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COMPARISON OF MOONLIGHT EFFECTS ON COVER USAGE AND SPATIAL LEARNING OF BLACK-FOOTED FERRETS (*MUSTELA NIGRIPES*) AND SIBERIAN FERRETS (*M. EVERSMANNII*)

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ABSTRACT

Marcum, Samantha N. Comparison of moonlight effects on cover usage and spatial learning of black-footed ferrets (*Mustela nigripes*) and Siberian ferrets (*M. eversmannii).* Published Master of Science Thesis, University of Northern Colorado, 2003.

The purpose of this study was to compare effects of different moonlight intensities on cover usage and spatial learning abilities of black-footed ferrets (*Mustela nigripes*) and Siberian ferrets (*M. eversmannii*). The black-footed ferret (BFF) is an endangered mammal in North America and the Siberian ferret (SF) is the congeneric extant relative. Trials were conducted in simulated new (0.05 lux), half (0.35 lux), and full (2.2 lux) moonlight levels. We tested activity patterns (i.e. use of open areas vs. cover) in an indoor chamber ($7m^2$) and spatial learning in a hexagonal indoor arena ($9m^2$). There were no significant differences within or between species regarding cover usage in different moonlight levels. Neither species decreased activity with increased moonlight. Black-footed ferrets did exhibit spatial learning skills, but moonlight levels appeared to have no effect on these abilities. However, through similar methodology, researchers found that Siberian ferrets exhibited spatial learning abilities and these skills appeared to be enhanced in half moonlight. Both species showed high individual variation in spatial learning trials. Understanding these aspects of animal behaviour may be critical to conservation efforts, particularly the success of captive breeding programs and species restoration.

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TABLE OF CONTENTS

CHAPTER		PAGE
I.	**INTRODUCTION**	1
	Observations and Hypothesis	4
II.	**LITERATURE REVIEW**	6
	Natural History	6
	Habitat and Prey Selection	10
	Predators and Competition	12
	Genetics and Reproduction	13
	Moonlight	15
	Spatial Learning	18
III.	**METHODOLOGY**	22
	Study Animals	23
	Apparatus I	24
	Procedure I	25
	Apparatus II	25
	Procedure II	27
	Statistical Analysis	28
IV.	**RESULTS**	30
	Activity and Moonlight	30
	Spatial Learning	32
V.	**DISCUSSION**	37
	Activity and Moonlight	37
	Spatial Learning	40
VI.	**LITERATURE CITED**	46

LIST OF FIGURES

Figure 1. Black-footed ferret in South Dakota..... 2

Figure 2. Current and historic range maps of black-footed ferret..... 8

Figure 3. Current range map of Siberian ferret..... 9

Figure 4. Siberian ferret at UNC Animal Facility..... 15

Figure 5. Black-footed ferret in moonlight chamber..... 24

Figure 6. Schematic overhead view of spatial learning arena..... 26

Figure 7. Schematic side view of spatial learning arena..... 26

Figure 8. Exterior and interior views of spatial learning arena..... 27

Figure 9. Open area activity index comparison..... 31

Figure 10. Individual black-footed ferret movements..... 33

Figure 11. Individual Siberian ferret movements..... 33

Figure 12. Comparison of mean distance traveled..... 34

Figure 13. Black-footed ferret individual range of movement..... 36

Figure 14. Siberian ferret individual range of movement..... 36

LIST OF TABLES

Table 1. Black-footed ferret open area activity index..... 31

Table 2. Siberian ferret open area activity index..... 31

Table 3. Appendix A: Distance traveled in 15 trials..... 53

Table 4. Appendix B: Ferret numbers and names from Figures 13 and 14..... 55

CHAPTER I

INTRODUCTION

Conservation biology and animal behaviour are fields of science that can potentially complement one another. Unfortunately, many conservation efforts for threatened or endangered species focus primarily on the demographics or genetics of a population and neglect the importance of incorporating animal behaviour studies when designing restoration plans. This is especially true for animals raised in captivity to be released into the wild. There is a need for a broader approach to conservation biology and captive management. Animal behaviour research is important for understanding the complex needs of each species to be managed or restored to its native range and can be an important part of the foundation for preservation of a species.

The black-footed ferret is a nocturnal carnivore in the family Mustelidae (Miller and Anderson 1993; Figure 1). This elusive predator once inhabited many areas of the western United States living in close association with three declining species of prairie dogs (*Cynomys ludovicianus, C. leucurus, C. gunnisoni*), which has helped contribute to its own endangered status (Biggins and Godbey 1995). Black-footed ferrets reside in the vast and open prairies of North America leading us to questions regarding their ability to orient themselves within their natural environment.

Figure 1. Black-footed ferret released in October 1999 in Buffalo Gap National Grasslands, South Dakota (Photo by Brent Horton).

The Siberian ferret (*M. eversmannii*), the congeneric closest living relative of the black-footed ferret, inhabits the steppe grasslands of Asia and Eastern Europe (Kydyrbaev 1988). They were used as a surrogate species for behavioural studies in the initial stages of restoration attempts for black-footed ferrets (Biggins 2000; Biggins et al. 1991). The black-footed ferret was once considered conspecific with (Hensel 1881; Hepner et al. 1967; Kostron 1948; Rempe 1970) or a subspecies of the Siberian ferret (Youngman 1982), but O'Brien et al. (1989) considered them to be distinct species based on biochemical genetic studies. Morphological differences do exist between the species and the geographical separation of North America and the steppes of Asia, along with natural selection, random mutations, and genetic drift may have led to divergence between the two forms (Biggins 2000). Siberian ferret prey is also more diverse in species, activity, and availability than that of the black-footed ferret.

Ferret survival depends on the ability to navigate within their dark environments and locate essential resources. Due to their nocturnal nature, moonlight may be an important factor in the logistics of navigation. Moonlight may also play an important role hunting or eluding predators, and may assist ferrets in forming spatial perceptions or memory of the landscape. Several small mammals are known to decrease their activity in bright moonlight (Clarke 1983; Falkenberg and Clarke 1998; Kotler 1984a; Kotler 1984b; Price et al. 1984). Ferrets, like many nocturnal animals, possess a tapetum lucidum, a reflective layer at the back of the eye that increases visual acuity in darkness (Ewer 1973). Black-footed ferrets and Siberian ferrets may rely on moonlight for different purposes due to evolutionary pressures involving habitat selection and prey availability. It is essential to recognize commonalties and discrepancies of behaviour and physiology between these species to properly manage their ecosystems for conservation and/or reintroduction efforts.

Spatial learning refers to an animal's ability to learn and remember the location of key features in the environment (Kimchi and Terkel 2001). Spatial learning research has been conducted on small mammals (Galea et al. 1994), birds (Bingman 1994), and reptiles (Holtzman et al. 1999), but to date only one study has investigated a non-domestic mammalian predator (Sheffer 2001). Ferrets may use spatial learning to locate potential mates, find prey, navigate in complex burrow systems, or avoid predators.

Captive ferrets released into the wild must be able to locate cover, attain food resources, and reproduce in order to achieve a successful self-sustaining population. It is important to address the behaviours of black-footed ferrets in varying moonlight levels and the use of spatial learning to navigate within their environment. Knowledge of these

behaviours can provide conservation biologists with insight into the optimal rearing environment for captive-bred animals, as well as the most appropriate times for an animal to be released into the wild. This knowledge could potentially be applied to Siberian ferrets and possible conservation efforts in the future.

Observations and Hypotheses

The primary objectives of this study were (1) to compare the effects of different moonlight intensities on the activity patterns (i.e. microhabitat use or cover usage) of black-footed ferrets and Siberian ferrets and (2) to examine spatial learning abilities of black-footed ferrets and compare to that of Siberian ferrets. Through field observations, Biggins (2000) found that black-footed ferrets tended to increase their activity in bright moonlight. This finding was surprising, because moonlight probably makes ferrets more susceptible to predation (as suggested by studies of other small mammals) and ferrets do not use light to hunt their prey in burrows. Similarly, a study of captive animals by Clarke and Cross (unpublished data) and a field study by Biggins (2000) found that Siberian ferrets did not decrease their activity in bright moonlight. Captive Siberian ferrets also exhibited enhanced spatial learning skills in brighter moonlight levels (Sheffer 2001). These observations suggested the following questions:

Q1 Does moonlight affect black-footed ferret and Siberian ferret activity patterns (i.e. microhabitat use)?

Q2 Do black-footed ferrets and Siberian ferrets differ between species in activity patterns in varying moonlight levels?

Q3 Do black-footed ferrets exhibit spatial learning skills?

Q4 If so, does moonlight affect the spatial learning abilities of black-footed ferrets?

The following hypotheses were proposed to address the previous questions:

H1 Moonlight has an effect on black-footed ferret and Siberian ferret activity patterns regarding their use of cover and open areas.

P1 Black-footed ferrets and Siberian ferrets will decrease their activity in open areas significantly with increasing moonlight levels.

H2 Black-footed ferrets and Siberian ferrets will not differ from each other in their activity patterns in each moonlight level.

P2 There will be no significant difference between black-footed ferrets' and Siberian ferrets' use of cover vs. open areas in new moonlight (0.05 lux), half moonlight (0.35 lux), and full moonlight (2.2 lux).

H3 Black-footed ferrets possess spatial learning abilities.

P3 Spatial learning will increase significantly with each successive trial. The distance traveled and the number of errors will decrease with each successive trial.

