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REPRODUCTION OF THE SAN JOAQUIN KIT FOX (Vulpes velox macrotis) ON CAMP ROBERTS ARMY NATIONAL GUARD TRAINING SITE, CALIFORNIA

September 1992

SANTA BARBARA OPERATIONS
130 Robin Hill Road
Goleta, California 93117

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REPRODUCTION OF THE SAN JOAQUIN KIT FOX (Vulpes velox macrotis) ON CAMP ROBERTS ARMY NATIONAL GUARD TRAINING SITE, CALIFORNIA

by

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ABSTRACT

The reproduction of a San Joaquin kit fox population (*Vulpes velox macrotis*) was investigated at Camp Roberts Army National Guard Training Site, California, from November 1988 through September 1991. Of 38 vixens radiocollared prior to parturition, 12 (32%) were successful in raising pups from conception to the point where pups were observed above ground. No yearling vixens were known to be reproductively active. The mean litter size during 1989 - 1991 was 3.0 (n = 21, SE = 0.28) and ranged from one to six pups. Both the proportion of vixens successfully raising pups and the mean litter size observed at Camp Roberts during this study were lower than those reported at other locations. Sex ratios of kit fox pups were male biased two of the three years, but did not differ statistically from 1:1 throughout the study. Whelping was estimated to occur between February 15 and March 5. Results of this study support previous reports that kit foxes are primarily monogamous, although one case of polygamy may have occurred. Both the proportion of dispersing radiocollared juveniles (26%) and the mean dispersal distance (5.9 km) of juveniles at Camp Roberts appeared low compared to other locations.

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1. INTRODUCTION

The San Joaquin kit fox population (*Vulpes velox macrotis*, until recently *Vulpes macrotis mutica*; Dragoo et al. 1990) was listed as endangered by the U.S. Fish and Wildlife Service in 1967 (U.S. Department of the Interior 1967), and classified as rare by the California Fish and Game Commission in 1971 (Morrell 1972). San Joaquin kit foxes primarily inhabit the semi-arid habitats of the San Joaquin Valley, California, although small populations do occur outside of the Valley (O'Farrell 1983).

The occurrence of San Joaquin kit foxes was confirmed at Camp Roberts Army National Guard Training Site in 1960, and the distribution and abundance of this species increased over the next two decades (Balestreri 1981). An investigation of the ecology of the San Joaquin kit fox at Camp Roberts was initiated in November 1988 to evaluate the effects of military activity on this species. One objective of this study was to investigate reproduction by San Joaquin kit foxes inhabiting Camp Roberts and develop information that might help determine if National Guard-authorized activities affect kit fox reproduction. Specific aspects of kit fox reproduction investigated were as follows: reproductive success of radiocollared females, timing of parturition, litter size, pup sex ratios, age-specific reproductive success, pair bonds, helping behavior, survival of pups to adulthood, and juvenile dispersal.

Few detailed studies have investigated the reproductive biology of San Joaquin kit foxes (Zoellick et al. 1987). Much of the available information on kit fox reproduction has been assimilated from descriptive life history and population trend studies or has been inferred from other fox species. Knowledge of kit fox reproduction is essential to understanding the effects of environmental factors on the population dynamics of this species. This information will facilitate management and conservation of the San Joaquin kit fox population on Camp Roberts.

2. STUDY AREA

Camp Roberts is a military training installation operated by the California Army National Guard and funded by the National Guard Bureau. The installation is located approximately 43 km east of the Pacific Ocean in the southern portion of the Salinas River Valley, approximately midway between San Francisco and Los Angeles along U.S. Highway 101 (Figure 1). Camp Roberts is bisected in an east-west direction by the Monterey-San Luis Obispo County line. The installation encompasses 172 km^2 consisting primarily of gently rolling hills that form a transition zone between the Salinas River floodplain and the steep foothills of the Santa Lucia Mountains. Portions of the Salinas, Nacimiento, and San Antonio Rivers traverse Camp Roberts. Elevations range from 161 to 521 m above sea level. Average annual rainfall is 28.5 cm, most of which (over 90%) occurs between November and April (Nakata and Associates 1987). Fog commonly occurs in the winter months. Annual mean maximum and minimum temperatures are 24°C and 6°C, respectively (Nakata and Associates 1987). The predominant vegetation associations are grassland, oak woodland (*Quercus* spp.), mixed chaparral, and riparian habitats. San Joaquin kit foxes occur primarily in grassland and low to medium density oak woodland habitats throughout the installation, and may also be found inhabiting the highly developed cantonment area (Reese et al. 1992). Additional information regarding the Camp Roberts environment may be found in National Guard Bureau (1991).

