The Journal of Wildlife Management 76(2):243–252; 2012; DOI: 10.1002/jwmg.247

*Management and Conservation*

# Effects of Roads on Survival of San Clemente Island Foxes

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**ABSTRACT** Roads generate a variety of influences on wildlife populations; however, little is known about the effects of roads on endemic wildlife on islands. Specifically, road-kills of island foxes (*Urocyon littoralis*) on San Clemente Island (SCI), Channel Islands, California, USA are a concern for resource managers. To determine the effects of roads on island foxes, we radiocollared foxes using a 3-tiered sampling design to represent the entire population in the study area, a sub-population near roads, and a sub-population away from roads on SCI. We examined annual survival rates using nest-survival models, causes of mortalities, and movements for each sample. We found the population had high annual survival (0.90), although survival declined with use of road habitat, particularly for intermediate-aged foxes. Foxes living near roads suffered lower annual survival (0.76), resulting from high frequencies of road-kills (7 of 11 mortalities). Foxes living away from roads had the highest annual survival (0.97). Road-kill was the most prominent cause of mortality detected on SCI, which we estimated as killing 3–8% of the population in the study area annually. Based on movements, we were unable to detect any responses by foxes that minimized their risks from roads. The probabilities of road-kills increased with use of the road habitat, volume of traffic, and decreasing road sinuosity. We recommend that managers should attempt to reduce road-kills by deterring or excluding foxes from entering roads, and attempting to modify behaviors of motorists to be vigilant for foxes. © 2011 The Wildlife Society.

**KEY WORDS** California Channel Islands, island fox, mortality, movement, road-kill, survival, *Urocyon littoralis*, vehicle.

Roads are a widespread and increasing feature on most landscapes throughout the world (Trombulak and Frissell 2000), including many small islands. Roads generate a breadth of negative ecological effects for wildlife, such as creating local population declines (Brockie 2007) or altering demography and population structures (Fahrig et al. 1995, Trombulak and Frissell 2000, Forman et al. 2003). Recent reviews indicate that negative effects of roads on wildlife outweighed positive effects by a factor of 5 (Fahrig and Rytwinski 2009), and that roads are a major contributor to loss of biodiversity (Benítez-López et al. 2010). However, of the studies examined, nearly all terrestrial species accounts were from the mainlands of Europe, North America, Australia, Africa, and India; and none were endemic to small islands.

Road-kills and avoidance of roads are among the most conspicuous and well-documented negative effects that roads have on wildlife (Forman and Alexander 1998, Trombulak and Frissell 2000, Litvaitis and Tash 2008, Shepard et al. 2008). Often, the severity of those effects was related to the size of road or volume of traffic (Rosen and Lowe 1994, Fahrig et al. 1995, Klöcker et al. 2006). In particular, roads have been recognized as having negative effects on various species of foxes; although rates of road-kills for foxes were often comparable or lower than other causes of mortality (Disney and Spiegel 1992, Farias et al. 2005, Gosselink et al. 2007). Many foxes have adapted to use habitats with roads (e.g., Riley 2006, Baker et al. 2007, Cypher et al. 2009), and some have reduced their risks of road-kills by avoiding large roads with high volumes of traffic on mainlands (Riley 2006, Baker et al. 2007).

The island fox (*Urocyon littoralis*) provides a good case study for examining the effects of roads on an island species. Island foxes evolved in isolation without high predation pressures, and have been reported to be less vigilant toward introduced threats (Roemer et al. 2001, Swarts et al. 2009), humans (Blake 1887, Grinnell et al. 1937, Laughrin 1977, Moore and Collins 1995), and likely vehicles (Gould 2010, Snow et al. 2011). Island foxes have demonstrated vulnerabilities to novel threats on 4 of 6 California Channel Islands, including 95% population declines on 3 northern Channel Islands from

Received: 21 January 2011; Accepted: 24 May 2011;
Published: 27 September 2011

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predation by colonizing golden eagles (*Aquila chrysaetos*) during 1993–1998 (Roemer 1999, Coonan et al. 2005), and an outbreak of canine distemper virus on Santa Catalina Island during 1999–2000 (Kohlmann et al. 2005, Timm et al. 2009).

Substantial development of roads and vehicular traffic did not occur on San Clemente Island (SCI) until the 1960s (Sturgeon 1999). Shortly after, road-kills were reported as a large source of mortality for island foxes (Laughrin 1977, Moore and Collins 1995, Roemer et al. 2004, Spencer et al. 2006). Various types of mitigation including warning signs, reduced speed limits, and mowing vegetation along roadsides have been implemented to reduce road-kills, but no reduction has been observed (Spencer et al. 2006, Snow 2009). Since 2000, approximately 30 foxes per year have been opportunistically found killed by vehicles on SCI (D. K. Garcelon, Institute for Wildlife Studies, unpublished data).

To our knowledge, no studies have addressed the impacts of roads on populations of island species. Our objective was to examine annual survival and causes of mortality for 3 samples of radiocollared island foxes on SCI, including: 1) a spatially balanced random sample from the entire study area, 2) a sample of foxes living near roads, and 3) a sample of foxes living away from roads. We also examined the movements of foxes in relation to roads, and characteristics of roads rhat influenced the probability of road-kills. We hypothesized that foxes living near roads would sustain lower survival. We also hypothesized that foxes would avoid roads with increased traffic, and would show less avoidance of roads during periods of low traffic. Lastly, we hypothesized that the probability of road-kills increased as foxes spent more time near roads; and for foxes that had home ranges near roads with increased traffic volume, traffic speed, paved surface, and reduced motorist visibility (e.g., increased road sinuosity).

## STUDY AREA

San Clemente Island is the southernmost of the California Channel Islands, located approximately 109 km west of San Diego, California. Our study area (80.6 km$^2$) was located on the northern portion of SCI, except for the extreme northern tip (2.1 km$^2$) and steep eastern escarpment (7.4 km$^2$), and covered approximately 55% of the island (Fig. 1). The vegetation was comprised primarily of maritime desert scrub (54%) and grassland (33%; Thorne 1976, Sward and Cohen 1980), although several other habitat types were interspersed (Roemer et al. 2004). About 7% of the island was designated as disturbed with naval facilities and roads, and foxes occurred in all habitats including the disturbed land (Roemer et al. 2004). The island was characterized as belonging to the Mediterranean Dry Summer Subtropical climatic type, with a cool summer regime (Kimura 1974, Yoho et al. 1999). The mean temperature was 17° C and annual precipitation averaged 13 cm with 95% falling during November through April, the wet season (Yoho et al. 1999).

San Clemente Island had a relatively extensive road network (Moore and Collins 1995). We focused on the primary roads of SCI, including Ridge Road (24.3 km) that ran north–south through the center of the island, and Perimeter Road (7.9 km) that encircled the airfield on rhe northern tip, resulting in a density of 0.32 km of roads/km$^2$ (Fig. 1). The surface of Ridge Road was a mixture of paved (68%) and gravel (32%), whereas Perimeter Road was entirely paved. The maximum speed limit was 56 km/hr, although 40 km/hr was posted in some urban and curved segments. Snow et al. (2011) used traffic recorders during 2007–2008 and determined that vehicles averaged between 47 km/hr and 60 km/hr and volume of rraffic averaged 60–366 vehicles/day, depending on the segment of road monitored. Approximately 90% of all traffic volume occurred during daytime hours (Snow 2009). All primary roads were 2 lanes and most did not have maintained shoulders. Other secondary roads were present on SCI, but were infrequently driven and not developed, and therefore were not included in our study.

