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Authors: King, Julie L., Duncan, Calvin L., and Garcelon, David K.

STATUS OF THE SANTA CATALINA ISLAND FOX
THIRTEEN YEARS AFTER ITS DECLINE

Julie L. King[1,3], Calvin L. Duncan[1], and David K. Garcelon[2]

ABSTRACT.—Santa Catalina Island was home to an estimated 1342 adult island foxes (*Urocyon littoralis catalinae*) in 1990. Nine years later, fox sightings declined and reports of dead or dying foxes increased. An island-wide trapping effort was initiated after a fox carcass tested positive for *Canine distemper virus* (CDV). In 1999, only 10 foxes were captured east of the Two Harbors isthmus during 1046 trap-nights. A multifaceted conservation plan was implemented in 2000 to conserve the Santa Catalina population of island fox. Initial recovery actions took place from 2000 to 2005 and resulted in the translocation of 22 juvenile foxes from the unaffected West End of the island to the depopulated eastern portion, the production and release of 37 pups from the captive breeding facility, and the vaccination of >80% of the wild fox population against CDV. Since 2006, fox recovery activities have included an annual island-wide population survey, vaccination of 300 foxes per year, weekly mortality monitoring of 50 radio-collared individuals, blood sampling to monitor the prevalence of CDV, veterinary treatment of injured foxes, and public outreach. Low mortality rates, successful breeding in the wild, and mitigation of the original cause of decline allowed for Catalina's fox population to grow to an estimated 1115 adults by 2012 and to be considered biologically recovered. The outbreak of another virulent canine disease on Santa Catalina Island, such as CDV or rabies, continues to be the greatest threat to the long-term survival of *U. l. catalinae* due to the species' restricted distribution and small population size, as well as the continued presence of domestic dogs on the island.

RESUMEN.—En 1990, la isla Santa Catalina fue el hogar de aproximadamente 1342 zorros adultos insulares (*Urocyon littoralis catalinae*). Nueve años más tarde, disminuyó la cantidad de avistamientos y aumentaron los informes de zorros muertos o moribundos. Se realizó un esfuerzo de captura en toda la isla después de que se encontró el virus del moquillo canino (CDV) en el cuerpo de un zorro. En 1999, sólo se capturaron 10 zorros al este del istmo Two Harbors durante 1046 capturas nocturnas. En el año 2000, se implementó un plan de conservación multifacético para conservar la población de zorros insulares de Santa Catalina. Las acciones de recuperación iniciales tuvieron lugar entre el 2000 y 2005 y resultaron en 22 zorros juveniles trasladados desde la parte occidental no afectada de la isla a la parte oriental despoblada, 37 crías producidas y liberadas de las instalaciones de cría en cautiverio y >80% de la población de zorros silvestres vacunados contra la CDV. Desde 2006, las actividades de recuperación del zorro han incluido un monitoreo anual de la población de toda la isla, la vacunación de 300 zorros al año, el monitoreo de mortalidad semanal de 50 individuos con radio-collares, la toma de muestras de sangre para monitorear la prevalencia de la CDV, tratamiento veterinario para zorros heridos y divulgación utilizando un zorro (no liberable) nacido en cautiverio. Las tasas de mortalidad bajas, la reproducción exitosa en el medio natural y la mitigación de la causa original de la disminución, permitieron el crecimiento de la población de zorros de Catalina a un estimado de 1088 adultos en 2012 y se le considera biológicamente recuperada. La mayor amenaza para la supervivencia a largo plazo de *U. littoralis catalinae* en la isla de Santa Catalina continúa siendo la aparición de otra enfermedad de virus canino como la CDV o la rabia debido a su distribución restringida, el tamaño pequeño de la población y la presencia continua de perros domésticos en la isla.

The island fox (*Urocyon littoralis*) represents one of 69 mammals in the United States currently listed as endangered under the Endangered Species Act (USFWS 2004). This small (1.8–3.5 kg) omnivorous canid inhabits 6 of the 8 California Channel Islands. This species has been isolated from its closest mainland relative, the gray fox (*Urocyon cinereoargenteus*), for approximately 9200 years (Hofman et al. 2015), with genetic evidence supporting separation of the species into 6 distinct subspecies, each inhabiting a single island (Gilbert et al. 1990, Collins 1993, Rick et al. 2009).

Prior to 1990, the subspecies on Santa Catalina Island (*U. l. catalinae*) had only been studied intermittently over the preceding 30 years (Propst 1975, Laughrin 1980). In 1989 and 1990, capture success on 3 established trapping grids on the eastern two-thirds of the island ranged from 10.4% to 31% (Roemer et al. 1994), and the population was estimated at 1342 adults. Trapping did not take place again until 1998 and was only conducted in selected

[1]Catalina Island Conservancy, Box 2739, Avalon, CA 90704.
[2]Institute for Wildlife Studies, Box 1104, Arcata, CA 95518.
[3]E-mail: jking@catalinaconservancy.org

areas. The 26% capture success recorded in 1998 suggested that foxes continued to be present at relatively high densities in areas on the eastern 84% of the island (Timm et al. 2009).

Beginning in early 1999, island residents reported a dramatic decrease in the number of island fox sightings, which was confirmed by biologists who were conducting crepuscular and nocturnal surveys for other species. The biologists only reported observing foxes west of the Two Harbors isthmus. The precipitous decline in fox observations east of the Two Harbors isthmus prompted the initiation of a population survey to determine the status of the population and possible causes of the decline. Surveys conducted in 1999 and 2000 indicated that the fox population had experienced a large (possibly >90%) decline on the eastern 84% of the island starting in late 1998 to mid-1999 (Coonan et al. 2010), with an estimated minimum of 28 individuals (Timm et al. 2009). *Canine distemper virus* (CDV) was identified as the probable cause of the fox decline on Catalina Island after a deceased fox tested positive for the disease and 2 live foxes had elevated blood titers for CDV. Foxes on the western 16% of the island appeared not to have declined (Timm et al. 2009).

Between 2000 and 2005, a series of fox recovery strategies were implemented that included (1) live-trapping foxes to determine abundance, distribution, and extent of the CDV outbreak; (2) translocating juvenile foxes from the western portion of the island; (3) vaccinating the wild fox population against CDV; and (4) implementing a captive-breeding program and release program. Here, we report on the management actions undertaken from 1999 to 2012 and the status of the population in 2012.

