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EFFECTS OF SUPPLEMENTAL FEEDING ON SURVIVORSHIP, REPRODUCTION, AND DISPERSAL IN SAN JOAQUIN KIT FOXES

February 1993

This report is unclassified:

Authorized Derivative Classifier

Work performed for the U. S. Departments of Energy,
Naval Petroleum Reserves in California, and Chevron U.S.A. through the
Nevada Field Office under DOE Contract No. DE-AC08-93NV11265

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ABSTRACT

Previous field studies at the Naval Petroleum Reserves in California indicated that a decline in the population size of the endangered San Joaquin kit fox (*Vulpes velox macrotis*) might be linked to declining prey abundance. To evaluate whether kit fox populations are limited by food resources; survival probabilities, sources of mortality, reproductive success, and dispersal rates were compared between foxes with access to supplemental food and foxes without access to supplemental food (controls). Of foxes born in 1988, the probabilities of supplementally fed foxes surviving to age one and age two were higher than corresponding probabilities of control foxes. Survival probabilities of fed foxes from the 1988 cohort also were higher than the average survival probabilities of foxes born in the previous eight years. Most foxes (73%) that died during their first year of life died in June, July, or August. Monthly probabilities of survival were higher for fed pups than control pups during the months of July and August of 1988. Survival probabilities of fed foxes originally captured as adults and fed foxes born in 1989 were not significantly different than survival probabilities of corresponding control groups. Most foxes (95%) for which a cause of death could be determined were killed by predators. The proportion of deaths attributable to predators did not differ between control and fed groups. Five of six (83%) adult females and four of eight (50%) yearling females from the supplementally fed groups whelped. In contrast, three of five (60%) control adult females and one of four (25%) control yearlings whelped. The proportion of male foxes from both cohorts that dispersed during their first year was higher for control foxes (0.63) than fed foxes (0.14). Average dispersal distances were not significantly different between fed and control groups but the two longest dispersal distances were made by control foxes. The average distance foxes died from their first known pupping dens was greater for control pups than fed pups of 1988 but did not differ between control and fed pups of 1989. These results indicate that food availability affects survival, reproduction, and dispersal by kit foxes and provides evidence that kit fox populations may at times be limited by food abundance.

ACKNOWLEDGEMENTS

The following staff from EG&G Energy Measurements, Inc. (EG&G/EM) collected or summarized data for this report: C. Bennett, B. Berry, L. Briden, L. Cain, K. Charlton, J. Dodge, N. Frost, K. Hammer, S. Hunt, O. Jones, M. Otten, W. Philpott, J. Scrivner, K. Spencer, R. Stafford, R. Stanfield, S. Tabor, G. Warrick, S. Woodward, and B. Zoellick.

G. Warrick and J. Scrivner designed the study, analyzed the data and wrote the report. T. O'Farrell helped design the study and reviewed the final report. B. Cypher, T. Kato, and W. Standley also reviewed the report and provided editorial comments.

Permission to trap, handle, and radiocollar San Joaquin kit foxes was granted by the U. S. Fish and Wildlife Service through permit PRT-683011 and a Memorandum of Understanding between the California Department of Fish and Game and EG&G/EM.

CONTENTS

<u>Section</u>	<u>Title</u>	<u>Page</u>
	ABSTRACT	i
	ACKNOWLEDGEMENTS	ii
1.	INTRODUCTION	1
2.	STUDY AREA	2
3.	METHODS	4
4.	RESULTS	7
4.1	SURVIVORSHIP	9
	4.1.1 Survivorship Curves	9
	4.1.2 Survival Probabilities	9
4.2	SOURCES OF MORTALITY	15
4.3	REPRODUCTIVE SUCCESS	17
4.4	DISPERSAL	17
4.5	INDICES OF MOVEMENT	19
4.6	ABUNDANCE OF KIT FOX PREY AND PREDATORS	19
5.	DISCUSSION	21
6.	LITERATURE CITED	24

TABLES

<u>Table</u>	<u>Title</u>	<u>Page</u>
1.	Survival probabilities ($\pm$ 95% confidence intervals) of kit foxes radiocollared as pups on the Naval Petroleum Reserves in California, 1980-1989.	12
2.	Monthly survival probabilities ($\pm$ 95% confidence intervals) and number of deaths per month during the first year of life of foxes born in 1988 on the Naval Petroleum Reserves in California.	13
3.	Monthly survival probabilities ($\pm$ 95% confidence intervals) and number of deaths per month during the first year of life of foxes born in 1989 on the Naval Petroleum Reserves in California.	14
4.	Survival probabilities ($\pm$ 95% confidence intervals) of breeding adult kit foxes on the Naval Petroleum Reserves in California, 1980-1988.	15
5.	Cause of death of kit foxes on the Naval Petroleum Reserves in California, 1988-1990.	16
6.	Proportion of female kit foxes that had pups on the Naval Petroleum Reserves in California, 1989-1990.	17
7.	Dispersal of kit foxes originally radiocollared as pups in 1988 and 1989 on the Naval Petroleum Reserves in California.	18

FIGURES

<u>Figure</u>	<u>Title</u>	<u>Page</u>
1.	Location of U.S. Department of Energy's Naval Petroleum Reserves, Kern County, California.	3
2.	Location of kit fox family groups that were supplementally fed (□) or designated as control groups (●) on the Naval Petroleum Reserves in California.	8
3.	Survivorship curves of supplementally fed and control foxes originally radiocollared as pups in 1988 and 1989 on the Naval Petroleum Reserves in California.	10
4.	Survivorship curves of supplementally fed and control foxes originally radiocollared as adults in 1988 on the Naval Petroleum Reserves in California.	11
5.	Dispersal by two control female foxes (#3934, #3936) from the 1989 cohort, Naval Petroleum Reserves in California.	20

1. INTRODUCTION

Populations of foxes (Englund, 1980; Lindstrom, 1989) and other canids (Clark, 1972; Todd et al., 1981; Messier, 1985a) are often influenced by the abundance of their primary prey. On Naval Petroleum Reserve No. 1 (NPR-1), lagomorphs are the primary prey (Scrivner et al., 1987a) of the endangered San Joaquin kit fox (*Vulpes velox macrotis*, formerly *Vulpes macrotis mutica*; Dragoo et al., 1990). On NPR-1, the kit fox population declined between 1981 and 1985 (Harris et al., 1987) concurrent with a decline in lagomorph numbers (Harris, 1986).