Military training activities occur throughout the year at Camp Roberts, with most occurring during the National Guard's Annual Training cycle (May through July). During this study, monthly utilization in terms of peak strength (number of individuals on the installation during the month) was lowest in January 1991 (1,214) and highest in June 1989 (13,784). Training activities include live-fire exercises from established ranges using weapons that range from .22 caliber rifles to 8-inch howitzers. Vehicles used during military activities range from motorcycles to tracked vehicles weighing over 66 metric tons. Although vehicle traffic mostly takes place along roads and tank trails, cross country travel does occur during certain training exercises.

Other activities authorized by the National Guard to occur on Camp Roberts include: 1) a livestock grazing program that allows restricted use by sheep and cattle during spring and summer; 2) controlled burning to reduce the spread of range fires accidentally started by training activities; 3) a hunting and fishing program operated by the California Department of Fish and Game; 4) a limited amount of pest control conducted to reduce rodent and insect populations within buildings and at the sanitary landfill; and 5) a wood cutting program that allows woodcutters to remove downed dead trees. A more detailed description of all activities that occur on Camp Roberts is included in Berry et al. (1992).

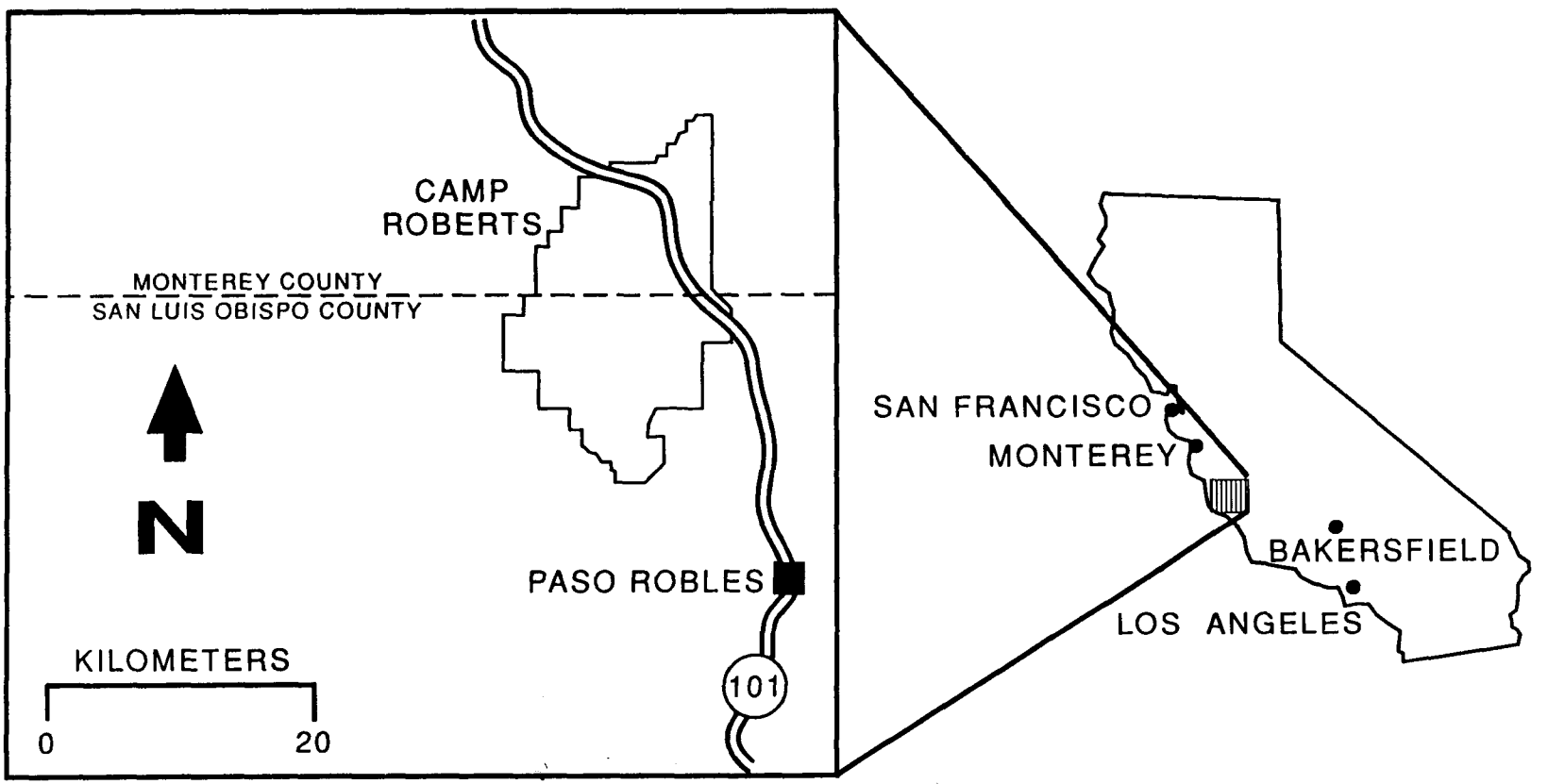

Figure 1. Location of Camp Roberts, Monterey and San Luis Obispo Counties, California.

3. METHODS

Radiotelemetry was used to estimate the proportion of female kit foxes that reproduced and to locate pupping dens (dens in which pups are whelped or reared). Adult San Joaquin kit foxes were captured using wire mesh live-traps following methods described by O'Farrell (1987). Live-trapping was primarily conducted during semi-annual trapping sessions (July-August and December-January) to gather population estimate information. Captured foxes were coaxed into a cloth bag to facilitate handling. Foxes were then weighed, sexed, eartagged, and their reproductive condition examined. Standard measurements were taken and selected foxes were fitted with radiocollars (Telonics, Mesa, AZ). Radiocollars weighed from 30 to 100 g, and each radiocollar weighed less than 5% of the body weight of the fox on which it was placed.

