Survival and cause-specific mortality of gray foxes (*Urocyon cinereoargenteus*) in southern California

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Abstract

From May 1997 to July 1999, 24 gray foxes *Urocyon cinereoargenteus* were radio-marked and their fates monitored in a natural area of southern California to identify rates of survival and cause-specific mortality, and thus to assess population sustainability. Pup (0.4–1.0 years old) foxes had an 8-month (September–April) survival rate (0.34) that was lower than the 8-month (0.77) or 12-month (0.58) estimates for adult foxes. Interference competition was evident; 92% (11/12) of fox mortalities were the result of predation by sympatric coyotes *Canis latrans* or bobcats *Felis rufus*. Also, five of seven gray fox mortalities were outside of, or on the border of, the home range of the killed fox. Calculations indicated that the fox population would remain stable if survival of pups during their first 4 months of life was 0.68 (*vs* 0.75 for adults during these months and 0.58 for older pups for 4 other months). This seems reasonable, yet sympatric carnivores, mainly coyotes, clearly influence the gray fox population in southern California.

Key words: bobcat, California, *Canis latrans*, carnivores, coyote, *Felis rufus*, gray foxes intraguild predation, mortality, survival, sympatry, *Urocyon cinereoargenteus*

INTRODUCTION

Gray foxes *Urocyon cinereoargenteus* are widely distributed from southern Canada to northern South America, and often the major source of their mortality is legal trapping (Cypher, 2003). In populations that are not trapped, gray foxes may more commonly be killed by other carnivores and raptors (Cypher, 2003) or by disease (e.g. distemper; Nicholson & Hill, 1984), which can cause local population reductions. The removal of larger predators has resulted in increases in the numbers of gray foxes, suggesting that predation limits some fox populations (Crooks & Soule, 1999; Henke & Bryant, 1999). Still, actual survival rates of gray foxes have previously been based only on age ratio analyses (Wood, 1958; Lord, 1961; Weston & Brisbin, 2003) rather than on fates of individually radio-marked animals, and cause-specific rates of mortality have not been calculated.

During an investigation assessing competition among mesocarnivores in the Santa Monica Mountains of southern California, U.S.A., Fedriani *et al.* (2000) found a negative relationship between the abundance of coyotes *Canis latrans* and gray foxes. Gray foxes seemed to be absent in regions of high coyote density, but apparently reached their greatest abundance in regions where coyotes were scarce (Fedriani *et al.*, 2000). In this study, the survival rates of gray foxes in the same area are identified, the relative importance of coyote and other predation as sources of mortality are documented, and an attempt is made to assess the effect of mortality on changes in the fox population. Whether foxes are more vulnerable to predation near the periphery of their home range is also explored (Sovada *et al.*, 1998; Kitchen, Gese & Schauster, 1999).

STUDY AREA

A population of gray foxes living within the Simi Hills portion of Santa Monica Mountains National Recreation Area (SMMNRA), which is adjacent to the metropolitan region of Los Angeles, was studied. The Simi Hills have large ($\geq 15\,000$ ha) core areas of protected parkland surrounded by undeveloped private and public lands (Riley *et al.*, 2003), and suburban developments at the parkland borders (National Park Service, 1994). More than $50\,000$ visitors/year frequent the area for outdoor activities such as hiking, mountain biking, and horse riding (National Park Service, 1996). No legal furbearer trapping was allowed in the area.

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Elevation in the Simi Hills ranges from 274 to 732 m (National Park Service, 1996). Mild, wet winters (November–April) and hot, dry summers (May–October) characterize the Mediterranean climate of the SMMNRA with annual minimum and maximum mean temperatures of 10.5 and 21.3 °C, and annual mean precipitation of 376 mm occurring primarily as winter rains. The meteorological phenomena 'El Niño' and 'La Niña' affected southern California during our study, however, producing very dry seasons in 1997 and 1998, and 231% of normal rainfall during the wet season in 1998 (National Oceanic and Atmospheric Administration, 1999).

Historic grazing, fire and urbanization have influenced the distribution and composition of plant communities in the Simi Hills (National Park Service, 1996). Cover types in our 3340-ha study site included northern mixed chaparral (with *Ceanothus* spp.), chamise chaparral (*Adenostoma fasciculate*), coastal sage scrub (*Artemisa* and *Salvia* spp.), coast live oak (*Quercus agrifolia*) woodland, valley oak (*Quercus lobata*) woodland, and grassland (with exotic annuals such as wild oat *Avena* spp. and black mustard *Brassica nigra*, native perennial bunchgrasses (*Stipa*, *Elymus* and *Melica* spp.) and native annual grasses (*Festuca* spp.)); developed residential areas and human-influenced cover types occurred on the park boundaries, but radio-marked foxes were never located there.