The simultaneous decline in the abundance of lagomorphs and kit foxes suggests a causal relationship but the interaction was complicated by an increase in coyote (*Canis latrans*) abundance during the same period. During a biological survey of NPR-1 in 1979, eight observations of coyotes were recorded (O'Farrell, 1980); while during a similar survey in 1984, 108 observations of coyotes were noted (O'Farrell and Mathews, 1987). Coyotes are the most frequent source of kit fox mortality on NPR-1 and the proportion of deaths of adult kit foxes due to predators increased between 1980 and 1986 (Berry et al., 1987). Because the changes in fox numbers, prey base, and coyote abundance occurred at about the same time, the role of food supplies in this relationship was uncertain.

Although food resources undoubtedly limit wildlife populations at some level, predation, disease, or territoriality may prevent a population from reaching a level where food becomes limiting. The question of whether food limits a population can be investigated by artificially manipulating the food supply and monitoring population responses. A large number of studies have assessed food limitation by providing food additions to a variety of terrestrial vertebrates (Boutin, 1989) but few of these studies have involved mammalian carnivores.

To investigate whether food is a limiting resource for kit foxes, foxes were supplementally fed and responses in population parameters were compared between fed foxes and foxes that were not provided additional food (controls). Specific objectives were to compare survival probabilities, sources of mortality, reproductive success, and dispersal rates between supplementally fed and control foxes.

2. STUDY AREA

The study was conducted on and adjacent to the U. S. Department of Energy's Naval Petroleum Reserves in California (NPRC). NPRC (Figure 1) consists of 77,325 acres and includes two petroleum reserves: NPR-1 and Naval Petroleum Reserve No. 2. These reserves encompass the moderately steep slopes of Elk Hills and Buena Vista Hills and some of the surrounding flat terrain. Elevations range from 290 to 1,551 feet above sea level.

Annual weather patterns consist of hot, dry summers and mild, humid winters (National Oceanic and Atmospheric Administration, 1989). Weather data recorded 26 miles east of NPRC in Bakersfield, California indicate that average daily maximum temperatures range from 99° F in July to 57° F in January and average daily minimum temperatures range from 39° F in December to 70° F in July. Most precipitation (90%) falls from October through April. Precipitation at NPR-1 averages 4.9 inches annually (EG&G Energy Measurements, Inc., 1993).

NPRC lies within the Valley Grassland vegetation type (Heady, 1977). The herbaceous vegetation is dominated by red brome (*Bromus rubens*) and red-stemmed filaree (*Erodium cicutarium*). Other grasses and forbs that are locally abundant include Arabian grass (*Schismus arabicus*), foxtail fescue (*Festuca megalura*), slender wild oats (*Avena barbata*), fiddleneck (*Amsinckia intermedia*), pepperweed (*Lepidium dictyotum*), crassula (*Crassula erecta*), and plantain (*Plantago insularis*). The most common shrub species is desert saltbush (*Atriplex polycarpa*) but other locally common species include spiny saltbush (*Atriplex spinifera*), bladderpod (*Isomeris arborea*), cheesebush (*Hymenoclea salsola*), and snakeweed (*Gutierrezia bracteata*).

The major land uses at NPRC are facility development and operational activities related to oil and gas production. Drilling and petroleum production began in the early 1900's. The Naval Petroleum Reserves Production Act of 1976 directed the Department of Energy to develop and produce petroleum resources at the maximum efficient rate consistent with sound engineering practices. Since then, oil field development on NPR-1 increased substantially. O'Farrell et al. (1986) and O'Farrell and Sauls (1987) provide a more thorough description of oil field activities and the natural environment at NPRC.

Figure 1. Location of U.S. Department of Energy's Naval Petroleum Reserves, Kern County, California.

3. METHODS

In spring of 1988 and 1989, fox family groups were located by searching from an airplane for trampled vegetation and sign of digging activity common near pupping dens. Dens were observed at dusk to confirm the presence of pups. Wire mesh live-traps were placed at dens and captured adult and juvenile foxes were eartagged, measured, and radiocollared (O'Farrell, 1987). Each radiocollar (Telonics, Mesa, AZ) contained a motion (mortality) sensor and weighed less than five percent of the fox's body weight.

Family groups of foxes were designated as either fed or control. Fed groups were chosen so they were at least one mile from the nearest control group to reduce the likelihood that control foxes had access to supplemental food. Fed groups were provided supplemental food *ad libitum* but no additional food was provided to control groups. A four-foot length of six-inch diameter polyvinylchloride pipe was set within ten yards of each den inhabited by a fed group of foxes. Dry and canned cat food was placed in the pipes three times per week. When the pups began using separate dens, three stationary feeder pipes were placed within the known denning ranges of each fed family group. At this time, feeder pipes were raised 18 inches off the ground to discourage other animal species from eating the cat food. Foxes were fed *ad libitum* for eleven months and then were provided a reduced amount of food for one month. A 35 mm camera activated by an infra-red beam was used to photograph animals using the pipes at night and automatic telemetry monitors were placed at pipes to record visits by radiocollared foxes. Also, observations of animals using the pipes were recorded when food was placed in the pipes.