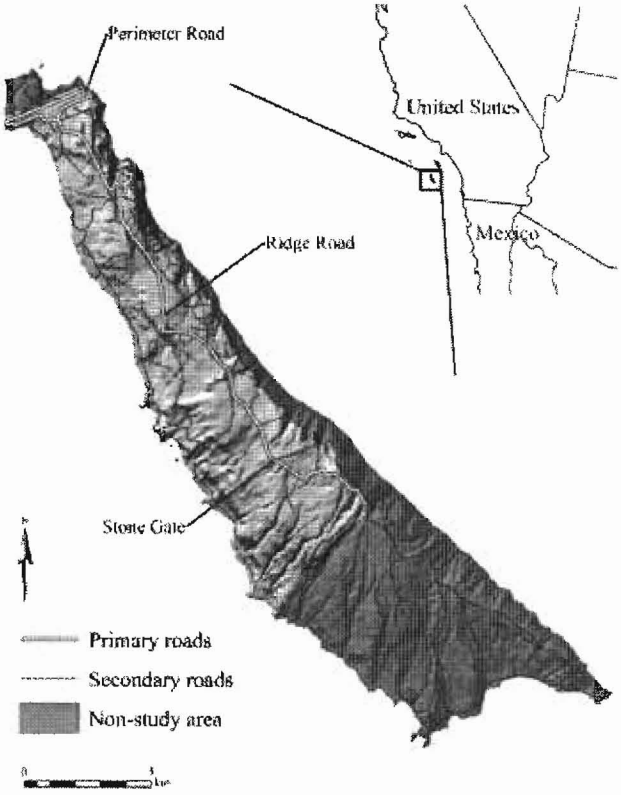


**Figure 1.** Study area for examining the effects of roads on survival of San Clemente Island foxes, California, USA, July 2006–December 2007.

## METHODS

### Random Sample

We used ArcGIS (v9.1; Environmental Systems Research Institute, Inc., Redlands, CA) and the Reversed Randomized Quadrant-Recursive Raster algorithm (Theobald et al. 2007) to generate random, spatially-balanced locations for capturing a random sample of foxes throughout the study area. During July to August 2006, we set cage traps (Tomahawk

Live Trap Co., Tomahawk, WI) equipped with acrylic glass on the inside of doors and chew-bars (i.e., polyethylene tubing) inside the traps to reduce potential injuries to animals for 2 nights at each location. We fitted all captured adult foxes ($\geq$1.4 kg) with approximately 45 g radio-telemetry collars ($\leq$3% of body weight) equipped with mortality sensors (M1930; Advanced Telemetry Systems, Isanti, MN). We replaced radiocollared foxes that died before March 2007 by capturing and collaring additional foxes at new trapping locations. Techniques for capturing, handling, collaring, and monitoring foxes were approved by Colorado State University's Institutional Animal Care and Use Committee (protocol 06-098A-01), and by a memorandum of understanding with California Department of Fish and Game.

We assigned ages to all radiocollared foxes at the time of capture according to amount of wear on the first upper molar (Wood 1958, Collins 1993): 0–12 months (age class 0), 13–24 months (age class 1), 25–36 months (age class 2), 37–48 months (age class 3), and $\geq$49 months (age class 4). To improve our estimates of age, we also verified and corrected our estimates using 2 methods. For all foxes found dead, we extracted an upper canine tooth to estimate age from tooth cementum layers (Matson's Laboratory, Milltown, MT). Also, because many foxes on SCI had been marked with Passive Integrated Transponders during previous studies, we referenced databases from previous years (D. K. Garcelon, unpublished data) to ascertain the year of birth. Following Wood (1958), we used the corrected estimates to calculate continuous estimates of age for each fox at the time of capture, assuming a consistent birthdate each year (i.e., 21 February; see Snow et al. 2011). We considered foxes estimated at $\leq$2 years as juvenile and young foxes, 2–6 years as intermediate-aged foxes, and >6 years as old foxes.

### Monitoring and Home Range

During July 2006 to December 2007, we triangulated most radiocollared foxes from 4 × 4 vehicles equipped with dual 6-element antennas connected to a receiver (R2000; Advanced Telemetry Systems), although some foxes were located on foot with a 3-element Yagi antenna. Most foxes were located using 3 bearings obtained <5 min apart with inter-bearing angles $\geq$20°, or by visual observations. We located most foxes every 1–1.5 weeks during 8-hr tracking periods (i.e., 4 locations at 2-hr intervals), alternated throughout the 24-hr cycle. We located reference radio-transmitters every month to estimate error of our telemetry equipment and to correct our bearings.

We estimated locations from triangulations primarily using the Andrews M-Estimator (White and Garrott 1990) within Location of a Signal (v3.2, LOAS™; Ecological Solutions Software LCC, Sacramento, CA) software. We discarded locations with larger than acceptable error tolerances (error ellipses $\geq$52,500 m$^2$ and error polygons $\geq$22,711 m$^2$) based on observations of our data, following Schmutz and White (1990). We estimated 95% fixed kernel home range boundaries (Worton 1989, 1995; Seaman and Powell 1996; Seaman et al. 1999) using least-squares cross-validation for bandwidth selection (Worton 1989, Seaman et al. 1999, Powell 2000) with the Animal Movement SA Extension (v2.04 beta; Hooge and Eichenlaub 2000) for ArcView (v3.3). We used home ranges to quantify characteristics of the primary roads inside each home range boundary, for use as covariates in analyses of survival.

### Road and Non-Road Samples

We divided Perimeter Road and Ridge Road (i.e., Perimeter Road to Stone Gate; Fig. 1) into equal segments (1.2 km), which approximated the diameter of home ranges reported for foxes on SCI (Schmidt et al. 2004). During August–September 2006, preliminary telemetry data indicated some radiocollared foxes in the random sample already occupied some segments of roads. We increased our sample size near roads by setting traps for 2 nights at random locations <10 m from the road, and radiocollating 1 captured fox in all unoccupied segments. We did not consider foxes intentionally captured near roads when making inference from the random sample to the entire population. We replaced radiocollared foxes that died or moved away from the road before August 2007 using new trapping locations along the original segment of road.

We drew the straight line paths connecting pairs of consecutive, 2-hr interval locations for each fox using Hawth's tools extension for ArcGIS (Hawth's Tools, www.spatialecology.com/htools/index.php, accessed 1 Nov 2010). We considered any temporary movement $\geq$1 km ourside the home range as an extraterritorial excursion (Adams et al. 2008, Skuldt et al. 2008). To quantitatively classify foxes as road foxes, we compared the proportions of movements considered as extraterritorial excursions to the proportion of movements that crossed roads. We classified foxes as part of the road sample if the proportion of movements crossing roads was greater than the highest proportion of excursions observed from any radiocollared fox. We classified all other foxes into the non-road sample. Foxes from the random sample were considered in road and non-road samples, respectively. We compared the proportions of males and females within the road and non-road samples using Fisher's Exact test ($P < 0.05$; PROC FREQ; SAS Institute Inc., Cary, NC).

