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SPACE USE AND DEN VISITATION BY THE ISLAND SPOTTED SKUNK (*SPILOGALE GRACILIS AMPHIALA*) AND ISLAND FOX (*UROCYON LITTORALIS*)

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ABSTRACT—On the California Channel Islands, wildlife researchers have hypothesized that the island fox (*Urocyon littoralis*) competes with the smaller-bodied island spotted skunk (*Spilogale gracilis amphiala*). Recent declines in spotted skunk captures have raised concerns about the status of the spotted skunk population on Santa Cruz Island and the potential role of foxes in the decline. From 2018 to 2019, we used global positioning system and very-high-frequency radio collars to assess patterns of space use by foxes and spotted skunks and deployed remote cameras to determine the potential for interaction between the two species at spotted skunk den sites. Spotted skunk home ranges were approximately five times larger than previously reported (range = 55–299 ha), and temporal patterns of space use differed between spotted skunks and foxes, with spotted skunks utilizing only 32% of their 6-month home range during a week, while foxes moved more widely over short time periods, covering 60% of their seasonal home range during 1 week. In spite of overall larger seasonal home ranges, the number of vegetation types used by spotted skunks (mean = 4) was smaller than that used by foxes (mean = 7) living in the same area, consistent with the narrow niche hypothesized for spotted skunks. More broadly, selection for vegetation types varied among individuals, within species, and across locations on the island. Based on camera trapping at spotted skunk den sites, we found a positive relationship between spotted skunk visitation rate and slope at den sites but no relationship with vegetation cover, suggesting more heavily used dens were in areas of steeper slope. Photographic evidence of a fox attempting to dig an adult spotted skunk from its den suggested predation at den sites could be a factor in spotted skunk mortality.

RESUMEN—En las Islas del Canal de California, el zorro isleño (*Urocyon littoralis*) ha se ha planteado la hipótesis de que compite con el zorillo manchada de la isla (*Spilogale gracilis amphiala*) de cuerpo más pequeño. Las recientes disminuciones en las capturas de zorrillos manchados han suscitado preocupaciones sobre el estado de la población de zorrillos manchados en la isla Santa Cruz y el papel potencial de los zorros en la disminución. De 2018 a 2019, utilizamos collares de radio GPS y VHF para evaluar los patrones de uso del espacio por los zorros y zorrillos moteados y desplegamos cámaras remotas para determinar el potencial de interacción entre las dos especies en los sitios de guaridas de zorrillos moteados. Los rangos de hogar estacionales (HR) de zorrillos manchados eran aproximadamente cinco veces más grandes de lo que se informó anteriormente, y los patrones temporales de uso del espacio diferían entre los zorrillos manchados y los zorros, con los zorrillos manchados utilizando solo el 32% de su HR de seis meses durante una semana, mientras que los zorros se movían más ampliamente en períodos de tiempo cortos, cubriendo el 60% de su FC estacional durante una semana. A pesar de los rangos de hogar estacionales más amplios en general, el número de tipos de vegetación utilizados por los zorrillos manchados fue menor que el utilizado por los zorros que viven en la misma área, en consonancia con el nicho estrecho hipotético para los zorrillos manchados. En términos más generales, la selección de los tipos de vegetación varió entre los individuos, dentro de las especies y entre los lugares de la isla. Basándonos en la captura de cámaras en los sitios de guaridas de zorrillos manchados, encontramos una relación positiva entre la tasa de visitas de zorrillos manchados y la pendiente en los sitios de guaridas, pero ninguna relación con la cubierta vegetal, lo que sugiere que las guaridas más utilizadas estaban en áreas de pendientes más pronunciadas. La evidencia fotográfica de un zorro que intenta sacar una mofeta moteada adulta de su guarida sugiere que la depredación en los sitios de guarida podría ser un factor en la mortalidad de la mofeta manchada.

Interspecific competition is an important mechanism structuring animal communities (Case and Gilpin, 1974; Schoener, 1974). Among carnivores, dominant competitors may restrict population size and distribution of subordinate species by both exploitative competition for limited resources and through interference competition in the form of mortality due to aggression and predation (Linnell and Strand, 2000; Prugh and Sivy, 2000; Ritchie and Johnson, 2009). At the scale of individual home ranges, subordinate carnivores may retreat into areas not occupied by dominant carnivores in order to limit agonistic interactions (e.g., Sargeant et al., 1987; St.-Pierre et al., 2006; Kamler et al., 2012; Vanak et al., 2013; Dröge et al., 2017). Intraguild predation among carnivores is an extreme form of competition and occurs most often when the dominant species is larger than the subordinate species (Palomares and Caro, 1999; MacDonald and Sillero-Zubiri, 2004;Donadio and Buskirk, 2006;Thompson and Gese, 2007). This additional mortality could increase the probability of extinction especially when the subordinate species becomes rare (Linnell and Strand, 2000). Thus, understanding resource selection and niche differentiation among carnivores may be critical for conservation of subordinate carnivore species.

The California Channel Islands are home to two mesocarnivore species, the island fox (*Urocyon littoralis*) and the island spotted skunk (*Spilogale gracilis amphiala*), with the fox characterized as the dominant competitor (Crooks and Van Vuren, 1995; Jones et al., 2008). While distinct subspecies of the fox exists on six of the eight Channel Islands, the spotted skunk is only present on two, Santa Rosa and Santa Cruz Islands. Historically, foxes and spotted skunks have coexisted on the islands of Santa Cruz and Santa Rosa since each species independently colonized the islands, with estimates of arrival for both species falling between 7,100 and 11,500 years ago (Floyd et al., 2011; Hofman et al., 2015). During the mid- to late 1990s, golden eagles (*Aquila chrysaetos*) colonized the northern Channel Islands (Sonsthagen et al., 2012). Golden eagles preyed heavily on foxes, reducing fox numbers to the point that the U.S. Endangered Species Act eventually federally listed them as endangered. During this period of declining fox numbers, spotted skunk captures on trapping lines increased exponentially, suggesting a release from competition with foxes (Crooks and Van Vuren, 2000; Roemer et al., 2002; Jones et al., 2008). As fox populations have increased in the last decade, a corresponding decrease in capture rates of spotted skunks has led to concern over the long-term viability of the spotted skunk population (Dillon et al., in litt.).