H4 Given H3 is true, moonlight level will affect spatial learning in black-footed ferrets.

P4 Spatial learning will increase significantly as moonlight intensity increases. In successive trials, distance traveled and number of errors will decrease as moonlight intensity increases.

CHAPTER II

LITERATURE REVIEW

Natural History

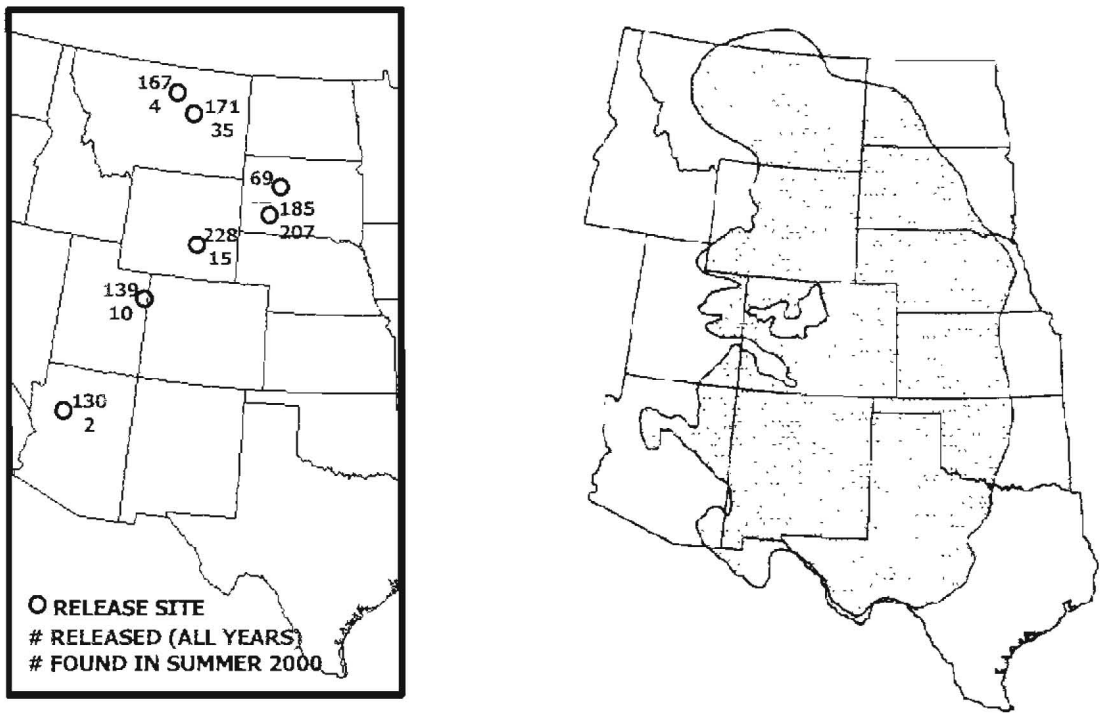
Black-footed ferrets

The former geographic range of black-footed ferrets (Figure 2b) extended from southern Canada, across the Great Plains, and into the southwestern United States and northern Mexico (Clark 1989). The decline of black-footed ferret populations throughout the 20th century can be attributed to many causes. At one time, the ferret was a predominant predator of prairie dogs in the prairie ecosystem. Before the Europeans arrived in North America, prairie dogs were an abundant and stable food resource with burrows that made homes for ferrets (Miller et al. 1996). At this time, short-grass prairies covered nearly a fifth of North America from Canada to Mexico (Anderson et al. 1986). In less than 100 years, the impact of human development on the prairies drastically reduced prairie dog numbers and nearly eradicated ferrets (Miller et al. 1996).

Black-footed ferrets were officially listed as endangered in 1967 and were included under the Endangered Species Act of 1973 (Cole 1989). They had reached near extinction by the 1970's (Biggins et al.1999). Little was discovered about black-footed ferrets before a steady decline in numbers and habitat fragmentation made them difficult to study (Biggins and Godbey 1995). The initial declines were primarily attributed to prairie dog control campaigns beginning before 1900 and climaxing in the 1920's and

1930's (Biggins and Godbey 1995). These shooting and poisoning campaigns reduced prairie dog numbers by over 90% in the last century (Hoogland 1995). The eradication programs indirectly poisoned black-footed ferrets and/or created isolated islands of habitat, which made them more susceptible to stochastic events such as epizootics of plague or canine distemper (Clark 1989; Miller and Anderson 1993). Stochastic events have a much greater chance of driving such island populations to extinction as opposed to large panmictic populations (Gilpin and Soule' 1986). By the time a recovery plan was developed and approved by the United States Fish and Wildlife Service in 1978, black-footed ferrets were unlocatable (Meffe and Carroll 1998). In 1981, a population was discovered near Meeteetse, Wyoming. An epizootic of canine distemper was responsible for the eradication of that population (Miller and Anderson 1993). The remaining 18 wild ferrets were captured between 1985 and 1987 and a captive breeding program was established at the Sybille Wildlife Research and Conservation Education Unit near Laramie, Wyoming (Williams et al. 1991).

Currently, black-footed ferrets are listed as an endangered species in North America. Their geographic range consists of reintroduced populations inhabiting prairie dog towns in the Phillips County, Montana, several locations in South Dakota, with a few in Aubrey Valley, Arizona, Shirley Basin, Wyoming, and near Dinosaur National Monument, Utah (Figure 2a). There are estimated to be more than 300 black-footed ferrets from reintroduced and translocated populations living in the wild (Biggins et al. 1998; Miller et al. 1994; Vargas and Anderson 1999).



(a) (b)

Figure 2. **(a)** Current range map and release sites for black-footed ferrets from 1991-2000 and **(b)** historic range map (Courtesy of Dean Biggins, USGS).

Siberian ferrets

Siberian ferrets are found throughout the steppe, semi-arid, and desert zones of Eastern Asia, Siberia, and Eastern Europe (Kydyrbaev 1988; Figure 3). Their numbers depend primarily on the population density of small rodents, such as ground squirrels (*Citellus rufescens*), hamsters (*Cricetus cricetus*), and pikas (*Ochotona* sp.) (Kydyrbaev 1988). Siberian ferrets, like black-footed ferrets, suffer from a history of exploitation and lack of information regarding their behaviours. The main factors influencing the dynamics of Siberian ferret populations are food availability, use of chemical methods to

combat rodent pests, spring-summer trapping of fur-bearing mammals, massive plowing of virgin lands, poisonous chemicals used for agriculture, and unrestricted cattle grazing (Kydyrbaev 1988). In the 1930s, poisoning of suslik (*Citellus pygmaeus*) burrows, a prey species of Siberian ferrets, along with ferret popularity in the fur trade, caused a massive decline in their numbers (Sviridenko 1935). At that time, ferret pelts accounted for 50% of the fur industry in Kazakhstan (Kydyrbaev 1988). Today, the status of most populations of Siberian ferrets is unknown and the principle questions regarding its biology remain poorly understood, thus hindering the development of scientifically sound methodology for the study and protection of the species (Kydyrbaev 1988). However, Mead et al. (1990) suggested Siberian ferrets were widely distributed and abundant in parts of the Soviet Union, Eastern Europe, and Eastern China in the 1980's.

Figure 3. Current range map of Siberian ferret (Courtesy of Dean Biggins, USGS).

Habitat and Prey Selection

Black-footed ferrets

Black-footed ferrets are fossorial and live primarily in prairie dog burrows (Meffe and Carroll 1998). They are endemic to North America and have no subspecies, in contrast to the Siberian ferret, which has 17 subspecies (O'Brien et al. 1989; Ognev 1931). In Meeteetse, wild-born ferrets were documented traveling 7 kilometers in a night and animals at Shirley Basin were known to travel even greater distances (Biggins et al. 1986; Biggins et al. 1999). Typically, males travel further than females during the mating season or when yearling males disperse from their mothers in early fall (Biggins et al. 1999). They are solitary hunters that usually kill their prey underground and they live in burrows acquired from prairie dogs that they consume (Clark 1989). Ferrets are extreme specialists in both food choices and habitat; however, they are also known to consume lagomorphs, rodents, birds, and insects (Henderson et al. 1969). In 1972, a study in South Dakota revealed that the black-tailed prairie dog (*C. ludovicianus*) comprised 91% of the 82 ferret scats examined and mice comprised the remaining 9% of material (Sheets 1971). In Meeteetse, WY, Campbell et al. (1987) found 87% white-tailed prairie dog remains in 86 ferret scats examined, with deer mice (*Peromyscus maniculatus*), sagebrush vole (*Lagurus curtatus*), meadow vole (*Microtus montanus*), and Nuttal's cottontail (*Silvalagus nuttali*) comprising the remaining ingredients.

An ethogram of captive ferrets revealed four elements in their predatory sequence: 1) stalk; 2) grasp; 3) avoidance of retaliation by shake, throw, or roll; and 4) kill bite (Miller and Anderson 1993). Prairie dogs are about the same size as ferrets, so learning efficient placement of the kill bite to penetrate the throat is essential for ferret

survival (Miller and Anderson 1993). Due to the behavioural differences of ferrets (nocturnal) and prairie dogs (diurnal), there may be a reduced risk of injury to ferrets by hunting at night when prairie dogs are inactive (Miller and Anderson 1993). It is also feasible that ferrets are exhibiting predator avoidance behaviour by concentrating most of their activity at times when coyotes (*Canis latrans*) and other predators are least active (Biggins 2000).