Radiocollared foxes were located approximately three times a week throughout the reproductive season (December through July) to locate pupping dens and examine dens for sign of pups such as matted vegetation, scats and prey remains. For purposes of this report, the reproductive season was considered to be the period consisting of conception, gestation (December - February), and pup-rearing (March - July) following Zoellick et al. (1987). Radiotelemetry also provided ancillary information regarding pair bonds and additional adults (known as helpers) found at pupping dens. The fidelity of pairs was monitored from one year to the next when both members of a pair were radiocollared. Dispersal movements and mortality of radiocollared juvenile foxes were also monitored throughout the study. Occasionally, military activity prevented access to certain areas temporarily precluding the monitoring of some foxes. The proportion of radiocollared female kit foxes successfully raising pups was determined annually. Females trapped and radiocollared post-partum were not used to determine measures of reproductive success.

Automatic telemetry monitors (ATMs) were placed at the dens of selected vixens during February and March to determine dates of parturition. The ATM continuously monitored the immediate vicinity of the den for the presence or absence of the radiocollared fox. ATMs were examined daily to determine if the vixen had changed dens. Pregnant foxes typically spend much of the night away from their dens, but usually remain in their dens the night of parturition. Data from the ATMs were analyzed to determine the percentage of time between 1800 and 0600 that the vixens were present in their dens. These proportions were then graphed and the period in which parturition occurred was assigned. Parturition was assumed to have occurred when a vixen spent over 70% of the night in the same den for four consecutive nights; the date of parturition was assumed to be the first night of this period. Subtracting an estimated gestation period of 49 - 55 days (Egoscue 1962) from the time of parturition gave an approximate range of dates for conception.

Average litter sizes and pup sex ratios were determined annually by observations and live-trapping at pupping dens. Beginning in April of each year, dens of radiocollared vixens were observed in the evenings to determine the presence or absence of pups. If pups were observed, the litter size was recorded. Beginning in May, smaller live-traps (28 x 30 x 81 cm) baited with canned mackerel were placed within 15 m of pupping dens to capture pups. Pups were handled and processed in the same manner as previously described for adult foxes. Efforts were made to capture every pup to verify litter sizes and determine sex ratios.