Researchers have characterized the island fox as the dominant competitor with a broad ecological niche based on their extensive use of various habitats on the island, omnivorous diet, and cathemeral activity patterns (Crooks and Van Vuren, 1995). In contrast, spotted skunks display a narrower range of habitat use, have a mostly carnivorous diet, and are primarily nocturnal (Crooks and Van Vuren, 1995). Previous studies of spotted skunks on Santa Cruz Island were conducted in 1992 when spotted skunks were considered rare and foxes abundant (Crooks and Van Vuren, 1995) and in 2003 when spotted skunks were considered abundant and foxes rare (Jones et al., 2008). In the first study, when researchers studied both spotted skunks and foxes simultaneously in two locations, at one site spotted skunks selected scrub oak and ravine habitats more than expected and underutilized fennel grassland habitat, while foxes showed the opposite pattern. However, at the other study site, spotted skunks selected grasslands and foxes showed no preferential selection, at least in the wet season (Crooks and Van Vuren, 1995). In the second study, spotted skunks selected certain vegetation types more than expected but did not consistently select the same vegetation types across sites or seasons (Jones et al., 2008). These variable results warrant further investigation of the extent to which habitat selection may reduce competition between the species.

Jones et al. (2008) hypothesized that a shift of spotted skunk den sites to more open, unprotected locations in the period when foxes were rare was due to a release from predation by foxes on spotted skunks at den sites, suggesting intraguild predation may be important in these species' interactions. Individual spotted skunks will use multiple dens (Crooks, 1994; Doty and Dowler, 2006) and different individuals may use the same den (Lesmeister et al., 2009). Den locations can be highly variable, though studies of den sites of mainland spotted skunks suggested that dens were associated with higher vegetation cover (Doty and Dowler, 2006; Lesmeister et al., 2009) and steeper slopes (Lesmeister et al., 2009). On Santa Cruz Island, Crooks (1994) documented spotted skunks denning under shrubs, in open grassland, rock cavities, root cavities, tree cavities and under human structures. Researchers have not investigated how slope and vegetation cover of a spotted skunk den site could affect visitations by spotted skunks.

The main objectives of this study were to explore patterns of space use by spotted skunks and foxes over time by using global positioning system (GPS) telemetry and to use remote cameras to quantify the potential for interaction between the two species at spotted skunk den sites. More generally, understanding habitat selection patterns of these two competing insular endemic species will inform our understanding of the mechanisms allowing coexistence among sympatric competitors.

Materials and Methods—*Study Area*—Santa Cruz Island (34° 00′ 7.80″ N, 119° 43′ 20.99″ W) is the largest of the California Channel Islands, encompassing 249 km^2. It is located approximately 30 km off the coast of southern California. The Nature Conservancy owns and manages approximately 76% of the island and the United States National Park Service owns and manages the remaining 24%. The island is approximately 34 km long and ranges from 3 to 11 km wide with a system of interior valleys running east to west enclosed by mountain ranges to the north and south (Schoenherr et al. 1999). Mount Diablo is the highest peak at 740 m. Climate is maritime Mediterranean with hot, dry summers and cool, wet winters. The island supports several types of vegetation including chaparral, coastal sage scrub, grassland and pine and oak woodlands (Junak et al., 1995). Other land mammals include the deer mouse (*Peromyscus maniculatus*), western harvest mouse (*Reithrodontomys megalotis*), and at least 11 species of bats (Laughrin, in litt.; Brown and Rainey, 2018).

Trapping—We conducted trapping over three timeframes: June–August 2018 and December–February 2019 to deploy all collars, and June–August 2019 to recover collars. We captured spotted skunks and foxes using Tomahawk single-door box traps (Tomahawk Live Traps Co., Tomahawk, Wisconsin) baited with wet/dry cat food and loganberry lure (U-Spray, Inc., Lilburn, Georgia). Once an animal was in hand, we weighed, sexed, and categorized animals as a young of the year, subadult, adult, or senior adult by first upper molar wear (Wood, 1958; Collins, 1987). Additionally, we assigned each fox and spotted skunk a body condition score from 1 to 5 based on guidelines described by the American Animal Hospital Association for pets, with 1 being thin and 5 being obese (Baldwin et al., 2010). We immobilized spotted skunks receiving collars with a ketamine (20–25 mg/kg)–xylazine (2 mg/kg) mixture. Once collaring was complete, we returned spotted skunks to traps and released them 1 to 2 hours later to ensure full recovery after immobilization. We handled foxes without anesthesia due to their docile nature and immediately released them after collaring was completed. We completed all animal procedures in accordance with Northern Arizona University IACUC Protocol 18-007.

GPS Telemetry—During June–August 2018 and December 2018–February 2019, we fitted 10 adult spotted skunks >500 g with Lotek LiteTrack20-RF Swift Fix GPS collars (Lotek Engineering Inc., Newmarket, Ontario, Canada). During August 2018, we trapped eight adult foxes >1.4 kg in the vicinity of sites where we captured GPS-collared spotted skunks and fitted them with Lotek LiteTrack60-RF Swift Fix GPS collars (Lotek Engineering Inc.). Given differences in activity patterns and limitations of collar battery life, we programmed fox and spotted skunk GPS collars to collect data differently for the two species. First, to determine space use over a longer time period, hereafter referred to as "rolling fixes," we programmed collars to take one GPS fix every 3 days at 2200 h (spotted skunks) or one GPS fix at 0100, 0300, 0600, 1200, 1800, and 2200 h every 3 days (foxes) for the life of the collar. Second, to determine space use in greater detail at specific periods of the year, hereafter referred to as "week fixes," we programmed collars to take one GPS fix every 30 min between 1900 and 0700 h for 1 week during the fall (October), winter (February), spring (May), and summer (July; spotted skunks), or one GPS fix every 30 min between 0000 and 2359 h for 1 week every month (foxes). Based on this programming, we approximated that the expected time of operation for spotted skunk and fox GPS collars was 1 year.

Before initial analyses, we projected all coordinates from geographic latitude and longitude to Universal Transverse Mercator coordinates. We then screened the GPS data based on horizontal dilution of precision. According to the manufacturer, horizontal dilution of precision values <2 were ideal and values >10 should be treated with caution. However, intensive screening of GPS points may bias datasets toward lower canopy cover and open terrain (Ironside et al., 2017), thus we chose a liberal horizontal dilution of precision (≤10) as a cutoff for our analysis. We then attributed data points with the following information: distance between consecutive points, distance from nearest road, degree slope, percentage of vegetation cover, and vegetation type (LANDFIRE, 2014; U.S Geological Survey, 2017; The Nature Conservancy, in litt.).

