 2 years after release by calculating (1) the number of hours invested in trapping and monitoring, ($t + m$); (2) the total number of prairie dogs required (n); and (3) the total number of acclimation cages and holding cages (a and H) for each of the two treatment methods.

Results

The FT prairie dogs outperformed NFT prairie dogs in survival and reproductive success (Fig. 1). Family translocation increased survival by a factor of five compared with NFT (Fig. 1a). The importance of family relationships for survival was further demonstrated by the pattern of sex differences. Adults of both sexes in the FT colonies survived at higher rates than NFT animals; however, the differences were greater for adult females than for adult males. Independent of sex and translocation method, adults survived at higher rates than juveniles.

The FT females showed higher reproductive success 1 year after release than did NFT females (Fig. 1). Among the
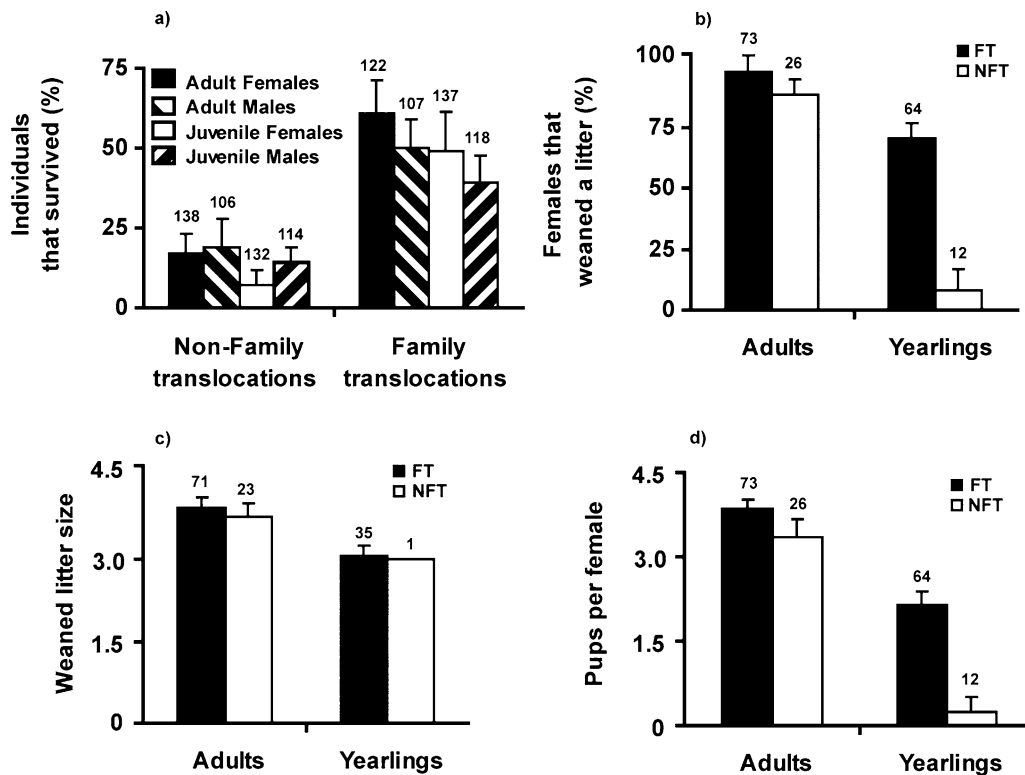
Figure 1. (a) Survivorship of family translocations (FT) versus survivorship of nonfamily translocations (NFT) of black-tailed prairie dogs (hierarchical general linear modeling): translocation method, t = 4.92, df = 534, p < 0.0001 for all age and sex classes combined; translocation method × sex, t = 2.44, df = 961, p = 0.015; translocation method × age, t = 2.81, df = 961, p = 0.005). Differences in reproductive success of FT verses NFT adult and yearling females in terms of (b) mean number of pups per female (for all females that survived on a colony, + SE), multiple Poisson regression (Wald χ^2 = 54.37; translocation method, OR = 20.08, p = 0.003; age, OR = 934.49, p < 0.0001); (c) mean litter size (for females that weaned a litter + SE), multiple Poisson regression (Wald χ^2 = 39.11; translocation method, OR = 2.41, p = 0.381; age, OR = 518.01, p < 0.0001); and (d) percentage of surviving females that weaned a litter + SE), multiple Poisson regression (Wald χ^2 = 21.96; translocation method, OR = 27.39, p = 0.001; age, z = 29.08, p = 0.001). The number above each SE line is the sample size.

