

**Social and Ecological Influences on the Survival Skills
of Black-tailed Prairie Dogs (*Cynomys Ludovicianus*):
A Role for Behavior in Conservation**

By

Debra Marie Shier

B.S. (University of California, Santa Barbara) 1992

M.A. Animal Behavior (University of California, Davis) 2002

M.A. Biology (San Francisco State University) 2003

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Animal Behavior
Behavior and Conservation of Wild Animals

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Donald H. Avery

Richard G. Coon

Neil Van Vorst

Committee in Charge

2004

Debra Marie Shier
December 2004
Animal Behavior

Social and Ecological Influences on the Survival Skills
of Black-tailed Prairie Dogs (*Cynomys Ludovicianus*):
A Role for Behavior in Conservation

ABSTRACT

The global extinction crisis had led to more active management of animal populations. But wildlife managers routinely design recovery plans for endangered species that do not take the animals' behavior into account. For example, captive-bred animals are often assumed, unrealistically to be "hard-wired" to avoid predators, or to be able to rapidly learn these skills following release. Many reintroduction programs have failed because of the lack of understanding of basic animal behavior.

There has been increasing awareness that behavior can play an important role in species conservation, but integration of behavior with conservation biology is still in its infancy. Survival and reproduction are the ultimate goals of translocation and captive breeding-reintroduction programs, yet these goals are rarely met. In the first few weeks following release, translocated animals often disperse from the new site and/or are more vulnerable to predation. Captive breeding-reintroduction methodology is fraught with additional problems. Captive environments often fail to provide the experiences necessary to ensure post-release survival of captive born young.

This research uses black-tailed prairie dogs (*Cynomys ludovicianus*) to investigate the importance of family social interactions for survival and the kinds of captive learning experiences required for effective antipredator behavior after release into the wild. Over the course of four field seasons, three experiments were conducted to examine 1) if

repeated early exposure to predators affects the development of effective antipredator behavior; 2) how the presence of experienced kin affects the development of defensive behavior; and 3) whether animals translocated in family groups show a higher survival rate following release than animals translocated without family members. Results reveal that juveniles trained with predators behave differently and survive at higher rates than untrained juveniles. Results also indicate that juveniles trained with experienced kin develop more appropriate antipredator behavior prior to release and survive at higher rates than juveniles trained without experienced kin. Finally, the results show that maintaining family groups significantly increases translocation success in terms of both survival and reproductive success and imply that any species that depends on social interactions for survival and reproduction may benefit substantially from the maintenance of social groups during translocations.

ACKNOWLEDGEMENTS

First, I would like to thank my committee members. I am grateful to my advisor and mentor, Dr. Donald Owings for his assistance, support and valuable advice. I am indebted to Dr. Owings for taking me on as a student and for directing me toward research on a most intriguing mammalian family, Sciuridae. I would also like to thank Dr. Owings for being a wonderful mentor. He was supportive of my goals both professionally and personally, regularly gave me encouraging feedback, and was sensitive to my trials and tribulations during my extended periods in the field. Dr. Dirk VanVuren provided his conservation expertise to my research while Dr. Richard Coss offered advice on statistics; both were enthusiastic and supportive from my very first year in the program. I would like to thank all of my committee members for their editorial advice on this manuscript. In addition to my committee members, I am grateful to Dr. Judy Stamps for many brainstorming meetings which broadened my thinking. I am grateful to the faculty and student members of the Animal Behavior graduate group who provided an exciting learning experience along with a supportive graduate environment. In particular, I would like to thank Amy Schilling and Aaron Rundus.

I thank D. Vackar for permission to work and stay on land at Vermejo Park Ranch and his staff (F. Sanders, C. Hooper and B. Coppedge) for logistical assistance. This study would not have been possible without the support of the Turner Endangered Species Fund (including D. Long, J. Truett, K. Bly-Honness, L. Temple and M. Phillips).

I would like to express my deepest gratitude and thanks to my dedicated field assistants who spent countless hours over long months working side by side with me to facilitate my research. Specifically, I am referring to Anita Shier Bruton, Whitney

Stiehler, Cory Unruh, Heidi Contrareas, Tanya Silva and Kim Okamoto, all of whom provided tireless support.

I wish to thank my family and friends for always supporting my choices and encouraging me to accomplish my goals. Specifically, I'd like to thank my father, Gary Shier, who is an amazing role model, source of strength and field companion. In addition to numerous telephone conversations and constant moral support, his assistance ranged from building the enclosures, nest boxes, and mesh barriers, to trapping and observing prairie dogs to taking me up in his Cessna aircraft to document colonies post release. My husband, Greg Grether, has been a pillar of support throughout my research and academic endeavors, has assisted in the field and in critiquing my manuscripts and happens to be one of the most brilliant biologists I know. In addition to being my first field assistant on the project, my sister, Anita Shier Bruton, has always been a source of encouragement, clarity and laughter and has helped me through many difficult days in the field. Taylor Shier brought her bright smile to my field site and assisted in trapping prairie dogs for the translocation and feeding animals in the enclosures. Finally, I am grateful to Judith Grether who assisted me in the enclosure experiments which allowed my full time field assistant a well deserved vacation.

Last, but definitely not least, I thank the prairie dogs for being such inspirational creatures and for teaching me patience, perseverance, and peace of mind. I dedicate this dissertation to those individuals who lost their lives while participating in my experiments. I can only hope that this some of what I have learned will be applied to the conservation of prairie dogs and the grassland ecosystem.

This research was funded by fellowships and grants from the National Science Foundation, University of California, Davis, American Society of Mammalogists, Animal Behavior Society, American Museum of Natural History, and Sigma Xi.

TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS	iv
CHAPTER 1: EFFECTS OF PREDATOR TRAINING ON BEHAVIOR AND POST-RELEASE SURVIVAL OF CAPTIVE PRAIRIE DOGS (CYNOMYS LUDOVICIANUS)	1
ABSTRACT	2
INTRODUCTION	3
METHODS	6
Subjects and Housing	6
Experimental Protocol	7
Measuring reintroduction success	8
Data Analysis	9
RESULTS	10
Treatment effects.	10
Trial effects for trained juveniles.	11
Period effects for trained juveniles	11
Post-release Survival	12
DISCUSSION	12
REFERENCES	16
TABLES AND FIGURES	19
CHAPTER TWO: EFFECTS OF SOCIAL CONTEXT ON PREDATOR TRAINING IN JUVENILE BLACK-TAILED PRAIRIE DOGS (CYNOMYS LUDOVICIANUS)	23
ABSTRACT	24
INTRODUCTION	26
METHODS	30
Experimental Manipulation of Predator Experience	31
Subjects and Housing.	31
Experimental Protocol.	31
Pre-Training Tests.	32
Developmental Conditions - Training	33
Post-training tests.	34
Comparison to Wild-reared Counterparts.	34
Analysis of Behavioral Responses.	34
Measuring training success.	36

RESULTS	36
Description of alarm behavior	36
Pre-training tests	37
Effect of social context on training	37
Relationship to demonstrator behavior	40
Captive vs. Wild-reared Juveniles	40
Training Success	41
DISCUSSION	41
REFERENCES	46
TABLES AND FIGURES	49
CHAPTER 3: FAMILY SUPPORT INCREASES THE SUCCESS OF TRANSLOCATED PRAIRIE DOGS	55
ABSTRACT	56
INTRODUCTION	57
METHODS	59
Study Site.	59
Site selection and establishment.	60
Study Subjects.	61
Determining coterie membership and capturing and holding animals for release.	61
Release to new site.	62
Post-Release Behavior.	63
Burrow Establishment.	63
Habitat Features.	64
Vegetation cover	64
Soil quality and slope	65
Measuring Translocation Success.	65
Population Viability.	66
Data Analysis.	66
RESULTS and DISCUSSION	69
REFERENCES	77
TABLES AND FIGURES	80

**CHAPTER 1: EFFECTS OF PREDATOR TRAINING ON BEHAVIOR AND
POST-RELEASE SURVIVAL OF CAPTIVE PRAIRIE DOGS
(*CYNOMYS LUDOVICIANUS*)**

ABSTRACT

Reintroduction of captive animals to the wild is a conservation strategy that has rarely succeeded. For many species, the blame has been placed on ineffective post-release behavior. In particular, predation on newly released animals can be devastating. To deal with this problem, biologists have initiated programs of pre-release predator training. However, the success of these programs as a function of long-term post-release survival has yet to be measured.

The development of effective antipredator behavior is known to be dependent upon experience. In social species, this experience may involve hearing alarm vocalizations, observing a conspecific interacting with a predator, or encountering a predator in the presence of an experienced group member. Here I examine the effects of training captive juvenile black-tailed prairie dogs (*Cynomys ludovicianus*) with presentations of a black-footed ferret, red tailed hawk, prairie rattlesnake predators, and a nonpredator control (cottontail). Training consisted of presenting appropriate alarm vocalizations during predator exposure. Playbacks of alarm vocalizations enhanced antipredator behavior toward these predators. Results revealed that training had an immediate and lasting effect on juveniles prior to release to the wild and that these differences appeared to promote post-release survival.

INTRODUCTION

The ultimate goal of captive breeding programs is reintroduction, yet there are problems with reintroducing captive-bred animals into the wild. Captive environments often fail to provide the experiences necessary to ensure survival upon release of captive born young into native habitat (Beck et al. 1994; Beck 1995b). Numerous studies have shown that captive-born animals have a higher mortality rate than wild-caught animals after release in the wild (Beck et al. 1994; Miller et al. 1994). In fact, the survival skills of wild-caught individuals may even erode while in captivity (Yoerg & Shier 1997; Yoerg & Shier 2000). In several species, this increased mortality has been linked to ineffective antipredator behavior (Biggins et al. 1999; Fischer & Lindenmayer 2000; Frantzen et al. 2001; Wallace 1994).

Anti-predator behavior often must be functional when a predator is first encountered, but animals can improve their responses with experience (Shriner 1995). A substantial empirical literature demonstrates that animals that initially show no recognition or fear can be conditioned to respond to live and model predators (Griffin et al. 2000; Mineka & Cook 1988). The type of experience required will elucidate the factors that affect the development of survival skills, and therefore plays an important role in the establishment of predator training protocols.

Because experience is critical for developing antipredator behavior, and because a high percentage of reintroduction attempts (62 – 89%) have failed (Beck 1995a), there is increasing interest in developing predator training protocols. To date, training research has focused primarily on fish (Brown & Laland 2001; Chivers & Smith 1995; Kelly & Magurran 2003; Mirza & Chivers 2000), birds (McLean et al. 1999; Maloney & McLean

1995) and marsupials (McLean et al. 2000; Griffin et al. 2001; Griffin & Evans 2003), with a few studies attempting training in other mammals (Miller et al. 1994; Mineka & Cook 1988; Yoerg & Shier 1997). While these studies have advanced our understanding of the efficacy of predator training on pre-release behavior, the success of these programs in terms of actual post-release survival has yet to be measured.

I tested the effectiveness of predator training on pre-release behavior and post-release survival in captive-born black-tailed prairie dogs (*Cynomys ludovicianus*). Prairie dog numbers have declined as much as 99% in North America. All species in the genus (*Cynomys*) are rare, threatened, or endangered, thus knowledge of their behavior is directly applicable to conservation efforts. They are considered keystone species that influence environmental heterogeneity, nutrient cycling, and biodiversity and therefore play an integral role in grassland ecosystems. The National Wildlife Federation filed a petition in 1998 to list the black-tailed prairie dog as threatened under the Endangered Species Act (ESA). In 2000 the U.S. Fish and Wildlife Service found the status of the species to be "warranted but precluded" from listing and the case is currently reviewed annually. This federal action has stimulated involvement by 11 states in the species' original range and by private organizations. Current efforts to conserve prairie dogs have relied in part on translocating animals to supplement small populations or to restore extirpated ones (Truett & Savage 1998) and captive breeding has been suggested.

Black-tailed prairie dogs are prey to a variety of predators, including weasels (*Mustela* spp.), coyotes (*Canis latrans*), bob cats, (*Lynx rufus*), several species of raptors and snakes. Prairie dogs are a colonial species that live in social groups called coterie which typically contain one adult male, several adult females, yearling males and females

and juveniles (young of the year)(Hoogland 1995). In the presence of mammals and avian predators, adult prairie dogs bark repetitiously, warning offspring and nondescendant kin of impending danger (Hoogland 1995). Upon hearing a bark alarm call, prairie dogs scan for predators and if one is detected, run to a burrow mound and either enter or begin calling while facing the predator (Hoogland 1995). Behavior toward snakes is very different, probably because most snakes cannot kill adults. During interactions with snakes, adults typically orient towards and approach the snake in an elongated posture, sniff, jump away and give distinct jump-yips calls and/or footdrum (Owings & Owings 1979; Owings & Loughry 1985). In fact, these confrontational interactions often result in attacks, and, occasionally, adults may kill the snake (Loughry 1987).

Newly emergent juveniles remain close to burrows, are vigilant and forage little (Loughry 1992). Juveniles jump-yip at higher rates upon emergence than in subsequent weeks (Loughry 1992), but rarely bark or footdrum until they have been above ground for a few months (Hoogland 1995).

The current study is the first in a series of experiments designed to determine whether captive-born juveniles trained with predators develop more effective antipredator behavior and survive in higher numbers than control juveniles. Specifically, in this study I compare the behavior and survival of juvenile prairie dogs trained by pairing predators with playbacks of antipredator vocalizations to those exposed to neither predators nor vocalization playbacks.

METHODS

Subjects and Housing

Subjects were 18 captive-born juvenile prairie dogs (10 females, 8 males) from 3 litters trapped within 2 weeks of emergence from the Spring River Park Zoo, Roswell, New Mexico during spring 2002. Juveniles were from 3 litters of a single coterie unit and were therefore housed in a single enclosure with their mothers. This population has not been exposed to natural predators since they were brought into captivity in 1963. These juveniles were trapped with their mothers, and transferred immediately to the Vermejo Park Ranch, Colfax County, New Mexico (36° N, 104° W, elevation 1850 m). All 21 animals were housed in a single wire mesh field enclosure (2 x 2 x 3 m) with a metal frame set into the soil 0.3 m with a mesh canopy over the top that prevented attacks by raptors but allowed exposure to other potentially important environmental cues. Animals were provided with two wood nest boxes with a latrine box (all 25.4 x 25.4 x 30.5 cm) in the middle that could be accessed from either nest box. A burrow system of corrugated black PVC tubing was attached to each nest box to allow access from above ground. Nest boxes and tubing were surrounded by dirt to simulate natural burrow systems. All animals remained together in the enclosure for the duration of the experiment. Animals were ear-tagged and dye-marked (Nyanzol D) for individual identification and allowed to habituate to the enclosures for 1 week prior to testing.

Experimental Protocol

Treatment groups. Following habituation to the enclosure I randomly assigned juveniles to one of two treatment groups: training = predator exposure coinciding with an alarm-call playback and control = no animal or alarm call ($n=9/\text{treatment}$). The adult females were randomly assigned to either group.

Testing. All testing occurred in the animal's home cage. The test cage was divided into four equal-sized quadrants delineated on the side of the cage for the observers (the barrier was placed between Quadrants 3 and 4 during snake tests and the mesh box was placed in Quadrant 4 during tests with the ferret and cottontail; Quadrant 1 was furthest away.). Approximately three weeks after emergence, I began testing each focal juvenile in the training treatment with each of the following stimulus animals: 1) a live black-footed ferret (*Mustela nigripes*); 2) a moving, taxidermically-mounted red tailed hawk (*Buteo jamaicensis*); 3) a live prairie rattlesnake (*Crotalus viridis*) and 4) a live desert cottontail (*Sylvilagus auduboni*) as a nonpredator control. Tests were 10 min in duration and divided into periods: (1) Pre-training: 2.5 min exposure to a predator or cottontail; (2) Training: 5 min predator or cottontail exposure paired with playbacks of either prairie dog alarm barking (ferret and hawk tests), jump-yipping (snake tests) or no playbacks (cottontail tests); and (3) Post-training: 2.5 min continued exposure to a predator or cottontail. During the training trials I removed the mother and all siblings except the focal subject from the home cage (to eliminate the effects of the social environment during exposure), and placed a mesh barrier or box in the home cage. With the exception of the hawk, I then placed the selected predator or cottontail behind the barrier or in the box. The hawk was hooked to a cable and released 5 min into the test to enter the

enclosure at a -45° angle from the top of a 5m tower. Thus, the hawk was observable throughout the 10-min tests, but released to "fly" into the enclosure midway through the tests. At the end of the 5 min training period, the predator or cottontail remained in the enclosure, but the playbacks of alarm vocalizations were terminated. Juveniles in the training treatment were exposed to each stimulus animal once per week for 2 weeks (Trial). Three exemplars of each stimulus animal were used to limit pseudoreplication. Alarm vocalization playbacks were recorded from multiple adults from each focal subject's coterie to simulate natural variation in alarm calls. The calls were randomly assigned to focal individuals. Animals in the control treatment group (no exposure to predators or cottontail) were subjected to the same experimental procedure (four tests per week for two weeks paired in time with predator tests), but were not exposed to stimulus animals or playbacks. Each test was video taped; the order of stimuli was counterbalanced to avoid order effects. An observer unfamiliar with the experimental questions scored the video tapes.

I used four measures of behavior to quantify the effects of predator training on juvenile prairie dogs: (1) time allocated to vigilance, defined as orientation toward stimulus animal and alert posture, (2) frequency of antipredator vocalizations (barking and jump-yipping), (3) time spent in or near shelter, (4) activity, measured by the number of quadrant changes.

Measuring reintroduction success

At the end of the experiment (June, 2002) animals were reintroduced to an established prairie dog town with uninhabited burrow systems in place. All animals were treated as a single coterie unit as they were trapped together and therefore were kept

together during release to decrease stress and dampen post-release dispersal. I measured reintroduction success by retrapping all ear-tagged animals present at the release site (June-July 2003). Dye marking and observation were used to verify that all prairie dogs remaining at a colony had been successfully retrapped. I also walked the area in grids to determine if 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. No distinction was made between dispersal and mortality since dispersing animals do not contribute to the population viability of a release site.