Home Range Analysis—We used minimum convex polygon (MCP) and kernel density estimates (KDE) to estimate home range size. We calculated MCP using the minimum bounding tool in ArcMap (10.4; Esri, Redlands, California) with 100% isopleths to estimate MCP for each timeframe (rolling and week). We used ArcMET (Wall, 2014), an add-on tool for ArcMap, to analyze KDE. We estimated 95% isopleths using an optimum smoothing parameter (h-ref) chosen by the ArcMET program. All values are reported as hectares ± *SE*. We used all GPS points (rolling and week) to calculate MCP, but used only rolling GPS fixes to calculate KDE.

To determine how space use by individual spotted skunks and foxes changed through time and across seasons, we used different subsets of telemetry locations to answer the following questions: 1) What percentage of an area across a 3-month period does an individual use within a single week and does that differ between fall and winter? 2) How does the area used by an individual during 1 week in either fall or winter compare to the area used by the same animal over 6 months from August 2018 to February 2019? 3) How much does the area used during 1 week in October 2018 overlap with the area used by the same animal during 1 week in February 2019? Because of limited data and collar life, we restricted our analyses to fall and winter. However this allowed us to compare movement during a nonbreeding period and a breeding period (fall season), when Rocky Mountain spotted skunks (*Spilogale gracilis gracilis*), a close relative of the island spotted skunk, have been recorded to breed (Mead, 1968). To answer the first question, for each individual, we calculated the MCP using 1 week of intensive fixes in October 2018 to the area used across 3 months that bracketed that period (August–October 2018 rolling fixes) and then intersected the two timeframes using the intersect tool in ArcMap. We used the same approach using the week of intensive fixes in January or February 2019 and compared it to the 3 months of rolling fixes from December 2018 to February 2019. To answer the second question, we repeated this process but compared MCP based on the week of intensive fixes in either fall or winter to the MCP based on all the fixes from August 2018 to Feburary 2019. We answered the third question by comparing MCPs calculated for each animal based on locations during 1 week in October 2018 to those collected during 1 week in January or February 2019. We reported results for each question as the mean percentage overlap averaged over all individuals of each species when data for more than one individual was available.

Habitat Analysis—We calculated 3-month and 6-month MCPs for fall and winter for four foxes and two spotted skunks living in the same area of the island to determine habitat selection within and between seasons. We limited our analysis to this subset of animals because vegetation types and availability varied strikingly across different regions of the island and comparing animals living in different regions would have confounded patterns of spatial variation in vegetation communities with selection for specific vegetation types. Using the random point generator in ArcMap, we generated two sets of random points for fall and winter within the MCP boundary. The number of random points were unique for each animal and matched the amount of GPS points collected during each season (fall and/or winter). To determine vegetation cover, we downloaded raster percentage of vegetation cover data from the most recent available layer (LANDFIRE, 2014) at a 30-m resolution. We then clipped rasters to the island layer to exclude ocean values. We removed vegetation categories from analysis if there were fewer than five GPS and random points within them. We compared the proportion of GPS points to the proportion of random points using a χ^2 goodness of fit test to determine if animals were using habitat relative to availability for each species (Manley et al. 1993). To determine if habitat selection differed among different seasons, we used a χ^2 contingency test. We considered tests significant for $P < 0.05$. We calculated confidence intervals (95%) for each vegetation category following procedures in Lin et al. (2013) and assigned positive or negative selection for a vegetation category if proportion of random points fell below or above the confidence interval for the observed values.

Den Site Characteristics and Visitation—To locate spotted skunk den sites we fitted 9 adult spotted skunks >500 g with Holohil RI-2D very-high-frequency (VHF) collars (Holohil Systems Ltd, Carp, Ontario, Canada) during January and February 2019. We considered a site where we found a spotted skunk resting during the day as a den. We located individual spotted skunks in their dens one to two times per week during daylight hours, weather and road access permitting. Once we located a spotted skunk, we recorded the location using a handheld GPS unit (Garmin, Olathe, Kansas) along with a written detailed physical description of the den and a photo of the den entrance.

To compare prevalence of den types to previous studies, we categorized spotted skunk dens using a modified version of the Jones et al. (2008) structure classification, which separated dens into five categories: 1) dense woody vegetation: dens under woody plants which provided dense cover at ground level, 2) open woody vegetation: dens under/inside woody plants that did not provide significant cover at ground level, 3) herbaceous: dens in open areas covered by herbaceous plants not associated with woody vegetation, 4) human made: nonrock dens under human-made structures including log piles, and 5) rock: dens among rock. We also classified dens based on exposure type as either: 1) protected: den underground or within a tree trunk, or 2) exposed: den above ground not within a trunk. We reported all numbers as value ± *SE*.

To assess how often spotted skunks and foxes visited dens, we placed Reconyx PC800 or MR5 remote cameras (Reconyx Inc., Holmen, Wisconsin) approximately 2–5 m from the openings of spotted skunk dens that we located during VHF tracking. We set the cameras at medium-high sensitivity and to shoot a burst of three consecutive photos when triggered. We calculated fox and spotted skunk detection rates by dividing the number of each species' occurrences at the den site by the number of days the camera was operational. We defined a detection as each time a fox or spotted skunk entered the camera frame. We considered consecutive photos of the same species within a 30-min time frame the same individual and counted those as a single detection unless the animals in the sequence could be distinguished as a different individual based on an obvious characteristic such as presence of a radio collar on one individual and not another. We calculated vegetation cover, vegetation type, and slope for each den site in ArcMap using the same methods described for habitat analysis. We used linear regression to test for relationships between 1) spotted skunk detections and vegetation cover, 2) spotted skunk detections and slope, and 3) spotted skunk detections and fox detections. We considered tests significant if $P < 0.05$.

Statistical Analysis—We used program R (version 3.5.1; http://www.R-project.org/) and Microsoft Excel (version 16.43, Microsoft, Redmond, Washington) for all statistical analyses. Throughout the manuscript we report all means as mean ± *SE*.

Results—*GPS Telemetry*—We deployed 18 GPS collars on adult animals, including 8 foxes (male [M] = 5, female [F] = 3) and 10 spotted skunks (M = 8, F = 2) and 9 VHF collars on spotted skunks (M = 8, F = 1) in various locations around the island (Fig. 1). The mean body condition score for a collared fox was 2.75 (range 2–3) and, for a collared spotted skunk, 2.4 (range 2–3), indicating healthy individuals. We acquired partial datasets from 14 individuals, including all 8 foxes and 7 spotted skunks (M = 5, F = 2) through remote download or physical capture. By the end of field study in summer 2019 we were able to physically recover 6 of the 8 fox GPS collars and 3 of the 10 spotted skunk GPS collars. We observed extensive damage on the recovered collars. All collars were missing antennas and were no longer transmitting very-high-frequency (VHF) signals. Bite marks covered all fox collars and 3 were missing the GPS unit entirely. We recovered carcasses of a collared fox and spotted skunk but cause of death could not be determined in either case.