Survival was monitored using radio telemetry equipment while driving or walking through areas occupied by radiocollared foxes a minimum of three times per week. An airplane equipped with wing mounted antennas was used to search for radiocollared foxes that could not be located from the ground. When a radiocollar was heard transmitting a mortality signal, the signal was tracked to its source and if the fox was dead, it was recovered for necropsy. Transmitter signals also were tracked to their source, a minimum of once per week, and these locations were plotted on topographic maps. When only a radiocollar was recovered, the location of death was assumed to be where the radiocollar was found. A fox's date of death was estimated to be the midpoint between the date the last "normal" (non-mortality) radio signal was received and the date when the carcass or radiocollar was recovered. Fox survival was monitored while foxes were provided supplemental food and monitoring continued for one year after feeding was discontinued.

The percentage of radiocollared foxes surviving to the end of each month was determined and these values were used to produce survivorship curves. Survivorship curves were developed for fed and control foxes from the 1988 and 1989 cohorts of pups and the adult foxes of 1988. Too few adult foxes were radiocollared in 1989 to provide a meaningful survivorship curve for this group.

The computer program MICROMORT (Heisey and Fuller, 1985) was used to calculate survival probabilities. The number of transmitter days (days radiocollared foxes were known to be alive) and the number of mortalities within a given time interval were entered into MICROMORT to estimate survival probabilities. For foxes that died during capture attempts or whose radio-signals stopped being detected before the study ended, the number of transmitter days were entered into MICROMORT but no mortality data were included.

Probabilities of survival were compared between fed and control foxes from the 1988 and 1989 groups. Survival probabilities also were calculated for foxes radiocollared during previous field studies (1980-1987) to provide other points of comparison with fed foxes. Consistent interval lengths were used when comparing survival probabilities of foxes radiocollared as pups in different years. The day supplemental feeding was initiated in 1989 (14 June) was chosen as the start of the interval and an approximation of the birth date of foxes (15 February; Zoellick et al., 1987a) was used as the end of an interval. Therefore, the probabilities of surviving to age one and age two were based on interval lengths of 246 and 611 days, respectively. To insure that pups included in the analyses were radiocollared at a similar stage in life, no pups originally radiocollared after July were included in the analyses. The probabilities that foxes originally collared as breeding adults would survive for one and two years also were calculated. Foxes were designated as breeding adults if they were captured with pups or were known to den with pups during April and May.

During necropsies, cause of death was determined based on observed injuries and abnormalities. If the fox had contusions associated with lethal injuries caused by tooth punctures, predators were considered the cause of death. Vehicle impact was considered the cause of death when foxes were found on or adjacent to a road and had evidence of massive trauma. If the cause of death could not be determined because the carcass was badly decomposed or scavenged, cause of death was classified as unknown.

To evaluate reproductive success, live-traps were placed near dens inhabited by adult and yearling female foxes in April and May. If pups were captured, or if the target female showed signs of lactation, it was assumed she had given birth that year.

Foxes were considered to have dispersed when their first and last locations were more than an average home range diameter (1.5 miles) apart (following Lindstrom, 1989; Woollard and Harris, 1990). Home ranges of kit foxes on NPRC average 1.78 square miles in size (Zoellick et al., 1987b). Therefore, assuming a circular home range, the average diameter of a home range would be 1.5 miles. During analyses of dispersal, the first pupping den a fox was captured at was considered the fox's first location and the last location was either a death site or the last radio location before the study ended.

For fox pups that died during April - August, the distances pups died from their original capture locations were determined and used as indices of movement. The maximum distance between dens that fox pups used during April - August also was used as

an index of movement. The period was limited to August because this encompasses the period of greatest mortality of kit fox pups and few pups were expected to live past this period.

In areas inhabited by 1989 family groups, the relative abundance of kit fox prey and coyotes near each control and experimental group was assessed. A line of ten scent stations (0.3 miles apart) was placed so that it passed through the denning range of each group of foxes. Scent stations were checked the following morning for tracks of coyotes and lagomorphs and the average number of visits per line were tallied and compared between fed and control groups. Although scent stations are commonly used as indices of carnivore abundance, they also have been used to index rabbit populations (Drew et al., 1988). Lagomorph abundance also was assessed while walking two one-mile long transects within the denning range of each family group of foxes. Rodent abundance was assessed by operating 15 small mammal traps for three consecutive nights at the center of each fox group's denning range. The average number of rodents captured during the session was compared between areas inhabited by fed and control groups.

Mass data collected between 22 April and 31 July 1988 were log transformed to correct for curvilinearity and then were regressed against the number of days since birth (assuming a 15 February birth date). Weights of individual foxes were not included in the analyses, if they were collected less than seven days apart. The slopes of the regression lines were compared using a Students t-test (Zar, 1984), to determine whether the rate of growth of fed and control foxes differed. Too few weights were obtained from fox pups in 1989 to be included in the analyses.

A Z-test was used to test for differences in the survival probabilities calculated using MICROMORT (Heisey and Fuller, 1985). Proportions of foxes dispersing were compared using a chi-square (χ^2) test. A chi-square test also was used to determine if the proportions of foxes killed by predators differed between fed and control groups. A Mann-Whitney U test was used to test for differences in dispersal distances. The average distances that fed and control pups died from their original pupping dens were compared using a Mann-Whitney U test. A Mann-Whitney U test also was used to determine if there were differences in predator and prey abundance in areas occupied by control and fed groups of 1989. Differences were considered statistically significant when $P < 0.05$.

4. RESULTS

In 1988, 54 foxes from 11 family groups were radiocollared (Figure 2). Between 22 April 1988 and 24 May 1989, supplemental food was provided to five family groups that included 19 pups (9 males, 10 females) and nine adults (3 males, 6 females). Supplemental food was not provided to six family groups that included 18 pups (5 males, 13 females) and eight adults (5 males, 3 females). To increase sample size, three adult female foxes were added to the control group to evaluate reproductive success in spring 1989.