Coyotes, bobcats *Felis rufus*, raccoons *Procyon lotor*, gray foxes, and striped skunks *Mephitis mephitis* are common resident carnivore species in the study site, while spotted skunks *Spilogale putorius*, long-tailed weasels *Mustela frenata*, badgers *Taxidea taxus*, and mountain lions *Felis concolor* are locally rare (National Park Service, 1996). Lagomorphs comprise the largest component of fox, coyote, and bobcat diets in the Santa Monica Mountains (Fedriani *et al.*, 2000), but various other rodent species are also important for each carnivore.

METHODS

Gray foxes were trapped and radio-collared from May to November in 1997 and from April to October in 1998. To avoid injuries, $1^1/_2$ coil-spring, soft-catch leg-hold traps with padded jaws were used (Riley *et al.*, 2003). Gray foxes were immobilized by taping their muzzle and legs, and covering their eyes with a blindfold to reduce stress. Aggressive foxes were intramuscularly injected with 5–10 mg/kg of ketamine HCl (Seal & Kreeger, 1987). Numbered ear tags and a 60-g radio-collar with a 20-cm whip antenna and mortality sensor (LOTEK, Ontario, Canada, and ATS, Minnesota, U.S.A.) were attached to each fox. Pups wore loosely fitted radio-collars to allow for normal growth. Foxes were aged by tooth wear and body size (pup < 1.0 year old, or adult), sexed, weighed, measured, and released at the capture site.

Twenty-four gray foxes (5 adult females, 12 adult males, 4 pup females, and 3 pup males) were radio-marked and portable receivers (Model LA-12 AVM, California, U.S.A.) and 4-element, hand-held, directional Yagi antennas used to monitor them. Transmitter signals of individual foxes were checked 4–7 days per week to identify when each died. Every time a mortality signal was received, the carcass was recovered and examined within the next 30 h, and the physical evidence at the site used to help determine the cause of death. Physical evidence included tracks or scats of other species (for species designation), and diagnostic puncture wounds, blood, and location and condition of carcass (Dolbeer, Holler & Hawthorne, 1994) were used to identify potential scavenging *vs* predation. The universal transverse mercator (UTM) coordinates of each mortality location were determined using a portable global positioning system unit (GPS, Trimble Pathfinder® ProXR System).

To investigate the location of mortalities in relation to home-range boundaries, home ranges of predated gray foxes were quantified with at least 30 locations whose accuracy averaged ± 50 m (cf. Farias, 2000). Two estimators were used to evaluate the consistency of our results: the 95% minimum convex polygon (MCP), and the 95% fixed kernel density estimator (FK; Worton, 1989; Seaman & Powell, 1996; Seaman, Griffith & Powell, 1998; Powell, 2000). RANGES V software (Kenward & Hodder, 1996) was used for home-range estimation, and ARCVIEW 3.1 software with the ANIMAL MOVEMENT 2.0 beta extension (Hooge & Eichenlaub, 1997) to plot the results. Location of carcass recovery was considered the mortality location (Kitchen *et al.*, 1999). The mortality location of the predated gray foxes was analysed in relation to home-range boundary by plotting all isopleths of the home range to the nearest 5% isopleth, and then assessing the mortality location relative to these isopleths (Sovada *et al.*, 1998; Kitchen *et al.*, 1999). The mortality location was considered to be outside the home range if the dead fox was found outside of the 95% isopleth (Kitchen *et al.*, 1999). The home range was estimated for only 7 of 11 foxes killed by another predator, because the other 4 foxes were killed before enough locations could be obtained for an adequate home-range delineation.

Survival and cause-specific mortality rates of radio-marked gray foxes were calculated using the computer program MICROMORT (Heisey & Fuller, 1985). Mortality rates owing to 2 causes of death were computed: predation and unknown. Gray fox mortality rates were compared between years (1997–98 *vs* 1998–99), sexes, and ages (adults *vs* pups). Monthly gray fox survival and mortality rates were totalled for a 12-month period (annual rate from May to April) for adults and for an 8-month period (from September to April) for pups (no pups were marked before they were 4 months old).