### Movement Near Roads

Following findings of Lovallo and Anderson (1996), we designated the primary roads and a buffer extending 100 m on both sides as road habitat, representing 6.4 km$^2$ (7.9% of the study area). We calculated the proportions of locations estimated to be in road habitat for each fox (RD_LOCS). We compared RD_LOCS to the proportion of road habitat area inside each home range with a paired $t$-test (PROC TTEST). We also compared RD_LOCS between night and day, by considering night locations as 1 hr after sunset to 1 hr before sunrise (National Oceanic and Atmospheric Administration, www.srrb.noaa.gov/highlights/sunrise/sunrise.html, accessed 6 Nov 2009).

Considering most traffic occurred during the day, we examined the proportion of movements that crossed the primary roads (CROSSINGS) during the night and day. We

normalized CROSSINGS for levels of nocturnal and diurnal activity using the average lengths of movements (m) during nights and days for each fox (Baker et al. 2007). We compared the normalized CROSSINGS between night and day with a paired $t$-test.

We also considered how variation in daily traffic volume (VOLUME) and speed (SPEED) affected CROSSINGS, using averages estimated with traffic recorders for 6 uniform segmenrs of the primary roads (see Snow et al. 2011). We examined if CROSSINGS were influenced by VOLUME, SPEED, and the interaction using an analysis of variance (ANOVA; PROC GLM).

### Cause-Specific Mortality

We located dead foxes when we detected mortality signals, examined carcasses for obvious signs of death, and shipped them to University of California, Davis for necropsy. We performed comprehensive gross necropsies and microscopic examinations of major organs on intact carcasses. If foxes were extensively decomposed or scavenged, only skeletal remains were examined for evidence of trauma. We determined the primary causes of mortality, and classified each cause into 4 categories, including: 1) road-kill, 2) disease, 3) injury not from vehicle, or 4) undetermined because of advanced post-mortem decomposition. When the cause of mortality was considered undetermined, we could not eliminate road-kills as a potential cause because some foxes moved (or were moved) off the road following a collision.

We attempted to recover any non-radiocollared foxes that were road-kills. We drove the primary roads ($\leq$56 km/hr), and scanned for signs of dead foxes 4–7 times each week, while conducting radio-telemetry. We found dead foxes based on our observations of carcasses or blood spots on roads, and voluntary reporting by personnel on SCI.

### Survival

We examined our data for pairs of highly cortelated variables ($r \geq |0.7|$; PROC CORR) and found that none of our covariates required exclusion due to collinearity. We estimated annual survival rates for the random, road, and non-road samples using a known-fate, nest-survival model that incorporated telemetry data with staggered entties in Program MARK (White and Burnham 1999, White et al. 2001). We described variation in survival using a priori and biologically meaningful models (Freedman 1983, Anderson et al. 2000, Anderson and Burnham 2002, Burnham and Anderson 2002). We used weekly encounter histories starting with the date of capture and followed by subsequent relocations via radio-telemetry until the fox was found dead, the radio signal was no longer heard ($n$ = 5), or until the study ended.

For the random sample, we evaluated 22 a priori models that considered RD_LOCS, biological covariates (SEX, WT, AGE, and SEASON [wet or dry]), and the interaction of [RD_LOCS × AGE] for influences on survival, to make inferences to the fox population on northern SCI. We also considered $AGE^2$ to ascertain if survival rates were highest or lowest for intermediate aged foxes. Finally, we evaluated 3 post-hoc models, which included the interaction of [RD_LOCS × $AGE^2$].

To compare survival of the road and non-road samples, we evaluated 16 a priori models that considered influences from road or non-road status (STATUS), biological covariates (SEX, WT, AGE, $AGE^2$), and the interactions of [STATUS × SEX], [STATUS × AGE], and [STATUS × $AGE^2$] on survival. We excluded 1 fox because it died prior to determining its inclusion in the road or non-road samples.

We used the minimum corrected Akaike Information Criterion ($AIC_c$) to select the best models for predicting survival, and averaged over all models to estimate annual survival rates (Burnham and Anderson 2002, Anderson 2008). We estimated standard errors and 95% confidence intervals for coefficients with the Delta method (Seber 1982), and examined the intervals for overlap of zero to ascertain which covariates had clear effects on survival (Burnham and Anderson 2002). We interpreted top models by back-transforming from the logit scale and plotting changes in annual survival.

We estimated an annual mortality rate for each sample by subtracting the annual survival rate from 1. Then we multiplied the overall mortality rates by the proportion of road-kills to obtain the rates of road-kills for each sample. Because causes of death were occasionally undetermined, we estimated ranges for the rates of road-kills.

### Probability of Road-Kills for Road Sample

We examined the probability of a road-kill occurring using modified nest-survival models for the road sample. We considered foxes that were conclusively killed by vehicles as dead and foxes found dead from other causes as alive in the dataset, but their final encounter was their last date known alive (i.e., the telemetry location preceding their death).

We evaluated 38 a priori models to examine the influences of various characteristics of roads on the probability of road-kills. We calculated the average traffic SPEED and VOLUME of traffic inside each home range. We calculated the sinuosity of roads (SINUOSITY) inside home ranges by calculating the ratio of road length to straight-line distance (Ratzlaff 1991) with Hawth's tools extension. We also estimated the proportions of paved roads (PAVED) inside each home range. Finally, we examined for influences from movements near roads (RD_LOCS and CROSSINGS) and biological covariates (SEX, WT, AGE, and SEASON). We also evaluated some a priori interactions of these variables including [SPEED × VOLUME], [RD_LOCS × SPEED], [RD_LOCS × VOLUME], and [CROSSINGS × PAVED]. We discovered SEX could only be modeled alone, using a sine-link, because no male foxes were killed by vehicles. Therefore, we used ANOVAs to determine if any influential covariates differed by SEX.

## RESULTS

We radiocollared 72 island foxes, including 53 foxes for the random sample (proportion males = 0.45). Thirteen foxes

from the random sample and 18 foxes intentionally radiocollared near roads met our criteria for inclusion in the road sample. Forty foxes from the random sample, plus 1 additional fox (intentionally radiocollared near a road, but found to have a home range away from roads) comprised the non-road sample. The proportions of males in the road (0.36) and non-road (0.51) samples suggested little evidence of having a disproportionate sex ratio between samples ($\chi^2_1 = 1.77$, Fisher's Exact $P = 0.08$). The proportions of young, intermediate, and old-aged foxes were consistent among samples (Fig. 2). Overall, we relocated radiocollared foxes >8,200 times during 17 months of monitoring.

### Movement Near Roads

The boundaries of the 95% fixed kernel home ranges for all foxes in the road sample overlapped the primary roads. Foxes were proportionately located within the road habitat ($\bar{x} = 0.28$, SE = 0.03) similar to expected based on the proportion of road habitat area ($\bar{x} = 0.29$, SE = 0.02) in their home range ($t_{30} = -0.55$, $P = 0.587$). Also, we did not detect a difference between the proportion of locations in the road habitat between the days ($\bar{x} = 0.25$, SE = 0.04) and nights ($\bar{x} = 0.31$, SE = 0.03) for the road sample ($t_{30} = -1.44$, $P = 0.160$). Six of 8 radiocollared foxes killed by vehicles were killed inside or near the boundaries of their home ranges.

