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REPRODUCTION AND SPACING PATTERNS OF KIT FOXES RELATIVE TO CHANGING PREY AVAILABILITY

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Abstract: The occurrence of drought and a corresponding decline in the availability of the primary prey of San Joaquin kit foxes (*Vulpes macrotis mutica*) during 1990 and early 1991 provided a unique opportunity to document the effect of changing food resources on kit fox productivity and spacing patterns. Thus, we studied reproduction and spacing patterns of 38 kit foxes on a 110-km² study area of the Carrizo Plain Natural Area, California from December 1988 through November 1991. The primary effect of prey scarcity on kit foxes was to decrease reproductive success; none of 9 collared females reproduced in 1990. Home ranges of members of the same social group overlapped extensively ($\bar{x} = 70.0 \pm 3.0$ [SE] %, $n = 20$), whereas those of foxes in adjacent social groups overlapped only slightly ($\bar{x} = 14.0 \pm 2.0$ %, $n = 73$). Individual home ranges averaged 11.6 ± 0.9 km² ($n = 21$) and did not change in size for foxes monitored among years ($P = 0.31$). Overlap between home ranges of adjacent, same-sex foxes decreased ($P = 0.02$) during prey scarcity. Foxes apparently maintained relatively exclusive home ranges of sufficient size to sustain their own body mass and condition during periods of prey scarcity. The maintenance of large and relatively non-overlapping home ranges in kit foxes may be an adaptation to drought-induced periods of prey scarcity that are episodic and temporary in this region of the country.

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Although kit foxes typically eat a mixture of small rodents, lagomorphs, birds, and invertebrates (McGrew 1979), their primary prey often varies among sites (Zoellick and Smith 1992). In turn, the spacing systems of kit foxes appear to correlate with the type and availability of their primary prey. For example, kit foxes in California (Zoellick et al. 1987) and Utah (O'Neal et al. 1987) that fed primarily on abundant lagomorphs (i.e., high prey biomass) had small, overlapping home ranges, whereas foxes in Arizona (Zoellick and Smith 1992) that fed primarily on nocturnal rodents (i.e., low prey biomass) had large, exclusive home ranges. These results suggest that kit foxes have a flexible spatial organization and adjust their spacing system in response to changes in prey availability. Theoretically, kit foxes should maintain home ranges that contain enough prey to satisfy their energetic requirements, even during temporary prey scarcity (Macdonald 1981). However, if the availability of their primary prey declines and eventually stabilizes at some lower level, kit foxes should increase their home-range sizes to adjust to this new level (Macdonald 1981). Furthermore, kit fox density should decrease in response to prolonged declines in prey availability and, consequently, overlap among the home ranges of unpaired adults also may decrease (Zoellick et al. 1987). However, few quantitative

data have been collected to support these predictions.

Numerical responses by foxes relative to availability of primary prey also have been reported. For example, Zabel and Taggart (1989) found that the productivity of red foxes (*Vulpes vulpes*) on Round Island, Alaska decreased as their primary prey declined. Similarly, Egoscue (1975) reported that the proportion of non-reproducing kit foxes in Utah increased as their primary prey declined. Those females apparently could not switch to, or were unable to sustain themselves on, alternate prey (Egoscue 1975). Thus, during periods of prey scarcity there should be fewer breeding females, smaller litters, or fewer pups.

In 1989, we initiated a study of the San Joaquin kit fox on the Carrizo Plain Natural Area, California. Extremely low rainfall resulted in poor plant production during 1990, and most plant species failed to set seeds. Because seeds are an important part of the diet of many nocturnal rodents in this area, they reproduced poorly or not at all during 1990, and population levels declined drastically (Williams and Germano 1992). Nocturnal rodents were the primary prey of kit foxes on the Carrizo Plain, composing about one-half of the diet during 1989 and 1990 (C. A. Vanderbilt White, Univ. Calif., Davis, pers. commun.). Thus, we were

provided with an opportunity to compare the reproduction and spacing patterns of kit foxes during periods of low and high prey availability. We predicted that a substantial decline in prey availability would reduce the productivity of females (Egoscue 1975), decrease overlap between home ranges of adjacent, unpaired foxes (Zoellick et al. 1987), and perhaps, if prey numbers stabilized at some lower level, increase home-range size (Macdonald 1981).