females that successfully weaned pups, there was no difference in litter size between FT and NFT colonies. However, females in FT colonies were more likely to produce weaned young (Figs. 1c & 1d). Overall, the mean number of emergent pups per reproductive female was higher for FT than NFT colonies (Fig. 1b). These treatment effects appeared to be driven primarily by yearling females (multiple Poisson regression: yearlings, Wald χ^2 = 5.47, OR = 10.38, p = 0.019; adults, Wald χ^2 = 0.73, OR = 2.36, p = 0.392; Figs. 1b–d).

For both treatment groups in this study, survival decreased significantly with predation pressure (as estimated from predator signs and sightings, not predation events) (Fig. 2b). However, the difference in the survival rate between FT and NFT colonies could not be attributed to differential predation pressure because FT colonies tended to experience higher predation pressures than NFT colonies: 5.19 ± 0.12 versus 2.81 ± 0.09 (mean ± SE, n = 5 colonies each). In the FT treatment, survival

increased with family size (logistic regression: Wald χ^2 = 25.06, OR = 1.06, p < 0.0001).

Survival increased steadily during the summer months. Late season (August) translocations had the highest survival regardless of predation pressure and translocation method (Fig. 2a). This pattern was more pronounced in juveniles than adults (HGLM interaction between age and time of release: t = −1.99, n = 961, p = 0.038). Both age from emergence and weight were significant predictors of survival for FT juveniles (multiple logistic regression: Wald χ^2 = 32.73, age, OR = 1.02, p = 0.035; weight, OR = 1.00, p = 0.039; age data not available for NFT animals, but weight data were not significant [logistic regression: Wald χ^2 = 20.75, OR = 4.95, p = 0.110]).

Behavioral differences between FT and NFT animals were apparent upon release at the translocation sites and the nature of those differences helped explain the greater success of FT translocations. Within the first 2 hours after release, prairie dogs translocated with family members
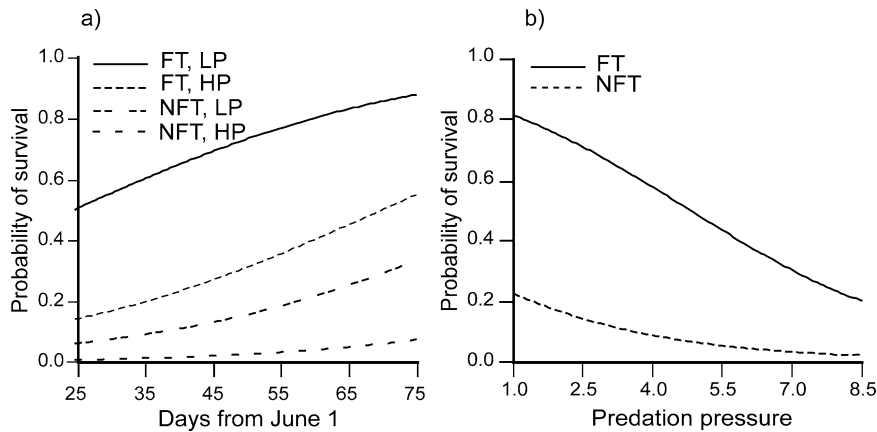
Figure 2. (a) Predicted probability of survival from best-fitting model in relation to time of release for family translocated (FT) and nonfamily translocated (NFT) prairie dogs under low predation (LP) (2 points) and high predation (HP) (8 points). Predation was scaled from 1 to 10 points. (b) Predicted probability of survival from best-fitting model of FT and NFT (info. provided in key) under full range of predation pressure (1–10) (hierarchical general linear modeling; predation pressure, t = −1.35, df = 534, p < 0.02).

largely remained near the acclimation cages in which they were released and traveled between adjacent acclimation cages. These individuals exhibited interactions typical of family groups (e.g., tactile greetings,"ID kissing; " [King 1955]), play, and allogrooming; [Hoogland 1995]) and were seen foraging and alarm calling. In contrast, NFT prairie dogs appeared disoriented on release and ranged outside the release sites. With only one exception (a yearling male), all the animals that dispersed and were trapped in other newly established colonies were translocated without their family members ($n = 9$ adult males and 5 adult females).