For the road sample, the distances moved (m) between locations during the days ($\bar{x} = 174.2$, SE = 16.1) and nights ($\bar{x} = 401.3$, SE = 22.1) showed higher activity at night ($t_{60} = -8.30$, $P < 0.0001$). Similarly for the non-road sample, the distances moved during the days ($\bar{x} = 205.2$, SE = 19.2) and nights ($\bar{x} = 330.7$, SE = 18.5) showed higher activity at night ($t_{58} = -4.70$, $P < 0.0001$). The proportion of movements that crossed roads during days ($\bar{x} = 0.08$, SE = 0.01) and nights ($\bar{x} = 0.32$, SE = 0.03) showed more crossings occurred at night when normalized for levels of activity ($t_{60} = -2.47$, $P = 0.016$). However, CROSSINGS were not influenced by speeds of traffic ($\beta = -0.03$, 95% CI = −0.06–0.002), volume of traffic ($\beta = -0.004$, 95% CI = −0.01–0.002), or the interaction ($\beta = 0.0001$, 95% CI = −0.00002–0.0002). On average,

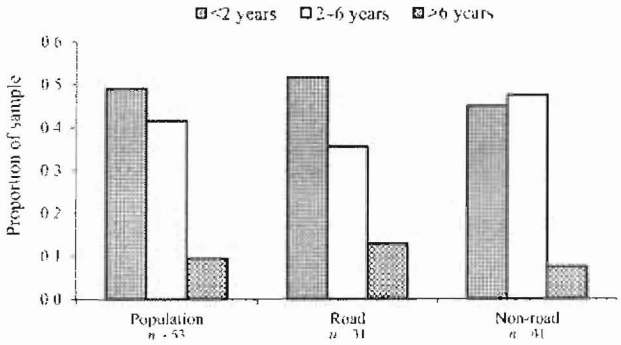


**Figure 2.** Distribution of ages (estimated in years) for each sample of island foxes captured on San Clemente Island, California, USA, July 2006–December 2007. Foxes estimated at ≤2 years were considered as juvenile and young foxes, 2–6 years were intermediate-aged foxes, and >6 years were old foxes.

foxes in the road sample crossed the primary roads at least twice in a 24-hr period, with 72% of all crossings occurring at night. We also detected 38% (20) of foxes in the random sample crossed the primary roads at least once during our study.

### Cause-Specific Mortality

We found 7 of 53 (13%) foxes in the random sample dead, including 2 road-kills (Table 1). We found 2 of the 3 undetermined mortalities dead near the primary roads and these foxes had home ranges that overlapped the roads; thus collision with a vehicle could not be excluded as a potential cause. Ultimately, between 3% and 6% of the random sample was killed by vehicles.

For the road sample, we found 11 of 31 (36%) foxes dead, including 7 road-kills (Table 1). For the non-road sample, we found 3 of 41 (7%) foxes dead. We found 1 non-road fox, presumed dead by road-kill, near a secondary road.

We recovered 34 non-radiocollared foxes killed by vehicles in our study area, which resulted in 42 road-kills including radiocollared foxes. This approximated 30 road-kills per year that were detected in the study area.

### Survival

We found a high annual rate of survival for our random sample, and survival of males and females did not differ (Table 2). The top model represented 74% of the model set weight, and indicated that the covariates RD_LOCS, AGE, AGE$^2$, RD_LOCS × AGE, and RD_LOCS × AGE$^2$ best fit our data (Table 3). By plotting this model, we identified that survival rates decreased as the proportions of road locations increased, particularly for intermediate-aged foxes (Fig. 3).

The road sample had considerably lower annual survival than the non-road sample, and survival for males and females did not vary within samples (Table 2). No model held a majority of the model-set weight, but the top models indicated that STATUS, AGE, and AGE$^2$ had the most influence on survival. Our top model indicated the strongest effects on survival were STATUS ($\beta = -2.11$, 95% CI = −3.46 to −0.76) and AGE$^2$ ($\beta = -0.10$, 95% CI = −0.19 to −0.01; Table 3). This model indicated that survival was highest for foxes living away from roads, and for intermediate aged foxes. Additionally, we found annual mortality rates from road-kills were highest for the road sample and lowest for the non-road sample.

### Probability of Road-Kills for Road Sample

Five of 8 radiocollared foxes were killed by vehicles during night from dawn to dusk, and times of death for 3 foxes were unknown. The average length of primary roads within the home ranges of each road fox was 1.2 km (SE = 0.12; range = 0.16–3.12 km). We found the post-hoc model with RD_LOCS ($\beta = 11.07$, 95% CI = 2.51–19.62), VOLUME ($\beta = 0.01$, 95% CI = 0.001–0.02), and SINUOSITY ($\beta = -14.96$, 95% CI = −27.63 to −2.29) best fit our data for predicting the probability of road-kills (Table 3). Foxes that were killed by vehicles were located in the road habitat a larger proportion of time ($\bar{x} = 0.34$, SE = 0.06) than those not killed ($\bar{x} = 0.26$, SE = 0.02).

Table 1. Causes of death for a random sample, a road sample, and a non-road sample of radiocollared island foxes on northern San Clemente Island (SCI), California, USA, July 2006–December 2007.

| Fox no. | Sex | Random sample[a] | Road sample[b] | Cause of death[c] | Estimated age at death (yrs) | Distance found from road (m) |
|---|---|---|---|---|---|---|
| 1 | F | Y | NA | Undetermined | 10 | 1,570 |
| 2 | F | Y | N | Undetermined | 5 | 190 |
| 3 | M | Y | Y | Undetermined | 3 | 310 |
| 4 | M | Y | N | Injury | 3 | 160 |
| 5 | F | Y | Y | Disease | 2 | 40 |
| 6 | M | N | Y | Disease | 7 | 270 |
| 7 | M | N | Y | Disease | 9 | 175 |
| 8 | F | N | Y | Road-kill | 6 | 20 |
| 9 | F | N | Y | Road-kill | 1 | 0 |
| 10 | F | N | Y | Road-kill | 1 | 0 |
| 11 | F | N | Y | Road-kill | 2 | 0 |
| 12 | F | N | Y | Road-kill | 5 | 0 |
| 13 | F | N | Y | Road-kill | 3 | 20 |
| 14 | F | Y | Y | Road-kill | 2 | 5 |
| 15[d] | F | Y | N | Road-kill | 10 | 195 |

[a] Radiocollared foxes captured using spatially balanced trapping locations from northern SCI.
[b] Radiocollared foxes that crossed roads on a greater than excursionary basis. Foxes in the road sample were captured as part of the random sample or were intentionally captured near roads.
[c] Causes of death included: 1) undetermined due to autolysis; 2) injury, non-vehicle related; 3) disease, impairment of health or normal function; and 4) road-kill.
[d] The likely cause of death for fox no. 15 was road-kill because type of injury (i.e., head trauma) was typical of collisions with vehicles.

Additionally, the home ranges of foxes killed by vehicles contained higher amounts of vehicles/day ($\bar{x}$ = 246.8, SE = 43.2) than those not killed ($\bar{x}$ = 151.2, SE = 19.6). Finally, the home ranges of foxes killed by vehicles had less road sinuosity ($\bar{x}$ = 1.08, SE = 0.07) than those not killed ($\bar{x}$ = 1.11, SE = 0.03).