Overall, the average GPS fix success rate was 87 ± 4% for fox collars and 66 ± 8% for spotted skunk collars. Total successful fixes for all fox collars (M = 5, F = 3) was 13,829 out of 16,533 fix attempts. Fox fixes were reduced to 12,157 after screening for position accuracy, averaging 1,519 ± 383 valid fixes per collar. Total successful fixes for all spotted skunk collars (M = 5, F = 2) was 901 out of 1,434 fix attempts. Spotted skunk fixes were reduced to 810 after screening for position accuracy, averaging 115.6 ± 33 fixes per collar. Number of GPS points varied across individuals and species due to collar damage and malfunctions. Of the seven spotted skunks, two spotted skunks (M = 2) had five GPS fixes, three spotted skunks (M = 3) had data for only fall (133, 144, and 177 fixes), one spotted skunk (F = 1) had data for only winter (103 fixes), and one spotted skunk (M = 1) had data for both fall (144 fixes) and winter (84 fixes). Of the eight foxes, five foxes (M = 3, F = 2) had data for only fall (449, 454, 455, 469, and 475 fixes) and three foxes (M = 2, F = 1) had data for both the fall (445, 455, and 477 fixes) and winter (604, 616, and 645 fixes). Only one spotted skunk (M = 1) and three foxes (M = 2, F = 1) collected concurrent week and rolling GPS data for both fall (August–October 2018) and winter (December 2018–February 2019) periods. Due to premature collar failure, we collected limited GPS data during spring and summer, which prevented analysis for those seasons.

Home Range—Across all GPS telemetry fixes for seven (M = 5, F = 2) spotted skunks, mean overall KDE home range size was 170 ± 3 ha (MCP = 80 ± 3 ha), with home range of the five males averaging 218 ± 3 ha (MCP = 80 ± 2 ha) and the two females 98 ± 4 ha (MCP = 79 ± 1 ha) Mean overall KDE home range for eight foxes (M = 5, F = 3) was 61 ± 1 ha (MCP = 116 ± 3 ha), with mean home range of the five males 72 ± 1 ha (MCP = 146 ± 5 ha) and the three females 45 ± 1 ha (MCP = 64 ± 3 ha; Table 1).

In general, home range sizes based on 1-week fixes, 3 months of rolling fixes, and 6 months of rolling fixes increased over time for spotted skunks but remained

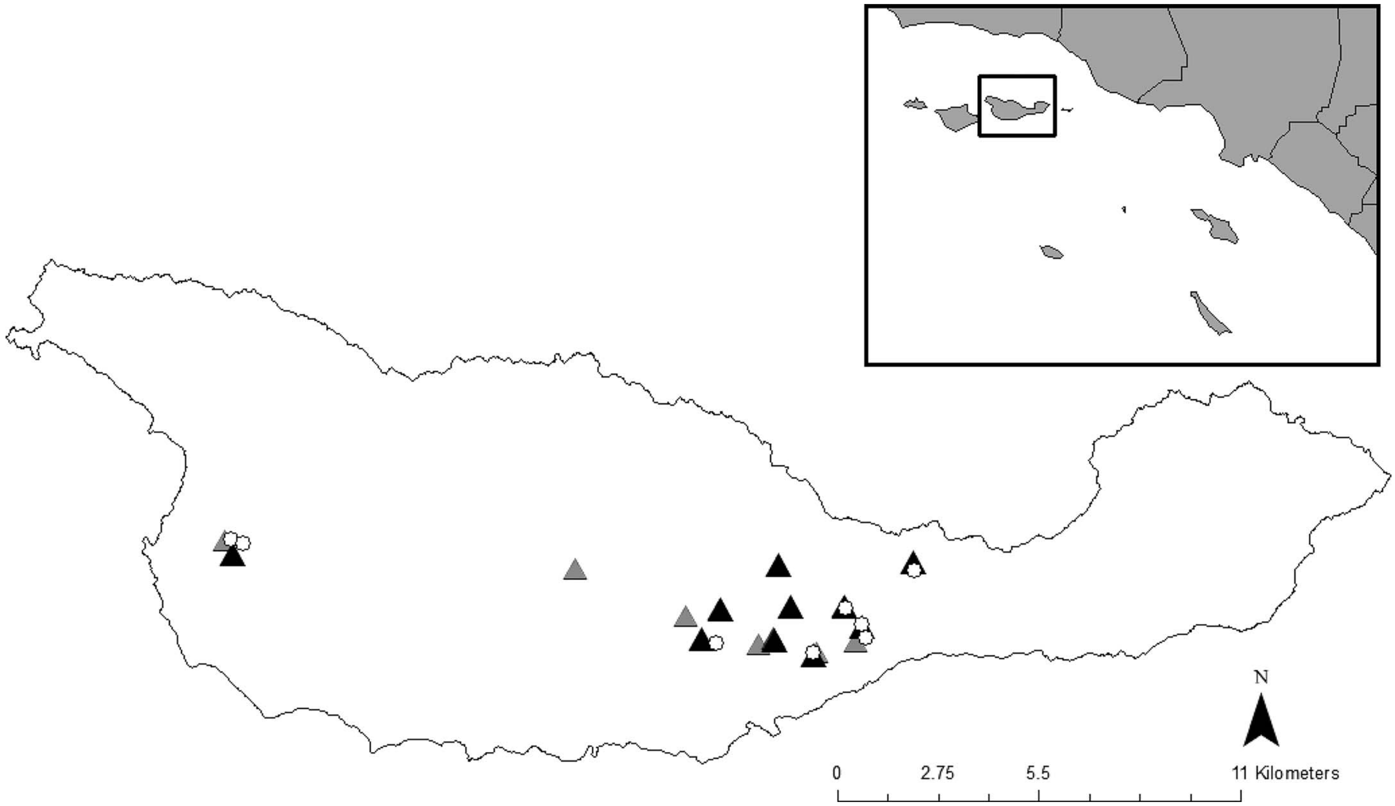


Fig. 1—Santa Cruz Island, California. Location of global positioning system (GPS; black triangle) and very-high-frequency (VHF; gray triangle)–collared island spotted skunks and GPS-collared island foxes (white circle).

similar for foxes (Fig. 2). Home range estimates for spotted skunks increased eightfold, from a mean KDE of 36 ± 7 ha (MCP = 33 ± 8 ha) based on 1-week fixes of three male spotted skunks to 205 ± 20 ha (MCP = 115 ±19 ha) based on 3 months of rolling fixes of the same three male spotted skunks, then to 299 ha (MCP = 169 ha) for one male spotted skunk with a collar that functioned for all 6 months (Fig. 2). In contrast, home range estimates of foxes remained similar regardless of sampling duration. Mean KDE home range size was 78 ± 24 ha (MCP = 66 ± 20 ha) for fall week fixes for eight foxes (M = 5, F = 3), 73 ± 14 ha (MCP = 87 ± 28 ha) for 3 months of rolling fall fixes for the same eight foxes, and 83 ± 23 ha (MCP = 100 ± 22 ha) for 6 months of rolling fixes for three foxes (M = 2, F = 1).