Data Analysis

Pre-release: Because prairie dogs behave differently in the presence of different predator types, statistical analyses were conducted separately for each species presented (ferret, hawk, snake, cottontail). For tests with each species, two-factor repeated measures analysis of variance (ANOVAs) were performed with predator exposure treatment (training vs. control) as the between-subjects factor and trial (weeks 1 vs. 2) as the within-subjects factor. Overall, juvenile prairie dogs significantly modified their behavior from first to second trials, at a statistically significant level, and this difference was almost exclusively produced by trained juveniles (see results; Fig. 1.1). Therefore, I assessed both multiple-trial effects and the immediate impact of training separately for the trained juveniles, using a two-way repeated measures ANOVA with period (pre vs. post training) and trial (weeks 1 vs. 2) as within subjects factors (see Table 1.1).

Post-release: To examine the effects of training on post-release survival, I used multiple logistic regression in the statistical package Stata (StataCorp 2004), to control for possible effects of weight and sex of juveniles. Because individuals were only from 3

litters and therefore not fully independent statistically, I used a generalization of Huber and White's estimator of variance (Huber 1967; White 1980; White 1982; Williams 2000) as implemented by STATA. This method adjusts for lack of independence by basing calculations on the clustered (litter) rather than on the individual observations. Degrees of freedom in the survival comparison are hence appropriately reduced, to control Type I error.

RESULTS

Treatment effects.

Training strongly influenced pre-release behavior in tests with all predatory stimulus animals but not with the nonpredatory stimulus animal (cottontail)(Fig. 1.1).

Averaged for weekly trials, juveniles exposed to the ferret and hawk spent significantly more time than control juveniles vigilant (ferret: $F_{1,16} = 20.339$, $P < 0.0001$; hawk $F_{1,16} = 16.372$, $P = 0.001$) and in or near shelter (ferret: $F_{1,16} = 14.865$, $P = 0.001$; hawk $F_{1,16} = 5.222$, $P = 0.036$), alarm called more (ferret: $F_{1,16} = 45.768$, $P < 0.0001$; hawk $F_{1,16} = 34.257$, $P < 0.0001$), and were significantly less active (ferret: $F_{1,16} = 19.460$, $P < 0.0001$; hawk $F_{1,16} = 9.408$, $P = 0.007$). In tests with the snake, trained juveniles spent significantly more time vigilant ($F_{1,16} = 22.087$, $P < 0.0001$), alarm called more ($F_{1,16} = 17.039$, $P = 0.001$), and spent significantly less time in shelter ($F_{1,16} = 4.860$, $P = 0.042$) than control juveniles not exposed to the snake. There was no statistically significant difference in activity between juveniles trained with the snake and untrained control animals ($F_{1,16} = 0.010$, $P = 0.922$).

Not only did trained juveniles exhibit different behaviors from juveniles that were not trained, but nearly all treatment by trial statistical interactions were statistically

significant (but see Hawk tests; Fig. 1.1). These interactions indicate that the effectiveness of training was even more pronounced after the first trial in all cases except for tests with the hawk.

Trial effects for trained juveniles.

Analyses of simple effects comparing the behavior during the first and second weeks indicated that training had a lasting effect on juvenile behavior (see Table 1; Fig. 1). Juveniles exposed to ferrets spent significantly more time vigilant and vocalized more during trial 2 than during trial 1. Similarly, juveniles exposed to the rattlesnake allocated more time to vigilance across training trials. However, juveniles spent less time in shelter and were more active in the presence of the snake in trial 2 compared to trial 1. Training also affected juvenile behavior in the presence of the cottontail. Juveniles spent reliably less time in or near shelter and were more active with the cottontail during the second trial than during the first trial. In contrast, there were no statistically significant trial effects for tests with the hawk when only trained juvenile behavior was examined. This finding suggests that hawk training was effective with the first exposure coupled with alarm vocalizations and that the subsequent exposure during the second week might not have been necessary.

Period effects for trained juveniles

More detailed analysis indicated that alarm vocalizations enhanced juvenile responses to the predators (Table 1.1; Fig. 1.2). In tests with all three predators, juvenile prairie dogs allocated more time to vigilance in the post-training period than in the pre-training period (Table 1.1; Fig. 1.2). Juveniles spent significantly more time in or near shelter following the training period when tested with the ferret, but spent significantly less time in or near

shelter following training with the snake. By contrast, juveniles were more active following training with the snake, but were less active during the post-training period in the presence of the ferret and hawk. There were no substantial differences in the rate of alarm vocalizations from pre- to post-training for tests with any of the predators or the cottontail presented to the juveniles.

Post-release Survival

Comparisons between trained and control juveniles revealed statistically significant differences in survival one year post-release. Trained juveniles showed significantly higher survival following release than their untrained counterparts (4 out of 9 or $44.4 \pm 17.5\%$ versus 2 out of 9 or $22.2 \pm 14.6\%$ (mean \pm SE); multiple logistic regression; $n = 18$, $\chi^2 = 13.10$, treatment: $z = 2.45$, $P = 0.014$; sex: $z = 1.23$, $P = 0.218$; weight: $z = 1.71$, $P = 0.087$).

DISCUSSION

The results of this study suggest that naïve juvenile prairie dogs learn to recognize predators when conditioned with alarm vocalizations. After undergoing training in which predators were paired with alarm vocalizations, juvenile prairie dogs became significantly more vigilant and alarm called more in response to all three predators, relative to a control group that was exposed to an empty compartment. However, training with the ferret and hawk caused juveniles to seek shelter, while training with the snake reduced this behavior compared to control animals. Ferrets and hawks pose a qualitatively different threat than snakes because of their hunting modes. Hawks are looming predators that are unable to attack prairie dogs within their burrows. Ferrets,

like weasels, primarily prey on prairie dogs in their burrows after they have retired for the night (Vargas & Anderson 1998). If detected above ground during the day, adult prairie dogs may harass the ferret and once it descends into a burrow, quickly plug the burrow with soil (Henderson et al. 1974). Due to their size and inexperience, young prairie dogs are likely more vulnerable to ferret predation than adults when detected above ground. Therefore, both hawks and ferrets likely elicit shelter seeking behavior by juveniles upon detection (Giles 1984; Bolbroe et al. 2000). By contrast, snakes rely almost entirely on stealth to surprise their prey. Snakes are dangerous because they are visually camouflaged and can enter the burrow undetected and prey on pups or wait for an ambush in or near a burrow. Therefore, once detected by a juvenile prairie dog, a snake may not remain a significant threat. The newly emergent juvenile prairie dog's antipredator strategy, therefore, should be to remain vigilant following detection, investigate, and alarm call to summons an adult coterie member. Juvenile behavior will likely shift toward more adult-like behavior over subsequent weeks (Loughry 1987; Loughry 1992).

Alternatively or in conjunction, the type of alarm vocalization presented with the predator may have elicited the different behavior. The presentation of the ferret and hawk were paired with barking vocalizations. Upon hearing a bark alarm call in the wild, prairie dogs scan for predators and if one is detected, run to a burrow mound and either enter or begin calling (Hoogland 1995). Results presented here show similar behavior in response to training. By contrast, presentation of the snake was paired with jump-yipping vocalizations. Jump-yipping appears to promote contact with snakes in wild prairie dogs (Owings & Owings 1979; Owings & Loughry 1985). Immediately following a bout of

jump-yipping, prairie dogs at a distance often move toward the interaction and investigate, while prairie dogs participating in the interaction may move away (Owings & Owings 1979). Again, results from this study indicate that captive training induces behavior that mimics natural behavior in the wild. In response to training with the cottontail control stimulus, there were no significant behavioral differences between the two groups, perhaps because no alarm vocalization was paired with the cottontail presentation in the training group.

While it is clear that training juveniles with a predator in conjunction with alarm vocalizations elicited effective antipredator behavior, future studies will need to separate the roles of predator exposure and vocalization experience to determine their respective contribution to successful predator training. It will be important to see if barking vocalizations can induce antipredator behavior to ecologically neutral cottontails as a test of "learning preparedness" (see Mineka & Cook 1988).

A second training period enhanced these pre-release differences for all stimulus animals except the hawk. By the second week of training, juvenile prairie dogs were more wary in the presence of the ferret compared to the first week, while exhibiting elevated confrontational behavior with the snake typical of wild prairie dogs (Hoogland 1995). The looming nature of the hawk may have been sufficient to generate predator recognition and avoidance in only one trial as has been observed in other such studies (Giles 1984). Regardless, it seems likely that juvenile prairie dogs learn rapidly, as in other predator recognition studies, which have typically shown that predator avoidance can be acquired in only one to two trials (Chivers & Smith 1995; Magurran 1989; Mineka & Cook 1988).

Is this rapid learning in captivity predictive of post-release survival? The answer appears to be yes. Results from this study indicate that juveniles exposed to predators in conjunction with conspecific alarm vocalizations survive to one year post-release in higher numbers than predator naïve juveniles. These results encourage the training of animals to recognize predators and respond "appropriately" by demonstrating a direct link between behavioral responses during training and post-release survival.

REFERENCES

- Beck, B. 1995a. Reintroduction, zoos, conservation, and animal welfare. In: *Ethics on the Ark* (Ed. by Maple, T. L.), pp. 155-163: The Smithsonian Institute.
- Beck, B. 1995b. Reintroduction, zoos, conservation, and animal welfare. In: *Ethics on the Ark* (Ed. by Maple, T. L.), pp. 155-163: The Smithsonian Institute.
- Beck, B. B., Rapaport, L. G. & Wilson, A. C. 1994. Reintroduction of captive-born animals. In: *Creative Conservation* (Ed. by Feistner, A.), pp. 265-286. London: Chapman and Hall.
- Biggins, D., Vargas, A., Godbey, J. L. & Anderson, S. H. 1999. Influences on pre-release experience on reintroduced black-footed ferrets (*Mustela nigripes*). *Biological Conservation*, **89**, 121-129.
- Bolbroe, T., Jeppesen, L. & Leirs, H. 2000. Behavioral response of field voles under mustelid predation risk in the laboratory: More than neophobia. *Annales Zoologica Fennici*, **37**, 169-178.
- Brown, C. & Laland, K. N. 2001. Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, **59**, 471-493.
- Chivers, D. P. & Smith, R. J. F. 1995. Free-living fathead minnows rapidly learn to recognize predators. *Journal of Fish Biology*, **46**, 949-954.
- Fischer, J. & Lindenmayer, D. B. 2000. An assessment of the published results of animal relocations. *Biological Conservation*, **96**, 1-11.
- Frantzen, M. A. J., Ferguson, J. W. H. & de Villiers, M. S. 2001. The conservation role of captive African wild dogs (*Lycaon pictus*). *Biological Conservation*, **100**, 253-260.
- Giles, N. 1984. Development of the overhead fright response in wild and predator-naive three-spined sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, **32**, 276-279.
- Griffin, A. S., Blumstein, D. T. & Evans, C. S. 2000. Training captive-bred or translocated animals to avoid predators. *Conservation Biology*, **14**, 1317-1326.
- Griffin, A. S. & Evans, C. S. 2003. Social learning of antipredator behaviour in a marsupial. *Animal Behaviour*, **66**, 485-492.
- Griffin, A. S., Evans, C. S. & Blumstein, D. T. 2001. Learning specificity in acquired predator recognition. *Animal Behaviour*, **62**, 577-589.
- Henderson, F. R., Springer, P. F. & Adrian, R. 1974. The black-footed ferret in South Dakota. pp. 1-31. Pierre, South Dakota: Department of Game, Fish and Parks.

- Hoogland, J. L. 1995. *The black-tailed prairie dog: social life of a burrowing mammal*. Chicago, Illinois: University of Chicago Press.
- Huber, P. J. 1967. The behavior of maximum likelihood estimates under non-standard conditions. In: *Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability*, pp. 221-233. Berkeley, California: University of California Press.
- Kelly, J. L. & Magurran, A. E. 2003. Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries*, 4, 216-226.
- Loughry, W. J. 1987. The dynamics of snake harassment by black-tailed prairie dogs. *Behaviour*, 103, 27-48.
- Loughry, W. J. 1992. Ontogeny of time allocation in Black-tailed prairie dogs. *Ethology*, 90, 206-224.
- Magurran, A. E. 1989. Acquired recognition of predator odour in the European minnow (*Phoxinus phoxinus*). *Ethology*, 82, 216-223.
- Maloney, R. F. & McLean, I. G. 1995. Historical and experimental learned predator recognition in free-living New Zealand robins. *Animal Behaviour*, 50, 1193-1201.
- McLean, I., Holzer, C. & Studholme, B. 1999. Teaching predator recognition to a naive bird. *Biological Conservation*, 87, 123-130.
- McLean, I., Schmitt, N. T., Jarman, P. J., Duncan, C. & Wynne, C. D. I. 2000. Learning for life: Training marsupials to recognise introduced predators. *Behaviour*, 137, 1361-1376.
- Miller, B. D., Biggins, D., Hanebury, L. & Vargas, A. 1994. Reintroduction of the black-footed ferret (*Mustela nigripes*). In: *Creative Conservation: interactive management of wild and captive animals* (Ed. by P.J.S. Onley, G. M. M., A.T.C. Feistner). London: Chapman and Hall.
- Mineka, S. & Cook, M. 1988. Social learning and the acquisition of snake fear in monkeys. In: *Social learning: psychological and biological perspectives* (Ed. by Zentall, T. R. & Jr., B. G. G.). Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Mirza, R. S. & Chivers, D. P. 2000. Predator-recognition training enhances survival of brook trout: evidence from laboratory and field enclosure studies. *Canadian Journal of Zoology*, 78, 2198-2208.
- Owings, D. H. & Loughry, W. J. 1985. Variation in snake-elicited jump-yipping by Black-tailed prairie dogs: Ontogeny and snake-specificity. *Zeitschrift fuer Tierpsychologie*, 70, 177-200.

- Owings, D. H. & Owings, S. C. 1979. Snake-directed behavior by Black-tailed prairie dogs (*Cynomys ludovicianus*). *Zeitschrift fuer Tierpsychologie*, **49**, 35-54.
- Shriner, W. M. 1995. Yellow-bellied Marmot and Golden-mantled Ground Squirrel Responses to Conspecific and Heterospecific Alarm Calls. In: *Animal Behavior Graduate Group*, pp. 1-168. Davis: University of California, Davis.
- StataCorp. 2004. Stata Statistical Software. College Station, Texas: Stata Corporation.
- Truett, J. & Savage, T. 1998. Reintroducing prairie dogs into desert grasslands. *Restoration and Management Notes*, 189-195.
- Vargas, A. & Anderson, S. H. 1998. Ontogeny of black-footed ferret predatory behavior towards prairie dogs. *Canadian Journal of Zoology*, **76**, 1696-1704.
- Wallace, M. P. 1994. Control of behavioral development in the context of reintroduction programs for birds. *Zoo Biology*, **13**, 491-499.
- White, H. 1980. A heteroskedasticity-consistent covariance matrix estimator and a direct test of heteroskedasticity. *Econometrica*, **48**, 817-830.
- White, H. 1982. Maximum likelihood estimation of misspecified models. *Econometrica*, **50**, 1-25.
- Williams, R. L. 2000. A note on robust variance estimation for cluster-correlated data. *Biometrics*, **56**, 645-646.
- Yoerg, S. I. & Shier, D. M. 1997. Maternal presence and rearing condition affect responses to a live predator in kangaroo rats, *Dipodomys heermanni arenae*. *Journal of Comparative Psychology*, **111**, 362-369.
- Yoerg, S. I. & Shier, D. M. 2000. Captive breeding and anti-predator behavior of the Heermann's kangaroo rat. pp. 1-56. Sacramento, California: Department of Fish and Game.

TABLES AND FIGURES

Table 1.1 Period and trial effects for trained juveniles

Stimulus Animal	ANOVA factor					
	Trial (weeks 1 vs. 2)		Period (pre vs. post)		Trial x Period	
	$F_{1,8}$	P	$F_{1,8}$	P	$F_{1,8}$	P
Ferret						
Vigilance	11.951	0.009	20.311	0.002	0.282	0.610
Shelter	2.861	0.129	31.09	0.001	20.238	0.002
Alarm vocalizations	23.866	0.001	3.215	0.111	0.341	0.575
Activity	4.615	0.064	14.880	0.005	1.704	0.228
Hawk						
Vigilance	0.025	0.878	18.444	0.003	9.973	0.013
Shelter	5.284	0.053	4.479	0.067	2.385	0.161
Alarm vocalizations	4.242	0.073	0.637	0.448	4.025	0.080
Activity	3.012	0.121	33.379	0.001	2.783	0.134
Snake						
Vigilance	20.318	0.002	9.627	0.015	1.242	0.297
Shelter	12.366	0.008	24.758	0.001	9.952	0.014
Alarm vocalizations	4.824	0.059	2.711	0.138	8.943	0.017
Activity	24.557	0.001	11.183	0.010	0.119	0.739
Rabbit						
Vigilance	0.343	0.574	3.008	0.121	0.734	0.417
Shelter	16.86	0.003	1.938	0.201	0.899	0.371
Alarm vocalizations	3.91	0.068	0.037	0.853	0.357	0.567
Activity	33.608	0.000	0.235	.0641	0.013	0.911

Results of two-way (Trial x Period) repeated measures ANOVAs comparing the mean rate (secs/min) allocated to four behaviors by the trained prairie dogs in tests with each stimulus animal.

Figure Legends

Figure. 1.1 Time spent (a) vigilant and (b) in or near shelter; and (c) frequency of alarm calling (both barking and jump-yipping) and (d) quadrant changes (activity) by trained (\square) and control (\blacksquare) juvenile prairie dogs during trials 1 and 2 with four different stimulus animals (ferret, hawk, snake and cottontail). Control prairie dogs were exposed to an empty compartment whereas trained prairie dogs were exposed to the stimulus animals plus alarm calls. Means + SE are shown. Significant statistical interactions are indicated as follows: $* = P < 0.05$; $** = P < 0.01$.