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STUDY AREA

We conducted the study on a 110-km² area of the western portion of the Carrizo Plain Natural Area (T31S and T32S, R19E and R20E; San Luis Obispo County, Calif.). Woods (1982) and Twisselmann (1956) provided detailed descriptions of vegetation types, climate, and fauna of the area. Habitat types within the study area included valley grassland, alkali sink, and fallow grain fields (Woods 1982). Valley grassland was dominated by annual herbs such as red-stemmed filaree (*Erodium cicutarium*), locoweed (*Astragalus oxyphysus*), fiddleneck (*Amsinckia intermedia*), and grasses (*Bromus* spp.). The eastern portion of the study area bordered a dry alkali evaporative basin (Soda Lake) that was surrounded by alkali sink habitat, including salt-bush (*Atriplex* spp.) and iodine bush (*Allenrol-*

fea occidentalis). Wheat had previously been cultivated in much of the central portion of the study area, and these fields had been fallow for 1–5 years at the onset of the study. The western portion of the study area extended into the grassland foothills of the Caliente Mountains, and elevations varied from 580 to 850 m. Approximate summer high and winter low temperatures were 40 C and –10 C, respectively. Average yearly precipitation in the study area was 26 cm, occurring primarily as winter rains (Woods 1982).

Mammalian prey eaten by kit foxes on the Carrizo Plain Natural Area included Heermann's kangaroo rat (*Dipodomys heermanni*), giant kangaroo rat (*D. ingens*), San Joaquin kangaroo rat (*D. nitratoides*), deer mouse (*Peromyscus maniculatus*), California pocket mouse (*Chaetodipus californicus*), San Joaquin pocket mouse (*Perognathus inornatus*), desert cottontail (*Sylvilagus audubonii*), black-tailed jack-rabbit (*Lepus californicus*), and California ground squirrel (*Spermophilus beecheyi* [C. A. Vanderbilt White, Univ. Calif., Davis, pers. commun.]).

MATERIALS AND METHODS

From December 1988 through November 1990, we captured kit foxes using Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wis.), custom-made with 1.3- × 2.5-cm wire mesh to minimize the likelihood of a trapped fox breaking a canine tooth in the mesh. We determined the sex and body mass of each captured fox. Each fox was outfitted with a 50-g radio collar (Advanced Telemetry Systems, Inc., Isanti, Minn.) with a 17.5-cm cable antenna that extended along the back of the fox. We attempted to capture all known members of each social group within the study area. Uncollared foxes were trapped as soon as possible after they were observed. Foxes were considered to belong to a specific social group (i.e., male-female pair, trio) if they frequently and concurrently shared the same dens. Conversely, we assumed foxes were not paired if no other foxes were trapped or observed within their home ranges. Because opportunistic sightings of collared or uncollared kit foxes were rare, we estimated the minimum number of adult kit foxes on the study area each month by combining the number of collared foxes with sightings of uncollared individuals. This value was then divided by the size of the study area to estimate densities. Monthly density

estimates were averaged to obtain yearly estimates.

We radiotracked foxes to their denning sites daily. Only 1 denning location was obtained per fox per day. Foxes also were located at night from mid-June to mid-September of 1989 and from May 1990 to November 1991. During nocturnal sampling periods, foxes were located using a vehicle-mounted, null-peak system with 2 4-element Yagi antennas. Each radio location was obtained by an observer driving quickly from one reference point to another until 2–3 intersecting compass bearings were obtained. Reference points were chosen to minimize error polygons (Springer 1979) and to reduce the mean time between bearings (Schmutz and White 1990). Each fox was located at ≥ 2 -hour intervals to reduce autocorrelation between successive relocations. Only 4–6 locations were obtained per fox per night and nocturnal sampling periods for a given fox were generally separated by ≥ 1 week.