For foxes, MCP home range estimates based on fall 1-week fixes overlapped those based on 3 months of fall fixes by 77% (n = 8) and those based on 6 months of fixes by 64% (n = 3), indicating that foxes moved through slightly more than half of their 6-month MCP in a week. The MCP home range estimates based on 1 week of fall fixes for the spotted skunk overlapped that based on 3 months of fall fixes by 32% (n = 4) and based on 6 months by only 8% (n = 1), reflecting the tendency to use only a portion of a larger home range during a week (Figs. 2 and 3). The mean overlap between MCP in an October week and a January week for three foxes (M = 2, F = 1) was 60 ± 13% while there was no overlap between the MCP October week and February week for the male spotted skunk (Fig. 3).

Habitat Selection—Foxes used more vegetation types in both fall (7 ± 0.7) and winter (7 ± 1.5) compared to spotted skunks (4.75 ± 0.3 and 4 ± 0 fall and winter, respectively; Fig. 4). Although all individuals showed selection for some vegetation types relative to availability within each season, there was no consistent pattern of which vegetation types were overselected across individuals within species, even though we limited this analysis to the subset of animals living in the same region of the island so that variation in vegetative community types and availability were similar across animals (Fig. 4). Some patterns were suggestive, however. In the fall, two (M = 2) of the four spotted skunks underutilized island buckwheat scrub (*Eriogonum arborescens*) and four of the eight foxes underutilized California sagebrush scrub (*Artemisia californica*) and island buckwheat scrub. In the winter, both a male and a female spotted skunk underutilized island buckwheat scrub and two of the three foxes underutilized coastal and island scrub-oak chaparral (*Quercus pacifica*). Type of vegetation used differed between fall and winter for all individuals of both species (Fox31402 $\chi^2 = 41.3$, $df = 8$, $P < 0.001$; Fox31405 $\chi^2 = 34.6$, $df = 8$, $P < 0.001$; Fox31407 $\chi^2 = 99.8$, $df = 7$, $P < 0.001$; Skunk31269 $\chi^2 = 97.7$, $df = 8$, $P < 0.001$) but selection for a single dominant vegetation type was more prominent for the spotted skunk than three foxes (Fig. 4). During the fall, over 60% of GPS locations for

Table 1—Overall 95% kernel density estimates (KDE) and 100% minimum convex polygon (MCP) home range (HR) size in hectares for seven global positioning system (GPS)-collared spotted skunks and eight island foxes on Santa Cruz Island. We used only rolling points in the calculation of KDE, while we used all points within the timeframe for MCP. We show mean averages with standard errors.

			95% KDE		100% MCP	
ID	Sex	Months monitored	GPS points	HR size	GPS points	HR size
Skunk31259	Male	August–November 2018	20	159	133	78
Skunk31260	Male	July–November 2018	29	196	179	138
Skunk31261	Female	August–October 2018	25	55	146	74
Skunk31269	Male	July 2018–March 2019	49	299	238	169
Skunk31270	Female	December 2018–March 2019	16	140	105	84
Skunk31271	Male	January–February 2019	5	N/A	5	4
Skunk31273	Male	July 2018	5	N/A	5	13
			Average male skunk	218 ± 2.8		80 ± 2.4
			Average female skunk	98 ± 4.3		79 ± 0.6
			Average skunk	170 ± 3.0		80 ± 2.5
			95% KDE		100% MCP	
ID	Sex	Months monitored	GPS points	HR size	GPS points	HR size
Fox31400	Female	August–December 2018	252	32	1,117	49
Fox31401	Female	August–October 2018	152	39	459	30
Fox31402	Male	August 2018–February 2019	330	50	1,425	76
Fox31403	Male	August–November 2018, March–August 2019	494	73	2,319	357
Fox31404	Male	August–November 2018	171	72	463	103
Fox31405	Female	August 2018–July 2019	615	65	2,972	113
Fox31406	Male	August–October 2018	199	59	472	49
Fox31407	Male	August 2018–July 2019	648	107	2,925	144
			Average male fox	72 ± 1.4		146 ± 4.6
			Average female fox	45 ± 1.4		64 ± 3.1
			Average fox	62 ± 1.1		116 ± 3.5

the spotted skunk occurred in coastal and island scrub oak chaparral while only 16% of locations occurred in fennel (*Foeniculum vulgare*). However, in winter over 60% of locations occurred in fennel while only 8% of locations occurred in coastal and island scrub oak chaparral. Foxes used a mixture of various vegetation types in both time periods.

Den Site Characteristics and Visitation—Eighty-seven dens from 9 VHF-collared spotted skunks (M = 8, F = 1) were located and described. The majority of dens were associated with woody vegetation (82%, $n = 71$), with far fewer associated with herbaceous cover (9%, $n = 8$), human-made structures (5%, $n = 5$), or rock crevices (4%, $n = 4$). All human-associated dens were in harvested eucalyptus logs that were stacked in large piles. Of the dens identified, we classified 90% of the dens as protected and 10% as unprotected.

During 2018–2019, we monitored 15 spotted skunk dens across the island by remote cameras. The average number of days a single den was monitored was 133 ± 24 days (minimum = 6, maximum = 361). We excavated one den to recover a dropped GPS collar, but due to continued occurrences of spotted skunks at the site, we left the camera in place and continued monitoring. Cameras detected spotted skunks at 13 of the 15 dens, an average of 7 ± 2.7 times, ranging from 0 to 36 detections per month. It was often challenging to distinguish spotted skunk individuals apart thus we could not confidently report den reuse rate in this study. However, at seven of the den sites at least two different individuals visited the den on separate occasions as we collected photographs of both collared and uncollared spotted skunks. Additionally at another den, at minimum three different spotted skunks visited, as there were photos of uncollared, VHF-collared, and GPS-collared spotted skunks. Vegetation cover did not predict the number of spotted skunk detections at a den site ($R^2 = 0.172$, $df = 1$, $P = 0.140$) but slope was positively correlated with spotted skunk detection rates ($R^2 = 0.392$, $df = 1$, $P = 0.017$; Fig. 5). Of the 15 dens monitored, only one site did not record a fox on camera. There was no significant relationship between spotted skunk and fox detections at den sites ($R^2 = 0.167$, $df = 1$, $P = 0.146$), although the den site with the highest fox visitation had low spotted skunk visitation. At one den site, a series of photos captured a fox digging at the den entrance while an adult spotted skunk was inside. In this series, a spotted skunk entered the den at 0157 h then later that day at 1303 h a fox arrived and dug at the entrance until 1309 h, when the fox left and did not