Figure 1.2 Time allocated to a) vigilance, b) shelter, and c) alarm vocalizations and d) activity by trained juveniles in tests with a ferret, hawk, snake and cottontail during pre-training, training, and post-training periods in (\blacksquare) trial 1 and (\square) trial 2. Means + SE are shown.

Figure 1.1

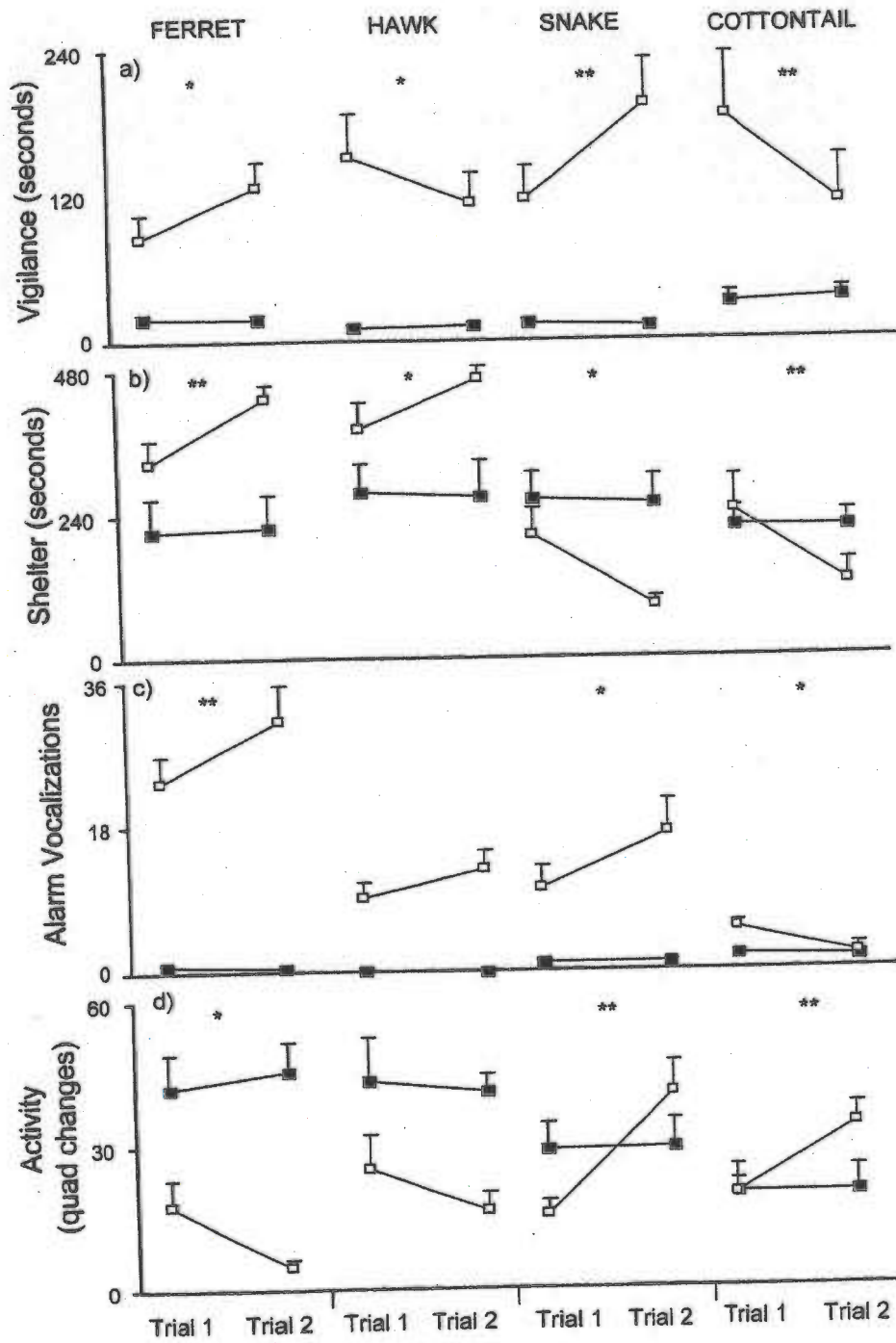
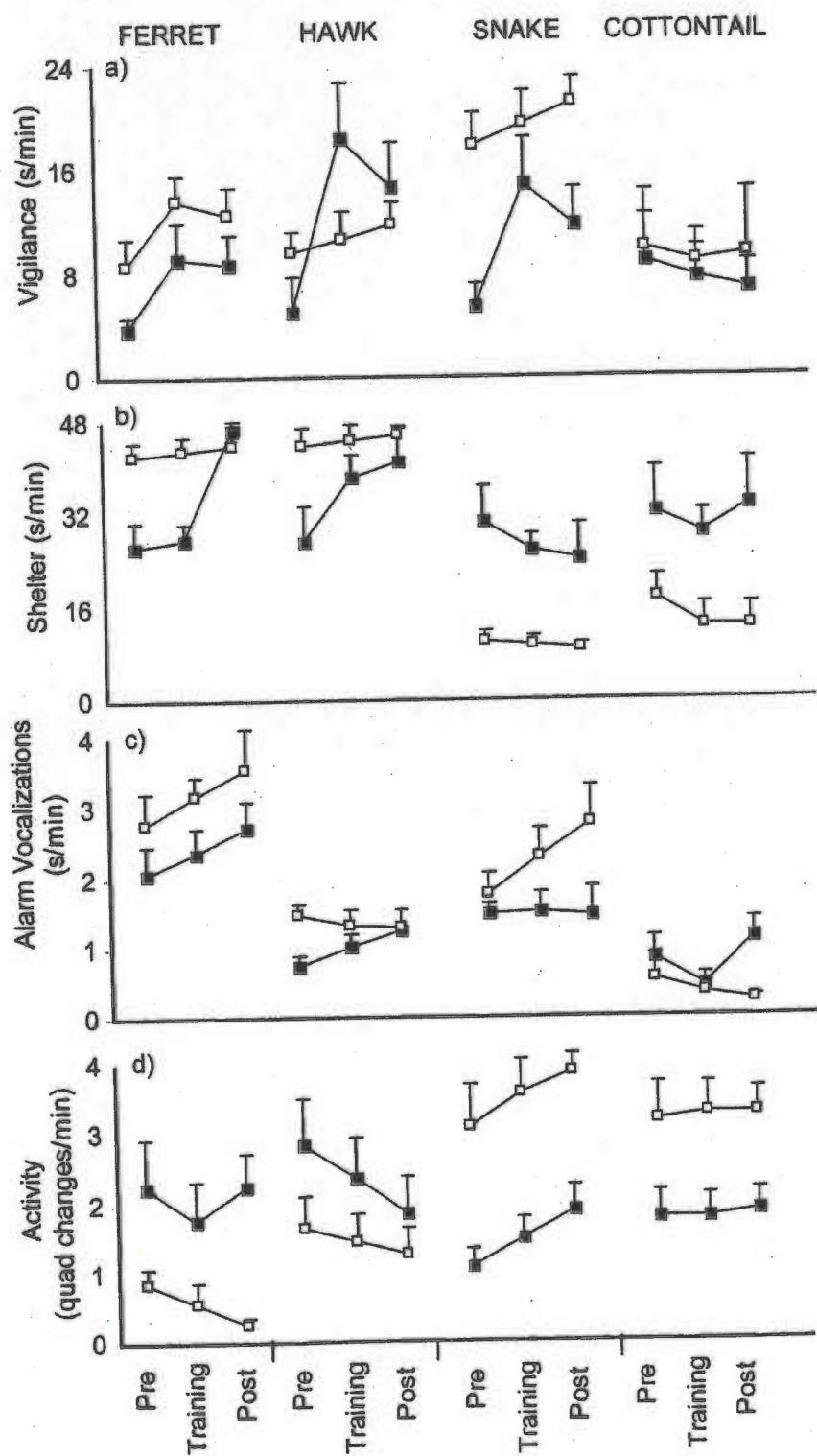


Figure 1.2



**CHAPTER TWO: EFFECTS OF SOCIAL CONTEXT ON PREDATOR
TRAINING IN JUVENILE BLACK-TAILED PRAIRIE DOGS
(*CYNOMYS LUDOVICIANUS*)**

ABSTRACT

I examined how social context and experience affected development of antipredator behavior and subsequent post-release survival in the black-tailed prairie dog, *C. ludovicianus*. The study involved three parts. Initially, juveniles newly emerged from their nursery burrows were wild-trapped and brought into captivity for experimental manipulation of predator experience (captive-reared). Next, remaining juveniles from the same families were wild-trapped approximately 7 weeks later (wild-reared) and transferred to captive enclosures. In captivity, the antipredator behavior of wild-reared juveniles was compared to that of the captive-reared animals who had received training with experienced adults. Finally, all juveniles were released and their survival was compared. Captive-reared juveniles were initially exposed to four stimulus animals: a live black-footed ferret, a live prairie rattlesnake, a mounted red-tailed hawk, and a desert cottontail control (pre-training tests). They were then divided into two developmental treatment groups: 1) trained with an experienced adult female or 2) trained without an experienced adult female. Training involved exposure to each stimulus animal two to three times over five weeks. After training, each juvenile was re-tested with each stimulus animal (post-training tests). At emergence from natal burrows (pre-training tests) juveniles responded differentially to the stimulus animals. They were least active with the snake, fled the most in tests with the hawk, and were less vigilant with the ferret than with the snake. Following training, juveniles trained with experienced adults were more wary with all four stimulus animals than juveniles trained without an experienced adult present. I then compared the antipredator behavior of the wild-reared juveniles to the post-training test behavior of the captive-reared juveniles who had been trained with

experienced adult females. The wild-reared animals behaved differently from the trained captive-reared juveniles. All juveniles were released together with remaining coterie members into artificial burrow systems at a newly established site. One year after release, juveniles trained with experienced adults were more likely to survive than juveniles trained without experienced adults, and wild-reared juveniles were more likely to survive than captive-reared juveniles. These findings provide the first evidence that social transmission of antipredator behavior during training can enhance survival following release.

INTRODUCTION

Mammalian development is embedded in a social context. Social context affects behavioral development both before birth (e.g. intrauterine position, Ryan & Vandenberg 2002), and after birth through basic regulatory processes known as "hidden regulators" (e.g., the effects of warmth, nutrients, olfactory or tactile stimulation Polan & Hofer 1999) and HPA effects of parenting style (Francis et al. 1999). Coupled with the extended interactions required for nursing young, these processes set the stage for extensive social influences on development, including learning. Social learning is important in the development of behavior in many taxa (Zentall & Galef 1988; Heyes & Galef 1996; Box & Gibson 1999). Consistent with this social learning context, early exposure to littermates and adults in complex situations is also known to enhance rodent brain development (reviewed in Coss 1991). Interactions with conspecifics can allow inexperienced young to learn about their environment without incurring the time, energy, and fitness costs associated with learning survival skills alone. For example, animals can modify their behavior as a result of observing a conspecific responding to a stimulus (observational conditioning), or an experienced conspecific can influence a naïve animal's development indirectly by bringing its attention to a particular stimulus or event in the local environment (local enhancement)(Galef 1988). Thus early social experience can lead to efficient development of effective foraging, mate selection, and antipredator behavior (Curio 1993; Brown & Laland 2001), and increase fitness (Mateo & Holmes 1997).

Social factors may strongly influence how experience shapes development. In some song birds, the presence of a live tutor extends the developmental period during

which species-specific song may be learned (see Petrinovich, 1988). Similar processes may be evident in the acquisition of anti-predator behavior. Young animals may first encounter predators or predator-related stimuli in the company of their parents, siblings, or other conspecifics (Curio, Ernst & Vieth, 1978; Poran & Coss, 1990). In Belding's ground squirrels, juveniles living with their mother after natal emergence were able to discriminate between alarm and non-alarm calls faster than juveniles living without their mothers (Mateo & Holmes 1997). Fathers can also play an important role in the development of effective antipredator behavior. In sticklebacks (*Gasterosteus aculeatus*), fry chased by their father and subsequently returned to the nest develop stronger avoidance responses toward a predator model than fry that are orphaned (Huntingford & Wright 1993).

The amount of parental influence on the ontogeny of antipredator behavior in young will likely vary with the time young are dependent on their parents. With extended parental care, young may have many opportunities to observe and learn from their parents' antipredator behaviors (e.g. Cheney & Seyfarth 1990; Poran & Coss 1990). Thus, the length of dependency on parents will influence the development of offspring's antipredator repertoires, and extended parental care may result in variable pathways of behavioral development, including social facilitation of responses to predators.

In highly social species, young animals may live and interact regularly with their own parents as well as other experienced adults (e.g. gregarious birds and colonial species). In these species several members of a group may produce offspring and therefore exhibit heightened vigilance associated with predators. Juveniles raised in these groups may not be restricted to learning skills from their own parents, but rather may

have the opportunity to learn life skills from other experienced group members. In general, we need to understand the role of conspecifics in the acquisition of appropriate anti-predator behavior. That role may be direct, e.g., observational learning of specific behaviors, or indirect, e.g., decreasing a threshold for response or distracting a potential predator.

Reintroduction of captive-bred endangered species is one context in which information on how animals learn about predators is of practical as well as theoretical importance (Kleiman, 1989). Captive environments may fail to provide the predator-related experiences necessary to ensure survival upon release into native habitat, and even the skills of wild-caught individuals may erode while in captivity (Kleiman 1989). Consequently, several recent studies, particularly in fish, have examined how animals learn to recognize and avoid predators (Kelly & Magurran 2003), and predator training (e.g., providing critical predator-related experiences) is becoming part of some captive breeding programs (Mirza & Chivers 2000; Jarvi & Uglem 1993; McLean et al. 1996; McLean et al. 2000; Yoerg & Shier 1997). But with training as well as with general theory, our understanding of the developmental processes supporting antipredator behavior is relatively poor (but see Miller et al. 1990; Yoerg & Shier 1997). To be most effective, antipredator training should mimic the critical features of ontogenetic processes in the wild: the experimental treatments used, the developmental timing of the training, and the social and physical context in which it occurs must all be appropriate.

The primary goal of the present study was to investigate how social context affects the development of antipredator behavior in juvenile black-tailed prairie dogs (*Cynomys ludovicianus*) and ultimately survival following release to the wild. Black-

tailed prairie dogs are prey to a variety of predators, including black-footed ferrets, raptors, snakes, coyotes, weasels and bobcats. They are a colonial species that lives in social groups called coterie which typically contain one adult male, several adult females, yearling males and females, and juveniles (young of the year)(Hoogland 1995). Adult antipredator behavior is well-studied. Adult prairie dogs bark repetitiously, warning offspring and nondescendant kin of impending danger in the presence of mammals and aerial predators (Hoogland 1995). Upon hearing a bark alarm call, prairie dogs scan for predators and if one is detected, run to a burrow mound and either enter or begin calling (Hoogland 1995). Interactions with snakes are characteristically confrontational. Adult prairie dogs typically orient towards and approach the snake in an elongated posture, sniff, jump away and give distinct jump-yips calls and/or footdrum (Owings & Owings 1979; Owings & Loughry 1985). They also attack snakes (i.e. biting, swatting; Owings & Loughry 1985) and have been observed to throw substrate at them (D. Shier, pers. obs.). Newly emergent juveniles remain close to burrows, are vigilant, and forage little (Loughry 1992). Juveniles jump-yip at higher rates upon emergence than in subsequent weeks (Loughry 1992), but rarely bark or footdrum until they have been above ground for a few months (Hoogland 1995).

It is likely that social experience is essential for the development of antipredator behavior in prairie dogs. Mothers call more often after first juveniles emerge than males or nonmaternal females (Hoogland 1995) and therefore may play an essential role in the development of effective anti-predator behavior. Newly emergent juveniles may benefit equally from all maternal females in their coterie since several females in a coterie may be reproductive at the same time (Hoogland 1995). Because newly emerged juveniles are

highly vulnerable to predation, individuals that can recognize life-threatening situations sooner may be more likely to escape from an otherwise fatal predator encounter.

The experiment was designed to determine: 1) whether newly emerged juvenile prairie dogs with no prior above-ground predator experience would exhibit functionally appropriate antipredator responses to 3 different predators under the influence of experienced adults (demonstrators); 2) if trained captive-reared juveniles behave similarly to wild-reared juveniles of the same age; and 3) whether juvenile prairie dogs trained with experienced adults (demonstrators) show higher survival than juveniles trained without experienced adults one-year after release.

METHODS

This experiment involved two groups of individuals. The first group was trapped at emergence from their natal burrows and brought into captivity for experimental manipulation of predator experience (captive-reared). The second group of juveniles was from the same coterries but raised in the wild (trapped 7 weeks later; wild-reared). I first compare the behavior of captive-reared juveniles raised and trained with experienced adult demonstrators and those exposed to predators without experienced adults. I then compare the behavior of a subset of the captive-reared juveniles to that of a subset of the wild-reared juveniles. Finally, all juveniles (captive and wild-reared) were released to the wild and survival was assessed one-year post release.

Experimental Manipulation of Predator Experience

Subjects and Housing.

Subjects were 36 prairie dog juveniles produced by 8 wild-caught females. Juvenile prairie dogs were live trapped on Vermejo Park Ranch, Colfax County New Mexico within 1-2 days of emergence to prevent mixing of litters within a coterie. I trapped all juveniles in a litter along with their mother and transferred them to field enclosures on the property. In order to control for genetic variation, females and litters were collected from the same ($r = 0.5$) or neighboring ($r > 0.375$) coteries (Hoogland 1995). Each female was housed with her litter in a separate wire mesh enclosure (2 x 2 x 3 m) with a metal frame and a mesh canopy over the top. The mesh canopy prevented attacks by raptors but allowed exposure to other potentially important environmental cues. Animals were provided with a burrow system of black PVC tubing and a wood nest box (0.3 x 0.3 x 0.5m), which was buried in 0.3 m of dirt to simulate natural burrow systems. Juveniles were dye-marked and eartagged for individual identification. Females and juveniles were allowed to habituate to the enclosures for 1 week prior to pre-training tests.