In 1989, 25 foxes from six family groups were radiocollared (Figure 2). Between 14 June 1989 and 23 May 1990 supplemental food was provided to three family groups that included 10 pups (6 males, 4 females) and four adults (2 males, 2 females). Supplemental food was not provided to three family groups that included 10 pups (3 males, 7 females) and one adult female. Not all members of the family groups from 1988 or 1989 were captured and radiocollared.

Cameras were set out for six nights and photographs of foxes using the pipes were obtained during four nights. Also, photographs of a badger (*Taxidea taxus*) using a feeder pipe were obtained one night. Automatic telemetry monitors were used to record fox visits to pipes during 10 of 21 nights. Although primarily nocturnal, kit foxes were observed on 13 occasions eating from the pipes during the day. Nelson's antelope ground squirrels (*Ammospermophilus nelsoni*) and ravens (*Corvus corax*) were observed eating from the feeder pipes on 26 and 7 occasions, respectively.

There was a significant correlation between the log of fox mass (variable y) and the number of days since birth (variable x) for fed male pups ($y = 0.68 + 0.006x$, $r^2 = 0.79$, $df = 22$, $P < 0.01$), fed female pups ($y = 0.70 + 0.005x$, $r^2 = 0.59$, $df = 18$, $P < 0.01$), and control female pups ($y = 0.74 + 0.004x$, $r^2 = 0.58$, $df = 24$, $P < 0.01$). The correlation between fox mass and days since birth approached statistical significance for male control pups ($y = 0.94 + 0.003x$, $r^2 = 0.29$, $df = 10$, $P = 0.09$). Rate of weight gain was significantly greater for fed male pups than control male pups ($t = 2.28$, $df = 30$, $P = 0.03$). However, rate of weight gain did not differ between fed and control female pups ($t = 0.39$, $df = 40$, $P > 0.50$).

Figure 2. Location of kit fox family groups that were supplementally fed (□) or designated as control groups (●) on the Naval Petroleum Reserves in California.

4.1 SURVIVORSHIP

4.1.1 Survivorship Curves

Foxes originally radiocollared as pups in 1988 and provided supplemental food had consistently higher survivorship than control pups (Figure 3). By the time the foxes were one year old in February 1989, 50% of the fed foxes were alive versus 6% of the control foxes. Between August 1988 and May 1989, the survivorship of fed foxes was more than 40% higher than control foxes. By the end of May 1990, 12% of the provisioned foxes were alive versus 6% of the control foxes.

Foxes originally radiocollared as pups in 1989, and provided food, had similar survivorship as control foxes until after July 1990 (Figure 3). By May 1991, 33% of the fed foxes were alive but all control foxes had died.

The survivorship of foxes originally collared as adults in 1988 was consistently higher for supplementally fed foxes (Figure 4). The greatest difference in survivorship between the fed and control groups occurred at the end of May 1989, when 62% of the fed adults and 25% of the control adults were alive. By May 1990, 33% of the fed adults and 25% of the control adults were alive.

Five adult foxes were captured in 1989 and all died before the end of the study. The control adult died in June 1990, and the four fed foxes died in June 1989, and March, June, and July 1990.

4.1.2 Survival Probabilities

The probability that fox pups of 1988 would survive to age one was significantly higher ($Z = 4.38$, $P < 0.01$) for fed foxes than for control foxes (Table 1). Similarly, the probability that fox pups of 1988 would survive to age two was significantly higher ($Z = 2.64$, $P = 0.01$) for fed foxes than for control foxes.

In 1989, the probability of surviving to age one was not significantly different ($Z = 0.31$, $P = 0.76$) between fed and control foxes (Table 1). The probability of surviving to age two also was not significantly different ($Z = 1.31$, $P = 0.19$) between fed and control foxes.

Figure 3. Survivorship curves of supplementally fed and control foxes originally radiocollared as pups in 1988 and 1989 on the Naval Petroleum Reserves in California.

Figure 4. Survivorship curves of supplementally fed and control foxes originally radiocollared as adults in 1988 on the Naval Petroleum Reserves in California.

Table 1. Survival probabilities ($\pm$ 95% confidence intervals) of kit foxes radiocollared as pups on the Naval Petroleum Reserves in California, 1980-1989.

Year	N	Probability of Surviving	
		To Age 1*	To Age 2**
1980	23	0.28 (0.14 - 0.56)	0.10 (0.03 - 0.34)
1981	15	0.26 (0.08 - 0.52)	0.02 (0.00 - 0.16)
1982	22	0.26 (0.13 - 0.50)	0.06 (0.02 - 0.23)
1983	29	0.09 (0.03 - 0.22)	0.01 (0.00 - 0.04)
1984	18	0.01 (0.00 - 0.11)	<0.01 (0.00 - 0.01)
1985	8	0.05 (0.00 - 0.54)	0.02 (0.00 - 0.46)
1986	7	0.36 (0.13 - 0.98)	0.07 (0.01 - 0.58)
1987	8	<0.01 (0.00 - 0.04)	<0.01 (0.00 - 0.00)
1988 (Fed)	19	0.56 (0.37 - 0.86)	0.28 (0.14 - 0.60)
1988 (Control)	18	0.02 (0.00 - 0.15)	<0.01 (0.00 - 0.03)
1989 (Fed)	10	0.40 (0.18 - 0.89)	0.23 (0.07 - 0.74)
1989 (Control)	10	0.33 (0.14 - 0.80)	0.04 (0.01 - 0.30)

* (14 June, year X) - (15 February, year X+1)

** (14 June, year X) - (15 February, year X+2)

Probabilities of surviving to age one for the 1980-1987 cohorts ranged from < 0.01 in 1987 to 0.36 in 1986. The average survival probability to age one for the 1980-1987 cohorts ($\bar{x}$ = 0.16, SE = 0.05) was significantly less than the probability for fed pups of 1988 (Z = 3.23, P < 0.01) but was not significantly different than the probability for fed pups of 1989 (Z = 1.46, P = 0.14; Table 1). Likewise, the average probability of surviving to age two for the 1980-1987 cohorts ($\bar{x}$ = 0.04, SE = 0.01) was significantly less than the survival probability for the fed pups of 1988 (Z = 2.31, P = 0.02), but was not different than the probability for fed pups of 1989 (Z = 1.39, P = 0.17).