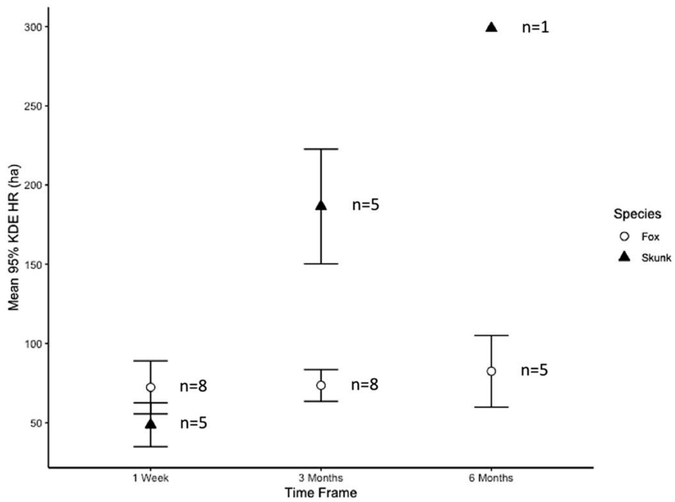


Fig. 2—Mean 95% kernel-density home range estimates for island spotted skunks (black triangles) and island foxes (open circles) followed using global positioning system–collars over a 1-week, 3-month, or 6-month period on Santa Cruz Island, California, in 2018 and 2019. Number of unique individuals in each sample is given as *n*.

return. That night at 1802 h the spotted skunk emerged and appeared unharmed.

Discussion—*Home Range*—For both the island fox and spotted skunk, we found larger home range sizes than previously reported on Santa Cruz Island. In 1992, Crooks and Van Vuren (1996) found mean fox home range size varied between 25 and 32 ha ($n = 12$) and in 1994, Roemer et al. (2001) reported an overall mean size of 55 ha ($n = 14$), both smaller than the mean 3-month range size of 73 ha in fall ($n = 8$) and mean 6-month home range size of 82 ha ($n = 3$) found in this study. Home range estimates of island foxes on other islands, however, were similar to or larger than those reported here, including 75 ha on San Clemente (island size = 147 km^2; Resnik, 2012), 105 ha on Santa Catalina (island size = 194 km^2; J. King, pers. comm.), 181 ha on San Nicolas (island size = 59 km^2; Powers, 2009) and 339 ha on Santa Rosa (island size = 215 km^2; Drake et al., 2015). Our seasonal estimates of home range in spotted skunks were also larger than previously reported, with a mean of 167 ha in fall ($n = 4$) and 225 ha in winter ($n = 2$) with an overall 6-month home range size of 299 ha ($n = 1$). In comparison, Crooks and Van Vuren (1995) reported mean spotted skunk home range sizes of 23 ha ($n = 7$) during the wet and 40 ha ($n = 1$) during the dry seasons and Jones et al. (2008) reported a mean seasonal home range size of 39 ($n = 33$) and annual home range size of 52 ha ($n = 6$). In these previous studies, authors utilized VHF collars and monitored animals over an entire year and included study sites on different parts of the island.

Home range estimates are sensitive to the number of locations collected for each animal with some studies estimating a minimum of 30–100 locations necessary to reach