METHODS

Study Area

Santa Catalina Island (194 km²), located approximately 31 km south of Long Beach, California, has mountainous terrain, with a central ridge running its length. A narrow isthmus (<0.8 km wide) located at the community of Two Harbors geographically separates the island into 2 distinct sides: the larger East End, comprising 84% of the entire island, and the smaller West End, comprising the remaining 16% (Fig. 1). The principal plant communities on Catalina are coastal sage scrub, coastal bluff scrub, island chaparral, island woodland, and coastal grassland (Schoenherr et al. 1999). Roughly 88% (170.5 km²) of Catalina is owned and managed by the Catalina Island Conservancy, a nonprofit land trust dedicated to the protection and management of the island's ecosystem. The remaining 12% is owned and managed by the Santa Catalina Island Company (11%) and the City of Avalon (1%), each with differing organizational missions. Catalina is home to a resident human population of over 3700 within the City of Avalon and 350 within Two Harbors (USCB 2010). Approximately 800,000 visitors per year (Catalina Island Chamber of Commerce and Visitors Bureau 2012) arrive by private vessel, daily commuter ferry, cruise ship, or airplane, making Catalina the most populous and easily accessible of all the California Channel Islands.

Estimates of Abundance

We monitored foxes annually using standardized, transect-based mark-recapture methods to compare relative abundance and distribution east of the isthmus, affected by the 1999 CDV outbreak, with that in the unaffected area west of the isthmus. We initiated live-trapping island-wide in 2000 in response to the extremely low East End capture success (0.7%) recorded in a 1999 preliminary investigation. Trapping was used to (1) estimate island fox density and distribution; (2) fit a subset of foxes with radio-collars in order to identify cause-specific mortality; and (3) vaccinate individuals against CDV and rabies. During October 1999 through April 2000, transects were established using 551 trap locations (102 West End, 449 East End) placed along the majority of the existing 300 km of dirt roads and hiking trails on the island. Traps remained open for 3 consecutive nights. This effort enabled direct comparison to predecline trapping efforts conducted during 1998. Trapping was conducted during 2002 using similar locations to those of 2000 and 2001, with additional sites added to allow for the continued capture of translocated and captive released foxes. Traps were open for 3 consecutive nights on the East End and 4 nights on the West End. Standardized (4-night) systematic, island-wide trapping was conducted from July through October annually between 2003 and 2009 using 603 trap sites. Road-based transects, rather than trapping grids, were used in response to 54% of
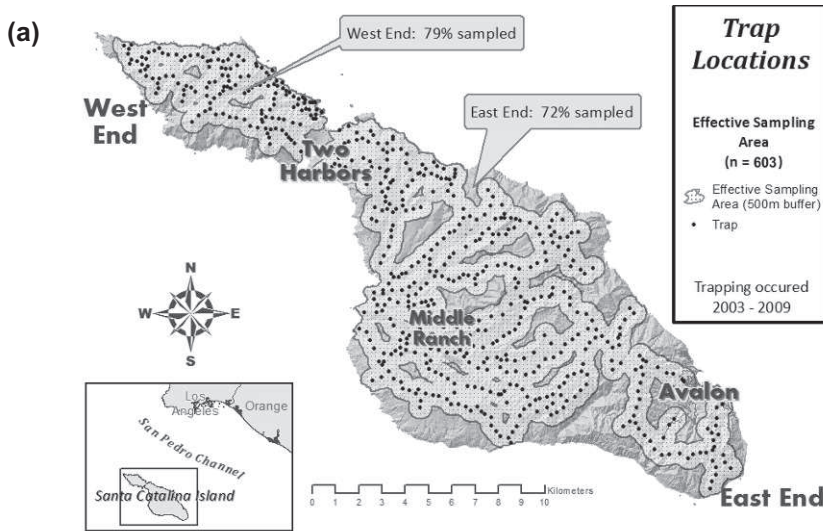
Fig. 1a–c (see facing page). Island fox trap locations ($n = 603$) used during systematic trapping conducted annually 2002–2009 on Catalina Island, California. Trapping during 2010–2011 used 400 of the 603 traps, while 243 of the 603 were used in 2012.

the East End and 74% of the West End, having terrain with slopes >30% (16.7°), which made fieldwork, especially trapping, hazardous to personnel and foxes. On the West End, we set traps on roads, ridgelines, and hiking trails with an average intertrap distance of 225 m. On the East End of the island where fox densities were low, we trapped only along established dirt roads and increased the average intertrap distance to 300 m. Intertrap spacing was based on modifications from Wood (1959) and Roemer et al. (1994) and met our criteria for having at least 4 traps per fox home range.

We defined the effective sampling area as the entire area covered (minus overlap) within a 500-m buffer placed around all traps. The buffer was added to characterize the entire area likely to be used by foxes entering traps, including areas used by foxes living adjacent to transects and captured in perimeter traps. This buffer was based on the approximate mean home range size for island foxes on San Clemente Island, California (0.65 foxes · km^{-2}) (authors' unpublished data), Santa Cruz Island, California (0.55 foxes · km^{-2}) (Roemer et al. 2001), and a cursory analysis of home ranges of translocated foxes on Catalina Island. Thus, the effective sampling area of the island totaled 73%, with 79% and 72% of the West End and East End sampled, respectively (Fig. 1a).

We adjusted our trapping efforts in response to changes in fox abundance as the East End population recovered and to high capture success in both subpopulations. Island-wide trapping efforts were downscaled to 400 of the original 603 trap sites during 2010 and 2011, representing a 55% effective sampling area (Fig. 1b). Trapping efforts were further decreased to 243 sites in 2012 (34% effective sampling area) (Fig. 1c). Annual surveys conducted during 2003–2009 were divided among 11–13 traplines consisting of 31–70 (average 50) trap sites per line, then decreased to 8–10 lines during 2010 and 2011, and ultimately to 6 lines of 32–49 (average 40) traps in 2012, with vegetation types sampled in rough proportion to their occurrence on the island. Traps were checked just after sunrise every 24 h for 4 consecutive nights.