Experimental Protocol.

Each focal juvenile was given a pre-training test (assessment of baseline antipredator behavior), a 5-week training period involving 2 exposures to predators each week, and a post-training test (Table. 2.1).

Pre-Training Tests.

At age 49 days (1 week following natural emergence), I began pre-testing each focal juvenile ($n = 36$; one test/day) with 1) a live black-footed ferret (*Mustela nigripes*), 2) a live rattlesnake (*Crotalus viridis*), 3) a moving, taxidermically-mounted red-tailed hawk (*Buteo jamaicensis*), and 4) a live desert cottontail (*Sylvilagus auduboni*) (non-predator stimulus). Black-footed ferrets and rattlesnakes are natural predators of prairie dogs (Hoogland 1995). The hawk (taxidermic mount with wings extended) served as a moving model aerial predator. Cottontails are also present in the natural environment of prairie dogs but are not predators. Different predators of prairie dogs have different hunting styles, thus it is important for captive born juveniles to experience the full range of types of threats from predators. The pre-training tests established baseline rates of behavior to be compared with the same behaviors in the post-training tests.

All testing occurred in the focal animal's home cage. During the pre-training tests I removed the mother and all siblings except the focal subject from the home cage (to eliminate the effects of the social environment during exposure and test habituation learning), placed a mesh barrier or box in the home cage, and then allowed the focal subject to habituate to the testing conditions for 10 min. I then placed the test stimulus behind the barrier or in the mesh box. The hawk presentation required a different procedure. The hawk was hooked to a cable and entered the enclosure at a -45° angle from the top of a 5 m tower. I presented the hawk midway through the tests. The order of stimuli was counterbalanced to avoid order effects. Ten-min tests were video taped. An observer blind to treatment conditions scored the tapes. Behaviors scored included:

vigilance (bipedal stand while oriented toward stimulus animal); shelter (time spent in or within 10 cm of nest box or burrow); activity (number of quadrant changes); and alarm vocalizations (frequency of barking or jump-yipping); fleeing (rapid movement away from the stimulus animal); and digging (movement of sand with either forefeet and/or hindfeet).

Developmental Conditions – Training

Following the pre-training tests, one juvenile from each litter was randomly assigned to one of two developmental treatments ($n = 18$ per treatment): (a) Experienced Adult (EA), in which the focal juvenile was trained with an experienced adult female demonstrator (raised and trained with either their mother or a close relative from their home coterie) or (b) Without Experienced Adult, (WEA) where the focal juvenile was “trained” without an experienced adult (raised and exposed to predators and the control stimulus animal with inexperienced littermates or raised with their mother but exposed to stimulus animals alone). Training periods were ten-min sessions in which either the ferret, snake or cottontail is placed behind a mesh barrier or in a mesh box in the focal prairie dog home cage or the hawk was presented via the pulley system midway through the session. Once juveniles were assigned to a treatment, they remained housed in that treatment for the duration of the experiment. Each juvenile from the two conditions was exposed to the ferret and rattlesnake two times and hawk and cottontail three times during the five-week period (two exposures/week; Figure 1). Littermates that were not chosen to be focal subjects participated as siblings in condition (b), to control for the presence of an experienced animal. In order to control for possible effects related to sex, the number

of male and female juveniles from each litter were divided equally among the two groups.

Post-training tests.

To measure the change in behavior, if any, due to predator exposure, each focal juvenile was tested after the five-week treatment period with each type of predator and the non-predator stimulus. The post-training tests followed the same guidelines and procedures as the pre-training tests. Four exemplars of each stimulus animal were used during training and tests to provide more natural variation in predator-based experience and to prevent habituation to a particular stimulus animal.

Comparison to Wild-reared Counterparts.

Once post-tests were complete, all remaining coterie members in the wild were trapped and brought into the enclosures ($n = 14$ adult males; 19 adult females; 14 juvenile males; 16 juvenile females). The newly trapped prairie dogs were given 1-3 days to habituate to the enclosures. A subset of the wild-reared juveniles (4 males; 5 females) were then tested with each stimulus animal following the same guidelines and procedures for the pre-training tests. The behavior of wild-reared juveniles and those captive-reared and trained with experienced adults were compared.

Analysis of Behavioral Responses.

I used t-tests for each dependent variable to test for sex differences in behavior in the pre-training test and again in the post-training test. All t-tests were statistically non-significant with $\alpha = 0.05$, therefore I combined males and females in subsequent analyses and did not include sex as a factor. I analyzed pre-training tests using one-way

ANOVA's with stimulus type (ferret, hawk, snake & cottontail) as a within subjects factor and used Bonferroni post hoc tests to examine pairwise differences in responses to each predator type and control.

Because prairie dogs behaved differently in the presence of different predator types during pre-tests, I conducted statistical analyses for each predator type separately (ferret, hawk, snake, cottontail). Therefore, to examine the effects of social context on training, for each predator a two-factor repeated measures ANOVA (pre vs. post-training tests) was employed with developmental treatment (EA vs. WEA) as the between subjects variable.

To determine if vigilance and alarm calling levels of demonstrators were predictive of juvenile prairie dog behavior, for each demonstrator I randomly selected one training period with each type of stimulus animal and determined the frequency of alarm calling and the amount of time the demonstrator spent vigilant. I then conducted regression analyses to determine if demonstrator behavior was predictive of juvenile responses during post-training tests.

To investigate differences in behavior between wild-reared and captive-reared juveniles trained with experienced adults, I used a two-factor repeated measures ANOVA with rearing condition (wild-reared vs. captive reared) as the between subjects factor and predator type (ferret, hawk, and snake) as the within subjects factor. Because juveniles behaved differently with the cottontail control stimulus during the pre and post-training tests, I analyzed tests with the cottontail separately using a *t*-test for each dependent variable. All statistical analyses were conducted using SPSS version 12 for Windows (SPSS Inc.).

Measuring training success.

At the end of the experiment all animals (captive reared; $n = 34$ and wild-reared; $n = 30$) in addition to all adults from their coterie were released in a newly-established prairie dog town to measure survival and reproductive success. I used "soft release" protocol established by Truett and Savage (1998) which allowed animals to habituate to the new site and remain protected from predators while digging new burrow systems. Coterie units were kept together to decrease stress and dampen post-release dispersal (see (Truett & Savage 1998).

I compared the frequency of survival of reintroduced and translocated animals in spring 2002 to determine if the survival rate of animals brought into captivity and trained differed from the survival rate of translocated animals from the same coterie.

RESULTS

Description of alarm behavior

Juvenile prairie dogs were very responsive to the three predators and desert cottontail control. Initially, they stood alert, often on their hind feet stretched upright, to scan the area and watch the predator or cottontail. Alert behavior was followed by either running to shelter and standing in bipedal or quadrupedal alert postures with tail erect, or repeatedly approaching the predator in an elongated posture and jumping or slowly moving away. Occasionally, prairie dogs gave barking or jump-yipping calls and/or footdrummed. While barking was observed during tests with all four stimulus animals, jump-yipping and footdrumming were only exhibited during tests with the snake. Prairie dogs either hit their hind feet on the ground during the jump-yipping calls or they stood in a quadrupedal posture and hit the proximal ends of their hind feet on the ground.

Pre-training tests

On first presentation, newly emergent juvenile prairie dogs behaved differently toward the four stimulus animals (Fig. 2.1). The predator and non-predator stimulus animals (ferret, snake, hawk and cottontail) evoked significantly different activity levels, amount of time allocated to vigilance, frequency of alarm calling and fleeing (respectively: $F_{3,132} = 4.093$, $P = 0.008$; $F_{3,132} = 3.001$, $P = 0.033$; $F_{3,132} = 76.173$, $P < 0.0001$; $F_{3,132} = 4.149$, $P = 0.008$, Fig. 2.1). Activity was substantially lower when juveniles were paired with the snake than with the ferret (Bonferroni post hoc test: $P = 0.025$), whereas juveniles spent significantly less time vigilant (oriented toward and alert) in the presence of the ferret than the snake (Bonferroni post hoc test: $P = 0.04$). The hawk elicited the most fleeing behavior (Bonferroni post hoc tests: vs. ferret, $P = 0.025$, vs. cottontail, $P = 0.036$, vs. snake, $P = 0.025$), while the snake elicited the most alarm vocalizations (Bonferroni post hoc tests: vs. ferret, $P = 0.0001$, vs. hawk, $P = 0.00001$, vs. cottontail, $P = 0.0001$). Juveniles did not, however, allocate time differently to shelter during pre-training tests with the different stimulus animals.

Effect of social context on training

The presence of an experienced adult demonstrator made a difference in the impact of training with the four stimulus animals (Fig. 2.2). In general, juveniles trained with an experienced adult present were much more wary following training with all four stimulus animals than juveniles trained without an experienced demonstrator.

During exposure to the ferret, juveniles in both groups exhibited significantly less activity during the post-training test than during the pre-training test (main effect: $F_{1,32} =$

16.424, $P < 0.0001$) while increasing their bark vocalizations (main effect: $F_{1,32} = 43.012$, $P < 0.000$), time spent vigilant (main effect: $F_{1,32} = 5.395$, $P = 0.027$) and time spent in shelter: (main effect: $F_{1,32} = 5.395$, $P = 0.027$). However, these differences during the ferret trials were driven by juveniles trained with an experienced adult demonstrator (statistical interaction effect between developmental condition and time (activity: $F_{1,32} = 4.576$, $P = 0.04$; bark vocalization: $F_{1,32} = 24.306$, $P < 0.0001$; vigilance: $F_{1,32} = 5.473$, $P = 0.026$; shelter: $F_{1,32} = 4.910$, $P = 0.034$; Fig. 2.2). In the presence of the hawk, there was no significant difference in activity or vigilance from pre- to post-training trials (activity: $F_{1,32} = 1.102$, $P = 0.302$; vigilance: $F_{1,32} = 3.235$, $P = 0.082$; Fig. 2.2). Albeit, juveniles trained without experienced demonstrators decreased time allocated to vigilance while juveniles trained with experienced demonstrators did not (developmental condition X time interaction: $F_{1,32} = 4.12$, $P = 0.050$; Fig. 2.2). There was an overall increase in bark vocalizations and time spent in shelter following training (bark vocalization: $F_{1,32} = 16.257$, $P < 0.0001$; $F_{1,32} = 23.677$, $P < 0.001$), and this effect appears much more pronounced for juveniles trained with experienced demonstrators (statistical interaction effect developmental condition X time: bark vocalization $F_{1,32} = 9.545$, $P = 0.004$; shelter: $F_{1,32} = 10.725$, $P = 0.003$; Fig. 2.2).

All juveniles were more active following training with the snake (main effect: $F_{1,32} = 9.781$, $P = 0.004$); however, the differences were greater for juveniles trained without experienced demonstrators (developmental condition x time interaction: $F_{1,32} = 4.810$, $P = 0.036$; Fig. 2.2). Overall, juveniles did not allocate time to vigilance or jump-yipping vocalizations differently during pre and post-training tests with the snake (vigilance main effect: $F_{1,32} = 0.879$, $P = 0.355$; jump-yipping vocalization main effect:

$F_{1,32} = 0.013, P = 0.909$), but juveniles trained with experienced demonstrators showed an increase in jump-yipping from pre to post-training while those trained without experienced demonstrators decreased jump-yipping vocalizations (ANOVA: developmental condition X time interaction: $F_{1,32} = 6.560, P = 0.015$; Fig. 2.2). There was a statistically significant decrease in the amount of time juveniles spent in or near shelter following training (main effect: $F_{1,32} = 8.369, P = 0.007$). This result appears to be driven by juveniles trained without experienced adults (developmental condition X time interaction: $F_{1,32} = 11.357, P = 0.002$; Fig. 3) as juveniles trained with experienced adults show a slight increase in time spent in shelter following training (Fig. 2.2).

Finally, in tests with the cottontail (control stimulus), juveniles were more active and less vigilant following training (activity main effect: $F_{1,32} = 7.178, P = 0.012$; vigilance main effect: $F_{1,32} = 14.030, P = 0.001$; Fig. 2.2). Again these results appear to be differentially driven by juveniles in the different treatment groups. Juveniles trained without experienced demonstrators show a striking increase in activity and substantial decrease in vigilance when tested with the cottontail, whereas juveniles trained with experienced demonstrators show virtually no behavioral differences from pre to post training trials (developmental condition x time interaction: activity $F_{1,32} = 6.508, P = 0.016$; vigilance: $F_{1,32} = 4.677, P = 0.038$; Fig. 2.2). There was no statistically significant difference in the frequency of alarm vocalizations or amount of time juveniles spent in shelter following training with the cottontail (alarm vocalizations main effect: $F_{1,32} = 2.105, P = 0.157$; $F_{1,32} = 2.447, P = 0.128$; Fig. 2.2).

Relationship to demonstrator behavior

During training, the vigilance behavior and alarm vocalizations of juveniles followed closely that of the demonstrator prairie dogs with which they were housed. Formal analysis revealed that demonstrator behavior during training was predictive of juvenile behavior during post-training tests (vigilance: $r^2 = 0.749$, $P < 0.001$; alarm vocalizations: $r^2 = 0.317$, $P = 0.01$).

Captive vs. Wild-reared Juveniles

Juveniles reared in captivity and trained with experienced adult females behaved differently during post-training tests than juveniles of the same age reared in the wild. In general, wild-reared juveniles were more wary, alarm calling and allocating more time to vigilance (alarm vocalization main effect: $F_{1,25} = 12.625$, $P = 0.002$); vigilance main effect: $F_{1,25} = 8.545$, $P = 0.007$), but spending less time in shelter than captive-reared juveniles (shelter main effect: $F_{1,25} = 10.134$, $P = 0.004$; Fig. 2.3). Overall, juvenile prairie dogs behave differently in the presence of different predators (ANOVA: predator type: alarm vocalization: $F_{2,50} = 7.942$, $P = 0.001$; vigilance: $F_{2,50} = 19.140$, $P < 0.0001$; shelter: $F_{2,50} = 11.590$, $P < 0.0001$; and activity: $F_{2,50} = 24.918$, $P < 0.0001$), and more specifically, the results suggest that captive-reared and wild-reared juveniles do not differentiate among the predators in the same way (statistical interaction of predator type X rearing condition (ANOVA: alarm vocalization: $F_{2,50} = 3.915$, $P = 0.026$; vigilance: $F_{2,50} = 13.029$, $P < 0.0001$; activity: $F_{2,50} = 19.600$, $P < 0.0001$). For example, captive-reared juveniles were more active than captive-reared juveniles in trials with the hawk,

but less active when tested with the snake. Finally, when tested with the cottontail control wild-reared juveniles were more active and spent less time in shelter than captive-reared juveniles trained with experienced adults (activity: $t_{1,25} = -2.899$, $P = 0.008$; and shelter: $t_{1,25} = 2.245$, $P = 0.034$).

Training Success

Social context and rearing condition affected survival following release. Juveniles raised and exposed to predators in the presence of an experienced adult female from their home coterie were more likely to survive for one year post-release than juveniles trained without an experienced adult ($X^2 = 5.7$, $P = 0.017$; Fig. 2.4a). Juveniles raised in the wild and translocated to a new site showed a significantly higher frequency of survival one-year post-release than juveniles raised in captivity, trained with predators, and reintroduced ($X^2 = 3.979$, $P = 0.043$; Fig. 2.4b). However, wild-raised juveniles were not more likely to survive than trained captive-raised juveniles ($X^2 = 0.119$, $P = 0.732$).

DISCUSSION

The results of this study show that at emergence juvenile prairie dogs differentiate among predators. During initial exposure with the three predators and cottontail control, juveniles were less active and more vigilant with the rattlesnake than with the ferret, alarm-called the most during interactions with the rattlesnake, and exhibited fleeing behavior almost exclusively in the presence of the hawk. The differences in alarm behavior with the different predator types suggest that the immediate pattern of stimulation presented by each predator influences the alarm behavior of juvenile prairie dogs. Snakes are ambush predators that rely on stealth, rather than speed, and prey

primarily on relatively young prairie dog pups (i.e. pre- and newly emerged juveniles; Loughry 1987). Like young ground squirrels (*Spermophilus beecheyi*), newly emergent prairie dogs may exhibit adult-like defensive behaviors in the absence of experience with snakes (Owings & Coss 1977; Poran & Coss 1990). However, because snakes enter burrows prior to juvenile emergence, some juveniles may have had experience with snakes before testing. While it is unlikely that juvenile prairie dogs had any prior experience with hawks, ferrets, or cottontails since they were trapped at emergence, hawks were a looming threat that may not require experience to elicit avoidance behavior (Giles 1984; Hanson & Coss 1997). Not surprisingly, newly emergent juveniles fled away from the flying hawk. Juvenile prairie dogs did not behave differently in tests with ferrets and cottontails at emergence, suggesting that distinction between these animals requires some form of experience or learning after emergence.

My findings may provide the first demonstration of observational conditioning in a small mammal. Antipredator responses were socially transmitted to predator-naïve juveniles. Juvenile prairie dogs that were trained with experienced adults from their home coterie became more wary when exposed to predators and the control stimulus animal than juveniles trained without experienced demonstrators. Following training, experienced-adult trained animals alarm called, were vigilant, reduced activity, and spent time in shelter in the presence of all four stimulus animals. In contrast, juveniles trained without experienced adults rarely alarm called, reduced vigilance, increased activity, and spent less time in shelter following training with the predators and the control animal. Further, levels of vigilance and alarm vocalizations in demonstrators during training were predictive of juvenile prairie dog behavior during the post-training tests. This pattern of

results suggests that juvenile prairie dogs attended to the behavior of the demonstrator, if present, and that this altered their subsequent responses to the predators and cottontail.