Minimum dispersal distances were determined for radiocollared juvenile kit foxes that moved greater than 1.6 km from the denning range of their parents, as adapted from Scrivner et al. (1987). The minimum dispersal distance for radiocollared juveniles was the straight line distance between its last known location within the parental denning range to the location where it was last monitored or recovered dead. Juvenile foxes that did not move greater than 1.6 km from their parental denning range were considered not to have dispersed.

Age estimates of reproductively active vixens were based on capture dates. Pups captured prior to June were considered young of the year. Foxes less than 10 months old were classified as juveniles. A yearling classification was given to those foxes 10 - 11 months old when entering the breeding season, and one year old during parturition in February of a given reproductive season (Zoellick et al. 1987). Foxes captured after June were categorized as probable young of the year or probable adults based on size and tooth wear. However, the exact age of probable pups and adults were considered unknown. Probable adults were assumed to be at least one year old. When possible, exact ages were later confirmed by tooth cementum annuli analyses (Matson's Laboratory, Milltown, MT) for each unknown age fox recovered dead.

Average litter size was compared between years using the Kruskal-Wallis tests. Annual pup sex ratios were compared using G-tests (Sokal and Rohlf 1981). Proportions of radiocollared females reproducing were compared among years using a Chi-square test for homogeneity. The proportion of radiocollared females reproducing and pup sex ratios were compared between developed and non-developed portions of Camp Roberts using G-tests. Mean litter size was compared between developed and non-developed habitat using a t-test. Foxes were considered to occupy the developed areas if they were located under a building more than 50% of the number of times they were tracked to either a den or a building. P-values ≤ 0.05 were considered statistically significant.

4. RESULTS

4.1 PERCENTAGE OF RADIOCOLLARED FEMALES SUCCESSFULLY RAISING PUPS

During 1989 - 1991, 38 female kit foxes were radiocollared prior to parturition and monitored throughout the reproductive season to estimate proportions of vixens successfully raising pups. Vixens were monitored for one to three reproductive seasons and located throughout the installation (Figure 2). Twelve of the 38 females (32%) were successful in raising pups from conception to the point where pups were observed above ground (Table 1). The success of vixens did not differ between years throughout the study period ($X^2 = 0.09$, df = 2, $P > 0.9$). Four (11%) vixens died while pregnant. Three of these females were killed by predators and one died of rabies. Four embryos in one female were in the process of reabsorption. Five (13%) of the 38 females died during the reproductive seasons of 1990 or 1991, but exhibited no evidence of having pups. The remaining 17 unsuccessful females (44%) lived throughout their respective reproductive seasons, but were neither observed nor trapped with pups. No pregnant or post-partum vixens were observed in the East Garrison portion of the installation (Figure 2).

Table 1. Percentage of radiocollared females successfully raising pups at Camp Roberts, 1989-1991.

YEAR	NUMBER OF VIXENS MONITORED	NUMBER OF SUCCESSFUL VIXENS (%)
1989	6	2 (33.3)
1990	14	4 (28.6)
1991	18	6 (33.3)
Total	38	12 (31.6)

Over the three years of this study, the proportion of vixens successfully raising pups in developed and non-developed areas was 14% (n = 7) and 36% (n = 31), respectively. However, these proportions did not differ significantly ($G = 1.22$, df = 1, $P > 0.3$). Measures of radiocollared females successfully raising pups between 1989 and 1991, were grouped in the above test due to small sample sizes.