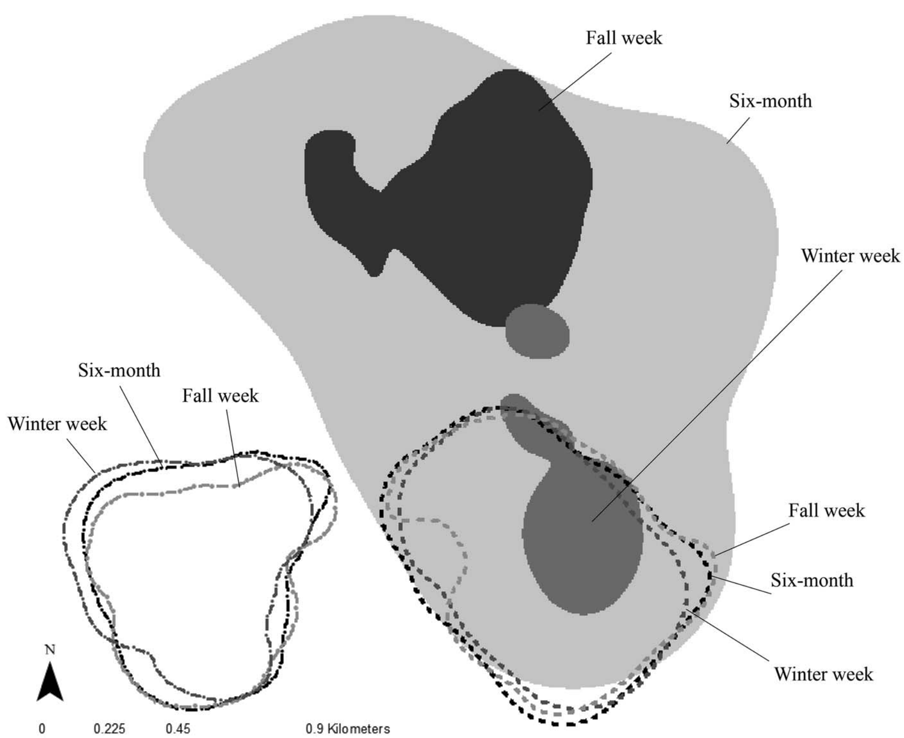
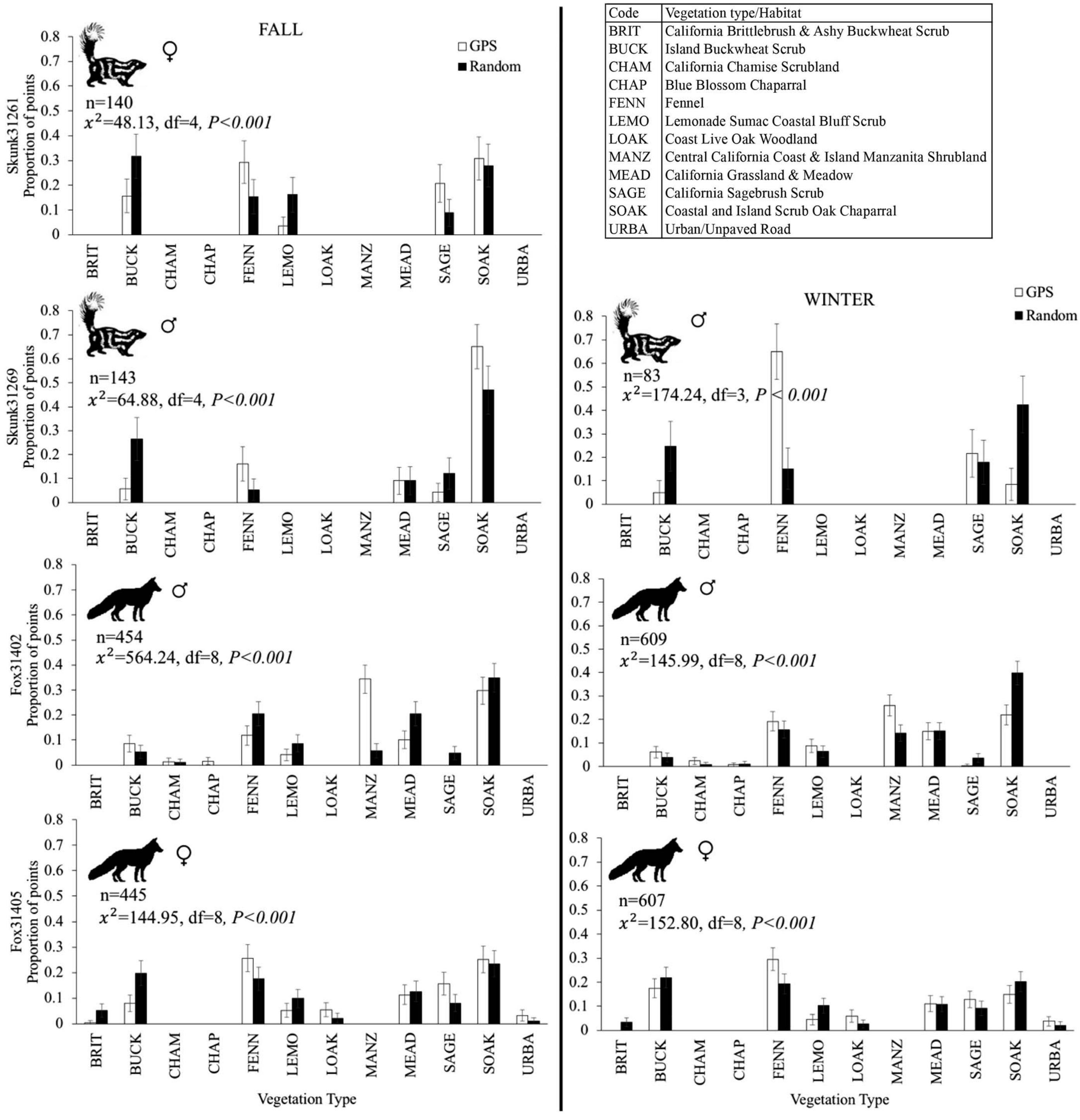


Fig. 3—Ninety-five percent kernel-density home range estimate based on fall week (October), winter week (January/February), and 6-month (August–February) rolling global positioning system fixes for two island foxes (dotted lines) and one island spotted skunk (filled polygons) living in same area of the central valley of Santa Cruz Island, California, in fall and winter 2018–2019.



Code	Vegetation type/Habitat
BRIT	California Brittlebrush & Ashy Buckwheat Scrub
BUCK	Island Buckwheat Scrub
CHAM	California Chamise Scrubland
CHAP	Blue Blossom Chaparral
FENN	Fennel
LEMO	Lemonade Sumac Coastal Bluff Scrub
LOAK	Coast Live Oak Woodland
MANZ	Central California Coast & Island Manzanita Shrubland
MEAD	California Grassland & Meadow
SAGE	California Sagebrush Scrub
SOAK	Coastal and Island Scrub Oak Chaparral
URBA	Urban/Unpaved Road

Fig. 4—Proportion ($\pm SE$) of global positioning system (GPS; open bars) versus randomly generated points (solid bars) within each individual's minimum convex polygon (MCP) home range during the fall and winter of 2018–2019 associated with each vegetation type for one spotted skunk and two foxes living in the same area of Santa Cruz Island, California. The number of GPS locations used for each analysis is given as *n*. No winter data were available for the female skunk.

an asymptote for estimates of seasonal home ranges and 300 for annual home ranges (Seaman et al., 1999; Girard et al., 2002). Previous studies of fox home ranges were determined by obtaining 632 VHF telemetry locations (mean = 26 per fox; Crooks and Van Vuren, 1996) and ~5,700 VHF telemetry locations (mean = 133 per fox, approximate; Roemer et al., 2001), compared to the ~13,000 (mean = 1,729 per fox) GPS locations collected in our study. Likewise, for island spotted skunks, previous studies relied on VHF collars and much smaller numbers of locations, with a

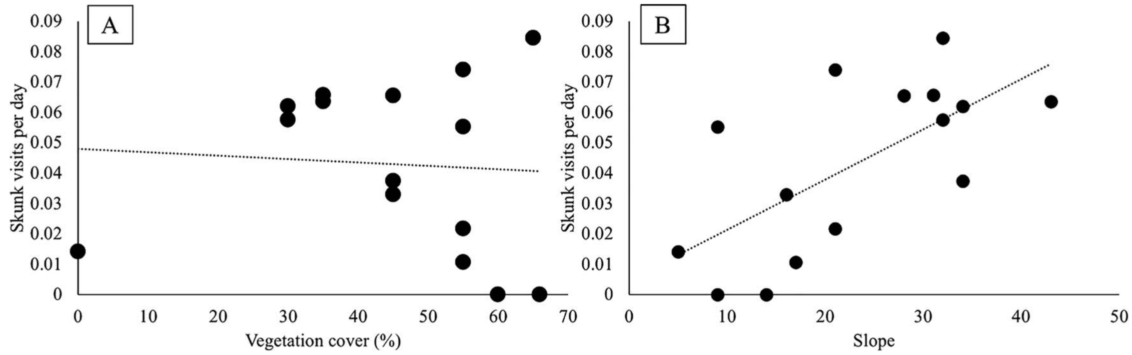


Fig. 5—Relationships between island spotted skunk visitation rates per day at spotted skunk dens with varying (A) vegetation cover (R^2 = 0.172, df = 1, P = 0.140) and (B) slope (R^2 = 0.392, df = 1, P = 0.017) on Santa Cruz Island, California, in 2018 and 2019.

seasonal average of 27 (Crooks and Van Vuren, 1996) or 29 (Jones et al., 2008) locations per spotted skunk compared to the ~900 (mean = 128 locations per spotted skunk) GPS locations of this study. Although we collected a large number of GPS locations per animal in our study, the number of unique individuals we followed was small and generalizations from our data should be interpreted with that important caveat.