Capture data were analyzed using program DENSITY 4.3 (Efford et al. 2004, Efford 2008) to estimate annual subpopulation density. East End and West End fox subpopulations were analyzed independently due to the known differences in abundance resulting from the 1999 CDV epidemic affecting only animals on the East End and the extremely limited cross-isthmus fox dispersal. We constructed a set of candidate statistical models of fox density in which detection probability (g0) remained constant (.) or varied due to
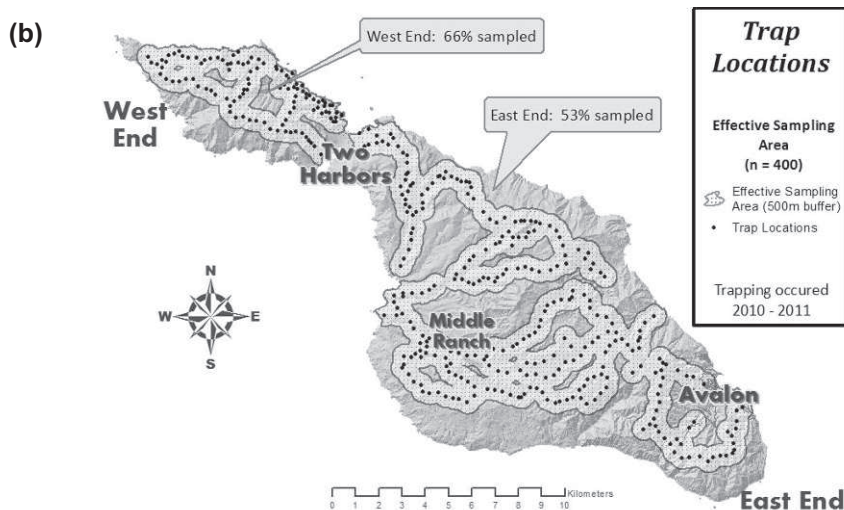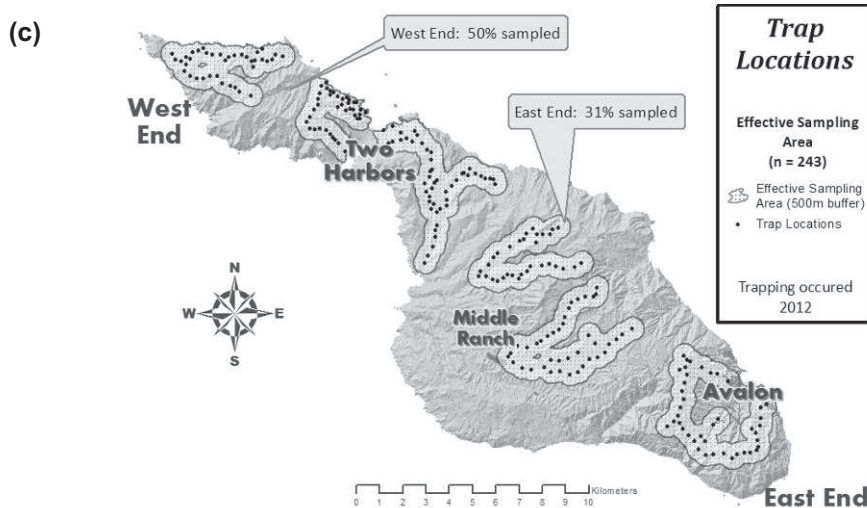
(b)

Fig. 1b.

(c)

Fig. 1c.

behavior (classic = b, Markov = b1) or heterogeneity (h2), while fox movement patterns represented by sigma (σ) remained constant (.) or demonstrated heterogeneity (h2). We used the minimum corrected Akaike information criterion (AIC_c) to select the best models for estimating density in each subpopulation. To address model uncertainty, ΔAIC and Akaike weights (w_i) were calculated, and models with Akaike weights <10% of the highest were excluded as suggested by Royall (1997). Parameter estimates and variances from each model were weighted and model-averaged in order to reduce bias and increase precision (Mazerolle 2006, Burnham and Anderson 2002).

Population estimates were calculated by multiplying the model-averaged density by the land area of the East End (162.53 km^2) and the West End (31.61 km^2). Annual island-wide adult fox population estimates were reported as the sum of the East End and West End subpopulation estimates determined via the best DENSITY models. Foxes were captured in all habitat types across the island, as well as

within the cities of Avalon and Two Harbors, so all available land area was considered potentially available.

Adult-only population estimates were also calculated using DENSITY to determine if population risk–based recovery criteria identified in the draft Recovery Plan (USFWS 2012) were being met. We used an interactive "Island Fox Recovery Tracking Tool" (Bakker and Doak 2009, Coonan et al. 2010) to determine whether the Catalina subspecies had attained a <5% risk of quasi-extinction (identified as ≤30 individuals) over a 50-year time period based on current mortality rates and population sizes. We plotted average adult mortality rate as determined through radio-collared individuals (see below) against the average estimated adult population size calculated over 3 years along with their 80% confidence intervals.

Standardized trapping did not take place during the March through June parturition season. Therefore, we estimated annual recruitment as the number of pups per total number of foxes captured during the summer/fall following the birth pulse. We tested for equal sex ratios expected for this species (Laughrin 1977, Crooks 1994), and estimated the proportion of new unmarked juveniles the following year to determine if pup capture had been underrepresented.

Capture and Handling

Foxes were captured in 23 × 23 × 66-cm wire-mesh cage-traps (Model #106, Tomahawk Live Trap Co., Tomahawk, WI) covered on top with landscaping shade cloth. Polypropylene tubing (1.8-cm diameter) was attached inside the back of each trap to serve as a bite bar to decrease trap-related tooth damage. Traps were lined inside and on top with dried grasses to provide thermal protection, then baited with wet and dry cat food and a loganberry lure (U-Spray, Inc., Lilburn, GA). Bait was placed in empty 5.5-ounce cat food cans to prevent traps from being dug out or robbed. All traps and bait cans were washed and disinfected weekly using a chlorhexadine solution to prevent disease and parasite transmission.

Island foxes are relatively docile compared to other canids and can be safely handled without anesthesia. To reduce stress, foxes were blindfolded using a small Quick Muzzle® designed for cats (Four Flags Over Aspen

Inc., St. Clair, MN), and handling time was minimized to approximately 10–15 min. Upon initial capture each year, foxes were weighed (±0.05 kg), sexed, and aged. Age was determined by the relative wear and dentin exposure observed on the first upper molar (Wood 1958, Collins 1993). All foxes captured between 1999 and 2002 were uniquely marked for identification with colored eartags (Roto-Tag, Nasco West, Stockton, CA). In subsequent years, eartags were removed and foxes were marked with 12.5-mm passive integrated transponder (PIT) tags (Biomark Inc., Boise, ID) inserted under the skin between the scapulae by using a sterile single-use syringe. Additional information recorded included reproductive condition, presence of ectoparasites, eye condition, general physical condition, and evidence of infectious disease or injuries. A blood sample of up to 10 mL from either the femoral or jugular vein was collected annually from a subset of captured foxes >5 months of age. These blood samples were used for determining disease exposure and efficacy of the CDV vaccine through measurements of antibody titer levels, for genetic analysis, or for archival purposes to allow future analyses. Blood samples were separated into their component fractions by centrifugation, and stored in a –86 °C freezer.