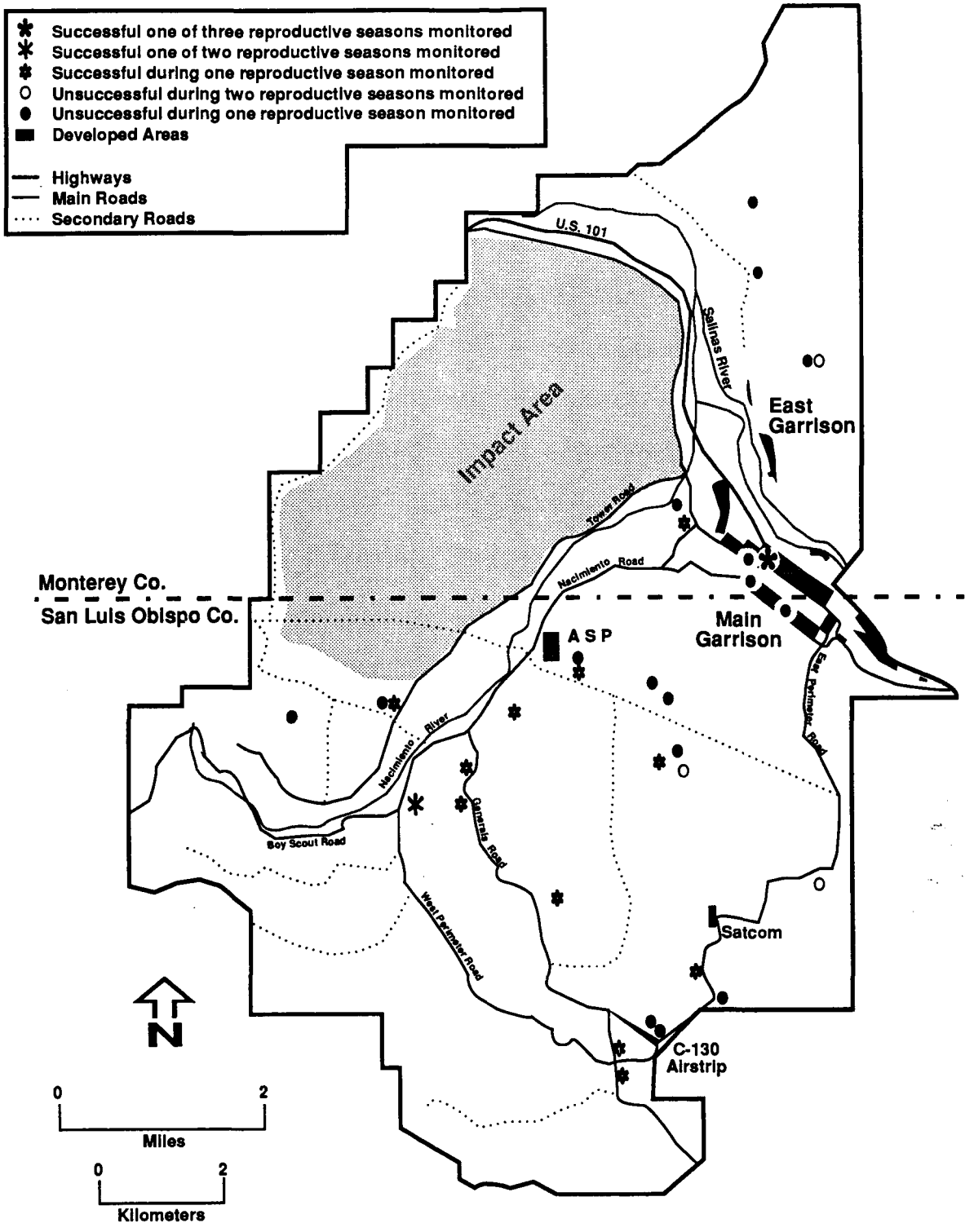

Figure 2. Capture locations of female kit foxes radiocollared to estimate proportions of vixens successfully raising pups at Camp Roberts, 1988-1991.

4.2 AGES OF REPRODUCTIVELY ACTIVE FEMALES

Vixens were considered reproductively active if they successfully raised pups or if they were recovered dead with embryos or placental scars. Vixens reproductively active for more than one annual reproductive season were considered separately for purposes of age analyses. The mean age of reproductively active females was 3.0 years (n = 19, SE = 0.33) and ranged from at least one year to at least six years (Table 2). This mean age represents a minimum estimate due to vixens for which an exact age could not be determined and a conservative age was recorded. No evidence of breeding by known yearling vixens was observed. Two vixens that were at least six years old were reproductively active. One of these vixens successfully raised pups in 1989. The other vixen, known to be at least six years old, was carrying six embryos when killed by a predator.

Table 2. Ages of reproductively active vixens at Camp Roberts, 1989-1991.