Control foxes of 1989 had significantly higher first year survival than the control foxes of 1988 ($Z = 2.09$, $P = 0.04$). The first year survival probabilities of fed foxes from 1988 and 1989 were not significantly different ($Z = 0.80$, $P = 0.42$).

Monthly survival probabilities for 1988 fed foxes ranged from 0.83 to 1.00 during their first year of life (Table 2). Most deaths occurred in June, when the probability of surviving was lowest. Monthly survival probabilities for control foxes ranged from 0.43 to 1.00. Most deaths, and the lowest survival probability for control foxes, occurred during July. Survival probabilities were significantly different between fed and control groups in July ($Z = 3.42$, $P < 0.01$). All other monthly comparisons were not significantly different, although comparisons of survival between fed and control groups in August approached statistical significance ($Z = 1.93$, $P = 0.05$). Many of the monthly survival probabilities were not statistically compared because there is no estimate of variance with probabilities of 1.00.

Table 2. Monthly survival probabilities ($\pm$ 95% confidence intervals) and number of deaths per month during the first year of life of foxes born in 1988 on the Naval Petroleum Reserves in California.

Month	Fed			Control		
	N	No. Deaths	Survival Probabilities	N	No. Deaths	Survival Probabilities
Apr/May	15	0	1.00	11	1	0.81 (0.53 - 1.00)
Jun	18	3	0.83 (0.67 - 1.00)	15	3	0.80 (0.63 - 1.00)
Jul	15	1	0.93 (0.80 - 1.00)	14	8	0.43 (0.24 - 0.77)
Aug	14	1	0.93 (0.80 - 1.00)	6	3	0.53 (0.25 - 1.00)
Sep	13	0	1.00	3	1	0.64 (0.27 - 1.00)
Oct	13	2	0.85 (0.68 - 1.00)	2	0	1.00
Nov	11	0	1.00	2	0	1.00
Dec	11	0	1.00	2	1	0.55 (0.17 - 1.00)
Jan	11	1	0.91 (0.76 - 1.00)	1	0	1.00
Feb	10	1	0.90 (0.73 - 1.00)	1	0	1.00

Monthly survival probabilities were not significantly different between fed and control foxes from the 1989 cohort. The lowest survival probabilities and the most deaths of fed foxes occurred in June and December (Table 3). The lowest survival probabilities and most deaths of control foxes occurred during July and August.

Table 3. Monthly survival probabilities ($\pm$ 95% confidence intervals) and number of deaths per month during the first year of life of foxes born in 1989 on the Naval Petroleum Reserves in California.

Month	Fed			Control		
	N	No. Deaths	Survival Probabilities	N	No. Deaths	Survival Probabilities
Jun	10	2	0.63 (0.33 - 1.00)	10	0	1.00
Jul	7	0	1.00	10	2	0.80 (0.58 - 1.00)
Aug	7	1	0.86 (0.64 - 1.00)	8	3	0.62 (0.35 - 1.00)
Sep	6	0	1.00	5	0	1.00
Oct	6	0	1.00	5	0	1.00
Nov	6	0	1.00	5	0	1.00
Dec	6	2	0.66 (0.37 - 1.00)	5	1	0.82 (0.55 - 1.00)
Jan	4	0	1.00	4	0	1.00
Feb	4	0	1.00	4	0	1.00

Most foxes (73%) that died during their first year died in June, July, or August (Tables 2 and 3); 83% of the first year mortalities of control foxes and 57% of the first year mortalities of fed foxes occurred during these months.

The one year survival probabilities for adult foxes in 1988 were not significantly different ($Z = 1.34$, $P = 0.18$) between fed and control foxes (Table 4). The two year survival probabilities for adult foxes also were not significantly different ($Z = 1.43$, $P = 0.15$) between fed and control groups.

Table 4. Survival probabilities ($\pm$ 95% confidence intervals) of breeding adult kit foxes on the Naval Petroleum Reserves in California, 1980-1988.

Year	N	Survival Probabilities	
		12 Months *	24 Months **
1980	15	1.00	0.74 (0.55 - 0.99)
1981	10	0.89 (0.72 - 1.00)	0.77 (0.54 - 1.00)
1982	22	0.47 (0.30 - 0.73)	0.25 (0.12 - 0.50)
1983	21	0.23 (0.11 - 0.48)	0.05 (0.02 - 0.20)
1984	20	0.28 (0.14 - 0.54)	0.09 (0.03 - 0.28)
1985	14	0.43 (0.23 - 0.80)	0.12 (0.03 - 0.48)
1986	7	0.22 (0.06 - 0.83)	0.06 (0.01 - 0.57)
1987	11	0.18 (0.06 - 0.56)	0.05 (0.01 - 0.32)
1988 (Fed)	9	0.64 (0.39 - 1.00)	0.45 (0.22 - 0.91)
1988 (Control)	8	0.33 (0.12 - 0.87)	0.16 (0.04 - 0.70)

* (22 April year X) - (22 April year X + 1)

** (22 April year X) - (22 April year X + 2)

The average probability that breeding adult foxes of 1980-1987 survived one year ($\bar{x}$ = 0.46, SE = 0.11) was not significantly different (Z = 1.05, P = 0.29) than the one year survival probability of fed adults of 1988. Similarly, the average two year survival probability of adult foxes from 1980-1987 ($\bar{x}$ = 0.27, SE = 0.11) was not significantly different (Z = 1.11, P = 0.27) than the two year survival probability of fed adults of 1988. Survival probabilities for 1989 adults were not calculated because of the small sample size (one control fox and four fed foxes).