Captured animals with minor injuries were treated in the field, and those with more serious or life-threatening injuries were transferred to the Conservancy's Middle Ranch Veterinary Field Clinic for medical treatment. Beginning in 2005, the ear canals of all foxes captured were observed by field staff via otoscopic exam for evidence of ear mite infestation, infection, and/or nodular tissue growth. Except for individuals requiring veterinary care, all foxes were released at the trap location immediately after handling. Foxes recaptured during the same year were scanned for their PIT-tag number then released without processing.

Vaccinations

All captive foxes and a large subset of captured wild foxes were vaccinated and provided boosters annually against CDV using 1 mL of live Canary Pox–vectored CDV vaccine (Purevax® Ferret Distemper Vaccine, Merial Ltd., Athens, GA) injected intramuscularly in the left thigh. See Coonan et al. (2010) for details

of vaccine development. Beginning in 2005, wild foxes were also vaccinated and given annual boosters with 1 mL of rabies vaccine (Imrab® 3 TF rabies vaccine, Merial Ltd., Athens, GA) injected subcutaneously in the right thigh as per veterinary protocol. A "vaccinated-core" strategy for population management was designed in 2006 (Cleaveland et al. 2006, Vial et al. 2006, Doak et al. 2013) and implemented on Catalina Island in 2007. We further incorporated recommendations generated from an island fox population viability analysis developed for Santa Catalina by Kohlmann et al. (2005) and set a goal of vaccinating a minimum of 300 individuals annually. Our vaccinated-core strategy assumed that in the event the population contracted to no less than the approximate size of the vaccinated core after an epizootic, 300 (150 in each subpopulation) survivors would be necessary to maintain a high degree of genetic heterozygosity and prevent demographic stochasticity. Prophylactic vaccination could then serve as a possible alternative to direct epidemic response and/or resumption of captive population maintenance in the event of an epidemic (Kohlman et al. 2005, Doak et al. 2013).

Captive Breeding

A captive breeding program was implemented in 2001 to protect a subset of the population against another catastrophic event and to produce offspring for assisting in the repopulation of the East End of the island. A 12-pen captive breeding facility located 1.8 km west of Middle Ranch was constructed during 2001 and was successfully operated through 2004. Each pen measured 9.15 × 30.5 m and housed a single adult breeding pair and their offspring of the year. All pens were equipped with 6 video cameras and infrared lighting for noninvasive behavior observation, and 2 insulated den boxes for pup rearing. The entire complex was surrounded by a perimeter fence topped with 3 strands of electric fence line, and the bottom was lined with buried chicken wire skirting to prevent access by bison, dogs, and other larger mammals that could potentially disturb the breeding foxes (see Coonan et al. 2010 for expanded details). Six West End foxes (3M:3F), held in captivity from February 2000 to February 2001 for experimental CDV vaccination testing, were placed into the first 3 of 12 pens constructed. All other adult foxes (6M:9F) were captured from the West End of the island and brought to the breeding facility during 2001 and 2002. Data collected during the 1999 and 2000 surveys investigating the population decline provided trapping information needed to target young mated pairs in good condition as candidates for the captive breeding program. Pups produced and surviving to dispersal age (6–7 months) were released from the breeding facility during November and December each year to various areas throughout the island's East End. The adults were not released until the breeding program ended in December 2004.

Captive animals were released using a "modified hard" technique wherein the animals were not held in transition pens, but were provided supplemental food placed in multiple wired-open traps baited with cat kibble for 9 weeks at release areas to enhance recapture probability. Foxes were targeted for recapture 1-, 2-, 4-, and 8-weeks post-release for health assessment. Animals losing more than 20% of their release weight during the first 8 weeks were returned to the Middle Ranch Veterinary Field Clinic for examination and supplemental feeding for several days to weeks, then released at their site of capture.

Translocations

An integral part of the recovery effort involved the capture and translocation of wild juvenile foxes from the higher-density West End to the nearly vacant East End during January and February 2001 and 2002. The surviving East End wild population had been reduced to an estimated 28 foxes living among 162 km^2. This low density raised concern that adult males and females would have difficulty finding one another to establish successful breeding pairs due to their small home-range sizes (0.36–1.05 km^2) and low natal dispersal distances (average 1.39 km) (authors' unpublished data, Roemer et al. 2001). All translocated individuals were wild-born yearling foxes that were independent from their parents but had not established pair bonds or permanent territories. These foxes were vaccinated against CDV and radio-collared prior to release.

Radiotelemetry

From 2001 to 2012, 259 foxes were fit with 39-g VHF radio-collars (model MI-2M,

TABLE 1. Results of systematic island-wide fox trapping conducted in 1999–2012 on Catalina Island, California. Mortalities in parentheses represent the number of radio-collared foxes comprised in the total. 1999–2001 population estimates represented all ages and were extrapolated from MNKA (minimum number known alive). EE = East End; WE = West End. All model-averaged densities were multiplied by the respective land areas: EE = 162.53 km², WE = 31.61 km².

Year	Traps: Number of traps	Traps: Trap-nights	Unique foxes captured EE	Unique foxes captured WE	Unique foxes captured Total	% Capture success EE	% Capture success WE	Adult model-averaged density EE (foxes · km⁻²)	EE Unconditional SE	WE (foxes · km⁻²)	WE Unconditional SE	Adult population estimate EE	WE	Total	CDV vacc EE	CDV vacc WE	Rabies vacc EE	Rabies vacc WE	Radio collars	Detected mortalities
1999	551	1183	10	49	59	0	50	0.07	N/A	1.04	N/A	28	75	103	0	4	0	0	12	2 (1)
2000	594	1808	10	143	153	2	42	0.06	N/A	4.59	N/A	14	143	157	2	104	0	0	21	8 (7)
2001	312	1205	24	101	125	9	33	0.08	N/A	5.10	N/A	31	161	192	0	45	0	0	26	6 (4)
2002	589	1812	50	67	117	6	27	0.73	0.26	3.28	0.81	119	103	222	16	28	0	0	41	9 (2)
2003	609	2193	70	65	135	7	21	0.33	0.09	1.81	0.55	54	57	111	69	63	0	0	57	5 (3)
2004	603	2412	103	106	209	11	43	0.66	0.15	3.75	0.54	107	118	225	0	0	0	0	71	9 (4)
2005	602	2408	145	105	250	20	48	0.93	0.13	3.82	0.54	150	120	270	0	0	126	104	29	12 (6)
2006	602	2408	207	123	330	24	49	1.23	0.14	7.10	0.94	200	224	424	182	101	182	101	55	14 (12)
2007	603	2412	246	119	365	30	46	2.30	0.38	5.79	0.84	374	183	557	221	113	221	114	76	16 (6)
2008	603	2412	342	165	507	35	61	2.74	0.68	4.34	0.66	445	137	582	215	160	218	160	75	16 (4)
2009	603	2412	401	153	554	42	64	2.96	0.38	5.47	0.51	481	173	654	227	60	249	71	70	17 (4)
2010	400	1600	350	139	489	56	71	2.99	0.36	6.30	1.04	486	199	685	264	125	264	128	69	31 (6)
2011	400	1600	422	148	570	60	67	5.45	0.59	7.79	1.24	886	146	1032	303	121	303	133	63	24 (4)
2012	243	972	277	98	375	67	68	5.79	0.92	5.44	1.08	942	172	1114	227	87	227	87	56	