Home range may also vary with age of the study animal, conspecific density, and food availability (Benson et al., 2006; Schradin et al., 2010). Foxes were abundant and spotted skunks uncommon during our study, similar to the previous study conducted in the early 1990s (Crooks and Van Vuren, 1996), so differences in density are unlikely to explain the differences in home range we documented. Likewise, body condition of foxes and spotted skunks trapped during our study did not indicate the kind of nutritional stress that would likely be associated with a major shift in food availability. Body conditions between 2 and 3 for foxes and spotted skunks are typical for healthy wild individuals (C. Gagorik, pers. observ.). The larger home range of spotted skunks relative to foxes we documented is consistent with the hypothesis that large home ranges result from subordinate species moving more widely through the landscape to avoid the dominant competitor (St. Pierre et al., 2006; Kamler et al., 2012). Alternate hypotheses for the larger home ranges of spotted skunks include low population densities, resulting in larger territory sizes, and more specialized diets, necessitating larger ranges to fulfil metabolic needs (Crooks and Van Vuren, 1995).

The temporal pattern of space use by foxes was strikingly different from that of spotted skunks in our study. Relative to foxes, spotted skunks tended to use a larger home range over time, but used only a fraction of that area over shorter temporal periods of weeks or months. A consistent pattern seen during the fall and winter periods was the tendency of island foxes to move through a large percentage of their trimonthly home range in the course of a single week. These weekly movements overlapped their 3-month seasonal home range by an average of 76% in the fall and 62% in the winter. In contrast, island spotted skunks showed more restricted movements across time, using a much smaller percentage of their trimonthly home range during a similar 1-week period. Weekly overlap between seasonal home ranges for a spotted skunk encompassed a mean of 32% in the fall and 34% in the winter, while no overlap of weekly home range occurred between fall and winter.

One caveat of this study is its basis primarily on male spotted skunks. Male spotted skunks tend to have larger home ranges (Jones et al., 2008), especially during the breeding season (Lesmeister et al., 2009). Western spotted skunks exhibit delayed implantation, with breeding occurring in the fall and parturition in the spring, and it is hypothesized island spotted skunks may follow the same pattern (Mead, 1968). Thus, the fall home range estimates we obtained may be inflated if males were travelling to find females during this period. This does not explain the equally large home range for the male spotted skunk we tracked in the spring. Further exploration of spotted skunk breeding ecology will aid in understanding movement patterns.

Habitat Selection—Island foxes in our study used a broader array of vegetation types than spotted skunks and selection for specific vegetation types in both species varied among individuals and across locations. In previous studies, island foxes showed selection for fennel grasslands and avoidance of ravines and scrub oak patches at one site and no selection for habitat types in another (Crooks and Van Vuren, 1995), while spotted skunks showed preferences for ravines, and coastal sage scrub and avoidance of fennel and scrub oak at one site and preferences for grassland at another (Crooks and Van Vuren, 1995). Jones et al. (2008) likewise reported spotted skunk selection for habitat types varied with both seasons and across sites. Consistent with our findings, a study of microhabitat associations using remote cameras and live trapping grids on both Santa Cruz and Santa Rosa islands during 2015–2017 found that spotted skunks had positive associations with rugged topography or woody vegetation including low shrubs and trees and stumps (Bolas et al., 2022). Foxes also had positive association with trees and stumps but did not respond to shrubs and had negative associations with rugged topography. Overall, these past and current studies suggest that spotted skunks may use denser cover and steeper slopes to avoid competition with foxes.

The one male spotted skunk monitored across seasons showed a strong preference for fennel in the winter, and a shift from selection for scrub oak in the fall to underutilization of that vegetation type in the winter. This variation in habitat selection across space and time may reflect seasonal changes in prey availability associated with different vegetation types. This finding contrasts with studies of mainland spotted skunks in less complex habitats like those in Arkansas where positive selection for shortleaf pine and hardwood stands was consistent across seasons (Lesmeister et al., 2009).

Den Site Characteristics and Visitation—Crooks (1994) first reported finding island spotted skunk dens in a variety of substrates but often under some form of cover. Later, during 2003–2004 when foxes were rare, Jones et al. (2008) documented spotted skunks using more unprotected den sites, suggesting a release from interference competition and that spotted skunks might avoid foxes by denning in more densely vegetated areas. We found no correlation between spotted skunk visits and fox visits at dens, which we would expect if dens were selected to minimize contact between species. However, we found a significant positive relationship between spotted skunk den visits and slope, suggesting spotted skunks may visit dens on steeper slopes more often, consistent with preference for slopes reported for some mainland spotted skunk populations (Lesmeister et al., 2009). We also observed that dens were most frequently associated with woody vegetation, similar to that reported for spotted skunks when fox densities were low (Jones et al., 2008), but also a shift toward more protected dens similar to when fox populations were relatively high in 1992 (Crooks and Van Vuren, 1994 1995).

Although previous researchers have hypothesized the potential for foxes to prey on spotted skunks in their dens, and have reported spotted skunks in the scat of island foxes (Cypher et al., 2014), we report the first evidence of a fox attempting to excavate a den while an adult spotted skunk was inside. Predation at den sites is not uncommon in systems where multiple carnivore species overlap in space and diet. For example, in Africa, cheetah (*Acinonyx jubatus*) cubs are vulnerable to predation by larger predators such as lions (*Panthera leo*) (Laurenson, 1994; Mills and Mills, 2014) and Creel and Creel (1998) have reported that spotted hyenas (*Crocuta crocuta*) disturb African wild dog (*Lycaon pictus*) dens sites and kill young. In Scandinavia, Frafjord et al. (1989) observed red foxes (*Vulpes vulpes*) digging at an arctic fox (*Alopex lagopus*) den and chasing and killing adults and cubs. Although our study focused primarily on male spotted skunks, females, especially those with kits, may be more vulnerable and therefore most sensitive to interactions with foxes. Den sites may provide opportunities for foxes to target young spotted skunks when mothers are away during foraging periods. The importance of fox predation at den sites and how such mortality could affect recruitment of young into the population remains an important question.

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