Siberian ferrets

Siberian ferrets are typically found in open grasslands with low, sparse foliage and can travel 5-18 km per night (Clark 1989; Kydyrbaev 1988; Heptner et al. 1967). Their diet varies with topography, geography, season, and abundance of prey species, but consists primarily of ground squirrels and susliks (Clark 1989; Kydyrbaev 1988; Serebrennikov 1929; Volchanetskii 1935). They also consume pikas, voles (*Microtus* sp.), jerboas (*Dipus* sp.), marmots (*Marmota* sp.), and hamsters (Clark 1989). When food is scarce, Siberian ferrets may prey upon some birds, reptiles, and amphibians (Volchanetskii 1935). Unlike black-footed ferrets, Siberian ferrets frequently kill more than they can consume at one time and cache dead prey in their burrows (Zverev 1931). Sviridenko (1935) reported that nest burrows usually contained 5-30 dead susliks, but one burrow was discovered containing 50 dead susliks. The tendency of Siberian ferrets to overkill is in stark contrast to the typical predatory behaviour of black-footed ferrets. This difference may be accounted for in the seasonal productivity fluctuations of their respective environments (Clark 1989).

As with black-footed ferrets, Siberian ferrets live and often hunt in burrows. They use the burrows for shelter and may stay for several successive years or only temporarily (Clark 1989). Siberian ferrets and black-footed ferrets rarely dig their own burrows and have occasionally been found in old sheds or haystacks (Clark 1989).

Predators and Competition

Black-footed ferrets

Black-footed ferrets serve as both predator and prey in the North American prairie ecosystems. In their subterranean world, they are relatively safe (aside from predation by badgers {*Taxidea taxus*}), but their role changes from predator to prey when they emerge on the surface. Behavioural traits are often influenced by the threats of predation, which is one of the primary forces of directional selection in many species (Miller et al. 1996). The main ferret predators are coyotes, badgers, great horned owls (*Bubo virginianus*), golden eagles (*Aquila chrysaetos*), and ferruginous hawks (*Buteo regalis*) (Miller et al. 1996).

Siberian ferrets

Siberian ferrets also play a dual role as both predator and prey in their ecosystem. Wolves (*Canis* sp.), domestic dogs (*Canis familiaris*), eagles (Family Accipitridae), foxes (*Vulpes* sp.), snowy owls (*Nyctea scandiaca*), black kites (*Milvus migrans*), and rough legged buzzards (*Buteo lagopus*) all prey upon ferrets (Kydyrbaev 1988). Evidence for intraguild predation (where elements of competition and predation combine) is provided by the failure of foxes to consume their Siberian ferret prey (Kydyrbaev 1988), which parallels the failure of coyotes to eat black-footed ferrets they have killed (Biggins 2000).

Humans are also enemies of Siberian ferrets due to hunting for the fur trade (Sviridenko 1935; Clark 1989).

Genetics and Reproduction

Black-footed ferrets

Black-footed ferrets are tan to yellowish in color with black feet, a mask across their eyes, and a black-tipped tail (Clark 1989). Males weigh 915-1125 grams and females weigh 645-850 grams (Clark 1989). The breeding season for black-footed ferrets extends from March toApril and gestation lasts 42-45 days (Clark 1989). Both females and males are sexually mature around one year of age (Miller and Anderson 1993). A study in ferret breeding facilities revealed proestrus to last about 2-3 weeks with captive females usually breeding within 32-42 days (Williams et al. 1991). Most breeding activity occurred in April and the average litter size was 3 kits (Williams et al. 1991). Breeding was most successful among females less than 3 years of age (Williams et al. 1991). The link of breeding success to female age may have contributed to the low mating success of the first individuals in the captive-breeding program.

In 1985, when the Meeteetse ferret population was brought into captivity, the primary objective was to increase the existing population size with genetic considerations becoming more important later (Russell et al. 1994). The low depressed founder genome that is attributed to the initially low female breeding success along with the high mating success of one male, Scarface, early in the captive program (Russell et al. 1994). Low genetic variation can also be attributed to the known bottleneck that the wild population encountered prior to captivity (Russell et al. 1994). A recent study by Wisely et al. (2002) examined museum specimens of black-footed ferrets, Siberian ferrets, and

European polecats (*Mustela putorius*). Historical genetic variation was compared to more recent populations. Researchers found three subpopulations of black-footed ferrets to be genetically distinct. Results showed black-footed ferrets to have less genetic diversity than Siberian ferrets, but a similar amount of polymorphic loci as European polecats. The most dramatic decrease in genetic diversity occurred between 1972 and 1985. This decline could most likely be attributed to the extinction of the last Great Plains subpopulations (Wisely et al. 2002).

Siberian ferrets

Siberian ferrets are yellowish to pale brown with dark feet, a mask across their eyes, and the terminal 1/3 of the tail is dark (Clark 1989; Figure 4). Siberian ferret size is more variable than the black-footed ferret, but they are still remarkably similar in appearance (Ognev 1931). Siberian ferrets begin to disperse about 90 days after birth and become sexually mature at about 9 months of age. The gestation period is 38-41 days and the kits are born in April or May (Clark 1989). The mean litter size of Siberian ferrets of 8-9 kits is notably larger than black-footed ferrets, but varies with geographic region (Kydyrbaev 1988).

Figure 4. Siberian ferret at UNC Animal Facility, 2001.

Moonlight

Moonlight affects the behaviour of many small mammals. As mentioned previously, several small mammals decrease their activity in bright moonlight, which may be advantageous for predator avoidance purposes (Clarke 1983, Falkenberg and Clarke 1998, Kotler 1984a, Kotler 1984b, Price et al. 1984). However, moonlight also provides illumination to a dark environment that allows animals to assess their surroundings.

Clarke et al. (1996) tested the effects of moonlight on the activity patterns of juvenile and adult prairie rattlesnakes (*Crotalus viridis viridis*). Six adults and eight juveniles were tested in the laboratory under a summer photoperiod of 14L:10D cycle. Snake activity was measured using an index of tracking trails left in a sand floor of the laboratory chamber. Each snake was tested in new, half, three-quarter, and full moonlight (0.06, 0.35, 1.00, 2.10 lux, respectively). Adults significantly increased their activity in open areas in new moonlight. Juvenile snakes displayed no significant

difference in their use of open versus covered areas in varying moonlight levels. These researchers believe that bright moonlight avoidance by adult prairie rattlesnakes may be a predator avoidance strategy as well as being influenced by the activity patterns of their nocturnal rodent prey. Juveniles' lack of moonlight avoidance may be attributed to diurnally active prey utilization, such as lizards and rodents (Clarke et al. 1996).

A study conducted by Julien-Laferriere (1997) compared activity levels of male and female free-ranging woolly opossums (*Caluromys philander*) during different moonlight levels. Woolly opossums did not shift their activity to parts of the night with lower moonlight intensities, but maintained a fairly constant activity level throughout the night. In low moonlight, males had a longer activity period than females. However, there was no difference in activity between males and females activity in medium moonlight levels. Males were more active in low or dim moonlight levels compared to bright moonlight and females had an average low amount of activity regardless of the moon phase. Reasons for the difference in activity between sexes are unknown (Julien-Laferriere 1997).

Zollner and Lima (1999) conducted a study on the role of illumination in the use of habitat patches by white-footed mice (*Peromyscus leucopus*). The purpose of the study was to gain a greater understanding of the interaction between behavioural and ecological influences and to help determine what factors affect animals' movements across landscapes. Male and female mice were live-trapped and released in a barren field near a woodlot. Previous data determined that mice orient themselves towards a woodlot for cover if they can detect it. Mice were released in varying moonlight intensities at distances of 30, 60, 90, and 120 meters from the edge of the woodlot. Mice released in

total darkness were allowed to view their environment at dusk from enclosures. Zollner and Lima (1999) proposed that white-footed mice, being primarily nocturnal, might be active at dusk so they can assess their landscape. Results were compared among each test group based on initial orientation towards the woodlot. Mice released under brighter moonlight conditions were able to navigate towards the woods from greater distances. Twilight-informed mice released in darkness were also able to orient towards the woodlot from distances of 30, 60, and 90 meters. These mice may have been using spatial learning skills to locate habitat patches for dispersal (Zollner and Lima 1999).

Barry and Franq (1982) also determined that white-footed mice increased their activity in bright moonlight, suggesting that the mice might be using the moon for orientation. They may also be processing physical cues from their environment for dispersal or habitat patch location. Kavanau (1969) tested the influences of light on the activity of least weasels (*Mustela rixosa*) and chipmunks (*Tamias striatus*). These animals ran in one direction when placed on a wheel. They were obtaining directional bearings for this orientation from nearby objects and the artificial illumination of the moon (Kavanau 1969). When discrete light sources were absent, the animals obtained bearings from other objects within the enclosure and experienced animals were able to maintain their directional bearings in total darkness, as shown by the unidirectional running on the wheel (Kavanau 1969).

Siberian ferrets, like white-footed mice, did not decrease their activity in bright moonlight in captive studies or wild studies (Clarke and Cross unpublished data; Biggins 2000). Biggins (2000) also observed black-footed ferrets being active on brightly moonlit nights in the field. This is interesting because they are presumably more

susceptible to predation in bright moonlight. They, too, may be assessing their environment for spatial learning of home ranges, to detect predators or competition, to locate mates, or to find burrows.