TABLE 2. Model selection results for the top 4 models used to estimate West End and East End subpopulation fox density (foxes · km^{-2}) during 2012 on Catalina Island, California, USA. Candidate models were ranked using change in Akaike's information criterion (ΔAIC_c). Model uncertainty was incorporated by calculating the Akaike weight (w_i) and weighting the ML density values. Only models with Akaike weights within 10% of the highest were maintained in the confidence set of candidate models. The model-averaged density estimate represents the sum of the weighted densities for each model.

Model[a]	K	ΔAIC_c	ΔAIC	ML density	Akaike weight (w_i)	Weighted density	Model likelihood	Weighted unconditional SE	95% CI
2012 WEST END									
g0(b1)s(.)	4	827.39	0.00	5.15	0.48	2.45	1.00	0.58	
g0(.)s(.)	3	828.38	0.99	5.58	0.29	1.62	0.55	0.21	
g0(h2)s(.)	5	829.90	2.51	6.13	0.13	0.83	0.33	0.21	
g0(b)s(.)	4	830.54	3.15	5.47	0.10	0.54	0.21	0.09	
Model-averaged estimate Unconditional SE				5.44			1.08		3.34–7.56
2012 EAST END									
g0(b1)s(.)	4	1476.00	0.00	5.69	0.35	1.99	1.00	0.27	
g0(b)s(.)	4	1476.26	0.26	5.09	0.31	1.58	0.88	0.33	
g0(.)s(.)	3	1476.73	0.73	6.34	0.24	1.52	0.69	0.22	
g0(.)s(h2)	5	1478.43	2.43	6.98	0.10	0.70	0.30	0.10	
Model-averaged estimate Unconditional SE				5.79			0.92		4.01–7.59

[a]g0(b1) = Markov behavior, capture probability influenced by previous capture (trap happy)
g0(b) = classic behavior, response to first capture influences subsequent events (trap happy/trap shy)
g0(.) = constant detection probability
g0(h2) = heterogeneity in detectability
s(.) = constant movement patterns
s(h2) = heterogeneity in movement patterns
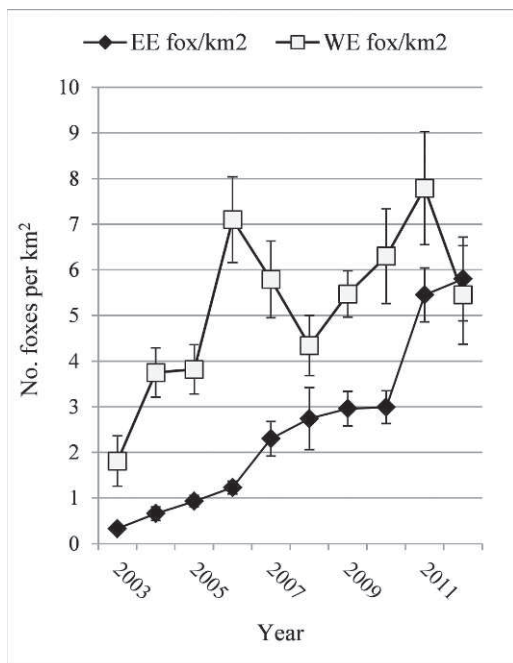K = number of parameters

Fig. 2. Annual estimated density (foxes · km⁻²) of adult island foxes reported for the East End (EE) and West End (WE) subpopulations on Catalina Island during 2003 through 2012. Maximum likelihood density estimates were derived from capture/recapture data analyzed using Program DENSITY. Error bars represent one standard error.

Holohil Systems, Ltd., Carp, Ontario, Canada) to quantify cause-specific mortality factors, as well as monitor the general use area and survival of translocated, captive-released, and wild controls. Beginning in 2006, we implemented a monitor-and-respond program using unvaccinated disease sentinels to act as an early detection system in the event of a potentially catastrophic disease outbreak.

For the first month post-collaring, all collars were monitored daily from the ground via a truck-mounted omnidirectional antenna or from a fixed-wing aircraft. Thereafter, monitoring continued at least once weekly. Radiocollars were placed on animals weighing more than 2.0 kg (collar <2% of body weight) and on animals known to be 7 months of age or older. VHF radio-collars were equipped with mortality sensors triggered after 12 h of nonmovement. All recoverable carcasses were transferred to the University of California–Davis Veterinary Medical Teaching Hospital or the California Animal Health and Food Safety Laboratory, Davis, California, for necropsy and identification of cause of death. Mortality factors were used to guide the Conservancy's threat abatement strategies and to establish trigger points for epidemic response.

We used known-fate models in Program MARK to estimate annual mortality probabilities from radiotelemetry data (2006–2012) (White and Burnham 1999). Our goal for this analysis was to generate year-specific estimates of annual mortality to be entered into the Island Fox Recovery Tracking Tool rather than test specific hypotheses about the causes of mortality. Therefore, we fit a single model in which survival was conditional on age, sex, and subpopulation (East End or West End).

RESULTS

Estimates of Abundance

Density estimates could not be calculated using Program DENSITY for trapping conducted during 1999, 2000, and 2001 due to extremely low capture probably (<0.1) when size of the eastern subpopulation was small. Fox abundance was estimated from the capture data during 1999–2001 using the minimum number known alive (MNKA): the total number of individuals caught in traps (as determined by eartag identification) per 1-km² grid plus radio-collared individuals not trapped but known to be alive via radiotelemetry. That density was then extrapolated to the entire island by multiplication with the sampled portion of the island (Table 1).