4.2 SOURCES OF MORTALITY

Of 63 foxes recovered dead, predators killed 35 (56%), one (1.5%) died after being struck by a vehicle, one (1.5%) died after being buried in a landfill, and 26 (41%) were too scavenged or desiccated to determine cause of death (Table 5). In addition, dogs killed one fox while it was in a trap and one fox died during an attempt to capture it in a pipe. These two capture related deaths were not included in the analyses of sources of kit fox mortality.

Table 5. Cause of death of kit foxes on the Naval Petroleum Reserves in California, 1988-1990.

Birth Year	Time Period	Group	N	Cause of Death							
				<u>Predator</u>		<u>Unknown</u>		<u>Vehicle</u>		<u>Buried</u>	
				N	(%)	N	(%)	N	(%)	N	(%)
1988	First Year	Fed	9	4	(44)	5	(56)				
		Control	17	10	(59)	7	(41)				
	Second Year	Fed	5	2	(40)	2	(40)	1	(20)		
		Control	0								
1989	First Year	Fed	5	2	(40)	3	(60)				
		Control	6	3	(50)	3	(50)				
	Second Year	Fed	1	1	(100)						
		Control	4	1	(25)	3	(75)				
Adults	Entire Study	Fed	8	5	(63)	2	(25)			1	(13)
		Control	8	7	(88)	1	(13)				
Total			63	35	(56)	26	(41)	1	(1.5)	1	(1.5)

Most predator caused deaths (30) could not be attributed to a specific species. The spacing of distinct paired puncture marks were measured on five foxes. Paired puncture mark spacings of 0.98 inches (± 0.04 inches) found on four foxes indicated the foxes were probably killed by coyotes. A measurement of 0.67 inches between a pair of punctures on one fox together with evidence that the fox was partially consumed, and then covered with grass indicated the fox was probably killed by a bobcat (*Felis rufus*).

The fox that was buried in a landfill was sent to a veterinary diagnostic laboratory for necropsy. The laboratory reported that the fox showed signs of acute aspiration, indicating the fox probably suffocated.

The proportion of fox deaths due to predators did not differ between fed and control groups from the 1988 cohort ($\chi^2 = 0.49$, $df = 1$, $P = 0.48$) or the 1989 cohort ($\chi^2 = 0.11$, $df = 1$, $P = 0.74$). The proportion of predator inflicted deaths also did not differ between fed and control adult foxes ($\chi^2 = 1.33$, $df = 1$, $P = 0.25$).

4.3 REPRODUCTIVE SUCCESS

Three of six yearling females and five of five adult females that were provided additional food had pups in spring of 1989 (Table 6). Of the control group, the only surviving yearling did not whelp but two of four adults had pups in 1989. In spring 1990, one of two fed yearling females and one of three control yearlings had pups. The fed adult female did not whelp but the control adult had pups. The proportion of fed yearlings from both cohorts that reproduced was twice as high as the proportion of reproducing control yearlings. The proportion of adult females that whelped during the two years also was higher for fed than control groups.

Table 6. Proportion of female kit foxes that had pups on the Naval Petroleum Reserves in California, 1989-1990.

Season/Year	Age	Proportion Reproducing	
		Fed	Control
Spring 1989	Yearling	0.50 (3/6)	0.00 (0/1)
	Adult	1.00 (5/5)	0.50 (2/4)
Spring 1990	Yearling	0.50 (1/2)	0.33 (1/3)
	Adult	0.00 (0/1)	1.00 (1/1)
Combined	Yearling	0.50 (4/8)	0.25 (1/4)
	Adult	0.83 (5/6)	0.60 (3/5)

4.4 DISPERSAL

A total of 14 foxes (9 males, 5 females) radiocollared as pups dispersed during the study. Similar proportions of provisioned foxes and control foxes from the 1988 cohort dispersed (Table 7). In contrast, the proportion of foxes born in 1989 that dispersed was approximately three times higher for control foxes than for foxes that received supplemental food. The proportion of the 1988 and 1989 cohorts dispersing was not significantly different between fed and control groups ($\chi^2 = 1.17$, $df = 1$, $P = 0.28$). However, the proportion of male foxes from both cohorts that dispersed during their first year of life was significantly higher for control foxes (0.63) than fed foxes (0.14) ($\chi^2 = 5.46$, $df = 1$, $P = 0.02$). This chi-

square test should be interpreted with caution however, because 50% of the expected values were less than five. The proportion of foxes from both cohorts that dispersed was significantly higher for males (0.41) than for females (0.16) ($\chi^2 = 4.34$, $df = 1$, $P = 0.04$).

Table 7. Dispersal of kit foxes originally radiocollared as pups in 1988 and 1989 on the Naval Petroleum Reserves in California.

Year	Group	Proportion Dispersing			Average Distance (miles)
		Males	Females	Total	
1988	Fed	0.25 (2/8)	0.11 (1/9)	0.18 (3/17)	2.6
	Control	0.20 (2/5)	0.08 (1/13)	0.17 (3/18)	2.4
1989	Fed	0.33 (2/6)	0.00 (0/3)	0.22 (2/9)	4.1
	Control	1.00 (3/3)	0.43 (3/7)	0.60 (6/10)	5.0

The average distance foxes from the 1988 cohort dispersed was not significantly different ($U = 4$, $n1 = 3$, $n2 = 3$, $P > 0.20$) between fed foxes ($\bar{x} = 2.6$, range = 1.8 - 3.7 miles) and control foxes ($\bar{x} = 2.4$, range = 1.9 - 3.4 miles). Average dispersal distance also was not significantly different ($U = 5$, $n1 = 2$, $n2 = 5$, $P > 0.20$) between fed foxes ($\bar{x} = 4.1$, range = 3.0 - 5.3 miles) and control foxes ($\bar{x} = 5.0$, range = 1.6 - 12.4 miles) from the 1989 cohort.