Spatial learning

Animals modify or adapt their behaviour by learning to respond efficiently to their environments (Cole et al. 1982). Spatial learning is valuable to many creatures for locating objects and places within the environment. Spatial learning refers to the memory of landmarks and physical cues in the environment relative to one's own position and movements (Alcock 1998). The localization of food and shelter are tasks that are facilitated by spatial learning (Holtzman et al. 1999). Additionally, spatial learning may aid animals in eluding predators or finding prey.

Research by Tinbergen (1958) on the beewolf wasp (*Philanthus triangulum*) was one of the first studies to recognize spatial learning. Tinbergen discovered that female wasps could distinguish their nest from other nests by circling in the air and locating environmental cues. When the landmarks were moved to another nest and placed in an identical arrangement around it, females circled incessantly in an attempt to locate a nest that was no longer present. When the environmental cues were replaced, female wasps were able to locate the burrow (Tinbergen 1958).

A study of hummingbirds by Cole et al. (1982) supports the hypothesis that if ecological and social conditions in which animals learn are variable, then the characteristics of learning also vary. Four black-chinned hummingbirds (*Archilochus alexandri*), two Rivoli's hummingbirds (*Eugenes fulgens*), and two blue-throated hummingbirds (*Lampornis clemenciae*), captured in southeastern Arizona, were trained

in "shift learning" and "stay learning". Cole et al. (1982) found significant differences between and within species regarding amount of time to learn the "shift" task relative to the "stay" task. For example, the slowest "shift" learner was the black-chinned hummingbird and the fastest "stay" learner was the Rivoli's hummingbird. These researchers believed that learning might depend on the influence of spatial and temporal scale resource depletion after feeding and that food and resource distribution in space and time generates important evolutionary influences on learning (Cole et al. 1982).

Lavenex and Schenk (1998) conducted a study on spatial learning with the presence of olfactory traces in rats (*Rattus norvegicus*). Trials were run in a hexagonal open-field arena with nineteen white plastic petri dishes arranged equal distances apart. Rats were trained to locate a food reward at a stationary location from different starting positions. In darkness, the rats needed supplementary olfactory cues, in addition to their own scent, to solve designated tasks. Rats trained in white light were more efficient at finding the food location than rats trained in darkness with irrelevant olfactory cues. This experiment demonstrated that rats rely on light and scent cues for spatial learning (Lavenex and Schenk 1998).

Holtzman et al. (1999) conducted a study on spatial learning in young corn snakes (*Elaphe guttata guttata*). They hypothesized that snakes could learn an open-field escape task. Snakes were trained to perform an escape task through one of eight holes in a brightly-lit arena. Learning was measured by changes in latency, path length to goal, and spatial preference for a particular quadrant in the arena. The data revealed that snakes form spatial memories and may use different mechanisms to orient themselves.

Additionally, Holtzman et al. (1999) noticed a qualitative difference in the routes taken by different snakes, showing intraspecific variation in choices among individual snakes.

Behavioural development is often affected by experience, especially those stimuli encountered early in an animal's life. For instance, Vargas and Anderson (1999) found that black-footed ferrets raised in "complex" environments were more likely to make successful kills than those raised in "deprived" environments. This could have serious implications regarding the effects of rearing conditions on the ability of a ferret to survive post-release into the wild. Similarly, rats raised in enriched cages were more likely to escape a predator model than those raised in empty cages (Renner and Rosenzweig 1987). Rats raised in cages with toys or other rats were more successful at completing mazes than rats raised alone and without aesthetic stimuli (Greenough and Juraska 1979).

The ability to remember routes in mazes is accomplished via spatial learning. This type of learning, associated with the hippocampus region of the brain (Sherry et al. 1984), may be a "use-it-or-lose-it" skill. The hippocampus region of the brain appears to be important for memory and information storage and may be associated with processing of sensory experiences that allow for proper development and learning (Sherry et al. 1984). Spatial learning skills of polygynous male meadow voles (*M. pennsylvanicus*) exceeded those of female voles during the breeding season when the males were moving about in search of mates (Gaulin and Fitzgerald 1989). However, in the non-breeding season, there were no significant differences in spatial learning abilities between sexes. Because males gain no reproductive advantage from spatial learning skills during the non-breeding season, the hippocampus region of the brain may shrink when extra tissue is not useful. A similar study conducted by Galea et al. (1994) with deer mice

(*Peromyscus maniculatus*), revealed no differences in spatial learning abilities between sexes during the non-breeding season, but males did exhibit superior spatial learning skills during the breeding season.

Spatial learning may be a necessary skill for black-footed ferret survival. Rearing environments and cage conditions may play a role in the opportunity for ferrets to retain spatial learning abilities and use them when released into the wild. The hippocampus region of the brain can change size in certain animal species that use spatial learning skills for navigational or food storage purposes (Burnea and Nottebohm 1994; Altman and Das 1964). Cage environment and experience seems to affect both the size of the hippocampus and the spatial learning capacity of some animals. This may also be true for black-footed ferrets raised in captivity.

CHAPTER III

METHODOLOGY

Research questions regarding activity patterns and spatial learning abilities of black-footed ferrets in moonlight were addressed using an indoor moonlight chamber and a hexagonal arena containing exterior spatial cues. Moonlight intensities were manipulated to simulate new moonlight (0.05 lux); half moonlight (0.35 lux), and full moonlight (2.20 lux) levels. To compare activities of black-footed ferrets and Siberian ferrets, I adhered to the same protocol and followed the same procedures as a previous moonlight study conducted on six Siberian ferrets at the University of Northern Colorado (UNC), Greeley in 1997-98 (Clarke and Cross unpublished data). Data from the previous Siberian ferret moonlight study was used for the comparison between species in this experiment. To test the spatial learning abilities of black-footed ferrets in three illumination levels, I adhered to similar protocol and procedures used in a study of Siberian ferrets by Sheffer (2001). Data from the previous Siberian ferret spatial learning study was used for the comparison between species in this experiment. I was constrained to conduct all tests consecutively in a 3-month period, compared to the tests of Siberian ferrets, which were conducted in a 12-month period with 3-4 month intervals between test sessions. The black-footed ferrets used in the test trials were either potential candidates for release to the wild soon after the tests, or they were critical to the black-footed ferret captive breeding program.

Study Animals

Eight adult male black-footed ferrets, 2-4 years old, from the National Black-footed Ferret Conservation Center breeding facility in Sybille, Wyoming, were used for these tests during May 15-August 15, 2001. The ferrets were housed individually in stainless steel cages (91 cm x 86 cm x 83 cm) at the University of Northern Colorado Animal Facility. Each ferret was provided a nest box, paper shavings, and a plastic tube (12 cm in diameter and 24 cm long). The ferrets were kept on an automated light cycle of 12L:12D with a lamp (40W bulb) that automatically turned on the first 30 minutes of each dark cycle to simulate dusk. The room temperature was maintained at 21-23 °C. Each day, the ferrets were fed 40 grams of dry food (Plymouth WI and Hill's Science Diet Adult Feline Maintenance, Hill's Pet Nutrition, Inc., Topeka, KS, 66601), 40 grams of horsemeat, and provided water *ad libitum*. Every other day, their cages were cleaned and their weights were measured to aid in assessing their health. Sheep Draw Animal Hospital (Greeley, CO 80631, Dr. Stephanie Buckholz) was designated for veterinary support. Surgical masks were worn to maintain disease prevention precautions, shoes were disinfected upon entry to the room housing ferrets, and the Black-footed Ferret Species Survival Plan protocol was followed. The data sets from two groups of 6 Siberian ferrets each, comparable in age to the black-footed ferrets used in this study, were utilized for species comparisons (Clarke and Cross unpublished data; Sheffer 2001).

Apparatus I

To determine black-footed and Siberian ferret activity in different light intensities, moonlight trials were conducted in an indoor chamber ($7m^2$) constructed of wood and glass (Figure 5). This chamber was located in a room containing no windows in the UNC Animal Facility. The study followed a similar procedure for research done with deer mice (*Peromyscus maniculatus*) by Falkenberg and Clarke (1998). Plastic tubes were secured in each corner of the chamber to serve as simulated burrows (i.e., cover). The chamber floor was covered with natural pine shavings. Illumination, using 105 bulbs (0.50W each) distributed evenly over the ceiling, was set via rheostat control. Reflectance values, reproducing illumination of clear nights with new, half and full moon were tested with a Gossen Luna Pro light meter and a 15% reflectance gray card. Trials were recorded using a ceiling mounted infrared camera (Sanyo), a VCR (Sanyo TLS-900), and a monitor (Sears Solid State).

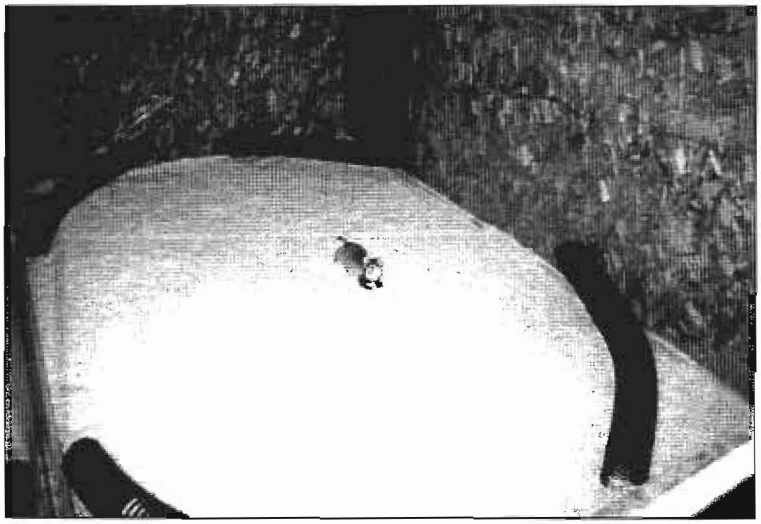


Figure 5. Black-footed ferret in moonlight chamber, UNC.