KNOWN AGE VIXENS		UNKNOWN AGE VIXENS	
AGE	NUMBER	AGE	NUMBER OF
1	0	≥ 1	2
2	1	≥ 2	4
3	1	≥ 3	6
4	2	≥ 4	0
5	1	≥ 5	0
6	1	≥ 6	1
Total	6	Total	13

4.3 PAIR BONDS

At least one member of five radiocollared kit fox pairs was monitored for two of the three annual reproductive seasons between 1989 and 1991. There were no apparent changes in pair bonds from one year to the next. Bonds between two fox pairs were maintained for at least two consecutive years. The death of a mate occurred with three (60%) of the five pairs monitored, but the surviving members were not subsequently observed with new mates. Pair changes caused by the death of a mate may have gone undetected if the surviving fox were to pair with an non-radiocollared fox.

4.4 HELPING BEHAVIOR

During 1989 and 1990, four non-reproducing adults were observed at pupping dens and were believed to be assisting reproducing pairs of foxes with pup rearing. All four of the helpers were females and their relationship to the four mated pairs was unknown. Two of the four helpers were known to be one year old, while the exact age of the remaining two helpers was unknown.

4.5 TIMING OF PARTURITION

Time of parturition was determined using ATMs for five vixens at Camp Roberts. In 1990, one vixen whelped on or within one day of February 19. An additional vixen whelped in 1990 during the second or third week of February. In 1991, three vixens whelped on or within one day of February 23, February 28, and March 5, respectively. Thus, dates of parturition ranged from approximately February 15 to March 6. By subtracting the estimated kit fox gestation period of 49 - 55 days (Egoscue 1962) from the range of parturition dates, conception dates ranged from approximately December 23 to January 17.

4.6 LITTER SIZE

The average litter size during 1989 - 1991 was 3.0 ($n = 21$, $SE = 0.28$) and ranged from one to six pups (Tables 3 and 4). Average litter size did not vary between years ($H = 2.41$, $df = 2$, $P > 0.40$). A multiple family group of eight pups raised by two vixens was observed in 1990, but was not included in litter size analyses. One of the vixens associated with this litter was recovered dead and had five prominent placental scars, indicating that she was indeed one of the mothers and that all eight pups were not her own.

Table 3. Average litter size of San Joaquin kit foxes observed at Camp Roberts, 1989-1991.

YEAR	AVERAGE LITTER SIZE
1989	2.9 ($n = 9$, $SE = 0.31$)
1990	3.8 ($n = 5$, $SE = 0.74$)
1991	2.6 ($n = 7$, $SE = 0.57$)
Total	3.0 ($n = 21$, $SE = 0.26$)

Table 4. Observed litter sizes of San Joaquin kit foxes at Camp Roberts, 1989-1991.

PUPS / LITTER	NUMBER OF LITTERS OBSERVED
1	2
2	5
3	9
4	2
5	2
6	1

During 1990 and 1991, the mean litter size in developed and non-developed areas was 3.7 ($n = 3$, $SE = 1.20$) and 2.9 ($n = 9$, $SE = 0.45$), respectively. The mean litter size pooled across the two years did not differ significantly between developed and non-developed habitats ($t = 0.76$, $df = 10$, $P > 0.4$). An additional litter of three pups was observed in the developed cantonment area in 1989, but these data were excluded from analyses because the parents were not radiocollared and their use of developed and non-developed habitats was unknown.

4.7 PUP SEX RATIOS

During the reproductive seasons of 1989 through 1991, 54 pups were live-trapped at pupping dens (Table 5). The ratio of male to female pups (1.3:1) did not differ from 1:1 ($G = 0.67$, $df = 1$, $P > 0.4$), and did not differ among years ($G = 0.96$, $df = 2$, $P > 0.6$). The male to female pup ratios pooled across years did not differ between developed (0.8:1, $n = 11$) and non-developed habitats (1.1:1, $n = 25$, $G = 0.13$, $df = 1$, $P > 0.7$). Sex ratio data from 1989, was not used in the above test due to insufficient information regarding the habitat use of the parents.

Table 5. Sex ratios of San Joaquin kit fox pups live-trapped at Camp Roberts, 1989-1991.