We used the Locate II plotting program to triangulate the locations (Pacer, Truro, N.S., Can.). To reduce error, estimated locations ≥ 3 km from the reference points were eliminated from further analyses. We used locations ≤ 3 km from reference points only if the angle of intersection of compass bearings was between 35° and 145° . To estimate minimum telemetry error, naive observers triangulated 126 locations of test collars placed 0.5–3.0 km from reference points. We calculated the absolute value of bearing errors and the mean distance between the estimated and true locations.

We estimated the sizes of home ranges (i.e., total area used by a fox in its normal activities; sensu Burt 1943) using the minimum convex polygon method (Mohr 1947). Slight autocorrelation of data does not significantly alter estimates of home-range sizes, provided that bursts of relocations are separated by relatively long inter-burst periods (e.g., 7 days) and data are collected over long time-periods (Andersen and Rongstad 1989). Thus, we calculated the sizes of home ranges for 21 foxes that were located for ≥ 175 days and 15 nights (i.e., ≥ 60 nocturnal locations). We calculated cumulative home ranges for the entire study as well as yearly home ranges. Locations from each member of a social group were combined to calculate the home ranges of groups. Using only nocturnal locations, we identified areas of intensive nocturnal use by calculating the area encompassed

by the 50% isopleth of the harmonic mean method (Dixon and Chapman 1980, Spencer and Barrett 1984). We calculated spatial overlap among home ranges of individual foxes by overlapping the polygon of each fox with a grid of 300-m² cells. Overlap was determined by multiplying the number of cells in the overlap area of the polygons by 2, and then dividing by the total number of grid cells in both polygons (Cole 1949).

We tested for differences in the capture probabilities of nocturnal rodents among years and the sizes of home ranges between sexes using unpaired *t*-tests. To determine if the home-range size of each fox differed between high prey availability (1989), low prey availability (1990), and continued low prey availability (early 1991) time-periods, we calculated the between-year differences (e.g., 1989–90, 1990–91) in the size of each fox's home range. We determined if these difference data varied significantly from zero using 1-group *t*-tests (Meese 1993). Significant *t*-tests were followed by a 2-sample *t*-test comparing the 2 between-year difference groups (e.g., 1989–90, 1990–91) against one another (Sokal and Rohlf 1981). Similarly, we used 1-group *t*-tests to examine between-year differences in the size of nocturnal activity areas, fox body masses, and overlap of home ranges between adjacent foxes. Differences in fox density among years were evaluated by analysis of variance. Statistical significance was inferred if $P < 0.05$.

RESULTS

Rainfall and Prey Availability

Total yearly rainfall was only 5.0 cm in 1990, compared with 11.5 cm in 1989 and 16.5 cm in 1991. Capture probabilities of kangaroo rats on the eastern portion of the Carrizo Plain Natural Area declined from an average of 69.0% during 1988–89 to 18.1% and 13.4% during 1990 and April 1991, respectively (Williams and Germano 1992). On our study area, capture probabilities were 3.4% and 1.7% during 1990 and 1991, respectively (C. A. Vanderbilt White, Univ. Calif., Davis, pers. commun.). These probabilities were 20–40 times lower than those obtained by Williams and Germano (1992) during 1988–89 and declined ($t = 3.44$, $P = 0.01$) between 1990 and 1991. Lagomorph counts derived from quarterly belt-transect surveys on the Carrizo Plain Natural Area declined from an average

of 0.58 ± 0.05 lagomorphs/km of transect during 1970–89 to 0.20 ± 0.03 lagomorphs/km of transect during 1990–91 (J. Lidberg, Calif. Dep. Fish and Game, pers. commun.). Also, ground squirrels were locally abundant in fallow portions of the study area during 1989, but were infrequently observed by 1991. This drought-induced decline in prey abundance appeared to be temporary. Winter rains during 1990–91 resulted in substantial plant production and by July, numbers of rodents were increasing (Vanderbilt White and White 1992). Capture probabilities on 2 alkali sink sites adjacent to our study area increased from 1.3% during May 1991 to 20.0% during August 1991 (Vanderbilt White and White 1992). Capture probabilities continued to increase on these sites, reaching 35.0% by May 1992 (Vanderbilt White and White 1992).