It was not possible to census or otherwise estimate the gray fox population in consecutive years. Therefore, to explore the effects of predation on gray fox numbers, the estimates of gray fox survival from this study and demographic parameters from the literature were combined into hypothetical calculations of potential population change. Because no published data were found on pup survival during their first months of life, the purpose of the calculations was to identify a hypothetical pup survival rate (i.e. from May to August) that would allow for the
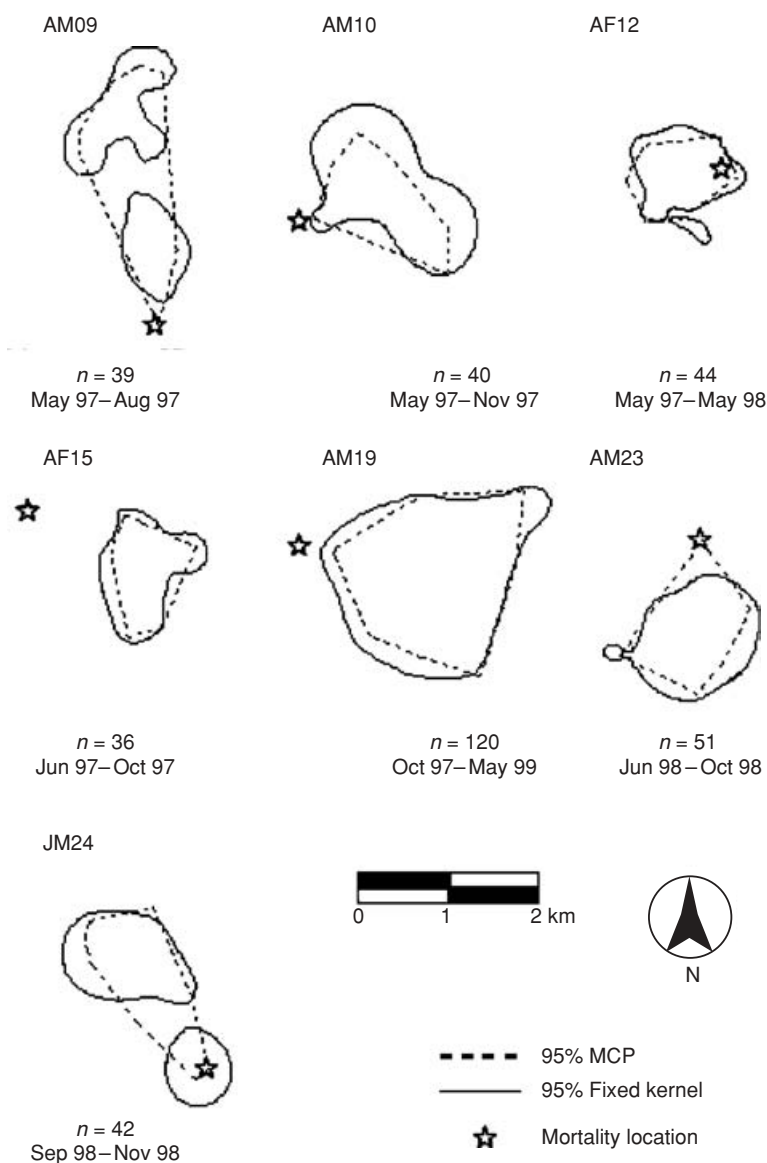
Fig. 1. Mortality locations of radio-marked gray foxes *Urocyon cinereoargenteus* in relation to 95% minimum convex polygon and 95% kernel estimate home-range boundaries. Dates of radio-monitoring and numbers of telemetry locations are indicated for each gray fox.

population to remain stable, and then assess whether or not the value was realistic. An unrealistically high value (compared to the range of published values for other canids) would suggest that the population could be declining. Conversely, a very low value would suggest that the population was not limited and had the potential to grow.

A closed population and a stable age distribution was assumed for these calculations. An even sex ratio was maintained for all age classes (Fritzell & Haroldson, 1982) by assuming that sex ratio at birth was even, and that survival of males and females was the same. It was also assumed that *c*. 95% of yearling and adult females reproduced (Cypher, 2003), and that every mated pair produced *c*. 3.8 offspring (Fritzell & Haroldson, 1982; Fritzell, 1987; Cypher, 2003). Finally, our estimated rates of annual adult survival (separated into a May–August rate and a September–April rate) and 8-month (September–

April) pup survival were used to produce the 4-month (May–August) pup survival rate.

RESULTS

Of the 24 foxes that were monitored, 12 died during the study (the others either survived or had collars that failed or fell off). Of the seven foxes dying of predation whose home ranges could adequately be described, three were found dead outside the home range, three were found dead on the 95% isopleth of the home range, and one was found dead on the 85% isopleth, using the MCP estimate. When using the FK estimate, five predated foxes were found dead outside the home range, and the other two predated foxes were found dead within the 75% isopleth of the home range (Fig. 1).