Procedure I

Each ferret was initially placed in the moonlight chamber for 30 minutes to engage in exploratory behaviours, so the chamber was no longer a novel environment. Ferrets were chosen from a randomized schedule for the actual trials, placed in the chamber, and recorded for 2 hours in each moonlight intensity: new moonlight, half moonlight, and full moonlight. Each trial began when the ferrets were 1hour into their night cycle, because this was a period of high activity for the ferrets (personal observation). Trials were recorded on a low-speed setting and thus each 2-hour trial lasted for 20 minutes of tape time. Trials were replayed and an acetate sheet with a grid was fitted to the monitor screen. A mark was made for a ferret's location every 5 seconds throughout the duration of each trial. Data were analyzed for percent time in a tube (i.e., cover, burrow, or edge) versus percent time in open for each moonlight intensity.

Apparatus II

Spatial learning trials were conducted in a hexagonal indoor arena ($9m^2$) in new, half, and full moonlight intensities. The original template for the arena was derived from a study conducted by Lavenex and Schenk (1998) that tested the spatial learning skills of rats (Figure 6). Light values for different moonlight levels were determined and confirmed through use of a light meter and a 15% gray reflectance card and manipulated via rheostat control. Two infrared light sources were mounted above the arena to provide illumination for recording the trials. A lamp with a 40W bulb was placed under the arena to allow for diffuse, even lighting.

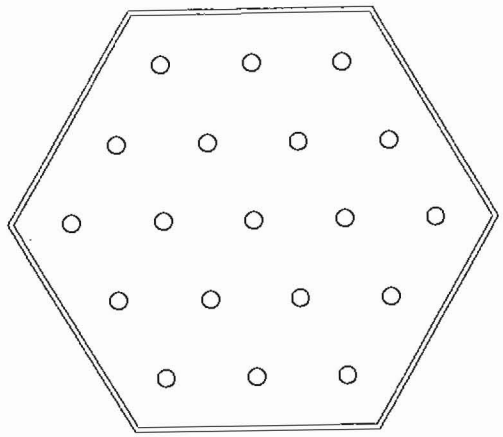


Figure 6. Schematic overhead view of spatial learning arena.

The floor and walls of the arena were made of plywood attached to a steel frame on wheels. Clear contact paper was placed on the floor so that it could be easily cleaned between trials. There was a removable door on one wall and "simulated doors" drawn on the other walls to present a uniform appearance. Nineteen holes or faux burrows (14 cm in diameter and 19 cm in depth) were spaced evenly on the arena floor. All the holes were fitted with a PVC pipe and removable cap, so that an elbow joint and PVC pipe (35 cm in length) leading to the food reward (goal), could be placed in different locations during each trial (Figures 7 and 8).

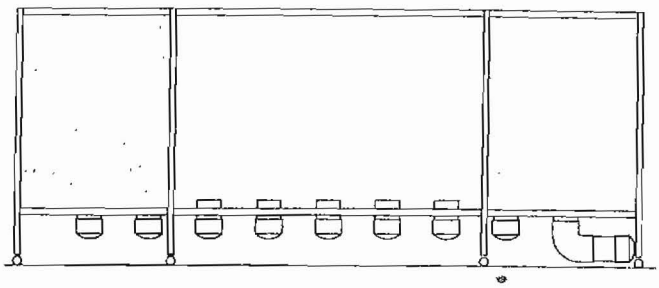
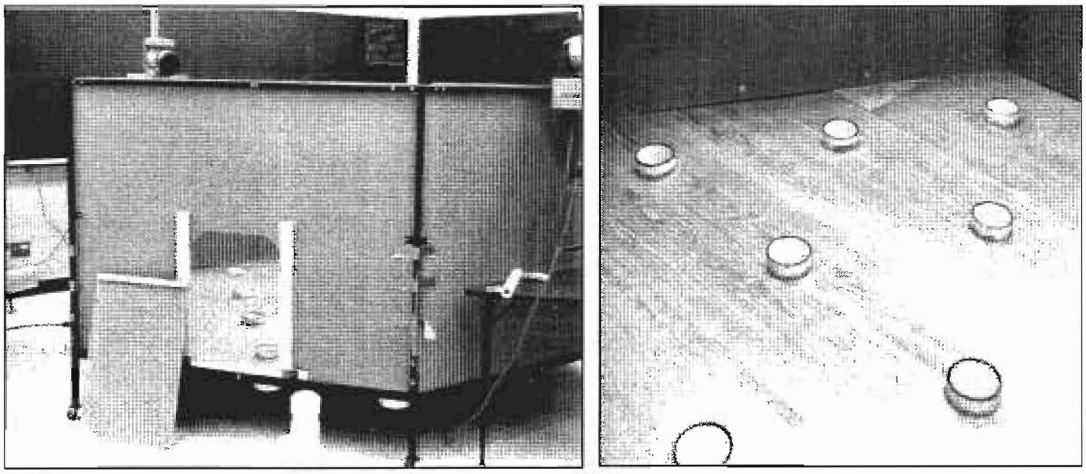


Figure 7. Schematic side view of spatial learning arena with movable goal location and faux burrows.

All trials were recorded using an infrared camera mounted in the ceiling above the arena, a mirror to capture the entire image of the arena, a VCR, and a monitor. The doors and windows of the room were covered to control the amount of light emitted within the arena, but the room was not soundproof. All possible sources of varying air currents were also covered.



(a) (b)

Figure 8. **(a)** Actual exterior view and **(b)** interior view of spatial learning arena.

Procedure II

Prior to each trial, the arena floor, burrows, and goal hole were wiped with ammonia-based cleaner and then dried with a fan to avoid any effects on subsequent behaviour associated with conspecific odors. Siberian ferrets were unable to locate the goal in total darkness (Sheffer 2001), providing evidence that this cleaning method was effective in removing scent cues. Approximately one teaspoon of Ferretvite, a palatable food supplement (Ferretvite High Calorie Concentrate, 8 in 1 Pro Products, Inc., Hauppauge, New York, 11788), was placed in the center of each blind-ended mock

burrow to produce scent prior to each trial. A tablespoon of Ferretvite was placed in the goal hole as the "reward" just before a ferret was released.

Upon beginning each trial, a ferret was brought from the Animal Facility to the arena room in its nest box. Researcher 1 stood outside the arena and released the ferret from the trap tube or nest box at predetermined location (using a randomized schedule) facing away from the entry door. Researcher 2 controlled the VCR to record all events. Trials lasted for 15 minutes or until the ferret found the goal. Upon trial completion, the ferret was returned to the Animal Facility.

Three or four ferrets were tested once per day for a total of five successive trials for each individual ferret. A trial set was complete after all ferrets had been tested in a particular moonlight intensity. Trial sets were alternated between new, half, and full moonlight. The goal was moved between each trial set. The trials were conducted between 1700 and 1900 hours each day. The tapes from each trial were used to measure the following variables: *a)* distance traveled from release point to goal "burrow" and *b)* number of errors. Ferret paths were traced with a marker on an acetate sheet placed on the monitor during replay of the trials. A map distance reader was used to measure the distance traveled. Calculations were necessary to account for image distortion of the arena on the monitor screen. The above procedures and analysis were used for each moonlight level in subsequent trials.

Statistical Analysis

Multivariate analysis with repeated measures design was used for analysis of data in the moonlight trials. The moonlight trials tested the use of cover versus open areas (i.e. microhabitat use) in new, half, and full moonlight and were compared in eight black-

footed ferrets and six Siberian ferrets. Spatial learning was analyzed for black-footed ferrets and Siberian ferrets via multivariate analysis with repeated measures design. Eight black-footed ferrets were used in five repeated trials in three moonlight levels (new, half, and full). Data from six Siberian ferrets were used in five repeated trials in three moonlight levels (new, half, and dark) conducted twice. Distance traveled was compared between species in new and half moonlight intensities. However, data were also analyzed for black-footed ferrets in full moonlight and for Siberian ferrets in total darkness. Number of errors was not analyzed due to apparent subjectivity in describing a "ferret error". Additional multivariate general linear modeling was done to assess variation between animals. For these analyses, movement distances were log-transformed to improve normality and homoscedasticity. This post-hoc statistical procedure was added after initial tests had been evaluated. An alpha of 0.05 was used for all tests.

CHAPTER IV

RESULTS

Activity and Moonlight

Black-footed ferret activity in open areas did not differ significantly between moonlight levels (new, half, full) (N=8 ferrets; N=24 trials; $F_{2,6}$=0.322; p=0.736). In all moonlight levels, black-footed ferrets exhibited high variation in percent activity in open areas (39.00- 41.67%; Table 1). Comparisons of the percentiles revealed a trend for highest variation in percent activity in open areas in full moonlight and the lowest variation in half moonlight (Figure 9a).

Similar to black-footed ferrets, use of open areas by Siberian ferrets did not differ significantly between moonlight levels (new, half, full) (N=6 ferrets; N=36 trials; $F_{2,9}$=2.069; p=0.182). In contrast, in the first trial set, Siberian ferrets tended to be less variable in their use of open areas in all moonlight levels (7.30-14.70%; Table 2). Comparisons of the percentiles suggested the highest variation in percent activity in open areas occurred in new moonlight and the lowest variation in full moonlight (Figure 9b).