Does training young prairie dogs in captivity elicit antipredator behavior similar to experience in the wild? The results suggest it does not. Prior to release, trained captive-reared juveniles spent less time vigilant and alarm calling and more time in shelter than wild-reared juveniles of the same age. These differences are most likely due to different environments during development. Disparity in the amount of time juveniles spent in shelter may be due to differential exposure to the enclosure itself. However, habituation can not fully explain the higher rates of alarm calling or vigilance exhibited by the wild-reared juveniles because these behaviors varied by predator type and therefore do not represent an overall heightened reactivity. Rather, these differences were likely due to critical features of the juvenile's social and physical environments during development. For example, wild-reared juveniles had the opportunity for above-ground experience with predators in the presence of multiple group members.

For individuals that live in stable groups, such as prairie dogs, a social group, rather than the individual or a single additional social partner, form the backdrop for social learning (Heyes & Galef 1996), and social training regimes are likely to be more effective because they mimic natural processes. Not surprisingly, research has begun to reveal the various influences of social context on learning (number of demonstrators, Galef & Whiskin 1997; Leland & Williams 1997; demonstrator status, Drea & Wallen 1999; Nicol & Pope 1999; and housing environment, Tscernichovski & Nottebohm 1998; Beecher 1996) and suggests that what an individual learns will depend on the context in which it is presented. In this study, naïve juveniles were exposed to predators with only

one demonstrator present. It is possible that the behavioral differences between captive and wild-reared individuals were simply due to the number of demonstrators present during interactions with predator stimuli. Alternatively or in addition, the complex interactions between multiple individuals and their environment may be required for the development of appropriate skills. It seems reasonable to assert that watching the fearful behavior of nearby individuals has contagious properties (see de Gelder et al. 2004). These types of interactions were not faithfully replicated in this captive setting. Further studies examining the effectiveness of predator training in the presence of intact social groups may shed light on this dynamic process.

Finally, pre-release behavior after training appears to translate to post-release survival. Previously, Shier (unpublished data) showed that training juvenile prairie dogs with predators increased survival following release compared with naïve juveniles. The present study provides the first evidence that social transmission of antipredator behavior during training can enhance survival following release. Juveniles trained with experienced demonstrators while in captivity were more likely to survive one year post-release than those exposed to predators without experienced demonstrators. These results encourage further investigation into the application of social experience and/or learning in predator training, particularly for species in which captive-breeding is the only viable alternative. However, they also imply that captive-breeding, training, and reintroduction should be used only as a last ditch effort. Wild-reared juveniles translocated to the same site were more likely to survive than trained captive-reared juveniles. Yet, there was no difference in the survival of juveniles brought into captivity at emergence and trained with experienced adult demonstrators and those translocated. Nevertheless, further

research is needed to examine the role of pre-emergent experience on the development of survival skills before captive breeding, training and reintroduction can be verified as a valid conservation strategy for this species. Therefore, if possible, translocation must continue to take precedent over captive-breeding reintroduction for populations in peril.

REFERENCES

- Beecher, M. D. 1996. Birdsong learning in the laboratory and field. In: *Ecology and Evolution of Acoustic Communication* (Ed. by Miller, D. E. K. E. H.), pp. 61-78. Ithaca, New York: Cornell University Press.
- Box, H. O. & Gibson, K. R. 1999. *Mammalian Social Learning*. Cambridge: Cambridge University Press.
- Brown, C. & Laland, K. N. 2001. Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, **59**, 471-493.
- Cheney, D. & Seyfarth, R. 1990. *How monkeys see the world*. Chicago: University of Chicago Press.
- Coss, R. G. 1991. Evolutionary persistence of memory-like processes. *Concepts in Neuroscience*, **2**, 129-168.
- Curio, E. 1993. Proximate and developmental aspects of antipredator behavior. *Advances in the study of behavior*, **22**, 135-238.
- de Gelder, B., Snyder, J., Greve, D., Gerard, G. & Hadjikhani, N. 2004. Fear fosters flight: A mechanism for fear contagion when perceiving emotion expressed by a whole body. *Proceedings of the National Academy of Sciences U.S.A.*, **101**, 16701-16706.
- Drea, C. M. & Wallen, K. 1999. Low-status monkeys 'play dumb' when learning in mixed social groups. *Proceedings of the National Academy of Sciences U.S.A.*, **96**, 12965-12969.
- Francis, D., Diorio, J., Liu, D. & Meaney, M. J. 1999. Nongenomic transmission across generations of maternal behavior and stress responses in the rat. *Science*, **286**, 1155-1158.
- Galef, B. G. 1988. Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by Galef, T. R. Z. B. G.), pp. 3-28. New Jersey: L. Erlbaum.
- Galef, B. G. & Whiskin, E. E. 1997. Effects of social and asocial learning on longevity of food-preference traditions. *Animal Behaviour*, **50**, 705-717.
- Giles, N. 1984. Development of the overhead fright response in wild and predator-naive three-spined sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, **32**, 276-279.

- Hanson, M. T. & Coss, R. G. 1997. Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to avian and mammalian predators. *Journal of Comparative Psychology*, 111, 174-184.
- Heyes, C. M. & Galef, B. G. 1996. *Social Learning in Animals: The Roots of Culture*. London: Academic Press.
- Hoogland, J. L. 1995. *The black-tailed prairie dog: social life of a burrowing mammal*. Chicago, Illinois: University of Chicago Press.
- Huntingford, F. A. & Wright, P. J. 1993. The development of adaptive variation in predator avoidance in freshwater fishes. In: *Behavioral ecology of fishes* (Ed. by Torricelli, F. A. H. P.), pp. 45-61. London: Harwood Academic.
- Jarvi, T. & Uglem, I. 1993. Predator training improves the anti-predator behaviour of hatchery reared Atlantic salmon (*Salmo salar*) smolt. *Nordic Journal of Freshwater Research*, 68, 63-71.
- Kelly, J. L. & Magurran, A. E. 2003. Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries*, 4, 216-226.
- Kleiman, D. G. 1989. Reintroduction of captive animals for conservation: Guideline for reintroducing an endangered species into the wild. *Biological Science*, 39, 152-161.
- Leland, K. N. & Williams, K. 1997. Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, 53, 1161-1169.
- Loughry, W. J. 1987. The dynamics of snake harassment by black-tailed prairie dogs. *Behaviour*, 103, 27-48.
- Loughry, W. J. 1992. Ontogeny of time allocation in Black-tailed prairie dogs. *Ethology*, 90, 206-224.
- Mateo, J. & Holmes, W. 1997. Development of alarm-call responses in Belding's ground squirrels: The role of dams. *Animal Behaviour*, 54, 509-524.
- McLean, I., Lundie-Jenkins, G. & Jarman, P. J. 1996. Teaching an endangered mammal to recognise predators. *Biological Conservation*, 87, 123-130.
- McLean, I., Schmitt, N. T., Jarman, P. J., Duncan, C. & Wynne, C. D. I. 2000. Learning for life: Training marsupials to recognise introduced predators. *Behaviour*, 137, 1361-1376.
- Miller, B., Wemmer, D., Biggins, D. & Reading, R. 1990. A proposal to conserve black-footed ferrets and the prairie dog ecosystem. *Environmental Management*, 14, 763-769.

- Mirza, R. S. & Chivers, D. P. 2000. Predator-recognition training enhances survival of brook trout: evidence from laboratory and field enclosure studies. *Canadian Journal of Zoology*, 78, 2198-2208.
- Nicol, C. J. & Pope, S. J. 1999. The effects of demonstrator social status and prior foraging success on social learning in hens. *Animal Behaviour*, 57, 163-171.
- Owings, D. H. & Coss, R. G. 1977. Snake mobbing by California ground squirrels: adaptive variation and ontogeny. *Behaviour*, 62, 50-69.
- Owings, D. H. & Loughry, W. J. 1985. Variation in snake-elicited jump-yipping by Black-tailed prairie dogs: Ontogeny and snake-specificity. *Zeitschrift fuer Tierpsychologie*, 70, 177-200.
- Owings, D. H. & Owings, S. C. 1979. Snake-directed behavior by Black-tailed prairie dogs (*Cynomys ludovicianus*). *Zeitschrift fuer Tierpsychologie*, 49, 35-54.
- Polan, H. J. & Hofer, M. A. 1999. Psychological origins of infant attachment and separation responses. In: *Handbook of Attachment: Theory, Research, and Clinical Applications* (Ed. by Shaver, J. C. a. P. R.), pp. 162-180. New York, NY: The Guilford Press.
- Poran, N. S. & Coss, R. G. 1990. Development of antisnake defenses in California ground squirrels (*Spermophilus beecheyi*): I. Behavioral and immunological relationships. *Behaviour*, 112, 222-245.
- Ryan, B. C. & Vandenberg, J. G. 2002. Intrauterine position effects. *Neuroscience and biobehavioral reviews*, 26, 665-678.
- Truett, J. & Savage, T. 1998. Reintroducing prairie dogs into desert grasslands. *Restoration and Management Notes*, 189-195.
- Tscernichovski, O. & Nottebohm, F. 1998. Social inhibition of song imitation among sibling male zebra finches. *Proceedings of the National Academy of Sciences U.S.A.*, 95, 8951-8956.
- Yoerg, S. I. & Shier, D. M. 1997. Maternal presence and rearing condition affect responses to a live predator in kangaroo rats, *Dipodomys heermanni arenae*. *Journal of Comparative Psychology*, 111, 362-369.
- Zentall, T. R. & Galef, B. G. 1988. *Social Learning: Psychological and Biological Perspectives*. New Jersey: L. Erlbaum.

TABLES AND FIGURES

Table 2.1 Experimental design

WEEK	TREATMENT	
	Trained with an experienced adult female	Trained without an experienced adult female
0	(pre-test)	(pre-test)
1	hawk	hawk
	cottontail	cottontail
2	ferret	ferret
	snake	snake
3	cottontail	cottontail
	snake	snake
4	hawk	hawk
	ferret	ferret
5	snake	snake
	cottontail	cottontail
6	(post-test)	(post-test)

Figure Legends

Figure 2.1. Differences in juvenile behavior during pre-training tests with different stimulus animals (Ferret, Hawk, Snake and Cottontail) in terms of a) alarm vocalizations; b) vigilance, c) fleeing and d) activity. Means \pm SEs are shown.

Figure 2.2. Effects of social context for juveniles raised and exposed to stimulus animals with experienced adults (\square ; mom and adult female) and without experienced adults (\blacksquare ; sibling and alone) and stimulus type (ferret, hawk, snake and cottontail) on a) activity, b) alarm vocalizations (barking and jump-yipping), c) vigilance, and d) time spent in or near shelter during pre and post-training tests. Means \pm SEs are shown.

Figure 2.3. Effects of rearing condition (captive-reared and trained with experienced adults during post-training tests (\blacksquare), and wild-reared (\square)) and stimulus type (ferret, hawk, snake & cottontail) on behavior: a) mean frequency of alarm vocalizations, b) mean time spent vigilant, c) mean time spent in or near shelter, and d) mean frequency of activity. Means \pm SEs are shown.

Figure 2.4. Differences in mean percent survival (\pm SEs) of juveniles a) exposed to predators with experienced adults vs. juveniles exposed to predators without experienced adults and b) captive-reared, trained and reintroduced vs. wild-reared and translocated. Mean percent \pm SEs are shown.

Figure 2.1.

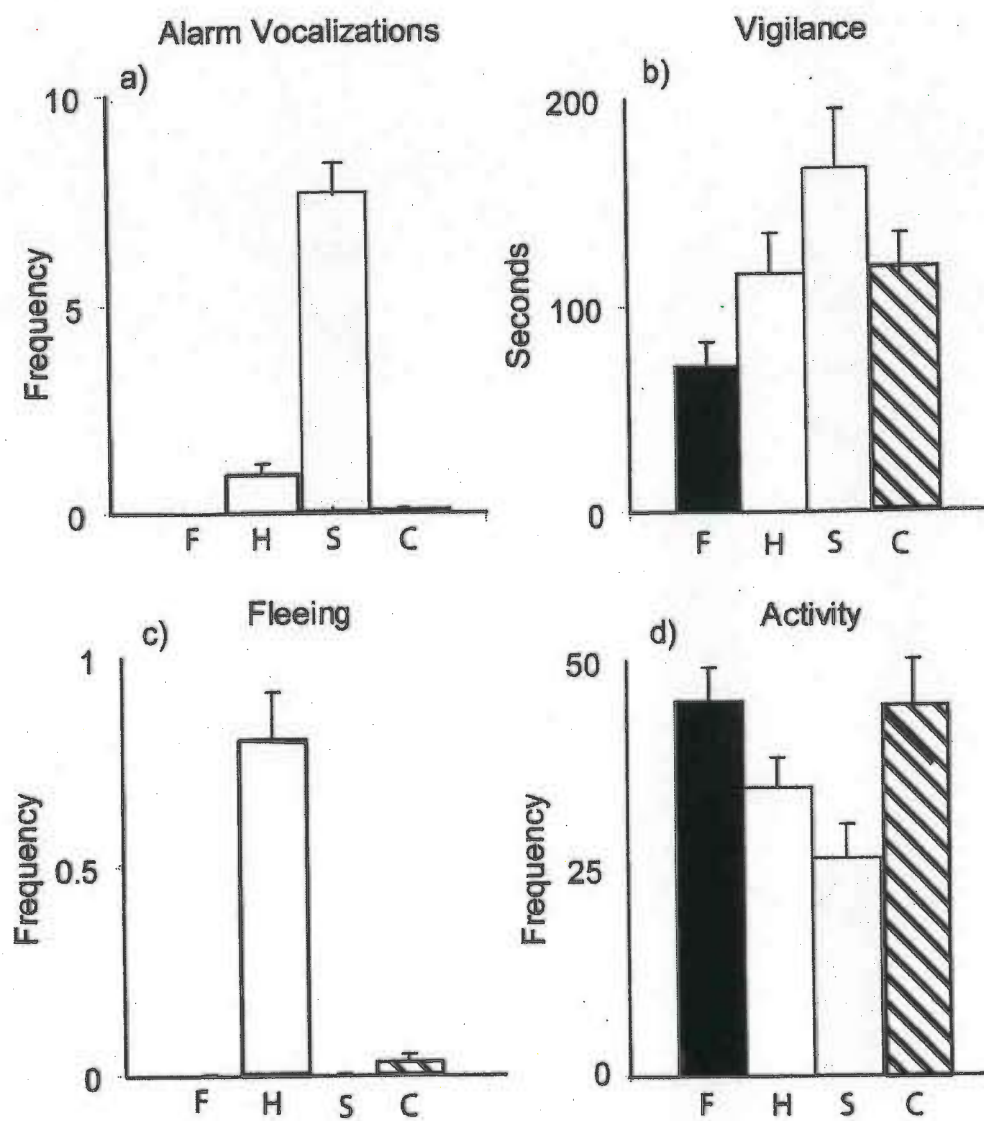


Figure 2.2.

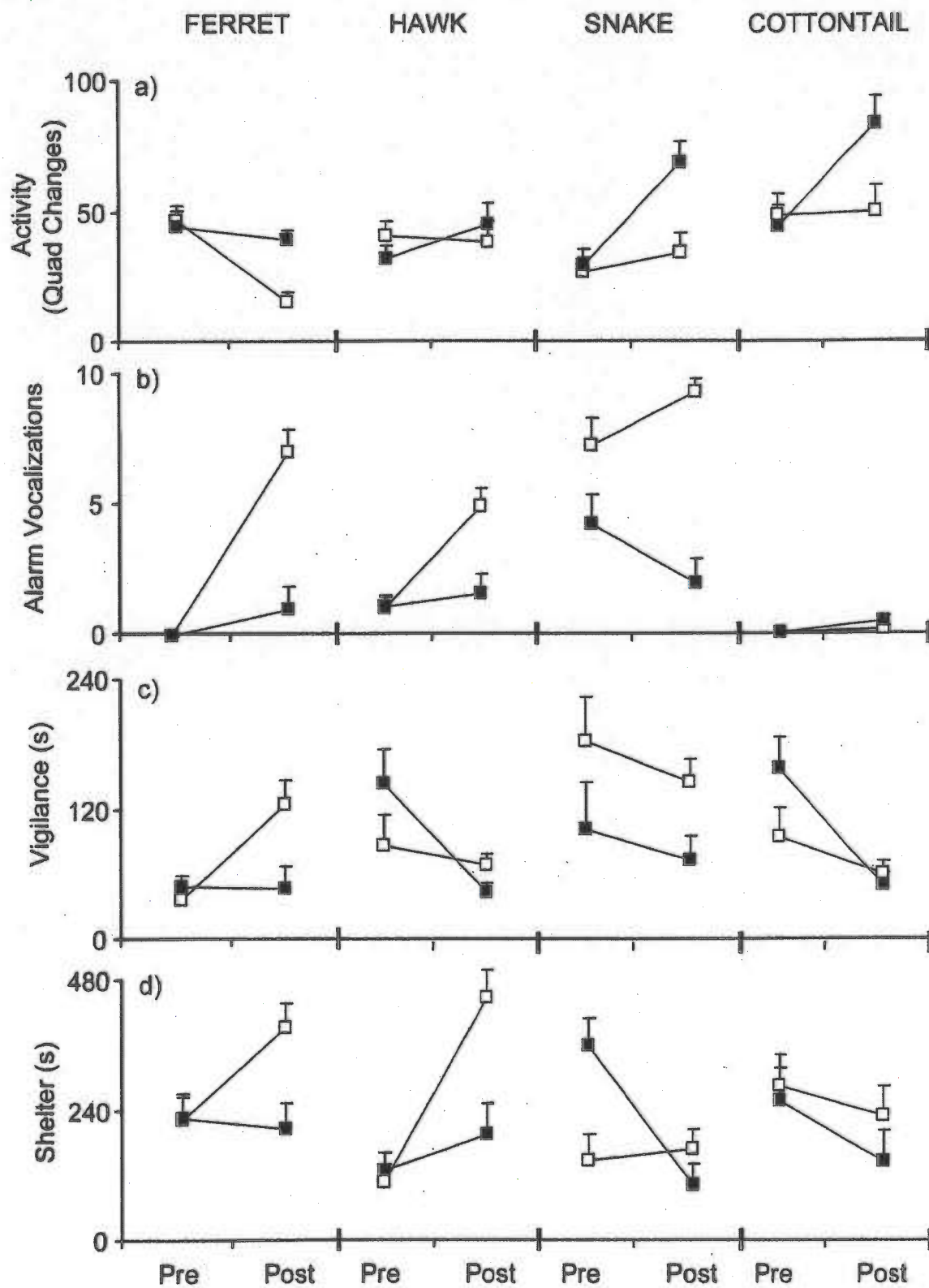


Figure 2.3.