These behavioral differences remained pronounced 2 weeks after release and persisted for at least 1 year (Figs. 3a & 3b). The proportion of individuals that were vigilant on a colony was higher for NFT than for FT colonies; FT animals spent more time foraging and digging burrows. Prairie dogs translocated in intact coterie units excavated more burrow entrances and did so faster than NFT prairie dogs over the 2 years following release (Fig. 4).

The most parsimonious model for the probability of survival contained all three predictor variables (deviance = 2752.013, $n = 973$, $K = 13$, AIC = 2778.013, Δ_i = 0.00, $w_i = 0.608$). Candidate models included only translocation method and predation pressure (deviance = 2758.663, $n = 973$, $K = 11$, AIC = 2780.663, $\Delta_i = 2.65$, $w_i = 0.161$) or translocation method and time of release (deviance = 2756.056, $n = 973$, $K = 12$, AIC = 2780.056, $\Delta_i = 2.043$, $w_i = 0.2189$). Translocation method was the best predictor of survival, followed by predation pressure (given the candidate models and data; parameter importance weights were translocation method = 1.00, predation pressure = 0.827, time of release = 0.769).
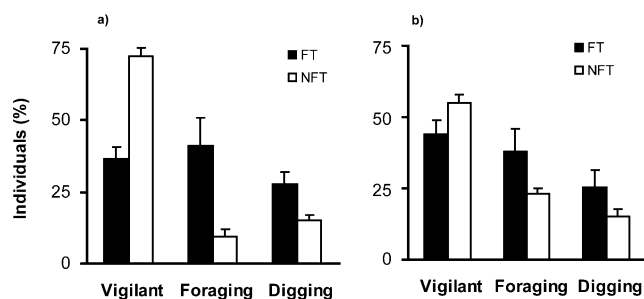

Figure 3. (a) Behavioral differences 2 weeks after release for family translocated (FT) and nonfamily translocated (NFT) prairie dogs in terms of the proportion (+ SE) of individuals that were vigilant on a colony (F = 60.50, df = 1,4, p < 0.001), foraging (F = 62.1, df = 1,4, p < 0.001), or digging (F = 16.05, df = 1,4, p < 0.02). (b) Behavioral differences 1 year after release (proportion vigilant, F = 4.84, df = 1,8, p = 0.048; proportion foraging, F = 5.59, p = 0.04; proportion digging, F = 6.83, df = 1,8, p = 0.034).
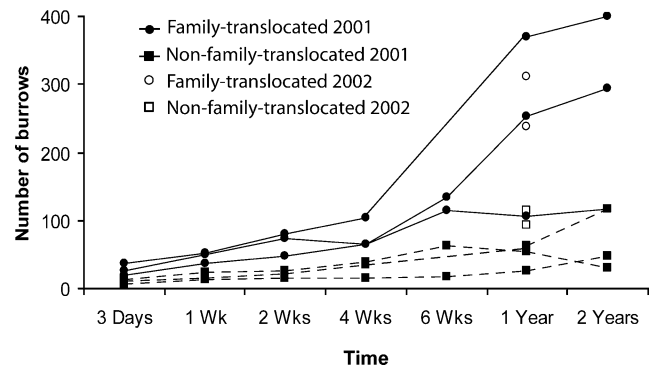

Figure 4. Length of time for burrow establishment for each of 10 prairie dog release sites. For six releases in 2001, burrow counts are provided for three family translocated (FT) and three nonfamily translocated (NFT) colonies over the first 2 years after release (3–5 days, 1 week, 2 weeks, 4 weeks, 6 weeks, 1 year, and 2 years; repeated measures ANOVA, F = 8.48, p < 0.04). For four releases in 2002, burrow counts at two FT and two NFT prairie dog colonies were made only once, at 1 year after release.