No significant differences existed between species in any moonlight level regarding use of open areas versus cover (N=14 ferrets; N=42 trials; $F_{1,18}$=1.780; p=0.199). In order to standardize the data sets, only the first set of Siberian ferret trials was used to compare species (Table 2; Figure 9).

Table 1. Mean, median, maximum, and minimum values for open area activity index (%) of black-footed ferrets (N=8; N=24 trials) in new, half, and full moonlight.

Moonlight	Mean (%)	Median (%)	Maximum (%)	Minimum (%)
New (0.05 lux)	11.20	3.96	42.00	1.30
Half (0.35 lux)	8.12	1.46	39.00	0
Full (2.2 lux)	9.11	4.38	42.00	0.33

Table 2. Mean, median, maximum, and minimum values for open area activity index (%) of Siberian ferrets (N=6; N=18 trials) in new, half, and full moonlight.

Moonlight	Mean (%)	Median (%)	Maximum (%)	Minimum (%)
New (0.05 lux)	4.39	3.16	14.70	0
Half (0.35 lux)	3.86	4.21	10.50	0
Full (2.2 lux)	4.91	3.68	8.40	1.10

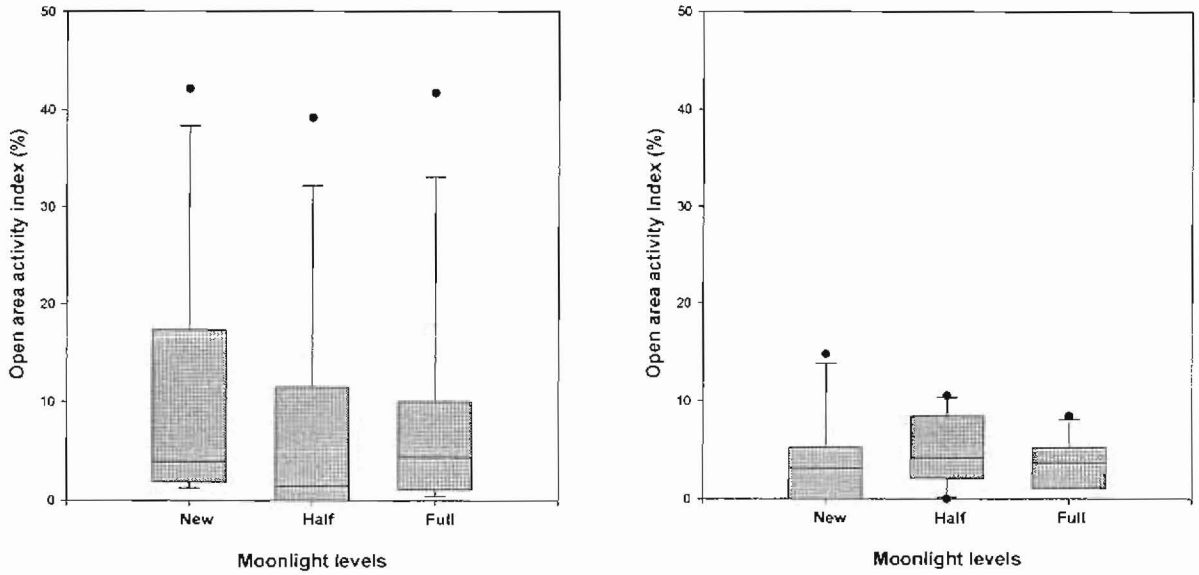


Figure 9. **(a)** Black-footed ferret (N=8 ferrets; N=24 trials) and **(b)** Siberian ferret (N=6 ferrets; N=18 trials) open area activity index in new, half, and full moonlight levels. Boxes indicate 25th to 75th percentiles with median lines. Whiskers are 5th and 95th percentiles. Dots are outlying data points.

Spatial learning

Black-footed ferret data were pooled regarding moonlight level because there were no significant differences in the ferrets' spatial learning abilities between moonlight levels (N=8 ferrets; N=120 trials; $F_{2,6}$=1.084, p=0.396). Only distance traveled relative to trial sequence was measured. Distance traveled declined linearly with trial sequence for black-footed ferrets (N=8 ferrets; N=120 trials; $F_{1,7}$=36.588; p=0.001; Figures 10 and 12). Within subjects, the mean distance traveled decreased in 15 consecutive trials with an exponential tendency, from 27.651m in Trial 1 to 6.517m in Trial 15 (Appendix A, Table 3). Similar results were obtained for Siberian ferrets when the data were pooled regarding moonlight level. Siberian ferrets' mean distance traveled declined linearly within subjects in 15 consecutive trials, from 38.835m in Trial 1 to 12.731m in Trial 15 (N=6 ferrets, N=90 trials; $F_{1,5}$=13.375, p=0.015; Figures 11 and 12; Appendix A, Table 3). The greatest decline in distance traveled occurred between Trial 1 and Trial 2 for black-footed ferrets (27.651m to 7.807m, respectively) and for Siberian ferrets (38.835m to 18.285m, respectively). Although both species exhibited the greatest decrease in distance traveled between Trial 1 and Trial 2, Siberian ferrets continued to linearly decline until Trial 5, whereas black-footed ferrets appeared to learn the location of the goal after one trial, suggesting that black-footed ferrets may learn faster (Figure 12). Black-footed ferrets tended to move less throughout all the trials (mean=9.070m; mean range=4.759m-27.651) compared to Siberian ferrets (mean=16.236m; mean range=8.467m-38.835m) who exhibited higher average distances traveled in 87% (13/15) of the trials.

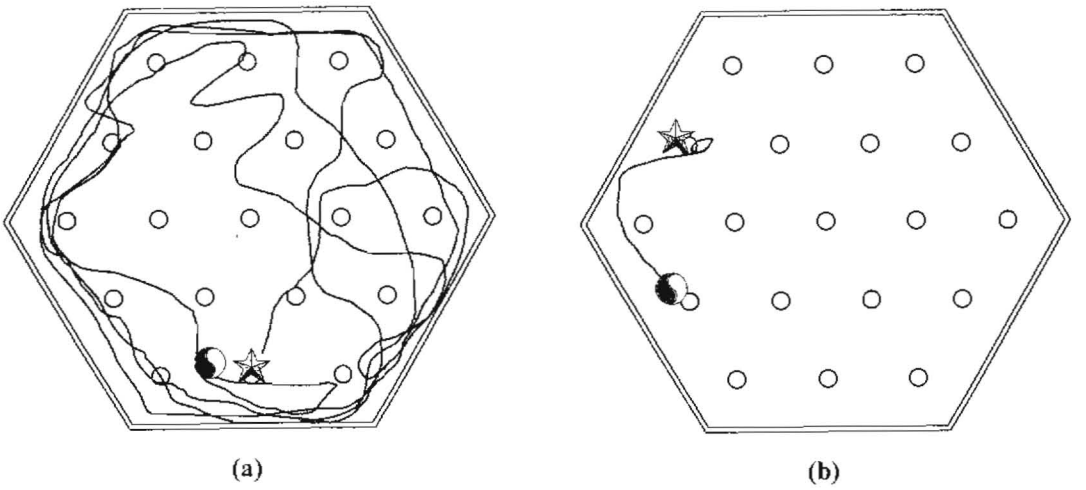


Figure 10. Illustration of an individual black-footed ferret's movements in **(a)** Trial 1 versus **(b)** Trial 15 (line on figures indicates route traveled; circle represents release point; star represents goal)

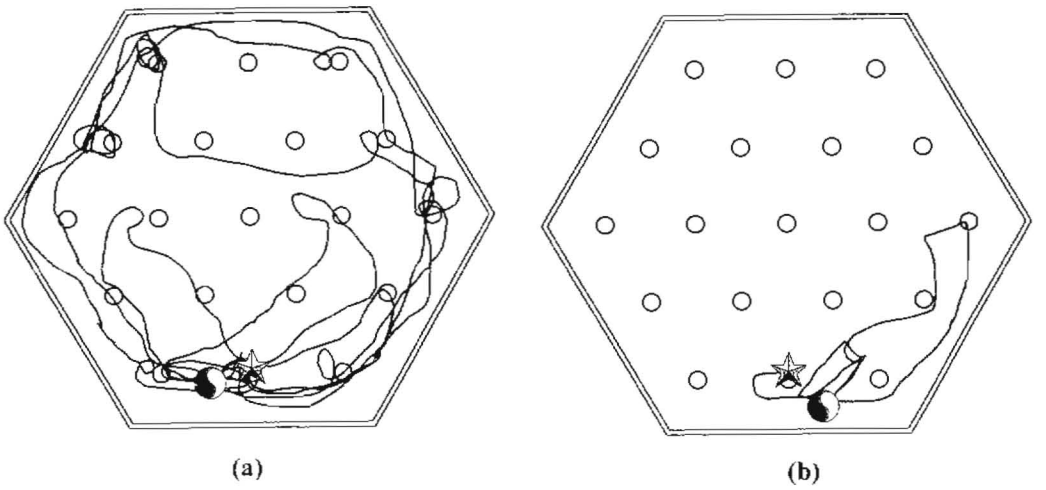


Figure 11. Illustration of individual Siberian ferret's movements in **(a)** Trial 1 versus **(b)** Trial 15 (line on figure indicates route traveled; circle represents release point; star represents goal).