We found 7 of 20 females and 0 of 11 males in the road sample were killed by vehicles, and therefore SEX was also a strong predictor of road-kills ($\beta$ = −0.17, 95% CI = −0.31 to −0.03). However, we did not detect any differences between males and females in RD_LOCS ($\beta$ = 0.16, 95% CI = −0.95–1.27), VOLUME ($\beta$ = −0.0006, 95% CI = −0.002–0.001), and SINUOSITY ($\beta$ = 0.33, 95% CI = −0.94–1.60).

## DISCUSSION

Overall, we identified that the population of foxes in our study area was experiencing a high rate of survival compared to foxes found on the mainland, United States (e.g., Farias et al. 2005, Gosselink et al. 2007). This result is not unexpected for SCI, based on a possible lack of interspecific competition (Phillips er al. 2007), predation, or outbreak of infectious diseases. Previous reports of island foxes have also suggested that survival was high (Moore and Collins 1995, Coonan et al. 2005), but only in the absence of major threats. When major threats did occur on other Channel Islands (e.g., predators or disease), survival rates dropped to nearly 0 (Coonan et al. 2005, 2010). On SCI, we observed that the proportion of time that foxes used the road habitat was the main contributor to reducing survival. Also, we identified road-kills as the largest source of morrality for the popularion.

We validated the results from the random sample by discerning that the road sample had substantially lower survival than the non-road sample. Road-kills were the largest source of mortality for the road sample. Foxes living away from the primary roads showed very high survival, and road-kills were not common. Studies of mainland foxes have indicated that road-kills affected survival (Farias et al. 2005, Gosselink et al. 2007), although no studies have compared survival of road and non-road samples within a population. In srudies where movemenrs and mortalities were analyzed in relation

Table 2. Annual survival and rares of road-kill for a random sample, a road sample, and a non-road sample of island foxes on northern San Clemente Island (SCI), California, USA, July 2006–December 2007.

| | | | Males and females | | Males | | Females | | |
|---|---|---|---|---|---|---|---|---|---|
| Sample[a] | $n$ | Deaths | $S$[b] | 95% CI | $S$ | 95% CI | $S$ | 95% CI | Annual rate of road-kill[c] |
| Random | 53 | 7 | 0.90 | 0.66–0.98 | 0.90 | 0.64–0.98 | 0.90 | 0.66–0.98 | 0.03–0.06 |
| Road | 31 | 11 | 0.76 | 0.57–0.89 | 0.78 | 0.55–0.91 | 0.75 | 0.55–0.89 | 0.15–0.17 |
| Non-road | 41 | 3 | 0.97 | 0.86–0.99 | 0.97 | 0.85–0.99 | 0.96 | 0.85–0.99 | 0.01–0.02 |

[a] Foxes were considered in the random sample if they were captured using sparially balanced trapping locations from northern SCI. Foxes were considered in the road sample if rhey crossed roads on a greater than excursionary basis. Foxes in rhe road sample were captured as part of the random sample or were intentionally captured near roads. Foxes not in the road sample were considered in the non-road sample.
[b] Annual survival rate estimated using known fate, nest-survival models and model averaging.
[c] We report a range because some causes of death were underermined and road-kills could nor be eliminated as a potential cause.

**Table 3.** Model selection results for the top 5 nest-survival models used to determine influences on survival and probability of road-kills on San Clemente Island, California, USA, June 2006–December 2007. We ranked candidate models within groupings using change in Akaike's Information Criterion ($\Delta AIC_c$) and Akaike weight ($w_i$).

| Candidate model by sample[a] | $K$[b] | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | Model likelihood | Deviance |
|---|---|---|---|---|---|---|
| Survival for random sample | | | | | | |
| RD_LOCS + AGE + AGE$^2$ + [RD_LOCS × AGE] + [RD_LOCS × AGE$^2$] | 6 | 86.863 | 0.000 | 0.741 | 1.000 | 74.838 |
| RD_LOCS + AGE + AGE$^2$ + [RD_LOCS × AGE] + [RD_LOCS × AGE$^2$] + SEX + WT + SEASON | 9 | 92.329 | 5.466 | 0.048 | 0.065 | 74.275 |
| RD_LOCS + AGE + [RD_LOCS × AGE] | 4 | 92.384 | 5.520 | 0.047 | 0.063 | 84.371 |
| AGE + AGE$^2$ | 3 | 92.903 | 6.040 | 0.036 | 0.049 | 86.896 |
| RD_LOCS + AGE + AGE$^2$ + [RD_LOCS × AGE] | 5 | 93.486 | 6.623 | 0.027 | 0.037 | 83.468 |
| Survival for road vs. non-road samples | | | | | | |
| STATUS + AGE + AGE$^2$ | 4 | 172.163 | 0.000 | 0.337 | 1.000 | 164.154 |
| STATUS + AGE + AGE$^2$ + SEX | 5 | 173.520 | 1.356 | 0.171 | 0.508 | 163.505 |
| STATUS + AGE + AGE$^2$ + [STATUS × AGE$^2$] | 5 | 174.149 | 1.985 | 0.125 | 0.371 | 164.134 |
| STATUS + AGE | 3 | 174.567 | 2.404 | 0.101 | 0.301 | 168.561 |
| STATUS + AGE + AGE$^2$ + SEX + WT | 6 | 175.452 | 3.289 | 0.065 | 0.193 | 163.431 |
| Probability of road-kill for road sample | | | | | | |
| RD_LOCS + VOLUME + SINUOSITY | 4 | 84.375 | 0.000 | 0.234 | 1.000 | 76.348 |
| SEX | 2 | 84.551 | 0.176 | 0.214 | 0.916 | 80.543 |
| CROSSINGS | 2 | 87.698 | 3.323 | 0.044 | 0.190 | 83.690 |
| RD_LOCS + SINUOSITY | 3 | 88.400 | 4.025 | 0.031 | 0.134 | 82.384 |
| Null | 1 | 88.622 | 4.247 | 0.028 | 0.120 | 86.619 |

[a] Nest-survival covariates: RD_LOCS = proportion of radio-locations within 100 m of primary roads, AGE = continuous estimate of age at the time of capture, SEX = male or female, WT = weight of fox (kg) at time of capture, SEASON = wet (Nov–Apr) or dry (May–Oct), STATUS = road or non-road sample, VOLUME = average daily traffic volume on primary roads inside 95% fixed kernel home range, SINUOSITY = sinuosity of primary roads inside 95% fixed kernel home range boundary, CROSSINGS = proportion of movements that crossed the primary roads during 8-hr tracking periods at 2-hr intervals, null = model with no covariates.

[b] No. of covariate terms plus an intercept.

to roads, gray foxes (*Urocyon cinereoargenteus*) and San Joaquin kit foxes (*Vulpes macrotis mutica*) in California did not experience frequent road-kills despite their frequent use of roads (Riley 2006, Cypher et al. 2009). This disparity suggests that other factors, such as behavior of foxes or visibility for motorists, may determine how vulnerable a species is to collisions with vehicles.