Study Population

During 1989, we studied 15 foxes, consisting of 3 male-female pairs, 2 trios (2 males and 1 female), and 3 unpaired foxes. During 1990, we studied 22 foxes, consisting of 5 pairs, 3 trios, and 3 unpaired foxes. Two trios consisted of 1 male and 2 females, and the third trio consisted of 2 males and 1 female. During 1991, we studied 16 foxes, consisting of 4 pairs, 1 trio (1 male and 2 females), and 5 unpaired foxes. We obtained nocturnal locations for all foxes except 3 in 1989 and 2 in 1991 that could not be accurately located using the available roads. Body masses of male ($n = 21$) and female ($n = 17$) foxes averaged 2.4 ± 0.01 and 2.1 ± 0.01 kg, respectively. Body masses of adult foxes that were recaptured did not change among years (1989–90: $t = 1.42$, 6 df, $P = 0.21$; 1990–91: $t = 0.27$, 11 df, $P = 0.79$).

Minimum densities of adult kit foxes were 1 per 4.1, 4.3, and 6.5 km² during 1989, 1990, and 1991, respectively. The density of adult foxes was similar between 1989 and 1990. However, the density of adult foxes was lower ($F = 78.1$, 2 df, $P < 0.001$) during 1991 than 1990.

Seven members of 4 fox groups were killed in 1989, 7 members of 6 fox groups were killed in 1990, and 7 members of 6 fox groups were killed in 1991. Predation by coyotes (*Canis latrans*) was the main cause of death. Members of trios and unpaired foxes that were killed ($n = 9$) were not replaced by other foxes during any year. During 1989 and 1990, members of pairs that died ($n = 7$) were replaced in ≤ 7 –

117 days by same-sex individuals. However, during 1991, only one of 5 members of pairs that died was known to be replaced. A female whose trio mates had been killed in 1990 left her original home range and moved about 7 km to that of a recently unpaired male. No resident foxes were known to abandon their home ranges following the death of a mate during 1989 or 1990.

Reproduction

Reproductive success in 1990 was likely lower than in 1989 and 1991. In 1990, none of 9 radio-collared females produced pups that appeared above ground. Also, no litters of pups were observed in areas adjacent to the intensive study area. Only 2 juvenile foxes were captured during trapping sessions later that autumn. In 1989, none of 3 collared females produced pups that appeared above ground. However, we observed 5 females with litters in areas adjacent to the intensive study area and trapped 7 juvenile foxes later that autumn. In 1991, four of 7 radio-collared females produced pups, with observed litters of 1, 2, 2, and 3 pups. Also, 2 females with litters were observed in adjacent areas. We did not trap for juvenile foxes in autumn of 1991.

Spacing Patterns

Absolute value of bearing error averaged 1.4 ± 0.2 degrees, and mean distance between estimated and true locations was 165 ± 13 m ($n = 126$). Neither value varied ($P = 0.66$) among observers. Mean time between bearings was 5 minutes. Distance between the antenna and estimated locations of foxes averaged 1.2 ± 0.1 km ($n = 1,244$).

Individual home-range size averaged 11.6 ± 0.9 km² ($n = 21$, \bar{x} locations = 432 ± 35 [SE]) over the course of the study, and did not change in size for foxes monitored among years (1989–90: $t = 0.68$, 4 df, $P = 0.54$; 1990–91: $t = 0.91$, 10 df, $P = 0.39$). Individual home ranges of the foxes in our study were 2–5 times larger than those of foxes in a nearby area of California (Zoellick et al. 1987) and in Utah (O'Neal et al. 1987; $F = 50.9$, 51 df, $P < 0.001$), but not different from those in Arizona (Zoellick and Smith 1992; $F = 1.9$, 27 df, $P = 0.18$). Home ranges of individuals within social groups overlapped an average of $70.0 \pm 3.0\%$ ($n = 20$), and sizes did not differ between the sexes ($t = 1.49$, 19 df, $P = 0.15$). Mean home-range size of fox social