The annual survival rate for adult foxes was 0.58 ($n = 17$), and the 8-month (September–April) survival rate

Table 1. Survival and cause-specific mortality rates (Heisey & Fuller, 1985) of radio-marked gray foxes *Urocyon cinereoargenteus* monitored in the Santa Monica Mountains during May 1997–May 1999

| | | No. of | | | Annual survival | | Cause-specific mortality rate | |
| | | Foxes | Radio-days | Deaths | | | Predation | Unknown |
Age	Sex				Rate	95% CI		
Adult	F	5	2028	2	0.69	(0.41–1.00)	0.31[b]	0.00
	M	12	3162	6	0.49	(0.27–0.88)	0.51[c]	0.00
	Both	17	5190	8	0.58	(0.39–0.85)	0.42	0.00
Juvenile	F	4	254	2	0.40[a]	(0.11–1.00)	0.38[d]	0.22
	M	3	324	2	0.30[a]	(0.06–1.00)	0.70[e]	0.00
	Both	7	578	4	0.34[a]	(0.11–0.99)	0.54	0.12

[a] 8-month mortality rate (September–April).
[b] One death caused by a coyote and one caused by an unknown predator.
[c] Five deaths caused by coyotes and one caused by a bobcat.
[d] One death caused by a coyote and one cause unknown.
[e] One death caused by a coyote and one caused by a bobcat.

Table 2. Calculations of potential population change for gray foxes *Urocyon cinereoargenteus* (hypothetical $n = 100$) in the Santa Monica Mountains, California, based on observed values in this study and on other values from the literature, and indicating (bold italics) the survival rate of 0.4-month-old pups necessary for a stable population (i.e. $\lambda = 1.00$)

| | No. of foxes | | | | | | |
| | Adults | | Yearlings | | Pups | | |
Date	M	F	M	F	M	F	Total
1 May	29	29	21	21			100
Reproduction	$(29 \times 0.95 \times 3.8) +$		$(21 \times 0.95 \times 3.8) =$		91.0	91.0	
Interval survival	0.75		0.75		*0.68*		
1 September	21.8	21.8	15.8	15.8	61.9	61.9	
Survival	0.77		0.77		0.34		
30 April	16.8	16.8	12.2	12.2	21.0	21.0	
1 May	29.0	29.0	21.0	21.0			100

for pup foxes from capture date until they were considered adults was 0.34 ($n = 7$) (Table 1). Statistical differences in survival rate estimates between years, sexes, or ages ($P > 0.50$) were not identified, probably because of low statistical power owing to small sample size. Nevertheless, adult gray foxes had an 8-month (September–April) survival rate of 0.77, which is more than twice the survival estimate of 0.34 for pups during the same interval.

Predation was the cause of mortality for 11 of 12 known deaths, while one female pup died of unknown cause (but not predation). Coyotes killed at least one female adult, five male adults, one female pup, and one male pup, while bobcats killed at least one male adult and one male pup. For one female adult, neither coyotes nor bobcats could be ruled out as the cause of death. The estimated annual probability of an adult gray fox being killed by a larger predator (coyote or bobcat) was 0.42 (because all dead adult foxes were preyed on).

Most predated gray foxes had puncture wounds in the neck, scapula, thoracic area, and vertebral column. One female adult, one male adult, and one female pup were partially eaten. One male adult and one male pup were partially consumed and cached (i.e. by a bobcat). Only one fox, a male pup, was fully consumed; everything except the head and limbs was eaten.

Based on our own data and those from the literature, our demographic calculations indicated that survival of pups during their first 4 months of life would need to be 0.68 (Table 2) for the hypothetical fox population to be stable from year to year. This is slightly lower than adult survival for the same interval (0.75), and a bit higher than a 4-month rate for older pups (0.58, based on an 8-month rate of 0.34). Overall, pup survival during their first year of life would be 0.23 (0.68×0.34) in our calculations.

DISCUSSION

Gray foxes live sympatrically with coyotes (Johnson, Fuller & Franklin, 1996), but they seem to avoid coyote activity areas temporally and/or spatially as a strategy to avoid fatal encounters (Ingle, 1990; Lovell, 1996; but see Neale & Sacks, 2001). It was found that most depredated foxes were killed outside or on the periphery of their ranges. This phenomenon has also been documented for swift foxes *Vulpes velox* by Sovada *et al.* (1998) and Kitchen *et al.* (1999), whose observations showed that predation of swift foxes usually occurred away from dens and core activity areas. These authors suggested that swift foxes are more vulnerable to coyote predation in peripheral

areas of their home range. Coyotes in southern California may be more successful in killing gray foxes in places not commonly visited by foxes, and gray foxes may have lower predation risk in familiar places where they may hide, climb shrubs or trees, or move fast enough to avoid confrontations with larger predators.