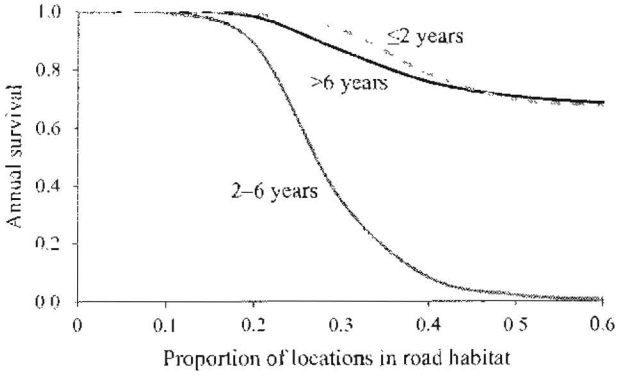


**Figure 3.** Plot of annual survival estimated with top nest-survival model used to predict survival for a random sample of island foxes ($n$ = 53) on northern San Clemente Island, California, USA, July 2006–December 2007. Foxes estimated at ≤2 years were considered as juvenile and young foxes, 2–6 years were intermediate-aged foxes, and >6 years were old foxes. The top model included influences from RD_LOCS ($\beta$ = 55.86, 95% CI = −5.38–117.10), AGE ($\beta$ = 0.99, 95% CI = −0.94–2.93), AGE$^2$ ($\beta$ = −0.14, 95% CI = −0.32–0.03), interaction of RD_LOCS × AGE ($\beta$ = −58.27, 95% CI = −116.16 to −0.39), and interaction of RD_LOCS × AGE$^2$ ($\beta$ = 9.41, 95% CI = −1.86–20.68). We considered road habitat the primary roads and a 100 m buffer on each side.

Based on the movements of island foxes, we were unable to detect any responses that indicated foxes were minimizing their risks associated with roads. Our data showed that radiocollared foxes did not avoid, but were also not attracted to, using roads and nearby habitats. We did not observe foxes shifting between road and non-road status during the study. We also found no indication that roads restricted the movements of foxes. Foxes crossed roads more at night, however, this appeared to be related to nocturnal behavior and not reduced traffic because non-road foxes were also most active at night, similar to island foxes on other Channel Islands (Swarts et al. 2009, Hudgens and Garcelon 2011). Additionally, we found no indication that varying volumes and speeds of traffic influenced the proportions of road crossings. More than half the road-kills occurred at night between dawn and dusk suggesting that increased crossings, even during periods of low traffic, increased the probabilities of road-kills. Also, our finding that 6 of 8 road-kills occurred within or near a home range boundary may be unique to SCI, because another study suggested that foxes were most vulnerable to road-kills in unknown territories, during extraterritorial excursions (Baker et al. 2007).

Our random sample indicated that between 3% and 6% of the population was killed by vehicles annually; however, our recovery of non-radiocollared foxes indicated slightly higher losses. Based on a 2007 population estimate of approximately 386 foxes (95% CI = 320–480) on northern SCI (Andelt

et al. 2009), up to 8% of the population was killed in a year (30 road-kills/386 foxes). However, we noticed that 4 of 8 radiocollared foxes moved (or were moved) off the road following a fatal collision with a vehicle, and likely would not have been found without the aid of radio telemetry. Therefore our detections of road-kills for non-radiocollared foxes were likely underestimates. We observed that approximately 25% of our random sample had home ranges that encompassed the primary roads, suggesting a moderate proportion of the population had increased vulnerability to road-kills.

Few studies have used attributes from animal movements to identify influential variables for predicting road-kills. We found island foxes with home ranges containing higher volumes of traffic had higher probabilities of road-kills, likely because those foxes were exposed to more encounters with vehicles. Our sample of radiocollared foxes experienced varied volumes of traffic within their home ranges (60–366 vehicles/day), but overall the volume on SCI was considerably lower than studies of mainland foxes. For comparison, Cypher et al. (2009) studied roads containing 800–1,500 vehicles/day in San Joaquin Valley, California, and found that San Joaquin kit foxes frequently crossed roads but rarely experienced road-kills. Another study by Grilo et al. (2009) contained roads with 330–2,161 vehicles/day, and suggested that high-volume road segments were barriers to movements and had less road-kill. Additional studies have shown that mainland foxes avoided roads with heavy traffic (Riley 2006, Baker et al. 2007). The volume of traffic on SCI was likely not high enough to elicit a similar response from island foxes.

Roads with fewer curves were also important predictors of road-kills for island foxes, contrary to our original prediction. These sections of roads may be related to locations where speeding motorists drove fastest. Motorists occasionally drove at speeds up to 128 km/hr on SCI (Snow 2009), but we could not differentiate speeds of vehicles actually involved in road-kills. However, in support of our original prediction, our finding that more road-kills occurred during night supports that visibility for motorists is important for predicting where road-kills occur. Furthermore, a recent study identified reduced visibility for motorists as an important characteristic for predicting the locations of road-kills on SCI (Snow et al. 2011).

Another predictor of road-kills for our sample was sex, which differs from other reports that road-kills were not gender-specific (Trombulak and Frissell 2000). Although we found females were killed more often, our results differed from a larger database for SCI, containing opportunistic observations of 223 road-kills since 1998, where 46% were female, 41% were males, and 13% were undetermined (D. K. Garcelon, unpublished data). Thus, we expect the preponderance of road-kills for females in our study might have been by chance alone. Regardless, road-kills of vixens during our study warrant concern because nearly all were of reproductive age, and 5 of 8 were killed when pups may have depended on them (e.g., during Feb–Aug).

Our results also suggested that roads had greater negative effects on survival of intermediate-aged foxes, which differs from findings for mainland foxes (e.g., Gosselink et al. 2007). For mainland species of foxes, age-specific mortality was also influenced by other large sources of mortality (e.g., predation and disease; Farias et al. 2005, Gosselink et al. 2007) that did not occur on SCI. Foxes on SCI were observed using roads for territorial behaviors, such as scent marking (Gould 2010), similar to other canids (e.g., Batja et al. 2005, Whittington et al. 2005). Because intermediate-aged island foxes are the primarily territory holders on SCI (Moore and Collins 1995), territorial behaviors along roads may have increased their risk of road-kills.

Another reason that island foxes on SCI are suffering frequent road-kills could be related to their evolution in isolation. Because island foxes apparently are naïve of predators (Roemer et al. 2001, Swarts et al. 2009) and possibly vehicles (Gould 2010, Snow et al. 2011), they may demonstrate fewer behaviors of avoidance and escape (see Griffin et al. 2000) when approached by vehicles compared to mainland foxes. For many island species, isolation has been reported to elicit ecological naïveté (Clevenger 1994, Blumstein and Daniel 2005), island tameness (Goltsman et al. 2005, Rödl et al. 2007), less vigilance (Blumstein and Daniel 2005, Mills 2007), and reduced probabilities of escape (Blázquez et al. 1997, Griffin et al. 2000, Rödl et al. 2007).

Finally, we observed that necropsies of 8 of 15 foxes revealed symptoms of systemic mineralization (mineralization of vasculature or soft tissues) and amyloidosis (abnormal deposits of amyloid proteins in organs or tissues). Although detection of these conditions was not formally part of our study design, our observations are consistent with previous reports of high prevalence on SCI (Munson 2010). These conditions may contribute to mortality of foxes by impairing normal function, however, the causes of these conditions have not been confirmed (Maxie and Newman 2007; D. Imai and L. Munson, University of California, Davis, unpublished data). Ingestion of cholecalciferol rodenticide (Quintox™; Bell Laboratories, Madison, WI) can be a contributing cause of systemic mineralization (see Capen 2007) and is suspected on SCI. Determining the causes of systemic mineralization and amyloidosis appear to be an important line of future research for the population of foxes on SCI.