We had sufficient data from 2002–2012 to calculate maximum likelihood density estimates with Program DENSITY. Several East End traplines with extremely low captures or no recaptures were joined with adjacent lines to allow for analysis of years 2002, 2003, and 2004. Maximum likelihood, model-averaged density estimates of the adult East End fox subpopulation increased annually beginning in 2003 from 0.33 foxes · km⁻² (SE 0.09, 95% CI 0.15–0.51) to 5.79 foxes · km⁻² (SE 0.92, 95% CI 4.01–7.59) in 2012. Density estimates on the West End ranged from a low of 1.81 foxes · km², following 2 consecutive years of translocations and removals for captive breeding, to 5.44 foxes · km² (SE 1.08, 95% CI 3.34–7.56) in 2012 (Table 2, Fig. 2).
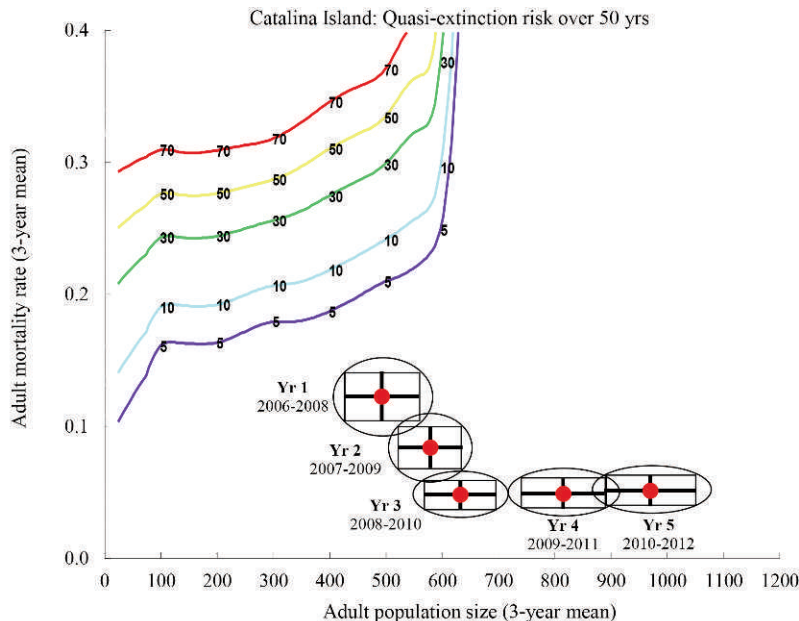
Fig. 3. An isocline figure showing quasi-extinction risk for Santa Catalina Island foxes over 50 years as a function of monitoring data. The colored extinction risk isoclines were calculated using an interactive "Island Fox Recovery Tracking Tool" (Bakker and Doak 2009); the number on each colored isocline represents the percent extinction risk. Three-year averaged mortality rates and population estimates 2006–2012 were plotted with 80% X and Y confidence intervals. The measured parameters, including the entire 80% confidence intervals, are required to fall below the 5% risk isocline (dark blue line) to qualify the subspecies for delisting. The quasi-extinction threshold was 30 individuals.

The rapid recovery of Catalina's island fox population from 2006 to 2012 greatly reduced extinction risk. The 5 consecutive 3-year average values of population size and mortality rate plotted against isoclines of extinction risk for 2006–2012 (generated from the interactive "Island Fox Recovery Tracking Tool" developed by Bakker and Doak 2009) show that the 80% confidence limits for both mortality and population size fell increasingly below the 5% isocline. This is considered an acceptable level of risk in the USFWS draft island fox recovery plan (Fig. 3).

Annual subpopulation recruitment, measured as pups per total foxes captured, varied annually over the 11 years (2002–2012) and was correlated with precipitation during the April–November breeding and parturition periods (Fig. 4). In years of above-average rainfall (>10.88 inches, 276 mm), the number of pups captured as a percentage of overall captures increased to >20%. Below-average rainfall was correlated with declining birth rates on both the West End to ($\leq$20%; r = 0.64) and the larger East End of the island

($<$22%; r = 0.53). The 11-year average recruitment for the eastern subpopulation was 29% versus 22% on the higher-density West End. Pups were approximately 5–8 months old when captured.

Vaccination

Large-scale vaccination of island foxes began in 2000 and continued for the duration of the study (Table 1). However, CDV vaccine shortage due to manufacturing complications at Merial Ltd. throughout 2004 and 2005 restricted our ability to vaccinate any free-ranging foxes during our standardized trapping period. The limited supply obtained in 2004 was used to vaccinate all 30 captives and provide boosters to 36 previously vaccinated animals. Once limited batches of CDV vaccine became available in late 2005, 16 East End and 18 West End foxes were targeted for vaccination. In 2006, new vaccination protocols were implemented that called for managers to vaccinate core group(s) totaling a minimum of 80–100 animals on the larger islands against CDV and rabies in strategic geographic
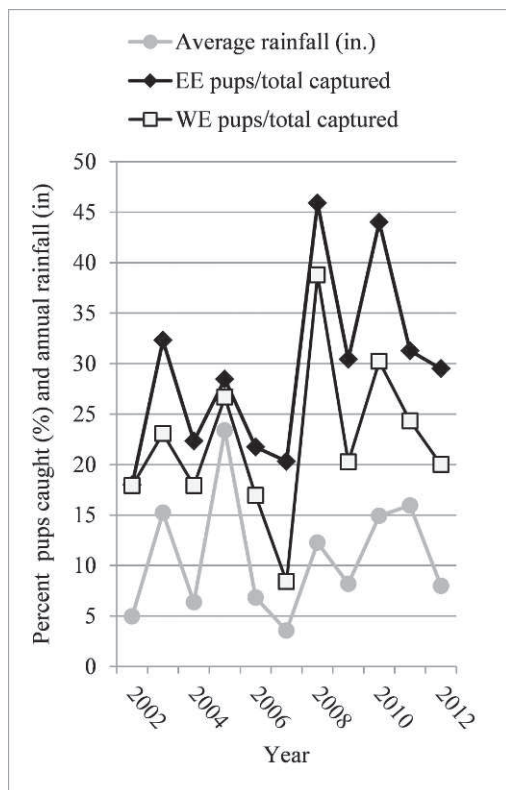
Fig. 4. Annual Catalina Island fox recruitment for the East End (EE) and West End (WE) subpopulations estimated by the number of pups captured per total foxes captured in the summer/fall following the birth pulse. Average rainfall reported between 1 November and 30 April annually from 3 weather stations located at the Airport in the Sky, Middle Ranch, and Avalon.
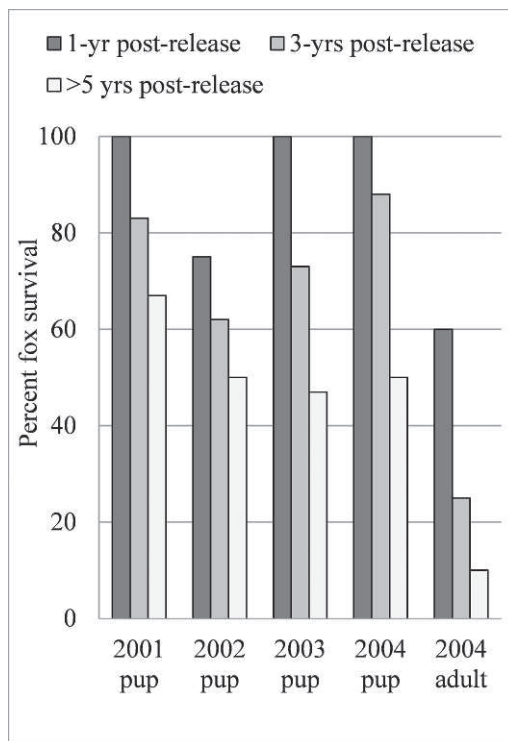