Two of the three NFT colonies released in 2001 had <7% survival by the following spring (colony 2001-01 had seven animals and colony 2001-03 had four). By June, one of these colonies (2001-01) had no remaining animals. Therefore, after the first year (summer 2002), additional animals ($n = 10–35$) were added to colonies 2001-01 and 2001-03. In spite of supplementation, NFT colonies continued to decline in size relative to FT colonies through the summer of the second year (NFT adults: 13.4 ± 4.7; NFT juveniles: 15.5 ± 11.7 vs. FT adults: 81.6 ± 39.9; FT juveniles: 199.8 ± 62.4 (mean $\pm$ SEs) paired t test: $t = -2.916$, $p < 0.05$).

Calculation of the cost-effectiveness of the two methods indicated that FT was considerably more cost-effective in terms of the number of hours invested per surviving prairie dog and the total investment in establishing 1000 prairie dogs 2 years after release (Table 1).

Discussion

My results indicate that black-tailed prairie dogs translocated in intact family groups were significantly more likely to survive than those translocated without family members and provide the first experimental evidence that founder-group familiarity significantly increases translocation success. This effect was more pronounced for adult females than for adult males and is consistent with the natural history of the species. In the wild, most females remain with their families their entire lives, whereas males typically disperse after the first year (Hoogland 1995).

Overall, FT females reproduced more than NFT females, but the yearling females drove this result. Yearling females translocated with family members were more likely to wean a litter than yearling females translocated without family members. Of surviving FT yearling females, 70.3% weaned a litter. Using 14 years of data on annual reproductive success, Hoogland (1995) showed that only 9% of yearling females successfully wean a litter on a well-established colony, perhaps because these females are under intense pressure from infanticidal females. In newly established colonies, however, competition for limited resources is reduced because food and space are abundant and yearling females may experience reduced infanticide.

This study was carried out in collaboration with the Turner Endangered Species Fund (TESF) biologists who have been conducting prairie dog translocations in South Dakota and New Mexico since 1995 (Long et al. 2006). Another translocation experiment conducted by TESF in South Dakota attempted to determine the effect of family translocation on survival. The results of this study suggest that no significant differences exist in post-translocation survival of NFT compared with FT groups (Bly-Honness et al. 2004; Long et al. 2006). However, in that study, no attempt was made to determine family membership and "same family" groups contained an average of only five individuals (range $n = 3–11$) trapped from one or occasionally two burrow entrances. Black-tailed prairie dog coterie territories are known to contain an average of 69 burrow entrances (range 5–214; Hoogland, 1995), and following emergence of young of the year, when prairie dogs are typically trapped for translocation, family groups can contain as many as 29 individuals (mean = 12.8, range 3–29; D.M.S., unpublished data). Thus, "same-family" groups in that study were most likely only small

Table 1. Cost-effectiveness of family translocation (FT) and nonfamily translocation (NFT) methods for black-tailed prairie dogs.

	Variable	Description	Treatment FT	Treatment NFT
Observed	b	no. of trapping hours invested for 3 new colonies	252	93
		no. of acclimation cages used	60	60
		no. of holding cages used	8	5
		total no. of prairie dogs present on colonies 1 year after release	383	43
	e	total no. of prairie dogs present on colonies 2 years after release (established)	810	103
	c	no. of trapping hours per prairie dog[a]	0.9	0.3
	i	no. of prairie dogs initially translocated	298	300
	s	total no. of prairie dogs added to a colony 1 year after initial translocation (supplemented)	0	45
		no. of colonies supplemented 1 year after initial translocation	0/3	2/3
Projected	n	no. of prairie dogs needed to establish 1000 prairie dogs 2 years after translocation[b]	368	3350
	a	no. of acclimation cages required	74.2	583
	b	no. of holding cages required	8	65
	m	total no. of hours to monitor new colonies for predators after release	90	150
	t	total no. of trapping hours required to establish 1000 prairie dogs 2 years after release[a]	309.0	1038.4

[a]*Rounded to the nearest tenth of an hour.*
[b]*Rounded to the nearest whole number.*

fractions of complete family units, and as a result the benefits of translocating animals with family members may have been negligible.