## MANAGEMENT IMPLICATIONS

The vulnerability of island foxes to novel threats has required managers to carefully consider the hazards to population persistence for each subspecies on the California Channel Islands. Currently, vehicle-caused mortalities are the most prevalent threat on SCI, and mitigation of these mortalities is becoming increasingly important because naval training activities, traffic, and urbanization are expected to increase (M. A. Booker, United States Navy Wildlife Biologist, personal communication). We recommend that managers should attempt to exclude or deter island foxes from entering roads. Fencing with underpasses can have unwanted impacts such as habitat fragmentation for small populations on

islands, therefore preliminary trials should ensure that underpasses provide effective movement corridors. Another option would be to alter the behaviors of motorists to be more vigilant for foxes on SCI by using dynamie warning signs, and oral and written information (see Snow et al. 2011).

## ACKNOWLEDGMENTS

We dedicate this manuscript to the memory of L. Munson. We thank K. P. Burnham, J. L. Dooley, J. S. Ivan, and G. C. White for statistical advice. We thank C. P. Herbst, M. E. Jacques, V. N. Logsdon, M. B. Maley, and J. P. Purdum for assisting with monitoring in the field, and entering and proofreading data. We thank M. A. Booker, M. K. Brock, and R. A. Guieb from the U.S. Navy for logistical snpport. R. O. Coleman and D. M. Theobald provided GIS support. D. L. Clifford, T. W. Vickers, and D. K. Garcelon provided training and veterinary assistance. The Institute for Wildlife Studies shipped fox carcasses. We thank anonymous reviewers, M. A. Booker, R. O. Coleman, K. R. Crooks, R. A. Guieb, L. M. Markovchick, D. S. Ouren, J. I. Ransom, and T. W. Vickers for reviewing an earlier draft of this manuscript. We thank numerous agency employees, particularly those from the U.S. Navy, California Department of Fish and Game, Institute for Wildlife Studies, and University of California, Davis for cooperation on this project. This research was funded by the Department of the Navy on behalf of the Command, Pacific Fleet. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by Colorado State University or the U.S. Government.

## LITERATURE CITED

Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. Wildlife Monographs 170:1–25.

Andelt, W. F., N. P. Gould, N. P. Snow, and J. R. Resnik. 2009. San Clemente Island (SCLI) fox conservation efforts: a researeh study of the biology and life history of the island fox on San Clemente Island, California. Final annual report: work conducted September 2007–July 2008. United States Navy, San Diego, California, USA.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, New York, USA.

Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management 66:912–918.

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912–923.

Baker, P. J., C. V. Dowding, S. E. Molony, P. C. L. White, and S. Harris. 2007. Activity patterns of urban red foxes (*Vulpes vulpes*) reduce the risk of traffic-induced mortality. Behavioral Ecology 18:716–724.

Barja, I., F. J. de Miguel, and F. Bárcena. 2005. Faecal marking behaviour of Iberian wolf in different zones of their territory. Folia Zoologica 54:21–29.

Benítez-López, A., R. Alkemade, and P. A. Verweij. 2010. The impacts of roads and other infrastructure on mammal and bird popnlations: a meta-analysis. Biological Conservation 143:1307–1316.

Blake, E. W. Jr. 1887 The coast fox. West American Scientist 3:49–52.

Blázquez, M. C., R. Rodríguez-Estrella, and M. Delibes. 1997. Escape behavior and predation risk of mainland and island spiny-tailed iguauas (*Ctenosaura hemilopha*). Ethology 103:990–998.

Blumstein, D. T., and J. C. Daniel. 2005. The loss of anti-predator behavior following isolation on islands. Proceedings of The Royal Sociery 272: 1663–1668.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Brockie, R. 2007. Notes on New Zealand mammals 4. Animal road-kill "blackspots". New Zealand Journal of Zoology 34:311–316.

Capen, C. C. 2007. The endocrine glands. Pages 364–366 *in* M. G. Maxie, editor. Jubb, Kennedy, and Palmer's pathology of domestic animals. Vol. 3. Saunders Elsevier, London, United Kingdom.

Clevenger, A. P. 1994. Habitat characteristics of Eurasian pine martens *Martes martes* in an insular Mediterranean environment. Ecography 17:257–263.

Collins, P. W. 1993. Taxonomic and bingeographic relationships of the island fox (*Urocyon littoralis*) and gray fox (*U. cinereoargenteus*) from western North America. Pages 351–390 *in* F. G. Hoochberg, editor. Third California Island symposium: recent advances in California Islands research. Santa Barbara Museum of Natural History, California, USA.

Coonan, T. J., C. A. Schwemm, and D. K. Garcelon. 2010. Decline and recovery of the island fox: a case study for population recovery. Cambridge University Press, United Kingdom.

Coonan, T. J., C. A. Schwemm, G. W. Roemer, D. K. Garcelon, and L. Munson. 2005. Decline of an island fox subspecies to near extinction. The Southwestern Naturalist 50:32–41.

Cypher, B. L., C. D. Bjurlin, and J. L. Nelson. 2009. Effects of roads on endangered San Joaquin kit foxes. Journal of Wildlife Management 73:885–893.

Disney, M., and L. A. Spiegel. 1992. Sources and rates of San Joaquin kit fox mortality in western Kern County, California. Transactions of the Western Section of the Wildlife Society 28:73–82.

Fahrig, L., J. H. Pedlar, S. E. Pope, P. D. Taylor, and J. F. Wenger. 1995. Effect of road traffie on amphibian density. Biologieal Conservation 73:177–182.

Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14:21.

Farias, V., T. K. Fuller, R. K. Wayne, and R. M. Sauvajot. 2005. Survival and cause-specific mortality of gray foxes (*Urocyon cinereoargenteus*) in southern California. Journal of Zoology, London 266:249–254.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–231.

Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanne, J. A. Jones, F. J. Swanson, T. Turrentine, and T. C. Winter. 2003. Road ecology: science and solutions. Island Press, Washington, D.C., USA.

Freedman, D. A. 1983. A note on sereening regression equations. American Statistician 37:152–155.

Goltsman, M., E. P. Kruchenkova, S. Sergeev, I. Volodin, and D. W. Macdonald. 2005. 'Island syndrome' in a population of Arctic foxes (*Alopex lagopus*) ftom Mednyi Island. Journal of Zoology, London 267:405–418.

Gosselink, T. E., T. R. Van Deelen, R. E. Warner, and P. C. Mankin. 2007. Survival and cause-specific mortality of red foxes in agricultural and urban areas of Illinois. Journal of Wildlife Management 71:1862–1873.

Gould, N. P. 2010. Reproduction, denning ecology, and behavior of the San Clemente Island fox. Thesis, Colorado State University, Fort Collins, USA.

Griffin, A. S., D. T. Blumstein, and C. S. Evans. 2000. Training captive-bred or translocated animals to avoid predators. Conservation Biology 14:1317–1326.

Grilo, C., J. A. Bissonette, and M. Santos-Reis. 2009. Spatial-temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. Biological Conservation 142:301–313.

Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. Fur-bearing mammals of California: their natural history, systematic status, and relations to man. University of California Press, Berkeley, California, USA.