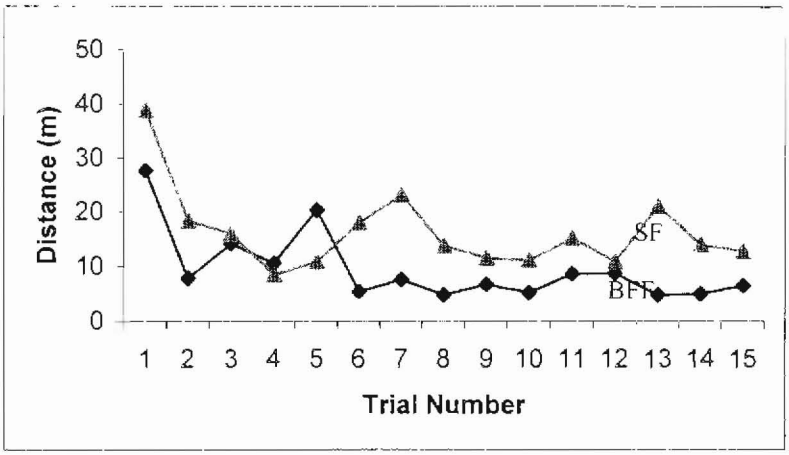


Figure 12. Comparison of mean distance traveled (m) by black-footed ferrets (BFF) and Siberian ferrets (SF) in 15 trials.

Siberian ferrets' spatial learning skills were affected by moonlight level in studies conducted by Sheffer (2001) using the same dataset. This previous study suggested that Siberian ferrets' spatial learning abilities were enhanced in brighter moonlight levels (Sheffer 2001). Non-parametric statistics were used and the trial schedule was non-randomized with regard to moonlight level (Sheffer 2001). Due to differences in statistical and sampling methods, direct comparisons between species regarding the effect of moonlight on spatial learning abilities could not be made.

A post-hoc comparison examined variation of individuals within species. Only the first ten trials were used for this analysis in order to standardize the time lapse between trials for both species. A general linear model indicated significant variation between individual black-footed ferrets regarding distance traveled in spatial learning trials (N=8 ferrets; N=80 trials; $F_{1,7}$=3.629; p=0.002; Figure 13; Appendix B. Table 4).

Individual Siberian ferrets also differed in the distances traveled in spatial learning trials (N=6; N=60 trials; $F_{1,5}$=3.455; p=0.009; Figure 14; Appendix B, Table 4). Distance from release point to goal was used as a control in data analysis to account for any individual variation due to release location. The release location had significant effects (i.e. positive correlation) on variation of distance traveled in black-footed ferrets (N=8 ferrets; N=80 trials; F_1=11.892; p=0.001) and Siberian ferrets (N=6 ferrets; N=60 trials; F_1=4.092; p=0.048) and was therefore, included in the general linear model.

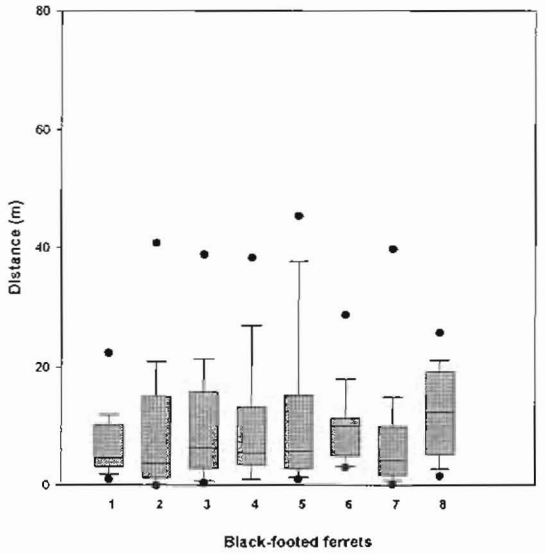


Figure 13. Range of movements (distance-m) for eight black-footed ferrets in 10 spatial learning trials. Boxes indicate 25th to 75th percentiles with median lines. Whiskers are 5th and 95th percentiles. Dots are outlying data points.

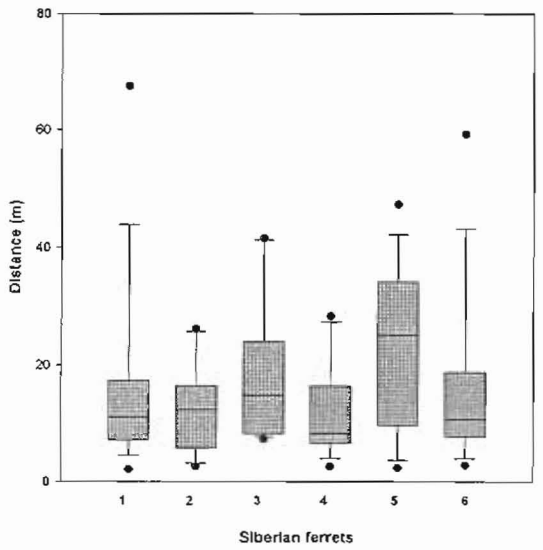


Figure 14. Range of movement (distance-m) for six Siberian ferrets in 10 spatial learning trials. Boxes indicate 25th to 75th percentiles with median lines. Whiskers are 5th and 95th percentiles. Dots are outlying data points.

CHAPTER V

DISCUSSION

Activity and Moonlight

As stated previously, many small mammals are known to decrease their activity in bright moonlight (Clarke 1983; Falkenberg and Clarke 1998; Kotler 1984a; Kotler 1984b; Price et al. 1984). However, black-footed ferrets and Siberian ferrets did not decrease their activity or use of open areas in full moonlight levels, as compared to new and half moonlight levels. These were surprising results, because bright moonlight makes them more visible on the surface and thus, presumably more susceptible to predation. A study by Barry and Franq (1982) with wild-reared white-footed mice was conducted in the field and in the laboratory to examine activity in varying illumination levels as well as visual acuity. There was no relationship between number of captures in a night relative to nocturnal cloud cover and moon visibility. These researchers concluded that visual cues are probably necessary for orientation and navigation within their environments, so therefore, white-footed mice are active on brightly moonlit nights (Barry and Franq 1982). Zollner and Lima (1999) examined how the landscape perception of white-footed mice is affected by varying moonlight intensities. Results indicated that white-footed mice possess greater perceptual abilities in brighter moonlight conditions. Results also indicated that mice were able to examine their environment in bright light levels and able to orient better when released in darkness. This suggests that

white-footed mice were using brightly-lit nights to gather information about their environment. However, they did not disperse in bright light, so perhaps predation risk influences dispersal in white-footed mice (Zollner and Lima 1999). Ferrets may also be using moonlight to examine their surroundings and disperse or move greater distances under darker light levels.

Biggins (2000) suggested that black-footed ferrets might be active during times that decrease their likelihood of intraguild predation. Intraguild predation and interference competition are possible selective forces that influence the behaviours of both ferret species, and could be responsible for the restricted niche of black-footed ferrets (Biggins 2000). Diurnal raptors hunt prairie dogs and could be a potential threat to ferrets as well (Biggins 2000). By avoiding activity periods of their diurnal prey, there is probably a decreased likelihood of ferrets encountering other predators and this may have induced the niche shift to nocturnality in black-footed ferrets (Biggins 2000). Coyotes are one of the main nocturnal predators and/or competitors of black-footed ferrets. Perhaps black-footed ferrets do not have the option to be inactive for entire moon phases due to high energetic demands. Instead, they may change activity levels during certain times of night regardless of moon phase. Lagomorphs (*Sylvilagus* sp.) are a prey source for coyotes, so it is possible that black-footed ferrets are least active when these lagomorphs and coyotes are most active. While living in the midst of a large biomass of potential prey, it may be critical for small predators to temporally avoid mid-sized predators (Biggins 2000). Telemetric studies conducted in Qinghai, China also revealed an avoidance pattern of red foxes (*Vulpes vulpes*) by Siberian ferrets in their natural habitat (Biggins 2000).

The nocturnal monkey, *Aotus trivirgatus,* did not decrease its activity with increasing moonlight intensity in a study by Wright (1981). This monkey's activity was actually higher during full moonlight or under full-moon brightness in captivity (Erkert 1974; Erkert 1976; Erkert and Grober 1986). Primates may be visually oriented and may require bright light to locate resources. This visual acuity may be necessary for ferrets as well. Female woolly opossums seemed to be active independent of moonlight levels in a study conducted by Julien-LaFerriere (1997). However, a nonlinear inverse relationship between light level and activity existed in male woolly opossums (Julien-LaFerriere 1997). This promotes questions regarding sexually dimorphic responses to moonlight levels and seasonal variation. The aforementioned studies reveal mammals that are active in bright light conditions or independent of moonlight level, which suggests that other factors of an animal's habitat may also affect behaviours. These factors may be constant or vary temporally.

The Indian crested porcupine (*Hystrix indica*), found in the southern highlands of Israel, displayed seasonal activity variation (Alkon and Saltz 1988). In a 1-year period, porcupines optimized winter (October-March) activity and had minimal exposure to moonlight. However, during late summer (August-September), there was no apparent moonlight avoidance. These seasonal changes in activity and moonlight exposure may have been due to available dark hours relative to surface-activity requirements or food-density fluctuations, but did not directly correspond to reproductive stages of porcupines (Alkon and Saltz 1988). This seasonal variation of activity may also exist in black-footed ferrets. This has not been studied, but differences between seasonal activity may occur relative to moonlight intensity as well as sexually dimorphic responses that may exist.