Moreover, the South Dakota study estimated survivorship from visual counts of aboveground individuals, which are known to vary in accuracy (e.g., Powell et al. 1994). In contrast, I determined family membership by observing behavioral interactions and sleeping patterns of ear-tagged, dye-marked prairie dogs. Following translocation, I estimated survivorship by exhaustive trapping of all ear-tagged individuals and their offspring 12 months after release. In striking contrast to the results I present here, aboveground counts at 2 months post-translocation revealed no differences in survival (D. Long, unpublished data as cited in Long et al. 2006). Whether this is because of the differences in the timing of the assessment (2 vs. 12 months) or because aboveground counts are unreliable is not clear.

Predation was a significant impediment to survival for both treatment groups. Although estimated predation pressure was higher on FT than on NFT colonies, mean survival was higher on FT colonies. Thus, family translocation appeared to reduce the success of predators on newly established prairie dog colonies.

It is well established that prairie dogs are adapted for living in large groups and are dependent on coterie members for predator detection and deterrence (Hoogland 1995). Larger groups and the presence of relatives are both associated with greater numbers of alarm-calling individuals, and prairie dogs spend less time scanning for predators when more adult coterie members are present aboveground (Hoogland 1995). The ability of prairie dogs to directly deter predators also depends on coterie membership. Prairie dogs attack small predators (e.g., weasels) as a group when they encounter them in their home coterie but not when they are encountered in other coteries (Hoogland 1995). If the presence of relatives provides antipredator benefits to translocated prairie dogs, then individuals moved with larger families should experience higher survival. As predicted, prairie dogs from larger families (>12 individuals) were more likely to survive than those from smaller families.

Time of release also affected postrelease survival. In general, translocations conducted later in the summer yielded higher survival, but timing of release appeared to be more important for juveniles than for adults. Survival of juveniles may depend, in part, on the amount of time they spend aboveground growing and improving in physical condition before translocation. Thus, translocation later in the summer may allow juveniles more time to develop and hone their survival skills through interactions with experienced kin. Antipredator vigilance is likely to be most crucial in the first half of the summer, while juveniles are small and lack knowledge of their environment. Foraging becomes of primary import later in the summer when vegetation is still plentiful and fat reserves

are required for survival through winter. A natural shift between vigilance and foraging can take several weeks (Loughry 1992), and young of the year need this time to increase body condition and skills prior to translocation.

Family translocation and NFT animals behaved differently immediately after release, and these behavioral differences persisted over time. Up to a year after translocation, FT individuals spent less time being vigilant and more time foraging and digging than NFT animals. Devoting less time to vigilance and more time to foraging and digging may have allowed FT prairie dogs to improve in physical condition and be more efficient at excavating their burrow systems. Consistent with this prediction, prairie dogs translocated in intact coterie units excavated more burrow entrances, and did so faster, than NFT prairie dogs over the 2 years following release.

Akaike parameter weights suggest that translocation method was the most important factor affecting survival, given the available data and candidate models. Thus, efforts of managers would best be directed at family group translocation, minimizing predator pressure and selecting the optimal release timing on the basis of the species' behavioral ecology.

Practicality is a concern when new methods may require additional time and money to conduct translocations. However, my results indicate that family translocation is more effective at increasing translocation success and provides a more efficient means of restoring prairie dogs to their former range. The FT animals must be trapped, marked, released, and observed to determine coterie membership, and specific individuals must then be targeted for trapping. Because the initial time investment is higher, FT might be expected to be less economical. However, the cost-effectiveness analysis showed that, despite the higher initial time investment in trapping intact families, the nearly ninefold difference in fitness 1 year after translocation (for the 2001 release) more than offset this added time cost. Differences between FT and NFT colonies remained pronounced by the second year after release, and supplementation did not offset these differences. Therefore, investing the time to determine and maintain the natural social grouping of the target species at the onset of a translocation project may minimize mortality of animals in the initial release and may save animal lives, time, and money by rendering supplementation unnecessary. In practice, less intensive methods may be just as effective. For example, wildlife managers could observe colonies to determine use of burrow entrances and exhaustively trap all animals from specific burrow clusters without using mark-recapture techniques.

My results have important implications for conservation and animal behavior. The data clearly demonstrate that for highly social prairie dogs, founder groups composed of intact family units were more successful in terms of post-translocation survival, reproductive success, and population viability. More broadly, these results suggest

that any species dependent upon social interactions for survival and reproduction may benefit substantially from the maintenance of social groups during translocations.