Hooge, P. N., and B. Eichenlaub. 2000. Animal movement extension to ArcView. Ver. 2.0. Alaska Science Center – Biological Science Office, United States Geological, Survey, Anchorage, Alaska, USA.

Hudgens, B. R., and D. K. Garcelon. 2011. Induced changes in island fox (*Urocyon littoralis*) activity do not mitigate the extinction threat posed by a novel predator. Oecologia 165:699–705.

Kimura, J. C. 1974. Summary of knowledge of the southern California coastal zone and offshore areas. Physical Environment 1:1–70.

Klöcker, U., D. B. Croft, and D. Ramp. 2006. Frequency and causes of kangaroo-vehicle collisions on an Australian outback highway. Wildlife Research 33:5–15.

Kohlmann, S. G., G. A. Schmidt, and D. K. Garcelon. 2005. A population viability analysis for the island fox on Santa Catalina Island, California. Ecological Modelling 183:77–94.

Laughrin, L. L. 1977. The island fox; a field study of its behavior and ecology. Dissertation, University of California, Santa Barbara, USA.

Litvaitis, J. A., and J. P. Tash. 2008. An approach toward understanding wildlife-vehicle collisions. Environmental Management 42:688–697.

Lovallo, M. J., and E. M. Anderson. 1996. Bobcat movements and home ranges relative to roads in Wisconsin. Wildlife Society Bulletin 24:71–76.

Maxie, M. G., and S. J. Newman. 2007. The urinary system. Pages 433–435 and 463-465 *in* M. G. Maxie, editor. Jubb, Kennedy, and Palmer's pathology of domestic animals. Vol. 2. Saunders Elsevier, London, United Kingdom.

Mills, L. S. 2007. Conservation of wildlife populations: demography, genetics, and management. Blackwell Publishing, Malden, Maryland, USA.

Moore, C. M., and P. W. Collins. 1995. *Urocyon littoralis*. Mammalian Species 489:1–7.

Monson, L. 2010. Diseases of island foxes. Pages 129–143 *in* T. J. Coonan, C. A. Schwemm, and D. K. Garcelon, editors. Decline and recovery of the island fox: a case study for population recovery. Cambridge University Press, United Kingdom.

Phillips, R. B., C. S. Winchell, and R. H. Schmidt. 2007. Dietary overlap of an alien and native carnivore on San Clemente Island, California. Journal of Mammalogy 88:173–180.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65–103 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

Ratzlaff, J. 1991. Sinuosity components of the Upper Saline River Valley, Western Kansas. Transactions of the Kansas Academy of Science 94: 46–57.

Riley, S. P. D. 2006. Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. Journal of Wildlife Management 70:1425–1435.

Rödl, T., S. Berger, L. M. Romero, and M. Wikelski. 2007. Tameness and stress physiology on a predator-naive island species confronted with novel predation threat. Proceedings of The Royal Society 274:577–582.

Roemer, G. W. 1999. The ecology and conservation of the island fox. Dissertation, University of California, Los Angeles, USA.

Roemer, G. W., T. J. Coonan, D. K. Garcelon, J. Bascompte, and L. Laughrin. 2001. Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. Animal Conservation 4:307–318.

Roemer, G. W., T. J. Coonan, L. Munson, and R. K. Wayne. 2004. Canid action plan for the island fox. Pages 97–105 *in* C. Sillero-Zubiri, J. R. Ginsberg, and D. W. Macdonald, editors. Canids: foxes, wolves, jackals and dogs: status survey and conservation action plan. Second edition. World Conservation Union, Gland, Switzerland.

Rosen, P. C., and C. H. Lowe. 1994. Highway mortality of snakes in the Sonoran desert of southern Arizona. Biological Conservation 68:143–148.

Schmidt, G. A., B. J. Willson, and D. K. Garcelon. 2004. Island fox monitoring and research on Naval Auxiliary Landing Field, San Clemente Island, California. Final report: work conducted June 2002–April 2003, United States Navy, San Diego, California, USA.

Schmutz, J. A., and G. C. White. 1990. Error in telemetry studies: effects of animal movement on triangulation. Journal of Wildlife Management 54:506–510.

Seaman, D. E., J. J. Millspangh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Griffin, London, United Kingdom.

Shepard, D. B., A. R. Kuhns, M. J. Dreslik, and C. A. Phillips. 2008. Roads as barriers to animal movement in fragmented landscapes. Animal Conservation 11:288–296.

Skuldt, L. H., N. E. Mathews, and A. M. Oyer. 2008. White-tailed deer movements in a chronic wasting disease area in South-Central Wisconsin. Journal of Wildlife Management 72:1156–1160.

Snow, N. P. 2009. Effects of roads on the San Clemente Island fox. Thesis, Colorado State University, Fort Collins, USA.

Snow, N. P., W. F. Andelt, and N. P. Gould. 2011. Characteristics of road-kill locations of San Clemente Island foxes. Wildlife Society Bulletin 35:32–39.

Spencer, W., E. Rubin, J. Stallcup, V. Bakker, B. Cohen, S. Morrison, and R. Shaw. 2006. Framework monitoring plan for the San Clemente Island fox with specific recommendations for the 2006 field season. U.S. Navy Region Southwest, and the Nature Conservancy, San Francisco, California, USA.

Sturgeon, W. J. 1999. San Clemente Island chronological military history (1934–2000). Naval Air Station, North Island, Coronado, California, USA.

Sward, W. L., and R. H. Cohen. 1980. Plant commnnity analysis of San Clemente Island. Report to Naval Ocean System Center, San Diego, California, USA.

Swarts, H. M., K. R. Crooks, N. Willits, and R. Woodroffe. 2009. Possible contemporary evolution in an endangered species, the Santa Cruz Island fox. Animal Conservation 12:102–127.

Theobald, D. M., D. L. Stevens, Jr., D. White, N. S. Urquhart, A. R. Olsen, and J. B. Norman. 2007. Using GIS to generate spatially-balanced random survey designs for natural resource applications. Environmental Management 40:134–146.

Thorne, R. F. 1976. The vascular plant communities of California. Pages 1–31 *in* J. Latting, editor. Plant communities of Southern California. California Native Plant Society Special Publication No.2, Riverside, California, USA.

Timm, S. F., L. Munson, B. A. Summers, K. A. Terio, E. J. Dubovi, C. E. Rupprecht, S. Kapil, and D. K. Garcelon. 2009. A suspected canine distemper epidemic as the cause of a catastrophic decline in Santa Catalina Island foxes (*Urocyon littoralis catalinae*). Journal of Wildlife Diseases 45:333–343.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Supplement): 120–139.

White, G. C., K. P. Burnham, and D. R. Anderson. 2001. Advanced features of Program Mark. Pages 368–377 *in* R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. Wildlife, land, and people: priorities for the 21st century. Proceedings of the Second International Wildlife Management Congress. The Wildlife Society, Bethesda, Maryland, USA.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

Whittington, J., C. C. St Clair, and G. Mercer, 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications 15:543–553.

Wood, J. E. 1958. Age structure and productivity of a gray fox population. Journal of Mammalogy 39:74–86.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794–800.

Yoho, D., T. Boyle, and E. McIntire. 1999. The climate of the Channel Islands, California. Pages 81–88 *in* Proceedings of the Fifth California Islands Symposium. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

*Associate Editor: Kevin McKelvey.*