Fig. 5. Percent survival by cohort of captive-born Catalina Island fox pups and wild-caught adult foxes following 1-year, 3-years, and >5-years post-release from the captive breeding facility (CBF) on Santa Catalina Island, California.

location(s) in perpetuity (Schwemm 2007, Doak et al. 2013). The CDV vaccine became widely available in this year as well. We vaccinated or boostered 283 (86%) and 334 (92%) foxes, respectively, against CDV. A total of 1368 of 1606 unique individuals captured between 2002 and 2012 were vaccinated at least once (range 1–7) against CDV. This represents 85% of all captured foxes being vaccinated, but not necessarily protected given the need for annual boosters. Rabies vaccine was also administered prophylactically at least once (range 1–7) to 1347 of 1606 (84%) unique wild foxes captured between 2005 and 2012.

Captive Breeding

A total of 37 (17M:20F) captive-born pups were released between 2001 and 2004 (2001

= 6, 2002 = 8, 2003 = 15, and 2004 = 8). Pups were released as a cohort in each year from 2001 to 2003 to a predetermined East End release site(s). Captive breeding efforts ceased in 2004, and 20 of 22 adult breeders accompanied by their 8 pups were released in family groups across the East End in November and December. Two geriatric foxes were deemed unreleasable due to health issues associated with ceruminous gland carcinoma. These foxes remained in captivity until they were humanely euthanized in September 2006.

Survival of released captive-born pups was high. Over 94% (35/37) survived 1-year post-release (Fig. 5). Three years after release, 78% (29/37) survived, and a minimum of 54% survived 5 years or more. Several foxes ultimately had unknown fates once radio-collars were removed and standardized trapping did not occur near their home range to allow for incidental capture.

Annual survival rates of captive-released adults were considerably lower than pup survival. The 20 mature adult breeders, having spent 2–4 years in captivity, had a 1-year post-release survival rate of 60%. Several factors contributed to high adult mortality: (1) release events took place during late fall, at the onset of the breeding season when males and females are most aggressive to conspecifics; (2) 15 of 20 adults had been in captivity for as many or more years than they had previously been in the wild; and (3) average age at release was 6 years, with 70% being 5–9 years old. Vehicle trauma (5 foxes), injuries inflicted by conspecifics (2), and unknown causes (1), accounted for the adult-breeder mortalities during the first year postrelease. By late 2007, only 5 (25%) captive-released adults had survived. Those foxes that survived established territories on the outskirts of human areas. Two adult females that survived >5 years postrelease in the wild were 3–4 years of age at release and had spent <2 years in captivity. In contrast, the adults that died had spent 3–4 years in captivity and were 5–9 years of age at time of release.

Most captive-released adults were also overweight. Average captive female weight was 2.55 kg ($n = 10$, range 2.10–2.95 kg) at time of release. That weight was significantly heavier ($t = 3.97$, df = 9, $P < 0.05$) than the average weight of East End wild females captured during the same year and season ($n = 30$, $\bar{x} = 2.19$ kg, range 1.85–2.70 kg). Similarly, the average captive male release weight of 2.95 kg ($n = 10$, range 2.35–3.90 kg) was significantly heavier ($t = 4.83$, df = 9, $P < 0.05$) than the average weight of 25 wild adult captured males from the same season and year ($\bar{x} = 2.42$ kg, range 2.20–2.95 kg).

Two 7-year-old males that received severe injuries (e.g., fracture and luxation of metatarsals) inflicted by other foxes were captured at 2- and 3-months postrelease and were returned to captivity for treatment. One of the males was released after 5 months of rehabilitation; however, he was recaptured 13 days later due to additional injuries and ultimately deemed nonreleasable. He spent the remainder of his life in captivity. The other male spent 8.5 months being rehabilitated following surgery to repair a fractured tarsal-metatarsal joint, yet only survived 5 months following his second release.

Translocations

Twenty-two wild-born juvenile foxes (11M: 11F) were translocated from the West End in 2001 ($n = 10$) and 2002 ($n = 12$). West End translocations ceased in 2003 when the subpopulation estimate for all age classes dropped below 150 foxes. Captive production in 2003 was high (15 pups), offsetting the lack of translocations in 2003. Survival of 2001 juvenile translocates 1 year postrelease was 90%, with 60% surviving >5 years. Comparatively, 1-year survival of West End juvenile controls (radio-collared, but not translocated), was 60% (6 of 10) in 2001. The 2002 translocate cohort had 100% survival at 2.5-years postrelease, with 70% surviving 5.5–9.5 years.