Across taxa, group living fosters social affiliation behavior that can affect an individual's fitness. Species for which social interactions enhance individual fitness would be especially likely to benefit from the maintenance of social groups during translocation. These species include those with kin-selected behaviors (e.g., ground squirrel alarm calls, Sherman 1977), those that rely on reciprocity (e.g., allogrooming [Silk et al. 1999]; communal nesting [Brown 1987]), and those that receive direct benefits from relationships with group members (e.g., coalition formation [Packer et al. 1991]; social foraging [Giraldeau & Caraco 2000]; sexually selected cooperation [Greene et al. 2000]; social learning [Galef & Laland 2005]; enhancement of immune function [Detillion et al. 2004]; reduced disease transmission [Traniello et al. 2002] and stress [Sachser et al. 1998]).

To illustrate this point, consider a species dependent on social facilitation for learning effective antipredator behavior. In the wild, animals must quickly and efficiently learn to protect themselves from predators. For many species, the development of effective predator-avoidance skills is socially learned (reviewed in Griffin 2004). During translocation animals are often moved into habitats that may include novel predators and/or young may be moved prior to learning these skills. Translocating individuals without group members would preclude young from learning effective predator avoidance skills from experienced group members and directly reduce fitness after translocation. In situations in which new habitats include novel predators, the benefits of social group translocation would not be limited to young animals. Through cultural transmission of acquired antipredator behavior, individuals (juveniles or adults) could become predator savvy much more quickly and with less risk than if they were to learn about the novel predator via trial and error. Maintaining the integrity of social groups during translocation may not only increase post-translocation fitness, it may also allow managers more flexibility in the timing of translocation. If young are translocated with experienced adult group members (e.g., mothers), they will continue to have opportunities to learn survival skills and/or fine-tune their antipredator responses to increase their effectiveness through observation following release (Griffin 2004).

My results also suggest future directions for basic behavioral research. Most research on the direct fitness costs and benefits of group living has focused on group composition, in particular group size, not on the relationships between individuals in a group. However, recent evidence indicates that, at least for primates, social bonds have positive effects on reproductive success (Silk et al. 2003). My results provide an example of how social relationships can also have survival value.

In addition, this research has implications for dispersal biology. To date most research on dispersal has focused on single propagules, and little attention has been directed toward mechanisms that underlie dispersal in social groups (Lambin et al. 2001). My results suggest that animals that disperse in groups might benefit from reduced predation and extended opportunities for learning survival skills. Other mechanisms may also confer advantages of group dispersal to individuals (e.g., information pooling among dispersers, Stamps 2001) and increased competitive ability (Lambin et al. 2001). Finally, my results highlight the importance of social factors in the development of effective survival skills, a topic rich with opportunities for future research.

Acknowledgments

Literature Cited

Anderson, G. W., T. E. Hilley, P. G. Martin Jr, C. R. Neal, and R. S. Gomez. 1982. Soil Survey I–IV. Pages 1–187. U.S. Soil Conservation Service, Washington, D.C.

Armstrong, D. P. 1995. Effects of familiarity on the outcome of translocations II A test using New Zealand robins. Biological Conservation **71:**281–288.

Bly-Honness, K., J. Truett, and D. Long. 2004. Influence of social bonds on post-release survival of translocated black-tailed prairie dogs (*Cynomys ludovicianus*). Ecological Restoration **22:**204–209.

Bodkin, J. L., B. E. Ballachey, M. A. Cronin, and K. T. Scribner. 1999. Population demographics and genetic diversity in remnant and translocated populations of sea otters. Conservation Biology **13:**1378–1385.

Brown, J. L. 1987. Helping and communal breeding in birds: Ecology and evolution. Princeton University Press, Princeton, New Jersey.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theorectic approach. Springer-Verlag, New York.

Causton, D. R. 1988. An introduction to vegetation analysis, principles, practice and interpretation. Unwin Hyman, London.

Detillion, C. E., T. K. S. Craft, E. R. Glasper, B. J. Prendergast, and A. C. DeVries. 2004. Social facilitation of wound healing. Psychoneuroendocrinology **29:**1004–1011.

Dobson, R. S., R. K. Chesser, J. L. Hoogland, D. W. Sugg, and D. W. Foltz. 1997. Do black-tailed prairie dogs minimize inbreeding? Evolution **51:**970–978.