Our results further confirm the suggestion that intra-guild predation is a common cause of mortality for gray foxes (92% (11/12) of known deaths) when sympatric with potentially interfering species such as coyotes and bobcats (Polis, Myers & Holt, 1989; Polis & Holt, 1992; Palomares & Caro, 1999). In our study, 67% (8/12) of gray fox deaths could be attributed to coyote predation, 17% (2/12) to bobcat predation, and 8% (1/12) to no specific predator. Other authors have reported similar magnitudes of intra-guild predation of foxes by larger carnivores. In the Carrizo Plains of California, larger predators accounted for 78% (18/23) of kit fox *Vulpes macrotis* mortalities: coyotes accounted for 64% (14/22) of deaths, red foxes *Vulpes vulpes* killed two kit foxes, and a domestic dog killed one (Ralls & White, 1995). In the Naval Petroleum Reserves of California, the mean annual proportion of mortalities of kit foxes caused by predation was 76% for adults and 83% for pups (Cypher & Spencer, 1998). Coyote-caused mortalities accounted for 63% (20/32) of swift fox deaths in western Kansas (Sovada *et al*., 1998) and 48% in Colorado (Kitchen *et al*., 1999). In north-western Texas, coyote predation on swift foxes was relatively higher where coyote density was higher, and subsequent removal of coyotes in one area resulted in increased survival, density, and recruitments of swift foxes (Kamler *et al*., 2003).

Most of our predated gray foxes were killed by coyotes but not consumed, suggesting that interference competition was the primary motivating factor. Other authors report that coyotes kill foxes to reduce interspecific competition, and that it is uncommon for coyotes to feed upon foxes. Disney & Spiegel (1992) reported that coyotes rarely ate carcasses of kit foxes. Sovada *et al*. (1988) reported that from 20 swift foxes killed by coyotes, only one fox was eaten and two were cached. Kitchen *et al*. (1999) found the carcasses of the majority of predated swift foxes intact, but caching of fox carcasses occurred occasionally. Ralls & White (1995) report that nine of 15 kit foxes killed by coyotes were partially eaten, but their study was conducted during a period when prey availability was low. Several authors have suggested an inverse relationship in population density between coyotes and gray foxes (Trapp & Hallberg, 1975; Soule *et al*., 1988; Johnson *et al*., 1996; Crooks & Soule, 1999; Fedriani *et al*., 2000), and the only experimental testing of the assumption (Henke & Bryant, 1999) supports this notion.

Our estimates of survival do not suggest that the studied population of gray foxes was greatly decreasing or increasing. Our adult annual survival rate (0.58) was somewhat lower than for a fox population in South Carolina that was not trapped (0.69; Weston & Brisbin, 2003), but about the same as that of a trapped population in Mississippi (0.56; calculated from data in Chamberlain & Leopold, 2000). The relatively low survival rates for pups in this study (compared to adult survival rates) are consistent with other estimates where coyote predation is the main cause of death for foxes. Ralls & White (1995) estimated the annual survival of adult kit foxes to be 0.58–0.61, and 0.21 for pups. Sovada *et al*. (1998) estimated an 11-month survival rate of 0.45 for adult kit foxes and a 6-month survival of 0.33 for pups. Cypher & Spencer (1998) reported an annual survival rate of 0.39 for adult kit foxes and of 0.20 for pups. Several authors document that the high reproductive rates of foxes may compensate for high mortality, but that predation may contribute to decreasing fox populations during periods of low reproduction (Ralls & White, 1995; Sovada *et al*., 1998).

Gray foxes in southern California may be avoiding the places and times of high predation risk (Fedriani *et al*., 2000) to coexist with coyotes and bobcats. Our radio-marked gray foxes were mainly nocturnal and crepuscular, probably to reduce predatory pressures during the day, and probably preferred northern mixed chaparral because dense vegetation provides escape cover and has a lower predator abundance (Farias, 2000). Gray foxes probably have a high predation risk outside or on the borders of their home ranges because these areas are less familiar places that provide less chance of avoiding agonistic encounters. Our estimate of predator-caused mortalities (92%) is high compared to other published estimates of intra-guild predation among mammalian carnivores (Palomares & Caro, 1999). Several authors identify coyotes as the primary cause of fox mortality, but it is common for foxes to be killed by more than one potential predator. The high percentage of mortalities caused by intra-guild predation in our study suggests that gray foxes in southern California may be more vulnerable to interference competition than other species of foxes of similar size.

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