Annual Survival

Between 2001 and 2012, 62 of 259 radio-collared foxes died. The number of detected mortalities ranged from 3 to 12 annually, while the number of radio-collared foxes each year ranged from 26 to 76. Causes of death for radio-collared individuals included dog attack (4), drowning (1), emaciation (13), euthanisia due to severe injuries (2), gunshot (1), septicemia (6), vehicular trauma (17), and undetermined due to advanced decay (17). Foxes that died due to emaciation and/or septicemia were geriatric animals that commonly also had been diagnosed with ceruminous gland carcincoma. Non-radio-collared deceased foxes were detected annually but were not included in the calculation of annual mortality rates. Total detected mortality averaged 14 individuals per year, with a high of 31 documented during 2011. Estimated annual mortality probability was 0.16 (80% CI 0.21–0.11) during 2006 and 2007 and declined to an average of 0.06 (80% CI 0.04–0.08) from 2008 to 2012 as the subset of collared individuals transitioned to disease sentinels and more closely represented the age and sex ratio of the adult population. Confidence intervals were calculated at 80% instead of 95% for consistency with the Recovery Tracking Tool.

DISCUSSION

Intensive management has enabled the island fox population on Santa Catalina Island to return to predecline numbers and to be considered biologically recovered. By the end of 2006, we estimated that 424 adults lived on

the island, indicating that after 6 years of conservation actions, *U. l. catalinae* had attained population sizes (minimum of 150 in each subpopulation) that had a high likelihood of long-term viability if survival remained high (Kohlmann et al. 2005). The density of adults on the West End in 2006 (7.10 foxes · km^{-2}) was similar to densities estimated in chaparral/woodland habitat on Catalina in 1989 and 1990 (5.9–7.4 foxes · km^{-2}), prior to the population decline and also comparable to pre-decline densities on Santa Cruz Island, California (7.0–7.3 foxes · km^{-2}) in 1993 (Roemer et al. 1994). In contrast, 2006 estimated densities for Catalina's East End (1.23 foxes · km^{-2}) were much lower than estimates for other healthy island fox populations during that time. Fox densities were reported as 7.6–13.7 foxes · km^{-2} in 2007 in grassland/scrub on San Nicolas Island and 3.9–4.8 foxes · km^{-2} in 2004 in grassland habitats on San Clemente Island (Coonan et al. 2010). Island fox populations on those 2 islands are not endangered and have remained relatively stable throughout the past 10 years. By 2012, however, adult densities on Catalina's East End had increased to 5.79 foxes · km^{-2} and exceeded estimated densities on the unaffected West End (5.45 foxes · km^{-2}) for the first time since 1999. West End subpopulation densities began to increase once yearlings were no longer translocated to the East End or taken into captivity as breeding stock. Continued West End population increases were also due to improved habitat and resource availability following the removal of thousands of feral goats and pigs between 1990 and 2002 (Schuyler et al. 2002, Garcelon et al. 2005).

The Catalina Island fox population decline documented in 1999 was assumed to have only affected the East End subpopulation, with the West End subpopulation being spared because of low fox dispersal across the Two Harbors isthmus. Annual trapping data collected between 2000 and 2012 document only 13 individual foxes (11 M:1 F), all juveniles, born on one side of the isthmus (6 East End, 7 West End) and dispersing to the opposite side in their first year. While this result demonstrates that the isthmus does not act as a complete barrier to fox dispersal, it does suggest that the rate of cross-isthmus dispersal is limited and may have ultimately saved *U. l. catalinae* from extinction.

Disease continues to be the greatest threat to the survival of the Catalina Island fox. Santa Catalina remains the only California Channel Island allowing visitors and residents to own and transport pets to and from the island. Pets coming to the island are not subject to quarantine, and proof of current vaccination is not required by the Catalina Express public ferry. Licensing of dogs (for rabies) is only required within the City of Avalon and for Conservancy employees and lessees with pets living in company-owned housing. Creating a pet passport system for the ferry that requires current proof of vaccination, and passing City of Avalon legislation requiring proof of vaccination would be positive steps in addressing the potential for introduced disease.

Island foxes vaccinated against CDV and rabies now occupy nearly every portion of the island. This ongoing management action will hopefully stop or slow the spread of CDV and rabies if those diseases are introduced to the island. Model simulations by Bakker et al. (2009), Doak et al. (2013), and Sanchez (2012) showed that the establishment of a vaccinated subset of the wild population was a more effective way to decrease the threat of epidemics than the rapid capture and vaccination of foxes following detection of an epidemic. Maintaining a "vaccinated core" of 300 individuals, versus the recommended number of 80–100 for just threat abatement, was also considered a possible alternative to the costly resumption of captive breeding in the event of a future epidemic. The Conservancy has therefore implemented this higher level vaccinated core ($n = 300$). Prophylactic inoculation has been identified as a cost-effective means for the Conservancy to protect its fox population, especially when boosters can be administered annually in conjunction with scheduled trapping for population estimation. Unvaccinated, radio-collared disease sentinel foxes also inhabit many areas of the island and are monitored weekly. These animals would likely act as an early detection mechanism in the event of another epidemic.

Additional disease introduction may take place when nonnative wildlife are inadvertently brought from the mainland. For example, 3 male raccoons (*Procyon lotor*) were discovered at separate locations during July 2007. At least one was confirmed as a "stowaway" on a private boat that had sailed from

Cabrillo Marina in San Pedro, California, to Avalon Harbor where the raccoon disembarked. An additional 3 adult raccoons have been detected and removed from Catalina between 2008 and 2012. Three of 6 animals were humanely euthanized, necropsied, and tested for evidence of rabies, CDV, and the roundworm nematode *Baylisascaris procyonis* found ubiquitously in raccoons. All 3 were negative for rabies and CDV, yet 2 of 3 were shedding *B. procyonis.* Most recently, a young female and a geriatric male opossum (*Didelphis virginiana*) were discovered and removed from Two Harbors during April and November 2013.

Threat abatement continues to be a priority for the Catalina Island Conservancy so that the number of human-caused fox mortalities may be minimized in the future. Preventative actions have included prophylactic vaccination of wild foxes (including CDV vaccine persistence research), annual serosurveys of unvaccinated foxes for disease monitoring, roadside signage, educational outreach programs, and implementation of a Pets and Wildlife Policy at all Conservancy-leased camps and coves. The Conservancy's Education and Communications departments incorporate island fox information into school curricula, radio programming, and social media.

In conclusion, *U. l. catalinae* has proven resilient and has staged a remarkably rapid recovery from a catastrophic population decline. Nevertheless, Catalina's island foxes will likely be "conservation-reliant" (Scott et al. 2005) for the foreseeable future due to their restricted distribution, small population size, and the continued presence of domestic dogs on the island. A continued investment in conservation management (average cost of $192,000 per year from 2000 to 2012), including prophylactic vaccinations and routine survival monitoring, will insure a self-sustaining wild population on Catalina Island.

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