Siberian ferrets may exhibit a seasonal variation of activity due to their temporal changes in food sources. They move great distances into habitats with new features and potentially novel predators in order to adapt to the prey available at a given time (Clark 1989; Kydyrbaev 1988; Serebrennikov 1929; Volchanetskii 1935).

Animal behaviour studies regarding activity patterns may be viewed as the examination of two conflicting demands: the activity required to maximize nutritional and reproductive needs, and the necessity to minimize the costs and risks inherent in the environment (Alkon and Saltz 1988). There are multiple factors affecting an animal's activity patterns. Among these factors, moonlight may play an important role in many nocturnal animals' lives. Physiological and evolutionary adaptations are numerous and complex for most species. It is crucial for ethologists, conservationists, and wildlife managers to learn as much as possible about how an animal acquires and processes information. This type of knowledge could affect conservation strategies and reintroduction plans for many species, including black-footed ferrets.

Spatial Learning

When data were pooled relative to moonlight level, black-footed ferrets and Siberian ferrets decreased their distance traveled in consecutive trials. They typically stayed close to the walls of the arena, behaviour known as thigmotaxy. The animals appeared to become "bored" with the trials quickly and would, therefore, not perform the task of locating the goal. There was a linear decrease in distance traveled from Trial 1 to Trial 10 and an effect of trial sequence for both species. The relationship of distance traveled was exponential for both species and followed a similar fluctuation pattern. Black-footed ferrets appeared to learn the goal location after Trial 1, while Siberian

ferrets continued to decrease distance traveled until Trial 5. It is possible that black-footed ferrets are faster learners than Siberian ferrets. However, both species traveled shorter distances in the last trials as compared to the first trials, indicating that they learned the goal location. Moonlight did not appear to enhance or detract from their spatial learning abilities. Conducting more research with larger sample sizes may reveal a more accurate representation of the spatial learning abilities of these species and if moonlight affects these skills. Ultimately, it would be best to test ferrets in the laboratory more extensively as well as in their native environments on the prairies of North America or the steppes of Asia.

In spatial learning studies conducted with polygynous voles (*Microtus* spp.), sexually dimorphic differences existed during the breeding season (Gaulin and Fitzgerald 1989). However, there were no sexually dimorphic differences in spatial learning among polygynous vole species in the non-breeding season (Gaulin and Fitzgerald 1989). These findings suggest that the male vole's need for navigation and mobility during the breeding season necessitates greater spatial learning skills, whereas females do not require the same skills due to their more sedentary role in breeding (Gaulin and Fitzgerald 1989). Similar results were found in a study with deer mice (Galea et al. 1994). Black-footed ferrets and Siberian ferrets are polygynous species and may exhibit sexual dimorphism in spatial learning skills. For example, if male ferrets have a need for increased spatial acuity during the breeding season, then it may be pertinent to examine how rearing environment affects their ability to retain skills necessary to survive within their environments.

The hippocampus region of the brain may play an important role in spatial learning and memory storage (Lee et al. 1998). The hippocampus can change size (based on need) in certain animal species that use spatial learning skills for navigational or food storage purposes (Burnea and Nottebohm 1994; Altman and Das 1964). Cage environment and experience could affect the size of the hippocampus and the spatial learning capacity of ferrets. Ultimately, the rearing environments may affect whether or not ferrets retain spatial learning abilities and use them when released into the wild.

In spatial learning studies with rats (Lavenex and Schenk 1998) and corn snakes (Holtzman et al. 1999), the animals decreased distance traveled and moved in more direct routes as trials proceeded. This appears to be true in trials with ferrets as well. However, black-footed ferrets and Siberian ferrets seemed to learn the goal location very quickly relative to other species. Ferrets exhibited typical exploratory behaviours in the novel environment during the first trial and then located the goal by traveling a more direct route in the second trial. Corn snakes developed much more direct routes in successive trials as well, and may have used exterior spatial cues as landmarks for locating the goal within the test arena (Holtzman et al. 1999). Rats appeared to use olfactory cues in the absence of visual cues, and moonlight did affect their ability to locate the goal (Lavenex and Schenk 1998). Ferrets may also utilize olfactory cues to aid in their memory and navigation within their respective environments. But as stated previously, moonlight level alone appeared to have no effect on the ability of black-footed ferrets to locate the goal.

In a similar study conducted with Siberian ferrets (the dataset used in this experiment), using non-parametric statistics and a non-randomized sampling schedule,

results suggested that moonlight level affected the ability of the ferrets to locate the goal (Sheffer 2001). Siberian ferrets also demonstrated thigmotaxy, but were unable to locate the goal in new moonlight or darkness. Distance traveled did not decrease in these dim light levels, but appeared random (Sheffer 2001). Interspecific variation among ferrets may be due to the environments to which each species is native. Although their habitats are similar, black-footed ferrets appear to be more nocturnal and are obligatory predators of diurnal prairie dogs. Siberian ferrets have fluctuating food sources that vary seasonally, which means they may be more active during daylight hours (less nocturnal) depending on the season, prey availability, and geographic location (Clark 1989; Kydyrbaev 1988; Serebrennikov 1929; Volchanetskii 1935). This seasonal variation could potentially lead to more plasticity in Siberian ferret behaviours. However, due to the differences in statistical sampling, only speculative, non-conclusive statements can be made. In order to compare the species, a post-hoc analysis was conducted.

A post-hoc investigation suggested high individual variation in both black-footed ferrets and Siberian ferrets (Figures 13 and 14). However, black-footed ferrets have undergone at least one genetic bottleneck and the gene pool of extant animals is much less diverse than Siberian ferrets (Wisely et al. 2002). Lower genetic diversity in black-footed ferrets could be lead to greater consistency of behaviours among individuals relative to Siberian ferrets. This comparison could be studied more in the future. These findings contradict assumptions made by Owen et al. (2000) regarding the adaptive abilities of black-footed ferrets. Although both species appear to be quite individualistic, some tests indicate that black-footed ferrets are more "hard-wired" and less plastic than their Siberian counterpart (Biggins 2000). They are dependent upon prairie dog towns

for their primary food source (Meffe and Carroll 1997) and living quarters and would likely perish in any other environment. Black-footed ferret dependence on a specific prey source may also affect their behaviour. Historically, Siberian ferrets evolved in their native Asian environment with plague (caused by *Yersinia pestis*), which may have caused large fluctuations in the rodent populations that are prey for ferrets (Biggins 2000). These fluctuations in prey availability could have led to more plasticity in behaviours of Siberian ferrets in response to varying food sources, and could feasibly affect their activity patterns.

Future studies could involve a comparison of eye anatomy and physiology between black-footed ferrets and Siberian ferrets to discern their physical abilities to navigate in a dark environment (Dean Biggins, pers. comm.). Genetic comparisons relative to behaviour could also be pursued between black-footed ferrets, Siberian ferrets, and other closely associated species. Spatial learning abilities of both species could be examined further to determine how cage rearing affects spatial learning skills of ferrets through time. If this is a skill that can be lost or fail to develop without appropriate stimuli, then modifications in captive breeding facilities may be necessary. Examination of the hippocampus in ferrets could reveal temporary or permanent changes and provide insight into the importance of various brain structures in learning. There are many more avenues of investigation to pursue with black-footed ferrets and Siberian ferrets, but larger sample sizes and appropriate sampling methodology is crucial for determining behaviour patterns and trends among such diverse and individualistic animals.

Incorporating animal behaviour research into genetic and demographic studies could be beneficial when implementing restoration plans for threatened or endangered species. Understanding the complexities of individual species could help biologists to design appropriate captive breeding facilities, species survival plans, and conservation programs. Animal behaviour studies could aid in the preservation of many species, especially for captive reared animals that will be released into the wild.

CHAPTER VI

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APPENDIX A

Table 3. Statistical mean and median distance traveled (m) in 15 consecutive trials by black-footed ferrets (BFF, N=8) and Siberian ferrets (SF, N=6).

Table 3. Statistical mean and median distance traveled (m) in 15 consecutive trials by black-footed ferrets (BFF, N=8) and Siberian ferrets (SF, N=6).

Trial #	BFF mean distance (m)	BFF median distance (m)	SF mean distance (m)	SF median distance (m)
1	27.651	33.224	38.835	37.041
2	7.807	9.739	18.285	17.286
3	14.129	13.653	15.933	23.988
4	10.556	9.639	8.467	9.701
5	20.326	13.719	10.848	6.350
6	5.368	3.922	18.021	12.347
7	7.585	3.897	23.077	14.111
8	4.759	4.761	13.758	9.172
9	6.665	4.571	11.524	13.053
10	5.175	4.521	11.083	9.348
11	8.640	4.936	15.139	10.417
12	8.757	8.609	10.833	11.528
13	4.782	4.221	21.088	15.972
14	4.949	2.884	13.912	7.361
15	6.517	6.415	12.731	8.333

APPENDIX B

Table 4. Ferret numbers and names from Figures 13 and 14 (page 36).

Table 4. Ferret numbers and names from Figures 13 and 14 (page 36).

Ferret #	Black-footed ferrets	Siberian ferrets
1	Chaka	Alberto
2	Fred	Kramer
3	Gloop	Odin
4	Jim	Pluto
5	Moses	Ricardo
6	Parsley	Yukon
7	Tashi	n/a
8	Wally	n/a