YEAR	MALE PUPS	FEMALE PUPS	RATIO M:F
1989	6	4	1.5
1990	17	10	1.7
1991	7	10	0.7
TOTAL	30	24	1.3

4.8 SURVIVAL OF PUPS TO ADULTHOOD

Because kit foxes appear to be physiologically capable of breeding in December of their birth year (Zoellick et al. 1987), juveniles were considered to become adults on December 1. Survival of kit fox pups to adulthood was monitored between May 30 (the earliest date any juvenile foxes were radiocollared) and November 30. The estimated mortality rate for juveniles between 1989 and 1991 was 0.80, with monthly mortality rates being highest in July and August (Standley et al. 1992).

4.9 JUVENILE DISPERSAL

Between 1989 and 1991, seven (26%) of 27 radiocollared juveniles dispersed. The minimum dispersal distances of the seven juveniles ranged from 2.3 to 6.6 km and the mean dispersal distance was 5.9 km (SE = 0.88). Two of the 27 juveniles (7%) were found dead at distances approximately 7 and 10 km from their respective last known locations.

5. DISCUSSION

Proportions of radiocollared vixens successfully raising pups measured at Camp Roberts between 1989 and 1991, were lower than proportions from the Naval Petroleum Reserves, California (NPRC). Both the proportions of females successfully raising pups in non-developed (36%) and developed (14%) areas at Camp Roberts were lower than those found for adult vixens in non-developed (51%) and developed (69%) areas of Naval Petroleum Reserve No. 1 (NPR-1) between 1980 and 1985 (Zoellick et al. 1987). The proportion of vixens successfully raising pups at Camp Roberts (32%) also was lower than that on Naval Petroleum Reserve No. 2 (55%) during 1985 (O'Farrell et al. 1987).

No information was obtained that would unequivocally indicate whether National Guard authorized activities did or did not affect reproduction in the kit fox population at Camp Roberts. All areas of the installation in which kit fox inhabit are subject to some degree of National Guard authorized activity and a control area was not available to compare aspects of reproduction. The reproductive success of the kit fox appears to be strongly influenced by prey availability (Egoscue 1975, O'Farrell et al. 1986). Prey abundance of kit fox at Camp Roberts appeared to be low between 1989 and 1991 (Logan et al. 1992), which may partially account for the low proportions of radiocollared vixens successfully raising pups observed during this study.

No known yearling vixens whelped during this study. Morrell (1972) concluded that yearling females do not successfully breed their first year. However, Zoellick et al. (1987) reported that female kit foxes are physiologically capable of reproducing as yearlings, and suggested that low measures of reproductive success may be indicative of difficulty in obtaining sufficient energy for both reproduction and growth. The proportion of radiocollared adult vixens successfully raising pups (59%) were found to be significantly greater than that of yearling vixens (16%) on NPR-1 between 1980 and 1985 (Zoellick et al. 1987). If reproductive success of yearlings is limited by energy, then some proportion of yearlings may successfully reproduce when food sources are abundant as observed during a supplemental feeding program conducted at Elk Hills during 1988 and 1989 (EG&G/EM 1991a, 1991b).

Of the three reproductively active females at Camp Roberts aged five years or older, one six year old was successful in raising pups. In western Utah, kit foxes over five years of age did not successfully breed (Egoscue 1975).

Results of this study support earlier reports that kit foxes are primarily monogamous (Grinnell et al. 1937, Egoscue 1962). Although no evidence of pair bond changes were observed, other studies have reported that kit foxes may change mates (Egoscue 1962, Morrell 1972, O'Farrell and Gilbertson 1986, Zoellick et al. 1987). Zoellick et al. (1987) reported that the majority of mate changes on NPR-1 occurred after the death of a mate;

and when these were excluded, 85% of the pairs maintained fidelity between years. The eight pups raised together by two vixens in 1990 may have been a result of polygamy, as only one male was observed with this family group. Polygamy has been reported in other kit fox studies (Egoscue 1962, Morrell 1972) and observed in red fox (*Vulpes vulpes*) as well (Moehlman 1989).