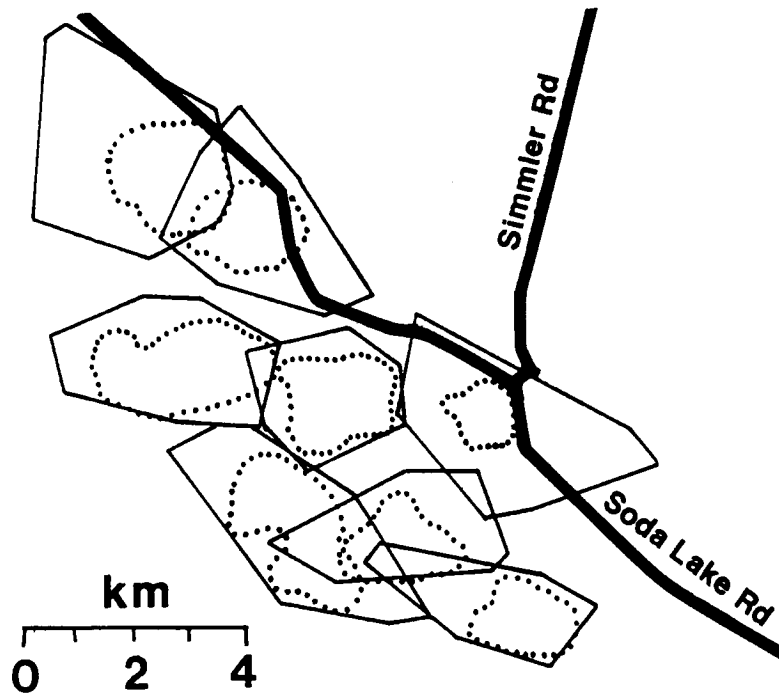


Fig. 1. Spatial arrangement of the home ranges (solid lines) and areas of intensive nocturnal use (dotted lines) of female kit foxes on the Carrizo Plain Natural Area, California, during 1990. Home ranges were plotted using the minimum convex polygon method, and areas used at night were plotted using the 50% isopleth of the harmonic mean method.

groups was $13.7 \pm 1.1 \text{ km}^2$ ($n = 10$; \bar{x} locations = 903 ± 98), which did not differ from the mean individual home-range size ($t = 1.43$, 29 df, $P = 0.16$).

The composition of social groups often changed during the course of a year due to mortality. Therefore, we compared home-range overlap between same-sex foxes belonging to adjacent social groups, rather than between social groups. Home ranges of female foxes belonging to adjacent social groups overlapped an average of $10.0 \pm 4.3\%$ ($n = 6$) during 1989, $9.7 \pm 4.2\%$ ($n = 14$) during 1990, and $5.1 \pm 3.5\%$ ($n = 4$) during 1991 (Fig. 1). Ranges of adjacent males overlapped an average of $19.2 \pm 5.5\%$ ($n = 6$) during 1989, $14.7 \pm 3.5\%$ ($n = 24$) during 1990, and $18.2 \pm 4.6\%$ ($n = 18$) during 1991. Overlap of home ranges did not differ ($t = 1.32$, 10 df, $P = 0.21$) between sexes. Home-range overlap between adjacent, same-sex foxes decreased slightly between 1989 and 1990 ($t = -3.43$, 5 df, $P = 0.02$), but did not differ between 1990 and 1991 ($t = 0.47$, 16 df, $P = 0.36$).

Areas of intensive nocturnal use, defined by the 50% harmonic mean isopleth, were rela-

tively exclusive whether we considered adjacent, same-sex individuals (Fig. 1) or adjacent social groups. The size of nocturnal activity areas did not change for foxes monitored among years (1989–90: $t = 1.78$, 4 df, $P = 0.15$; 1990–91: $t = -0.30$, 10 df, $P = 0.77$).