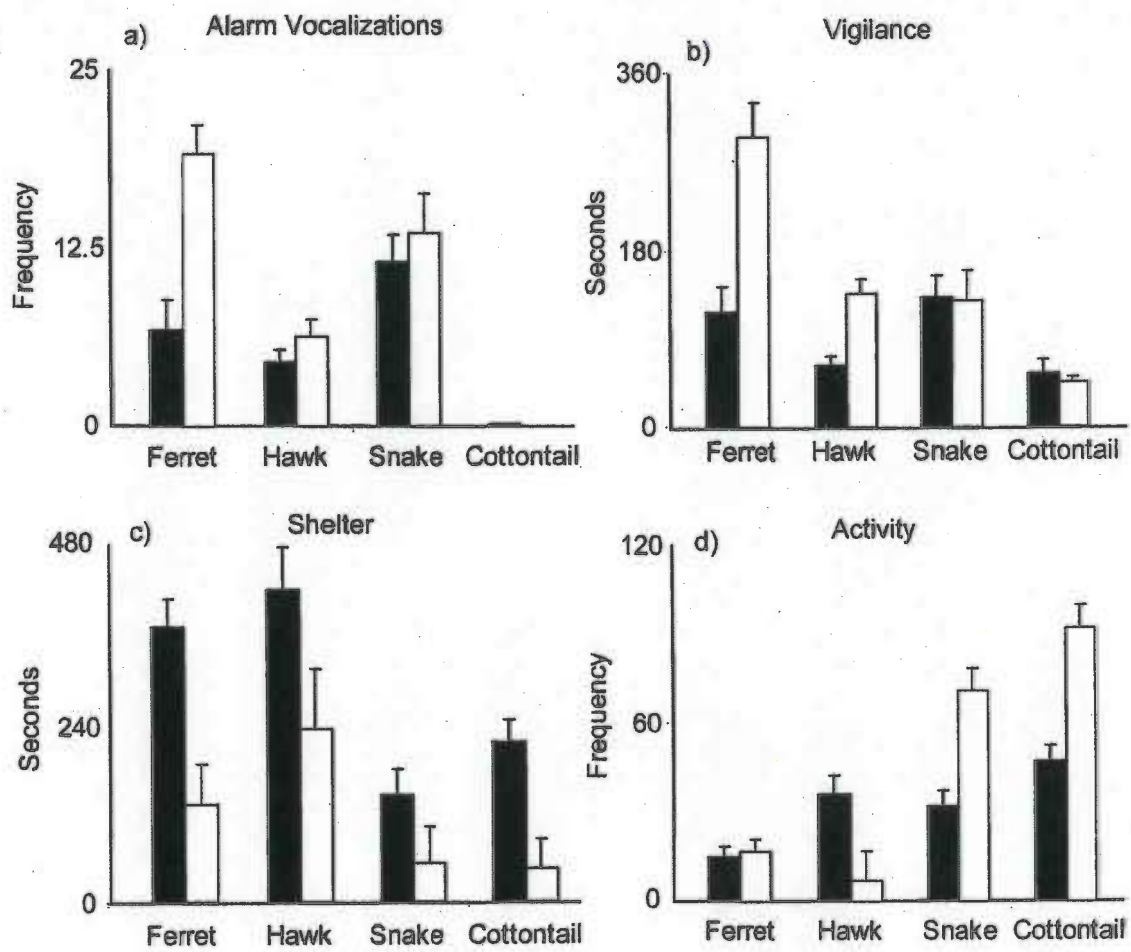
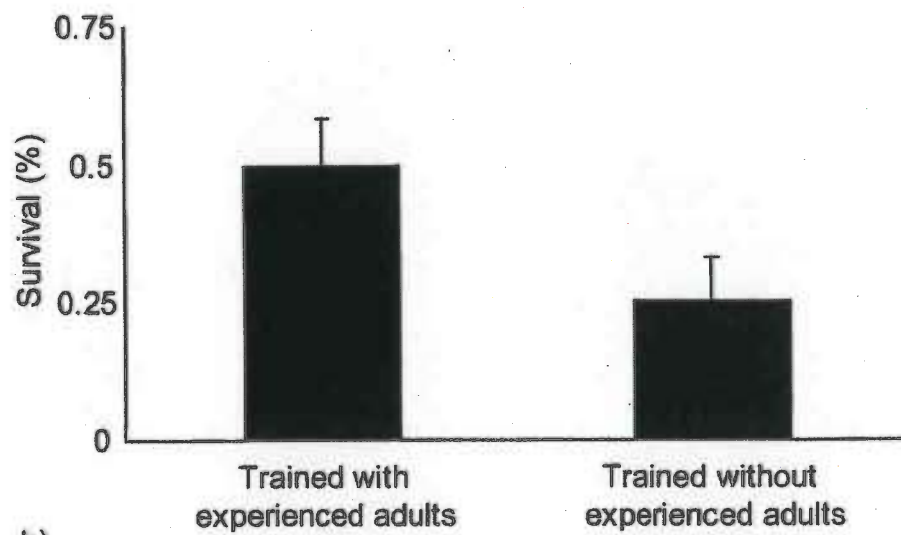
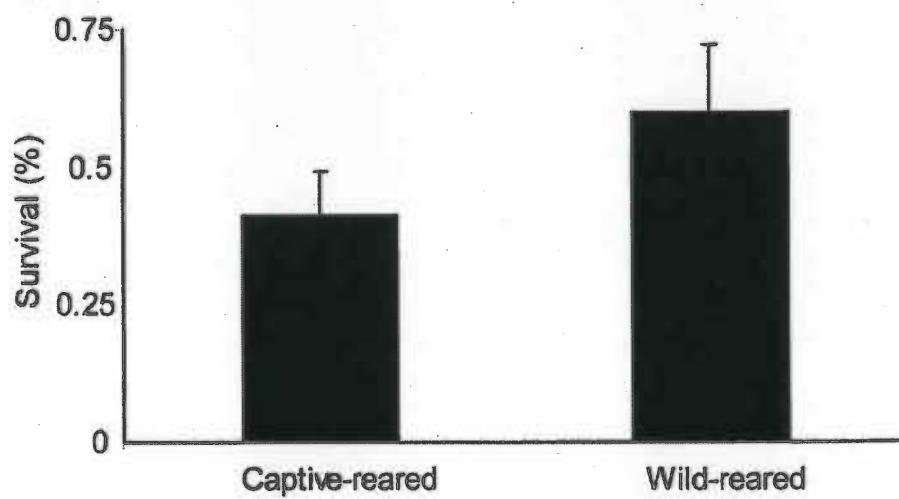


Figure 2.4

a)



b)



**CHAPTER 3: FAMILY SUPPORT INCREASES THE SUCCESS OF
TRANSLOCATED PRAIRIE DOGS**

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 post-release survival. Here, I show that maintaining family groups significantly increases translocation success in terms of both survival and reproductive success in the highly social black-tailed prairie dog (*Cynomys ludovicianus*). The results suggest that family-translocation may reduce the effects of predation on newly established prairie dog colonies and imply that any species that depends on social interactions for survival and reproduction may benefit substantially from the maintenance of social groups during translocations.

INTRODUCTION

The goal of translocation is to increase the viability of a species by releasing individuals into new sites within the species' historic range. Unfortunately, heavy mortality often limits the success of translocation programs. The blame for such mortality has long been placed on post-release behavior (Kleiman 1989), but tests of this hypothesis await controlled experimentation.

Upon release, animals need to find shelter and may have to modify the new site to accommodate their needs, e.g., by digging burrows. Until these modifications are complete, predation rates can be high. Vulnerability to predation may also be elevated by dispersal from a release site, a common response to translocation (Griffith et al. 1989). Dispersal may be high initially because animals are faithful to their previous locations, are not familiar with the biological and physical characteristics of their new surroundings, or lack social relationships with the individuals with whom they were released.

Recent efforts to enhance the effectiveness of translocation have turned to questions about founder group composition. Translocation research has begun to address elements of founder groups, such as age and sex ratios, and group size (Clarke & Schedvin 1997; Armstrong et al. 1999; Cooper & Walters 2002), but this research has essentially ignored the relationships between individuals, notably parent-offspring and siblings relationships (but see Armstrong et al. 1994b). The benefits of group living have been documented for many taxa (Alexander 1974; Slobodchikoff & Schultz 1988) and experienced kin can shape the development of appropriate survival skills in juveniles, from food-finding to predator defense to mate selection (see reviews in: Freeberg 2000; Galef 1989a; Griffin et al. 2000). Familiarity with conspecifics following translocation is

especially likely to enhance survival in social species (Kleiman 1989), but this factor has been examined in a controlled way only in less socially-complex territorial birds (Armstrong 1995).

In the present study, I examined the impact of maintaining family groups in a large scale translocation of black-tailed prairie dogs. Prairie dogs are obligatorily social and live in territorial harem-polygynous family groups (coteries) within larger colonies (Hoogland 1995). Females are philopatric and thus coteries contain highly related females (Hoogland 1995) and genetic differentiation between coteries can be as high as the differentiation between colonies (Dobson et al. 1997).

A keystone species (Kotliar et al. 1999), black-tailed prairie dogs play an integral role in the grassland ecosystem, influencing vegetative structure, grazing by ungulates, environmental heterogeneity, plant succession, hydrology, nutrient cycling, and biodiversity (Kotliar et al. 1999). Colonies of black-tailed prairie dogs provide habitat for an estimated 140 species, including several threatened or endangered species, such as black-footed ferrets (*Mustela nigripes*) (Sharps & Uresk 1990), burrowing owls (*Athene cunicularia*), ferruginous hawks (*Buteo regalis*), and tiger salamanders (*Ambystoma tigrinum*) (Hoogland 1995).

Black-tailed prairie dogs have declined an estimated 98% from the numbers that once occupied between 400,000 and 1 million km² of the Great Plains before European settlement (Mac et al. 1998). The sources of this decline include conversion of grassland to cropland, poisoning programs, recreational hunting, and sylvatic plague (*Yersinia pestis*) (Cully 1993). Most remaining towns of this species are <40 ha in size and isolated from other towns. The U.S. Fish and Wildlife Service recently designated the

black-tailed prairie dog as a candidate species, warranted for listing as threatened but precluded for administrative reasons. This case is currently reviewed annually (Service 2000). Such federal action has stimulated conservation involvement by private organizations as well as 11 states in the species' original range. Current efforts to conserve prairie dogs have relied in part on translocating animals to supplement small populations or to restore extirpated ones.

Prairie dog translocation methodology has been far from effective. Survival rates following translocations seldom exceed 40% and frequently are much lower (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.

The obvious alternative of keeping family groups together during translocation is not trivial because it requires marking and observing the animals prior to translocation. The main goal of this study was to determine whether maintaining family groups is both effective and efficient. Given the complex social nature of prairie dogs, I predicted that translocating intact family groups would increase translocation success.

METHODS

Study Site.

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. Vegetation is dominated by Blue grama (*Bouteloua*

gracilis), buffalograss (*Buchloe dactyloides*), and tobosagrass (*Hilaria mutica*), which are common in short grass prairies and adapted to heavy grazing.

Site selection and establishment.

During the springs of 2001 and 2002, ten uninhabited sites were selected by the wildlife manager on the property and myself within the historical range of black-tailed prairie dogs (Fig. 3.1), based on soil quality (deep well-drained soils of sandy loam clay texture), vegetation cover, slope (<6%) and location on the ranch. Sites were mowed to allow for good horizontal visibility by the animals. Pairs of family-translocated (FT) and non-family-translocated (NFT) sites were matched for soil, vegetation cover, slope, proximity on the ranch, and sex and age ratios to control for these factors, but also analyzed for differences in soil, vegetation cover, and slope (see below).

Sites were prepared for "soft release" in order to limit dispersal and allow prairie dogs to acclimate to the new site (Truett et al. 2001). Twenty artificial burrows were placed 25 m apart in a 5 x 4 grid configuration in each site. Artificial burrows consisted of a cylindrical underground wire retention basket (0.3 m diameter x 0.3 m) set 1 to 1.5 m underground, a corrugated plastic tube (10-cm diameter drainpipe), which connected the basket to the surface, and an above-ground retention cage (1 m x 1 m x .3 m). This design allowed movement of prairie dogs between the retention basket and the above-ground retention cage, but precluded escape during the acclimation period (Truett et al. 2001). Each grid was temporarily surrounded with a battery- powered electric-tape fence to deter predation attempts by coyotes and disturbance by bison (*Bison bison*).

Study Subjects.

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: family-translocated (trapped and translocated with family members; $n = 484$; 5 sites, 87-100/site) and non-family-translocated (trapped and moved without family members; $n = 489$; 5 sites, 88-103/site). Family members were transferred to uninhabited burrow systems at five sites. Nonfamily members from three source colonies were transferred into artificial burrow systems at five other sites (five individuals per burrow). I refer to areas where animals were to be released as sites, but changed this designation to colonies once prairie dogs established burrow systems in these sites.

Determining coterie membership and capturing and holding animals for release.

Coterie (family) membership is easiest to determine prior to pup emergence in May. Therefore, I determined coterie 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 coterie in five distinct source colonies. I chose coterie randomly from the edge and center of colonies to ensure variability in predator vigilance behavior and genotype. From mid-June to August, all animals from the designated coterie were trapped again, including previously marked individuals and emergent young. Animals were classified as adults if they were ≥ 1 year of age and juveniles if they were newly emergent young.

Prairie dogs were transferred to holding cages (Havahart rabbit hutches; 0.6 x 0.6 x 0.4 m) in an indoor temperature-controlled facility and held until 100 animals were

captured (<2 weeks). Nonfamily-translocated animals were trapped following standard methods (removing animals from large source colonies and mixing them in holding cages; (Truett et al. 2001) and were weighed, ear-tagged, aged, sexed and held in the holding facility under the same conditions. Prairie dogs were fed timothy hay, cattle block, and fresh vegetables daily and given water ad lib while in the holding facility. All transfers occurred between the end of June and August of 2001 and 2002. Translocation earlier in the season conflicts with pup emergence, and later in the season prairie dogs may not have enough time to establish new burrows prior to early snows in the fall.

Release to new site.

Once approximately 100 animals were captured, they were transported to above-ground retention cages at one of the new sites (Fig. 3.1). I placed four to seven animals in a retention 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 artificial burrow system. Otherwise I split the coterie among adjacent artificial burrow systems. For the nonfamily-translocated animals, one male, two females and two pups were placed into each retention cage at a new site. The ratio of adult males to adult females in retention cages varied slightly depending on the number of each released on a site. FT and NFT colonies in a matched pair were released within 2 weeks of each other to control for possible seasonal effects. All animals were provisioned with hay, cattle block, fresh vegetables and water every other day for 7 days. At the end of the acclimation period, the above-ground retention cages and electric fence were removed; underground retention baskets and artificial burrows were left in place. We attempted to minimize predation by

driving by and chasing potential predators off each pair of sites at least three times per week for the first month following release.

Post-Release Behavior.

My field assistants, the wildlife manager, and I observed the prairie dogs during the first 2 hours following release from the retention cages and documented the presence or absence of the following behaviors: alarm calling, allogrooming, foraging, ranging outside mowed areas, tactile greeting and play. Dispersal was documented only in cases where animals were retrapped at a different colony from which they were released. 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 (prairie dog in bipedal stance, oriented towards vehicle), foraging (prairie dog placing vegetation in mouth with forefeet), or digging (prairie dog moving dirt with forefeet, hindfeet, or both). One year post-release, each of the 10 new sites was observed 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 above ground with binoculars for 1 hour. Three to seven coterie were observed per day and all burrow systems were observed one to three times over the course of the summer for a total of 386 hours of focal coterie observation during the study.

Burrow Establishment.

My field assistants and I counted burrows and used a GPS receiver to document the position of each one established on each new site at seven different points following the 2001 release: 3-5 days, 1 week, 2 weeks, 4 weeks, 6 weeks, 1 year and 2 years. The

same procedure was used for the 2002 release, but burrows were assessed only once, 1 year post release. To quantify the amount of protective burrow room available in the early stages of establishment and the complexity of the burrow system as the season progressed, burrows were categorized as starter burrows (sheltered at least one-half of prairie dog body length, 0.15-0.25 m), full burrows (sheltered adult prairie dog completely, >0.25m) or mound burrows (full burrow with mound of dirt >0.15 m at opening; indicating extensive excavation). Only full or mound burrows with fresh digging and prairie dog scat were counted for burrow establishment analysis.

Habitat Features.

Though I paired colonies by vegetation cover, soil quality, and slope (see above), I assessed differences in these variables to confirm that no significant differences existed between sites within a pair.

Vegetation cover

I conducted vegetation analysis of sample plots at each new colony and each source colony to determine percent vegetation cover. I placed a 1 x 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 Corporation). Images were transferred to Adobe Photoshop and overlaid with a 10 x 10 cell grid to obtain estimates of mean total percent of vegetation cover and mean percent of open soil (methods follow Causton 1988). Cells (10 cm x 10 cm) with less than 25% cover were coded as 0, cells with 25-75% cover were coded as 0.5, and cells with greater than 75% cover were coded as 1.

For each quadrat, cell totals were summed, yielding a percent cover and total mean percent cover was calculated for each site.