A total of four foxes (1 male, 3 females) radiocollared as adults dispersed during the study. The proportion of adult foxes from the 1988 and 1989 family groups that dispersed was the same (0.13) for both fed and control groups. Of the 1988 adults, one supplementally fed female dispersed 2.0 miles, and one control female dispersed 1.7 miles. Of the 1989 adults, one fed male dispersed 1.7 miles, and one control female dispersed 1.9 miles.

Two control female foxes of the 1989 cohort dispersed greater than nine miles (Figure 5). One fox (#3936) moved 12.4 miles northwest to the Lokern Road area from her natal range in May 1990. In July 1990, this fox was found dead near Lokern Road. Another fox (#3934) dispersed 9.4 miles in May 1990 from her natal range to an area of the Little Santa Maria Valley approximately three miles west of the town of McKittrick. This fox also died in July 1990. Fox #3934 made an exploratory movement six months before she dispersed. In November 1989, this fox moved from her natal range to an area eight miles

to the northeast, and remained in the new area until she returned to her natal range in February 1990. A fed male fox from the 1989 cohort exhibited a similar movement pattern when he moved approximately five miles in December 1989 and stayed until June 1990, when he returned to the area in which he was born. In December 1990, he dispersed 5.4 miles to the area he first visited in December 1989.

4.5 INDICES OF MOVEMENT

During April - August of 1988, the average distance between the original capture locations of fox pups and the locations where they were recovered dead was significantly shorter for fed foxes ($\bar{x} = 0.4$, range = 0.2 - 0.7 miles) than for control foxes ($\bar{x} = 1.1$, range = 0.3 - 3.4 miles) ($U = 69$, $n_1 = 5$, $n_2 = 15$, $P < 0.01$). During the corresponding period for the 1989 pups, the average distance between capture and death locations was not significantly different between fed foxes ($\bar{x} = 1.1$, range = 0.1 - 3.0 miles) and control foxes ($\bar{x} = 1.3$, range = 0.4 - 2.0 miles) ($U = 9$, $n_1 = 3$, $n_2 = 5$, $P > 0.20$).

During April and August of 1988, the maximum distance between dens was not significantly different between fed ($\bar{x} = 0.7$, range = 0.5 - 1.9 miles) and control foxes ($\bar{x} = 0.8$, range = 0.4 - 2.3 miles) ($U = 217.5$, $n_1 = 19$, $n_2 = 18$, $P = 0.17$). The maximum distance between dens used by the 1989 cohort also was not significantly different between fed ($\bar{x} = 0.3$, range = 0.05 - 0.5 miles) and control foxes ($\bar{x} = 0.3$, range = 0.1 - 0.7 miles) ($U = 13$, $n_1 = 3$, $n_2 = 7$, $P > 0.20$).

4.6 ABUNDANCE OF KIT FOX PREY AND PREDATORS

The abundance of kit fox prey and coyotes within areas occupied by the 1989 groups was assessed in December 1989 and January 1990. There was no significant difference between the number of coyote visits recorded in fed group areas ($\bar{x} = 2.0$, range = 0 - 3) and control group areas ($\bar{x} = 0.3$, range = 0 - 1) ($U = 7$, $n_1 = 3$, $n_2 = 3$, $P > 0.20$); the number of lagomorph visits to scent stations in fed group areas ($\bar{x} = 3.00$, range = 1 - 4) and control group areas ($\bar{x} = 1.3$, range = 1 - 3) ($U = 7.5$, $n_1 = 3$, $n_2 = 3$, $P > 0.20$); the average number of lagomorphs observed during transect surveys in fed group areas ($\bar{x} = 2.0$, range = 0 - 3) and control group areas ($\bar{x} = 2.0$, range = 0 - 3); and the number of rodents captured in fed group areas ($\bar{x} = 2.7$, range = 1 - 5) and control group areas ($\bar{x} = 14.0$, range = 5 - 23) ($U = 8.5$, $n_1 = 3$, $n_2 = 3$, $P = 0.15$).

Figure 5. Dispersal by two control female foxes (#3934, #3936) from the 1989 cohort, Naval Petroleum Reserves in California.

5. DISCUSSION

In general, supplemental feeding appeared to have a positive influence on the survivorship of kit foxes. Of foxes born in 1988, probabilities of surviving to age one and age two were higher for fed foxes than control foxes. Survival probabilities of fed foxes from the 1988 cohort also were higher than the average survival probability of foxes born in the previous eight years. With the exception of some of the monthly survival probabilities, other comparisons of survival between fed and control groups were not statistically significant, but in all cases, the fed groups had higher point estimates of survival than control groups. Point estimates of survival were higher for fed foxes than for foxes collared in previous years in 92% (44/48) of the comparisons. Only adult foxes during a period of high lagomorph abundance (1980 - 1981; Harris, 1986) had higher point estimates of survival than adult fed foxes.

Although in 1988, fed male pups gained weight at a faster rate than control male pups, there was no evidence that control foxes were malnourished or died of starvation. The differential survival of control and fed foxes may instead be related to differences in foraging effort and vulnerability to predators. Because the control foxes presumably had less food available to them, they may have spent more time searching for food than supplementally fed foxes. Greater foraging effort by control foxes may have made them more vulnerable to predators. The high proportion of predator caused deaths and the longer distances between original capture locations and death sites of 1988 control pups supports this possibility. In addition, other field studies have demonstrated that as prey abundance declines, daily travel distances and movements by carnivores outside their territories increase (Mech, 1977; Messier, 1985b; Ward and Krebs, 1985; Knick, 1990) indicating an inverse relationship between food availability and foraging effort.