DISCUSSION

Although rainfall was below average in 1989, seed stores and reserves of seeds in the soil likely were sufficient to maintain high populations of nocturnal rodents (Williams and Germano 1992). Our data and results from concurrent studies (J. Lidberg, Calif. Dep. Fish and Game, pers. commun.; Vanderbilt White and White 1992; Williams and Germano 1992) of nocturnal rodents and lagomorphs on the Carrizo Plain indicate that prey availability declined during 1990, and remained low until mid-1991. The primary effect of drought on kit foxes on the Carrizo Plain Natural Area was to decrease reproductive success. The decline in food availability led to an increase in the number of females that did not successfully reproduce (non-breeding) in 1990, and lower densities of adult kit foxes by 1991. Similar increases in the numbers of non-breed-

ing females following reductions in prey availability have occurred in kit fox populations in Utah (Egoscue 1975) and red fox populations in Alaska (Zabel and Taggart 1989). Many females on the Carrizo Plain Natural Area may have conceived or produced pups in 1990, but failed to rear them to the age when they normally appear above ground. Prey declines in Utah and Alaska were followed by substantial reductions in the number of litters and pups that were successfully reared by kit foxes, arctic foxes (*Allopex lagopus*), and red foxes (Egoscue 1975, Eberhardt et al. 1982, Zabel and Taggart 1989). Furthermore, Macpherson (1969) provided evidence that breeding arctic foxes may abandon their dens or fail to successfully rear pups to weaning during periods of prey scarcity. This reproductive pattern might be expected when prey is scarce, because female mammals generally require more energy for lactation than gestation (Clutton-Brock et al. 1989). Surprisingly, several females on the Carrizo Plain Natural Area successfully weaned pups during 1991, although prey availability remained low. These females may have changed their diets slightly to include a greater proportion of alternate prey species and, thereby, obtained sufficient energy to rear pups (C. A. Vanderbilt White, Univ. Calif., Davis, pers. commun.). Red foxes in Alaska consumed a larger proportion of alternate prey species following a decline in the availability of their primary prey (Zabel and Taggart 1989). This change in diet apparently enabled some foxes to successfully rear pups during the second and third years of low prey availability (Zabel and Taggart 1989). Diminished productivity during periods of reduced prey availability suggests that surveys of pup production might provide a cost-effective indicator of population condition.

Despite the drastic decline in prey availability, home-range size did not change over the study. These results support the hypothesis of Macdonald (1981) that foxes would not modify home-range sizes in response to temporary changes in food availability. Our data are consistent with the suggestion of Macdonald (1981) that large home ranges are associated with low prey availability. Nocturnal rodents were the primary prey species of foxes on the Carrizo Plain Natural Area throughout the study (C. A. Vanderbilt White, Univ. Calif., Davis, pers. commun.) and in Arizona (Zoellick and Smith 1992). Prey biomass in both areas was <20%

that of the Naval Petroleum Reserves, California (Zoellick et al. 1987) and Utah (O'Neal et al. 1987), where lagomorphs were the primary prey. Overlap between the home ranges of adjacent, same-sex foxes we studied was 2–3 times less than in the Naval Petroleum Reserves (Zoellick et al. 1987) where prey biomass and fox density (1 fox/1.4 km²) were high, but similar to that in the Arizona study (Zoellick and Smith 1992) where prey biomass and fox density (1 fox/4.4 km²) were lower. As prey availability declined on our study area, there was a small, but significant, decrease in overlap between the home ranges of adjacent, same-sex foxes.

RESEARCH IMPLICATIONS

Foxes on the Carrizo Plain Natural Area apparently maintain home ranges of sufficient size to sustain their own body mass and condition during periods of prey scarcity. This is consistent with the hypothesis of Macdonald (1981) that red foxes maintain home ranges that prevent them from having to alter their spatial organization in response to temporary changes in food availability. Rainfall patterns suggest that periods of low prey availability are fairly common on the Carrizo Plain Natural Area. At least 4 droughts, with rainfall similar to 1989–90, have occurred within the last 50 years. Thus, the maintenance of large and relatively non-overlapping home ranges may be an adaptation to drought-induced periods of prey scarcity that are episodic and temporary.