Soil quality and slope

I obtained soil associations within the study site in paper map form (Anderson et al. 1982) from the U.S.D.A. for Colfax County, New Mexico. To determine soil quality, water permeability, rooting depth, and type of vegetation supported, I manually overlaid latitude/longitude coordinates of new prairie dog colonies on soil association maps.

Slope of sites were calculated using a clinometer.

Measuring Translocation Success.

I measured translocation success by retrapping all ear tagged animals present at the release site and counting emergent young in the spring/summer following release (May-July 2002 for the six colonies translocated in 2001 and May-June 2003 for four colonies translocated in 2002). Prairie dog colonies in a pair were trapped at the same time to avoid any effects of time of trapping on survival estimates. Dye marking and observation were used to verify that all prairie dogs remaining at a colony had been trapped. I walked the area in grids to determine if 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 a Cessna 182 aircraft at 90-150 m elevation and examined the landscape for any active burrows within a 4-km radius of each colony. No distinction was made between dispersal and mortality since dispersing animals do not contribute to the population viability of a release site. Nevertheless, successful dispersal

greater than 3 km is extremely rare in the wild (Garrett & Franklin 1988) probably because long-distance (>1 km) dispersers are prone to heavy mortality due to predation and injurious interactions with residents of colonies into which they are attempting to immigrate (Garrett & Franklin 1988). Therefore, prairie dogs were considered deceased if they were not trapped at the colony in which they were released, or if they were not trapped at another new colony located within 3 km of the release site (Fig. 3.1).

Population Viability.

In order to determine if 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 trapping and observing all animals at a random subset of burrow clusters (a set of active burrows separated from other burrows by ≥ 10 m) 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.

Data Analysis.

Because half of the animals were statistically nested within families, multilevel analytic techniques and regression with a cluster function were used 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 using HGLM (Hierarchical General Linear Modeling; Raudenbush et al. 2003) with SURVIVAL (0=not surviving at release colony; 1 = surviving at release colony) as the outcome variable because it allows modeling of nested data using binomial outcome variables. I employed a Bernoulli model among the

nonlinear multilevel model options. Analysis of the best fit model was conducted using likelihood ratio tests. Possible predictor variables included the following: 1) age 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 1-10 based on: the number of artificial burrows and underground retention baskets that were dug out by predators by the following spring, the total amount of coyote scat present on a colony, and the 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 quality (scaled from 1-10 based on: soil quality, water permeability, rooting depth and vegetation type supported; Table 3.1); 7) terrain (slope on 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:

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

$$\begin{aligned} \text{Log}[P/(1-P)] = & \gamma_{00} + \gamma_{01} * (\text{Pair1}) + \gamma_{02} * (\text{Pair2}) + \gamma_{03} * (\text{Pair3}) + \gamma_{04} * (\text{Pair4}) + \\ & \gamma_{05} * (\text{Translocation Method}) + \gamma_{06} * (\text{Predation Intensity}) + \gamma_{07} * (\text{Time of} \\ & \text{Release}) + (\text{SEX})[\gamma_{10} + \gamma_{11} * (\text{Translocation Method})] + (\text{AGE})[\gamma_{20} + \gamma_{21} \\ & * (\text{Time of Release})] + \mu_0 \end{aligned}$$

To determine whether translocation method, predation or time of release had a greater influence on survival post-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 ($w_i = \exp [-\Delta_i/2] / \sum \exp [-\Delta_i/2]$) (Burnham & Anderson 2002). For the best fitting model and each submodel, I calculated deviance values in HLM. The model with the smallest AIC value was the best fitting model and was in agreement with the likelihood ratio tests from the HLM analysis. I calculated AIC differences between the best model and the other candidate models to determine the relative ranking of the models. Parameter importance was assessed by summing the Akaike weights for each model in which a parameter was present.

Nonfamily-translocated prairie dogs were coded as having a unique family and consequently their family size was 1. Therefore, examination of the relationship between number of individuals in a family and survival was restricted to family-translocated animals and was analyzed using logistic regression in Stata Version 8.2 for Windows (STATA Corp, College Station, TX, USA), which allows for clustering by family. The relationship between juvenile weight at translocation and survival was examined using the same analytic technique.

Reproductive success was analyzed using a Poisson regression clustered by family membership in Stata Version 8.2 for Windows. Reproductive success was analyzed only for females that survived at the release site in terms of mean number of emergent pups per female, mean litter size (for females that weaned a litter), and percentage of females that weaned a litter. In family-translocated colonies, I observed behavioral interactions and sleep patterns to determine if family membership was maintained following release. Settlement was examined by calculating the observed proportion of each new coterie established 1 year after release that included individuals from the same original coterie but that were not in the same release cage (coterie effect).

Observed values were calculated using a 90% criterion. Therefore, if a coterie effect was present 90% of the prairie dogs in an individual's new coterie must have been from the same original coterie in order to count that individual as settling with coterie members.

Once observed values were calculated, I ran Monte Carlo simulations with 10,000 iterations to generate random expectations of new coterie membership using only surviving individuals at each new site. The observed and random expectations were then compared to generate a significance level. This analysis was replicated using individuals from the same release cage to examine if there was a release cage effect. The Monte Carlo simulations were implemented in Microsoft Excel with a Visual Basic macro.

The remaining statistical analyses were conducted using SPSS version 11 for Windows (SPSS Inc.) One-way analysis of variance was used to compare the proportion of individuals that were vigilant, foraging, or digging in the two translocation groups. Repeated-measures analysis of variance was used 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 statistically 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 ($t = 1.01$, $df = 4$, $P = 0.370$).

RESULTS and DISCUSSION

Family-translocated prairie dogs outperformed nonfamily-translocated prairie dogs in terms of both survival and reproductive success (Fig. 3.2). Family translocation increased survival by a factor of five compared with nonfamily translocation (Fig. 3.2A). The importance of family relationships for survival is further indicated by the pattern of

sex differences. Adults of both sexes in the family-translocated colonies survived at higher rates than nonfamily translocated animals, but the differences were greater for adult females than for adult males. This sex difference is consistent with the natural history of the species. Females remain with their families their entire lives, while most males disperse after the first year. Independent of sex and translocation method, adults survived at higher rates than juveniles.

Family-translocated females showed higher reproductive success one year after release than NFT females (Fig. 3.2). Among females that successfully weaned pups, there was no difference in litter size between FT and NFT colonies, but females in FT colonies were more likely to produce weaned young (Fig. 3.2, C and D). Overall, the mean number of emergent pups was higher for FT than NFT colonies (Fig. 3.2B). These treatment effects appear to be driven primarily by yearling females (Fig. 3.2, B to D).

Survival increased steadily during the summer months such that late season (August) translocations had the highest survival regardless of predation pressure and translocation method (Fig. 3.3A). This pattern was more pronounced in juveniles than adults (Fig. 3.3A). Survival of juveniles may depend, in part, on the amount of time they have above ground to grow and improve in physical condition before translocation. Alternatively or in addition, translocation later in the summer may allow juveniles more time to develop and hone their survival skills (learning effect). In a multivariate analysis both age and weight were significant predictors of survival (Multiple logistic regression, Wald $\chi^2 = 32.73$, $n = 254$, age: OD = 1.02, $z = 2.11$, $P = 0.035$; weight, OD = 1.00, $z = 2.07$, $P = 0.039$; data on number of days from emergence. Age data was not available for

NFT animals, but weight data was not significant (logistic regression: Wald $\chi^2 = 20.75$, $n = 247$, $P = 0.110$)).

Predation is a major cause of death following release in translocated prairie dogs (Truett et al. 2001). In this study, survival decreased significantly with the increase in predation pressure (as estimated from predator signs/sightings, not predation events within both treatment groups (Fig. 3.3B). However, the difference between FT and NFT colonies in survival could not be attributed to differential predation because FT colonies tended to experience higher predation pressures than NFT colonies: 5.19 ± 0.12 versus 2.81 ± 0.09 (mean \pm SE, $N = 5$ colonies each). Thus, family-translocation appears to reduce predation on newly established prairie dog colonies.

It is well established that this highly social species is adapted for living in large groups and is dependent on coterie members for predator detection and deterrence (Hoogland 1995). Larger groups and the presence of relatives are both associated with higher numbers of alarm-calling individuals, and prairie dogs spend less time scanning for predators when more adult coterie members are present above ground (Hoogland 1995; Loughry 1993). The ability of prairie dogs to directly deter predators is also dependent on coterie membership. Prairie dogs are known to attack small predators (e.g. weasels) as a group when they encounter them in their home coterie but not in other coterie (Hoogland 1995). If the presence of relatives does provide antipredator benefits to translocated prairie dogs, then individuals moved with larger families should experience higher survival. As predicted, in the FT treatment, survival increased with family size (Logistic regression: Wald $\chi^2 = 25.06$, $OD = 1.06$, $z = 5.01$, $n = 484$, $P < 0.0001$; Fig. 3.4).

Behavioral differences between FT and NFT animals were apparent upon release at the translocation sites. Within the first 2 hours after release, prairie dogs that were translocated with family members largely remained near the artificial burrows in which they were released and traveled between adjacent artificial burrows. 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 upon release and were observed to range outside the release sites. All but one of 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; Fig. 3.1). The one family-translocated disperser was a yearling male.

These behavioral differences remained pronounced 2 weeks after release and persisted for at least 1 year (Fig. 3.5 A and B). 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. This is consistent with what we know about prairie dogs in the wild. Individuals spend more time scanning for predators when fewer adult family members are above ground (Hoogland 1995). Family-translocated individuals spent less time being vigilant than non-family-translocated animals, which may have allowed them to forage more and improve in physical condition. Less time devoted to vigilance should also give individuals more time to excavate their burrow systems. Consistent with this prediction, prairie dogs translocated in intact coterie units excavated more burrow entrances and did so faster over the 2 years following release than NFT prairie dogs (Repeated-Measures ANOVA $F = 8.48$, $df = 1$, $P < 0.04$, Fig. 3.6).

Data from this study demonstrate that family membership significantly increases post-release survival and reproductive success. But, the question of how family membership affects survival remains. Were family-translocated individuals simply less physiologically stressed and therefore more likely to survive on their own; or does family composition allow individuals to benefit directly from well established social relationships? Evidence thus far suggests the latter. Individuals from larger families showed higher survival than those from smaller ones, and, fewer animals released with family members were vigilant 2 weeks and 1 year post release (Fig. 3.5, A and B). However, the true test of the benefits of long-term family membership should be revealed by settlement decisions. If individuals released with family members also settle with them, they will benefit from well established social relationships. Therefore, I examined settlement patterns of family-translocated prairie dogs to determine if they settled with coterie members more often than expected by chance. Family-translocated prairie dogs were: (1) more likely to settle with family members from a different release cage than with nonfamily members; but (2) not more likely to settle with family members from the same release cage than with family members from adjacent release cages (Table 3.2). This suggests that prairie dogs use long-term familiarity rather than short term association to make settlement decisions, providing further support for the importance of maintaining family membership during translocation.

In this study, survival was influenced by translocation method, predation pressure and time of release. The most parsimonious model for the probability of survival contained all three predictor variables and pair as a control variable (Deviance = 2752.013, $n = 973$, $K = 13$, $AIC = 2778.013$, $\Delta_i = 0.00$, $w_i = 0.608$), compared with candidate models that

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, $n = 973$, $K = 12$, $AIC = 2780.056$, $\Delta_i = 2.043$, $w_i = 0.2189$). All other candidate models had essentially no support. Of these factors, translocation method was the best predictor of survival (Parameter importance weight: translocation method = 1.00; predation pressure = 0.827; time of release = 0.769). Thus, efforts of managers would best be directed at family group translocation, while, if possible, also minimizing predator pressure and selecting the optimal release timing based on the species' behavioral ecology.

Beyond survival and reproductive success, the ultimate goal of translocation is population viability. Thus, when releases are not successful in establishing sustainable populations, supplementation is often conducted. In this study, two of the three nonfamily-translocated colonies released in 2001 were judged by the wildlife manager on the property to require supplementation due to low survival. Additional animals ($n = 10$ -35) were added to colonies 2001-01 and 2001-03 after the first year (Summer 2002). In spite of supplementation, nonfamily-translocated colonies continued to decline in size relative to family-translocated colonies through 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: $t = -2.916$, $P < 0.05$). These data indicate that differences between colonies established using different translocation methods become even more pronounced by the second year post-release and that supplementation does not offset these differences.

These results have important implications for conservation and animal behavior. Regarding conservation, the data clearly demonstrate that for highly social prairie dogs, founder groups composed of intact family units are more successful in terms of post-release survival, reproductive success and population viability. More broadly, these results suggest that any species which depends on social interactions for survival and reproduction may benefit substantially from the maintenance of social groups during translocations (e.g. wolves, elephants, primates). Thus, translocation methodology should be restructured to incorporate the target species behavior.

This method is not only extremely effective, but it also provides a more efficient means of restoring prairie dogs to their former range, even though the initial investment is substantially higher. Family-translocated animals must be trapped, marked, released, and observed in order to determine coterie membership, and specific individuals must then be targeted for trapping (e.g., estimated mean trapping time for coterie members in 2001 was 252 hours versus 93 hours for NFT animals). But the six-fold difference in survival rates (for the 2001 release) more than offsets this added time cost.

These results also suggest that wildlife managers would benefit from detailed knowledge of a species' behavior when they set the timing of translocation. For prairie dogs, late summer translocations showed the highest survival, apparently because juveniles are most vulnerable to predators just after emergence early in the summer. Antipredator vigilance is likely most important in the first half of the summer while juveniles are small and lack knowledge about the environment. Foraging then 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.

While the timing of translocation may not be as crucial for all adults, maternal females may also benefit from late season translocations. Maternal females are energetically constrained by reproduction and lactation and require high rates of foraging to increase body mass and condition during summer months. Therefore, lactating females translocated early in the summer may be less likely to survive. I examined the relationship between time of release and survival for lactating females and found that lactating females translocated later in the summer showed higher survival than those translocated early in the summer (Logistic regression: Wald $\chi^2 = 7.81$, OD = 1.03, $z = 2.79$, $n = 141$, $P < 0.005$, perhaps because females translocated later weighed more (Logistic regression of maternal female weight on survival: Logistic regression: Wald $\chi^2 = 4.36$, OD = 1.00, $z = 2.09$, $n = 141$, $P < 0.03$).

These results also have implications for basic behavioral processes. To date, most research on dispersal has focused on single propagules; however, the mechanisms that underlie dispersal in social groups have been little studied (Lambin et al. 2001). These data indicate that animals that disperse in groups would benefit from reduced predation and extended opportunities for learning survival skills. Still, other mechanisms may confer advantages of group dispersal to individuals (e.g. information pooling among dispersers (Stamps 2001) and increased competitive ability (Lambin et al. 2001)). Finally, evidence presented here highlights the importance of social context in the development of appropriate survival skills, a topic that is rich with opportunities for future research.

REFERENCES

- Alexander, R. D. 1974. The evolution of social behavior. *Annual Review Ecological Systems*, 5, 325-383.
- Anderson, G. W., Hilley, T. E., Martin Jr, P. G., Neal, C. R. & Gomez, R. S. 1982. Soil Survey I-IV. pp. 1-187: U.S. Soil Conservation Service.
- Armstrong, D. P. 1995. Effects of familiarity on the outcome of translocations II A test using New Zealand robins. *Biological Conservation*, 71, 281-288.
- Armstrong, D. P., Castro, I., Alley, J. C., Feenstra, B. & Perrot, J. K. 1999. Mortality and behavior of Hihi and endangered New Zealand honeyeater, in the establishment phase following translocation. *Biological Conservation*, 89, 329-339.
- Armstrong, D. P., Lovegrove, T. G., Allen, D. G. & Craig, J. L. 1994b. Composition of founder groups for bird translocations: does familiarity matter? In: *Reintroduction Biology of Australian and New Zealand Fauna* (Ed. by Serena, M.), pp. 105-111. Chipping Norton: Surrey Beatty & Sons.
- Burnham, K. P. & Anderson, D. R. 2002. *Model selection and multimodel inference: A practical information-theoretic approach*. New York: Springer, Verlag.
- Causton, D. R. 1988. *An introduction to vegetation analysis, principles, practice and interpretation*. London: Unwin Hyman.
- Clarke, M. F. & Schedvin, N. 1997. An experimental study of the translocation of Noisy Miners *Manorina melanocelphala* and the difficulties associated with dispersal. *Biological Conservation*, 80, 161-167.
- Cooper, C. B. & Walters, J. R. 2002. Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology*, 16, 471-478.
- Cully, J. F., Jr. 1993. Plague, prairie dogs, and black-footed ferrets. pp. 1-96: United States Fish and Wildlife Service.
- Dobson, R. S., Chesser, R. K., Hoogland, J. L., Sugg, D. W. & Foltz, D. W. 1997. Do black-tailed prairie dogs minimize inbreeding? *Evolution*, 51, 970-978.
- Freeberg, T. M. 2000. Culture and courtship in vertebrates: a review of social learning and transmission of courtship systems and mating patterns. *Behavioral Processes*, 51, 177-192.