The presence of the four non-reproducing vixens observed at pupping dens provides further evidence of helpers assisting a pair of kit foxes with pup rearing (Zoellick et al. 1987). Helping behavior, which may contribute to the survival of the pups, has been documented for red fox (MacDonald 1979). Helpers tend to be female in the smaller canid species, such as red fox (MacDonald 1979, Moehlman 1989), which is consistent with the helping behavior observed with kit foxes at Camp Roberts. However, Zoellick et al. (1987) observed helping behavior by male foxes on two of three occasions and an additional two instances of apparent helping behavior where male foxes were trapped at pupping dens of other radiocollared pairs. Further research is needed to determine whether helping behavior by kit fox is skewed towards females.

The range of parturition dates (February 15 - March 6) determined for Camp Roberts during 1990 and 1991 was later than that determined for vixens at NPR-1 (January 27 - February 19) between 1981 and 1984 (Zoellick et al. 1987). The breeding season of kit foxes at Camp Roberts, December 23 - January 17, was approximately two weeks later than the December 7 - 30 range found at NPR-1 (Zoellick et al. 1987). Other studies have suggested that the breeding season of kit foxes begins in December and ends in January or February (Egoscue 1962, Morrell 1972, O'Farrell and Gilbertson 1986), which is consistent with the breeding seasons observed at both Camp Roberts and NPR-1.

The mean litter size of kit foxes during this study (3.0) was lower than the mean litter size observed at Camp Roberts during 1981 (3.9; Balestreri 1981) and also lower than those reported for kit foxes between 1980 and 1985 on NPR-1 (4.3; Zoellick et al. 1987). Female canids in poor nutritional condition may have high fetal or neonatal mortality (Kleiman and Brady 1978). Egoscue (1975) reported low annual average litter sizes (2.8 and 3.0), which were similar to those observed during this study, during a decline of black-tailed jackrabbit populations in western Utah.

Although the sex ratio of male to female pups grouped over the study period (1.3:1) slightly favored males, no significant difference from 1:1 was found. Egoscue (1975) suggested that a positive correlation existed between male-biased sex ratios and adult population densities relative to food availability. In retrospect, the higher ratio of male to female pups in 1989 (1.5:1) and 1990 (1.7:1), although not statistically significant, may be biologically important. Mech (1975) suggested that a male biased sex ratio among gray wolf (*Canis lupus*) pups may result from marginal nutrition or intense competition for food among adults. A male biased ratio might be advantageous for monogamous canids during periods of stressful environmental conditions by providing potential helpers that are less competitive for food, denning sites, and other limited resources (Kleiman and Brady 1978).

Both the proportion of dispersing radiocollared pups (26%) and the mean dispersal distance (5.9 km) of pups at Camp Roberts appeared low compared to other locations. Between 1980 and 1986, 37% of radiocollared pups at NPR-1 dispersed an average of 8 km from the denning range of their parents (Scrivner et al. 1987). The average dispersal date of juvenile kit fox on NPR-1 was August 20 and the median was August 12 (Scrivner et al. 1987), which coincides with the estimated peak monthly mortality rates for juveniles at Camp Roberts (Standley et al. 1992). However, Scrivner et al. (1987), found no relationship between dispersing radiocollared kit foxes and mortality due to predators or vehicles. The estimated mortality rate of juveniles on Camp Roberts (0.80; Standley et al. 1992) is similar to that found on NPRC (0.74; Berry et al. 1987), but 74% higher than the rate reported on the Carrizo Plain (0.46; Ralls et al. 1990).

6. SUMMARY

1. No information was obtained during this study to unequivocally indicate that National Guard authorized activities affected the reproduction of radiocollared vixens.

2. Reproduction of radiocollared vixens appeared low compared to similar studies conducted during 1980 - 1985 on NPR-1.

3. No yearling vixens were known to be reproductively active.

4. Whelping was estimated to occur between February 15 and March 6.

5. Monogamy is prevalent among kit foxes at Camp Roberts.

6. The mean litter size of kit foxes during this study (3.0) was lower than the mean litter size observed on Camp Roberts in 1981 (3.9), and also lower than those reported for kit foxes on NPR-1 between 1980 and 1985 (4.3).

7. Sex ratios of pups trapped during this study did not differ statistically from 1:1, but were male biased two of the three years.

8. The proportion of dispersing pups and the mean dispersal distance of pups appeared low at Camp Roberts compared to similar studies on NPR-1.

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