Dugatkin, L. A. 1997. The evolution of cooperation. BioScience **47:**355–362.

Fischer, J., and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. Biological Conservation **96:**1–11.

Galef, B. G. J., and K. N. Laland. 2005. Social learning in animals: empirical studies and theoretical models. BioScience **55:**489–499.

Garrett, M. C., and W. L. Franklin. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. Journal of Mammalogy **69:**236–250.

Giraldeau, L., and T. Caraco. 2000. Social foraging theory. Princeton University Press, Princeton, New Jersey.

Greene, E., B. E. Lyon, V. R. Muehter, L. Ratcliffe, S. J. Oliver, and P. T. Boag. 2000. Disruptive sexual selection for plumage colouration in a passerine bird. Nature **407:**1000–1003.

Griffin, A. S. 2004. Social learning about predators: a review and prospectus. Learning and Behavior **32:**131–140.

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.

Hoogland, J. L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago.

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed Prairiedog Town in the Black Hills of South Dakota. Contributions from the Laboratory of Vertebrate Biology. The University of Michigan, Ann Arbor, Michigan.

Kleiman, D. G. 1989. Reintroduction of captive animals for conservation: guidelines for reintroducing an endangered species into the wild. BioScience **39:**152–161.

Kotliar, N. B., B. J. Miller, R. P. Reading, and T. W. Clark. 2006. The prairie dog as a keystone species. Pages 53–64 in J. L.Hoogland, editor. Conservation of the black-tailed prairie dog. Island Press, Washington, D.C.

Lambin, X., J. Aars, and S. B. Piertney. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. Pages 110–122 in J. C. E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, Oxford, United Kingdom.

Long, D., K. Bly-Honness, J. C. Truett, and D. B. Seery. 2006. Establishment of new prairie dog colonies by translocation. Pages 188–209 in J. L.Hoogland, editor. Conservation of the black-tailed prairie dog. Island Press, Washington, D.C.

Loughry, W. J. 1992. Ontogeny of time allocation in black-tailed prairie dogs. Ethology **90:**206–224.

Packer, C., D. A. Gilbert, A. E. Pusey, and S. J. O'Brien. 1991. A molecular genetic analysis of kinship and cooperation in African lions. Nature **351:**562–565.

Powell, K. L., R. J. Robel, K. E. Kemp, and M. D. Nellis. 1994. Aboveground counts of black-tailed prairie dogs: temporal nature and relationship to burrow entrance density. Journal of Wildlife Management **58:**361–366.

Proctor, J., B. Haskins, and S. C. Forrest. 2006. Focal areas for conservation of prairie dogs and the grassland ecosystem. Pages 232–247 in J. L.Hoogland, editor. Conservation of the black-tailed prairie dog. Island Press, Washington, D.C.

Raudenbush, S., A. Bryk, and R. Congdon. 2003. HLM hierarchical linear and nonlinear modeling. Scientific Software International Lincolnwood, Illinois.

Sachser, N., M. Durschlag, and D. Hirzel. 1998. Social relationships and the management of stress. Psychoneuroendocrinology **23:**891–904.

Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. Science **197:**1246–1253.

Silk, J. B., R. M. Seyfarth, and D. L. Cheney. 1999. The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. Behaviour **136:**679–703.

Silk, J. B., S. C. Alberts, and J. Altmann. 2003. Social bonds of female baboons enhance infant survival. Science **302:**1231–1234.

Stamps, J. A. 2001. Habitat selection by dispersers. Pages 230–242 in J. C. E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, Oxford, United Kingdom.

Traniello, J. F. A., R. B. Rosengaus, and K. Savoie. 2002. The development of immunity in a social insect: evidence for the group facilitation of disease resistance. Proceedings of the National Academy of Sciences of the United States of America **99:**6838–6842.

Truett, J. C., L. D. Dullam, M. R. Matchell, E. Owens, and D. Seery. 2001. Translocating prairie dogs: a review. Wildlife Society Bulletin **29:**863–872.

USFWS (U.S. Fish and Wildlife Service). 2000. Endangered and threatened wildlife and plants: 12-month finding for a petition to list the black-tailed prairie dog as threatened. Federal Register **65:**5476–5488.