- Galef, B. G. 1989a. An adaptationist perspective on social learning, social feeding and social foraging in Norway rats. In: *Contemporary Issues in Comparative Psychology* (Ed. by Dewsbury, D. A.), pp. 55-79. Sunderland, Massachusetts: Sinauer.
- Garrett, M. C. & Franklin, W. L. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. *Journal of Mammalogy*, 69, 236-250.
- Griffin, A. S., Blumstein, D. T. & Evans, C. S. 2000. Training captive-bred or translocated animals to avoid predators. *Conservation Biology*, 14, 1317-1326.
- Griffith, B., Scott, J. M., Carpenter, J. W. & Reed, C. 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*. Chicago, Illinois: University of Chicago Press.
- King, J. A. 1955. Social Behavior, Social Organization, and Population Dynamics in a Black-tailed Prairie dog Town in the Black Hills of South Dakota. In: *Contributions from the Laboratory of Vertebrate Biology: The University of Michigan*.
- Kleiman, D. G. 1989. Reintroduction of captive animals for conservation: Guideline for reintroducing an endangered species into the wild. *Biological Science*, 39, 152-161.
- Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. *Wildlife Monographs*, 3, 78.
- Kotliar, N. B., Baker, B. W., Whicker, A. D. & Plumb, G. 1999. A critical review of assumptions about the prairie dog as a keystone species. *Environmental Management*, 24, 177-192.
- Lambin, X., Aars, J. & Piertney, S. B. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. In: *Dispersal* (Ed. by E. Danchin, J. C., A.A. Dhondt, and J.D. Nichols), pp. 110-122. Oxford: Oxford University Press.
- Loughry, W. J. 1992. Ontogeny of time allocation in Black-tailed prairie dogs. *Ethology*, 90, 206-224.
- Loughry, W. J. 1993. Determinants of time allocation by adult and yearling black-tailed prairie dogs. *Behavior*, 124, 23-43.

- Mac, M. J., Opler, P. A., Puckett Haecker, C. E. & Doran, P. D. 1998. Status and trends of the nation's biological resources. pp. 437-964. Virginia: United States Department of the Interior, Geological Survey.
- Raudenbush, S., Bryk, A. & Congdon, R. 2003. HLM Hierarchical Linear and Nonlinear Modeling. Scientific Software International.
- Reading, R. & Matchell, M. R. 1997. Attributes of black-tailed prairie dog colonies in northcentral montana. *Journal of Wildlife Management*, 61, 664-673.
- Service, U. S. F. a. W. 2000. Endangered and threatened wildlife and plants: 12-month finding for a petition to list the black-tailed prairie dog as threatened. pp. 5476-5488. Federal Register.
- Sharps, J. C. & Uresk, D. W. 1990. Ecological review of black-tailed prairie dogs and associated species in western South Dakota. *The Great Basin Naturalist*, 50, 339-345.
- Slobodchikoff, C. N. & Schultz, W. C. 1988. Cooperation, aggression and the evolution of social behavior. In: *The Ecology of Social Behavior* (Ed. by Slobdchikoff, C. N.). New York: Academic Press.
- Stamps, J. A. 2001. Habitat selection by dispersers. In: *Dispersal* (Ed. by E. Danchin, J. C., A.A. Dhondt, and J.D. Nichols), pp. 230-242. Oxford: Oxford University Press.
- Truett, J. C., Dullam, L. D., Matchell, M. R., Owens, E. & Seery, D. 2001. Translocating prairie dogs: a review. *Wildlife Society Bulletin*, 29, 863-872.

TABLES AND FIGURES

Table 3.1. Soil characteristics of newly established colonies. While soils have little influence on prairie dog distribution (Koford 1958), some soils types are favored. Well-drained soils of sandy loam to clay loam soils with high water capacity are preferred over shallow well drained clay to silty clay soils with low water capacity (Reading & Matchell 1997). Soil quality was assessed on a 10 pt scale for data analysis; 1 = low; 10 = high.

Colonies	Soil Association	Soil Depth	Soil Type	Water Capacity permeability depth (inches)	Rooting Depth (inches)	Salinity	Vegetation Supported	Scale (1-10)
1,2,3	Mion Little	Moderately Deep	Clay loam	Slow	3-4	20-40	Low Sideoats grama (<i>Bouteloua curtipendula</i>) Fringed sagewort (<i>Artemisia frigida</i>) Yucca (<i>Yucca spp.</i>) One-seed juniper (<i>Juniperus monosperma</i>)	5
4	Swastika-LaBrier	Deep	Silt loam	Slow	7-8*	60+	High Inland Saltgrass (<i>Distichlis spicata</i> L.) Silkai sacaton (<i>Sporobolus airoides</i>)	7
5,6,10	Swastika	Deep	Silt loam	Slow	10-12	60+	Low Blue grama (<i>Bouteloua gracilis</i>) Western wheatgrass (<i>Agropyron smithii</i>) Galleta (<i>Pleuraphis jamesii</i>)	2
7,8,9	Dalhart	Deep	Sandy loam	Moderate	8-10	60+	Low Blue grama (<i>Bouteloua gracilis</i>) Sand dropseed (<i>Sporobolus Cryptandrus</i>) Prairie three-awn (<i>Aristida Oligantha</i>) Yucca (<i>Yucca spp.</i>)	1

* Seasonal water table 6 ft

Table 3.2. Settlement of family-translocated prairie dogs one year after release. *Expected values were generated using a Monte Carlo simulation that counted the expected number of individuals that settled with family members and generated a probability distribution (>90% of an individual's new family members were either from its original coterie but not from the same release cage, or from its original coterie and the same release cage).

New Colony	Settlement with family members		Settlement with release cage members	
	Percent (%) Observed	Significance	Percent (%) Observed	Significance
2001-2	16.6	P = 0.001	9.2	P = 0.649
2001-4	28.6	P = 0.001	14.2	P = 0.117
2001-6	20.3	P = 0.001	3.1	P = 0.871
2002-1	12.9	P = 0.012	11.1	P = 0.074
2002-3	27.1	P = 0.0001	10.1	P = 0.442

Figure Legends

Fig. 3.1. Map of the study site showing locations of 10 newly established prairie dog colonies and existing colonies within 3 km of new colonies. Solid black diamonds indicate sites into which prairie dogs were translocated with family members. Open circles designate nonfamily-translocation sites and crosses indicate existing colonies. Dashed lines show FT and NFT pair designations. Dispersal is indicated by solid arrows. Average dispersal was 0.914 ± 0.564 km (mean \pm SD). Note: Colonies 02-1 and 02-2 were only 0.359 km apart and therefore movement between the colonies was not considered long-distance dispersal. Only 15 cases of successful long-distance dispersal to newly established colonies were documented. Eight animals emigrated from 01-1 to 01-2, three emigrated from 01-3 to 01-4, two emigrated from 02-4 to 02-3, one emigrated from 02-1 to 02-4, and one emigrated from 02-2 to 02-3.

Fig. 3.2. (A) Survivorship of Family-Translocations versus survivorship of Nonfamily Translocations. HGLM, translocation method: $t = 4.92$, $df = 534$, $P < 0.0001$ for all age/sex classes combined; translocation method \times sex: $t = 2.44$, $df = 961$, $P = 0.015$; age: $t = 2.81$, $df = 961$, $P = 0.005$). Last three plots show differences in reproductive success of Family-Translocated (FT) vs. Nonfamily-Translocated (NFT) adult and yearling females in terms of: (B) mean number of pups per female (for all females that survived on a colony) (+ SEs), multiple poisson regression: Wald $\chi^2 = 54.37$, $n = 175$, trap method: $z = 3.00$, $P = 0.003$, age: $z = 6.84$, $P < 0.0001$; (C) mean litter size (for females that weaned a litter) (+ SEs), multiple poisson regression: Wald $\chi^2 = 39.11$, $n = 143$, trap method: $z = 0.88$, $P = 0.381$, age: $z = 6.25$, $P < 0.0001$; and (D) percentage of females

Fig. 3.6. Burrow establishment for each of 10 prairie-dog-release sites. For six releases in 2001, burrow counts are provided for three FT and three NFT colonies over the first two years after release. 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 (Repeated-Measures ANOVA, $F = 8.48$, $df = 1,4$, $P < 0.04$).

Fig. 3.1.

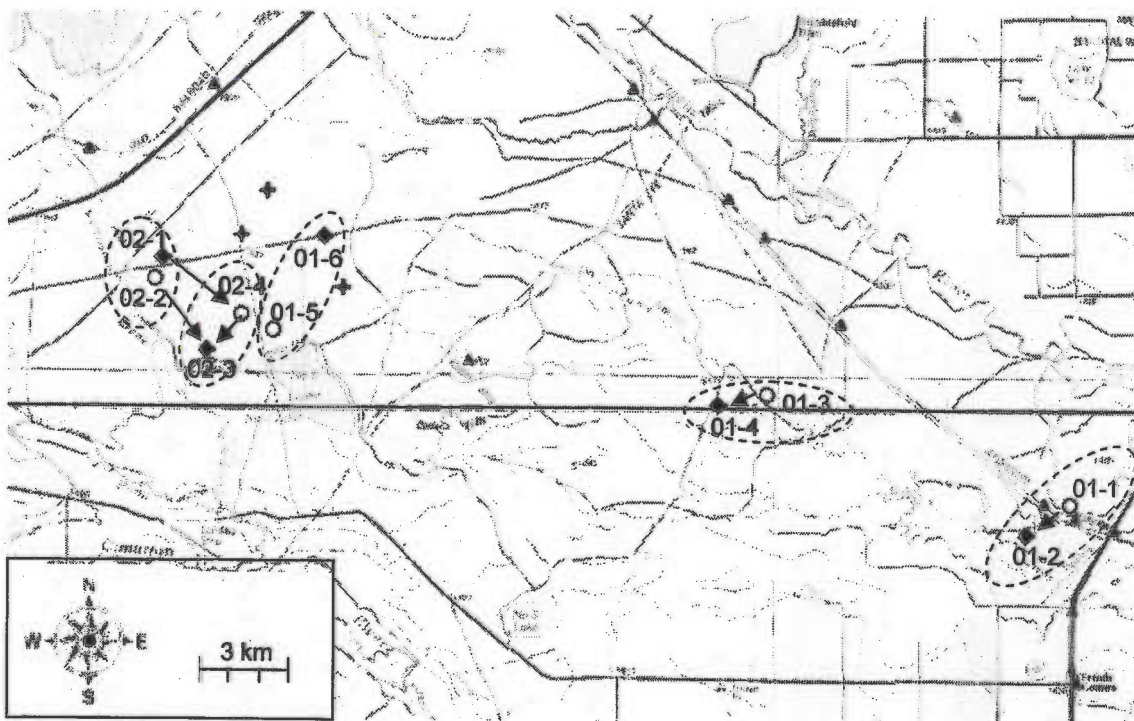


Fig. 3.2

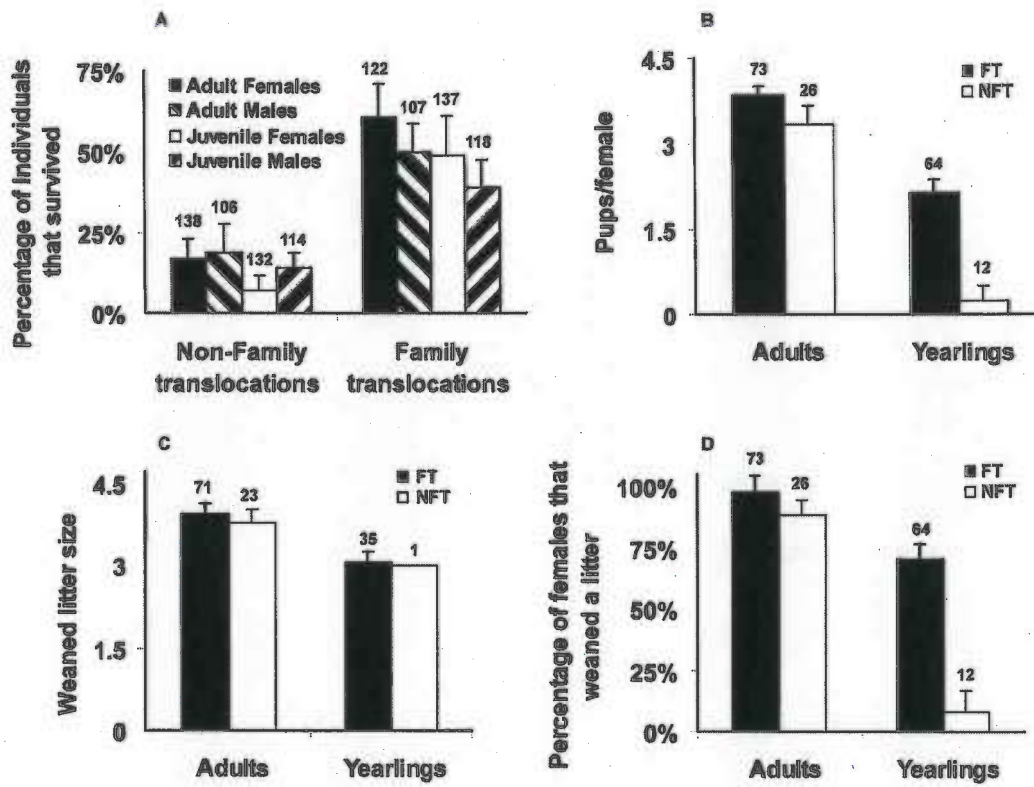


Fig. 3.3

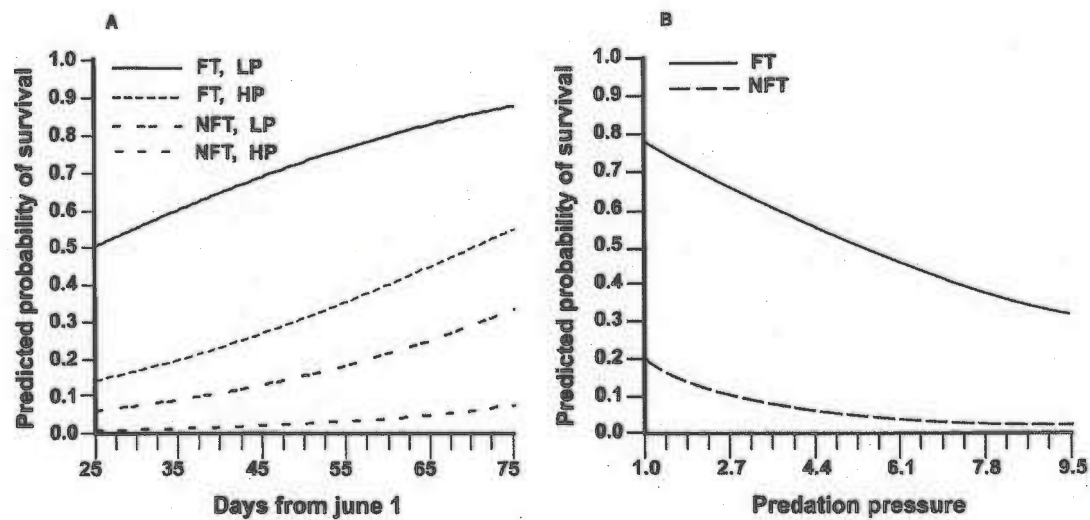


Fig 3.4.

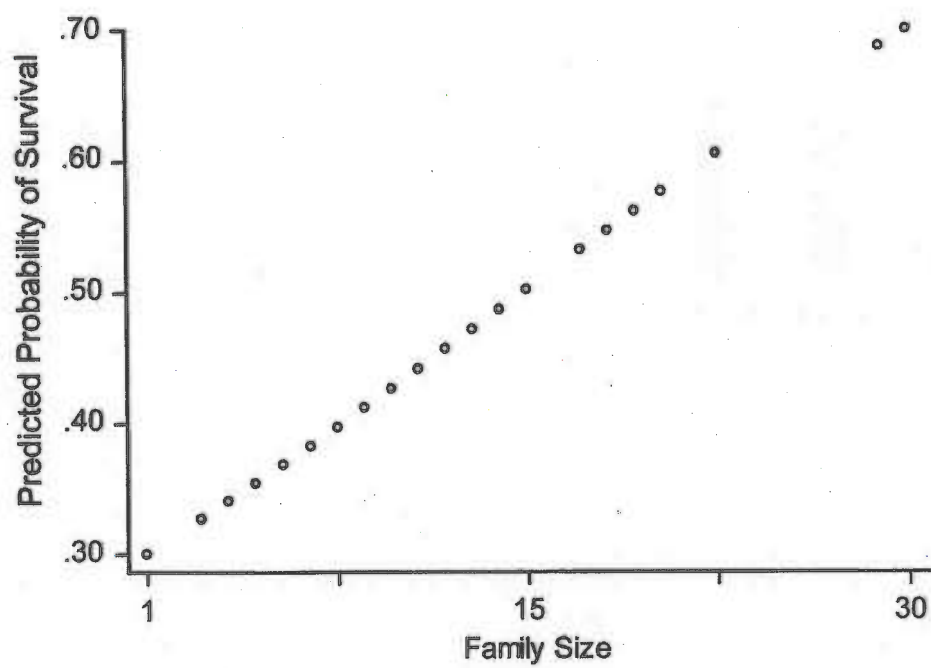


Fig. 3.5.

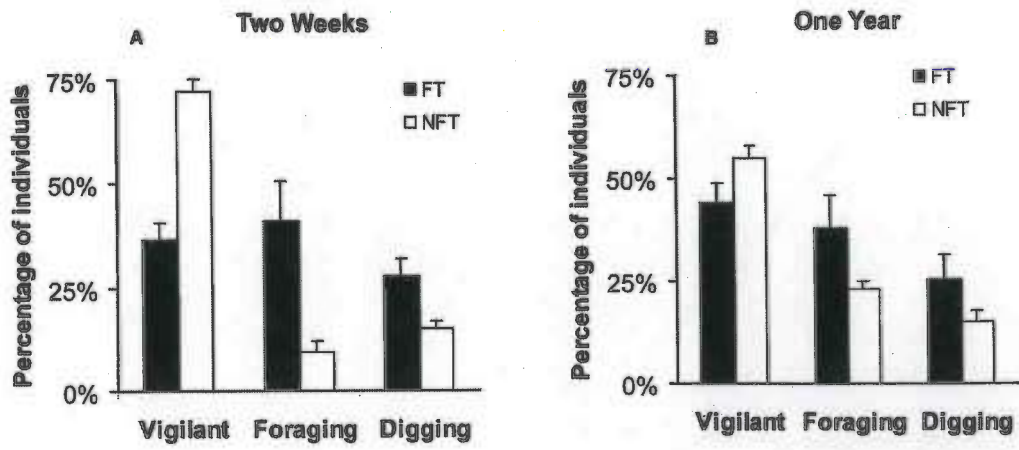


Fig. 3.6.