LITERATURE CITED

- ANDERSEN, D. E., AND O. J. RONGSTAD. 1989. Home-range estimates of red-tailed hawks based on random and systematic relocations. *J. Wildl. Manage.* 53:802–807.
- BURT, W. H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24: 346–352.
- CLUTTON-BROCK, T. H., S. D. ALBON, AND F. E. GUINNESS. 1989. Fitness costs of gestation and lactation in wild mammals. *Nature* 337:260–262.
- COLE, L. C. 1949. The measurement of interspecific association. *Ecology* 30:411–424.
- DIXON, K. R., AND J. A. CHAPMAN. 1980. Harmonic mean measure of animal activity areas. *Ecology* 61:1040–1044.
- EBERHARDT, L. E., W. C. HANSON, J. L. BENGTON, R. A. GARROTT, AND E. E. HANSON. 1982. Arctic fox home range characteristics in an oil-development area. *J. Wildl. Manage.* 46:183–190.
- EGOSCUE, H. J. 1975. Population dynamics of the kit fox in western Utah. *Bull. South. Calif. Acad. Sci.* 74:122–127.
- MACDONALD, D. W. 1981. Resource dispersion and

- the social organization of the red fox (*Vulpes vulpes*). Pages 918-949 in J. A. Chapman and D. Pursley, eds. Proc. Worldwide Furbearer Conf., Frostburg, Md.
- MACPHERSON, A. H. 1969. The dynamics of Canadian arctic fox populations. Can. Wildl. Serv., Rep. Ser. 8. 52pp.
- MCGREW, J. C. 1979. *Vulpes macrotis*. Mamm. Species. 123:1-6.
- MEESE, R. J. 1993. Effects of predation by birds on gooseneck barnacle (*Pollicipes polymerus* Sowerby) distribution and abundance. J. Exp. Mar. Biol. Ecol. 166:47-64.
- MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223-249.
- O'NEAL, G. T., J. T. FLINDERS, AND W. P. CLARY. 1987. Behavioral ecology of the Nevada kit fox (*Vulpes macrotis nevadensis*) on a managed desert rangeland. Pages 443-481 in H. H. Genoways, ed. Current mammalogy. Plenum Press, New York, N.Y.
- SCHMUTZ, J. A., AND G. C. WHITE. 1990. Error in telemetry studies: effects of animal movement on triangulation. J. Wildl. Manage. 54:506-510.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry: the principles and practice of statistics in biological research. Second ed. W. H. Freeman and Co., New York, N.Y. 859pp.
- SPENCER, W. D., AND R. H. BARRETT. 1984. An evaluation of the harmonic mean measure for defining carnivore activity areas. Acta Zool. Fennica 171:255-259.
- Springer, J. T. 1979. Some sources of bias and sampling error in radio triangulation. J. Wildl. Manage. 43:926-935.
- TWISSELMANN, E. C. 1956. Flora of the Temblor Range. Wasmann J. Biol. 14:161-300.
- VANDERBILT WHITE, C. A., AND P. J. WHITE. 1992. Population status of the short-nosed kangaroo rat on the Carrizo Plain Natural Area, California. Trans. West. Sect. Wildl. Soc. 28:30-33.
- WILLIAMS, D. F., AND D. J. GERMANO. 1992. Recovery of endangered kangaroo rats in the San Joaquin Valley, California. Trans. West. Sect. Wildl. Soc. 28:93-106.
- WOODS, C. 1982. An inventory of the terrestrial vertebrates of the Carrizo Plain, San Luis Obispo County, California. M.S. Thesis, California Polytechnic State Univ., San Luis Obispo. 109pp.
- ZABEL, C. J., AND S. J. TAGGART. 1989. Shift in red fox, *Vulpes vulpes*, mating system associated with El Niño in the Bering Sea. Anim. Behav. 38:830-838.
- ZOELICK, B. W., T. P. O'FARRELL, AND T. T. KATO. 1987. Movements and home range of San Joaquin kit foxes on the Naval Petroleum Reserves, Kern County, California. U. S. Dep. of Energy Topical Rep., EG&G/EM Santa Barbara Operations, Natl. Tech. Inf. Serv., Springfield, Va. 38pp.
- , AND N. S. SMITH. 1992. Size and spatial organization of home ranges of kit foxes in Arizona. J. Mammal. 73:83-88.

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