The reasons the 1989 control pups had higher survivorship than the 1988 control pups were unclear. There was no evidence that prey available to the 1989 cohort was greater than that available to the 1988 cohort. The number of lagomorphs counted on NPRC was lower during the first year of life of the 1989 cohort (676/312 transect miles) than the corresponding period for the 1988 cohort (780/312 transect miles; EG&G Energy Measurements, Inc., 1992b). The number of rodents captured in northeast NPR-1 was similar in summer 1989 (23/100 trap-nights; EG&G Energy Measurements, Inc., 1991) and summer 1988 (21/100 trapnights; EG&G Energy Measurements, Inc., 1989). From 1985-1990, coyotes were killed on NPRC in an attempt to increase the abundance of kit foxes (Cypher and Scrivner, 1992). Although the coyote control program between 1985 and 1988 probably had little positive effect on kit foxes (Cypher and Scrivner, 1992) an expanded coyote control program initiated in 1989 may have reduced this major source of mortality for foxes born in 1989. In 16 months (January 1989 - April 1990), 242 coyotes were killed

at NPRC and 164 coyotes were killed within a 15-mile buffer area surrounding NPRC. However, if the expanded coyote control program caused an increase in the survivorship of 1989 control pups, a similar increase in survival of the 1989 fed pups would have been expected.

Survivorship of fed yearling foxes did not decline noticeably after supplemental feeding was terminated. This was not surprising because survival probabilities of foxes increase after the first year. Floit and Barnthouse (1991) found that survival rates of kit foxes on NPRC from birth to age one and from age one to age two were 0.27 and 0.47, respectively. Therefore, the risk of mortality had probably decreased for foxes by the time supplemental feeding was discontinued.

Most foxes (73%) that died during their first year, died in June, July, or August. Berry et al. (1987) also found that most pups died in these months. By June, pups are generally more independent of their parents and may be more vulnerable to predators. Hunting skills and ability to detect and avoid predators are probably not as effective in young foxes, and this, in combination with increasing independence, may explain the higher risk of mortality of juvenile foxes during the summer months.

Most foxes (95%) for which a cause of death could be determined were killed by predators. The proportion of deaths attributable to predators did not differ between fed and control groups and was similar to results from other studies (Berry et al., 1987; Ralls et al., 1990; Standley et al., 1992). Although cause of death could not be determined for 41% of the foxes, a large proportion of these deaths probably were caused by predators.

Evidence from this study and other field studies supports the idea that reproductive success of foxes can be limited by food availability. Although sample sizes were too small to make statistical comparisons of reproductive success, supplementally fed vixens tended to have higher reproductive success than control females. This was most apparent in the proportion of yearling females breeding. The proportion of yearling fed foxes that reproduced (50%) was not only higher than the proportion of control yearlings that reproduced but also was higher than the average proportion of yearling foxes that successfully raised pups in previous years (16%) on NPRC (Zoellick et al., 1987a). Other authors have concluded that reproductive success of foxes can be limited by the abundance of food resources. Angerbjorn et al. (1991) provided supplemental food to arctic foxes (*Alopex lagopus*) and concluded that under poor dietary conditions their reproduction was limited by available food. Studies of red foxes have found that as prey abundance decreases, a lower proportion of females breed (Lindstrom, 1989; Zabel and Taggart, 1989). Also, data collected on NPRC indicates that a recent increase in reproductive success of female kit foxes from 18% (3/17) in 1991 to 100% (6/6) in 1992 occurred as rodent populations increased substantially (EG&G Energy Measurements, Inc., 1993).

Food availability may have contributed to the observed differences in dispersal rates between control and fed foxes. The proportion of male foxes that dispersed during their first year of life was significantly higher for control foxes and three times as many control foxes as fed foxes dispersed from the 1989 cohort. Although Scrivner et al. (1987b) found no evidence that rate of dispersal of kit foxes at NPRC was inversely related with food availability, food shortage has been associated with increased dispersal of red foxes (*Vulpes vulpes*) (Englund, 1980; Lindstrom, 1989) and abandonment of home ranges by other carnivores (Ward and Krebs, 1985; Mills and Knowlton, 1991). By 1990, the number of lagomorphs observed during transect surveys was the lowest in eight years (EG&G Energy Measurements, Inc., 1992b), indicating that food availability may have been exceptionally low for foxes from the 1989 cohort. By May 1991, 60% of the control foxes from the 1989 cohort had dispersed, which was a higher proportion dispersing than has been previously reported for foxes at NPRC (Scrivner et al. 1987b).

The higher proportion of males dispersing was similar to results obtained from other studies of foxes (Storm et al., 1976; Tullar and Berchielli, 1982; Scrivner et al., 1987b; Lindstrom, 1989). Although the two longest dispersal distances were made by female foxes, there was no significant difference in average dispersal distances between the sexes. Scrivner et al. (1987b) also found that the distances male and female kit foxes dispersed were similar. However, Storm et al. (1976) found that tagged red fox males were recovered farther away from their natal ranges than females.

Two foxes moved long distances (> 5 miles) and then returned to their natal ranges before dispersing. This pattern indicates that for some kit foxes, dispersal is a gradual process that is preceded by one or more preliminary trips as has been documented in wolves (*Canis lupus*) (Van Ballenberghe, 1983; Messier, 1985b). This pattern may be seldom noted however, because most kit foxes that "disperse" as pups die soon afterwards (26 ± 9 days; Scrivner et al., 1987b). Much of what is termed dispersal may actually be exploratory trips during which the fox is killed.

Supplemental feeding has been used to replace diminished supplies of natural food of threatened and endangered species (Wilber et al., 1974; Knight and Anderson, 1990). The results of this study indicate that food additions could have a positive affect on kit fox populations in some years. However, supplemental feeding of kit foxes in the San Joaquin Valley should be used with caution. There are other threatened or endangered species in the San Joaquin Valley and some are prey for kit foxes. The giant kangaroo rat (*Dipodomys ingens*) is an endangered species that has disappeared from at least one area of NPRC (EG&G Energy Measurements, Inc., 1992a) after two years of below average precipitation (1989, 1990) and this species appears to be slow in recolonizing. An artificial increase in the fox population, due to supplemental feeding, could put additional predation pressure on giant kangaroo rats or other sensitive species and could threaten small populations with extinction.

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