



Original research article

Multi-population comparison of resource exploitation by island foxes: Implications for conservation



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ABSTRACT

Imperiled island foxes are inherently resource-limited by their insular ecology. We examined food use on all 6 islands where they occur to assess resource exploitation patterns. Over 40 different food items were identified with item use varying among islands. Sixteen items occurred with $\geq 10\%$ frequency in annual fox diets: deer mice, birds, lizards, beetles, beetle larvae, Jerusalem crickets, silk-spinning sand crickets, grasshoppers, earwigs, snails, and fruits of toyon, manzanita, prickly pear cactus, ice plant, Australian saltbush, and summer holly. Foxes used a diversity of food items with variations among islands attributable to island-specific availabilities. Deer mice in particular appeared to be preferred. Foxes also exhibited extensive use of non-native items, such as ice plant fruits, European snails, and earwigs, and foxes may even be dependent on these items on some islands. To increase food security and promote population stability, we recommend (1) continuing and enhancing habitat restoration efforts on all islands, (2) increasing the abundance of native items in association with any removals of non-native species used by foxes, and (3) monitoring annual trends in abundance of key food items as well as periodic monitoring of item use by foxes to determine functional responses to changes in item availability.

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1. Introduction

Island foxes (*Urocyon littoralis*) are endemic to the 6 largest Channel Islands off the coast of southern California. Populations on each island are considered unique subspecies and no natural interchange occurs between islands. Pre-1994 population estimates on the islands ranged from 450 foxes on San Miguel to 1465 foxes on Santa Cruz (US Fish and Wildlife Service, 2012). Due to relatively small population sizes, restricted distributions, and no chance for population rescue by natural dispersal, the island fox was listed as Rare by the State of California in 1971, and reclassified as Threatened in 1985. In the mid to late 1990s, fox populations on 4 of the 6 islands declined markedly due to golden eagle (*Aquila chrysaetos*) predation (San Miguel, Santa Rosa, and Santa Cruz) and canine distemper disease (Santa Catalina). On these 4 islands, captive breeding colonies were established using surviving animals, and for several years there were no (San Miguel, Santa Rosa) or very small (Santa Cruz, Santa Catalina) wild populations. Consequently, the foxes on these 4 islands were listed as Federally Endangered in 2004 (US Fish and Wildlife Service, 2004, 2012).

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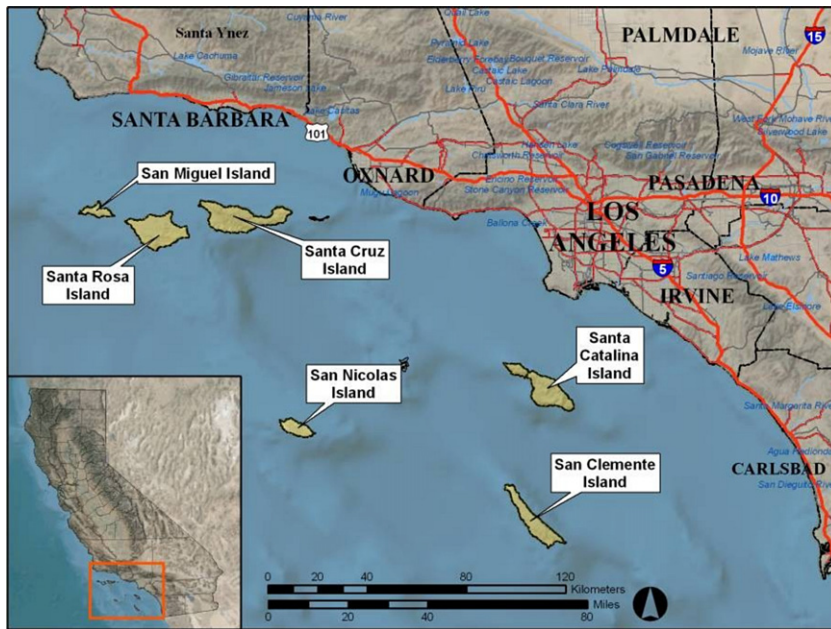


Fig. 1. Locations of the 6 Channel Islands with inhabited by island foxes off the coast of southern, California.

Beginning in 2001 on Santa Catalina and 2004 on other islands, releases of foxes from the captive colonies were initiated, and wild populations are again present on all 6 islands. The catastrophic declines of fox numbers on the 4 islands highlighted the vulnerability of these insular populations. In addition to the immediate recovery actions (e.g. captive breeding and reintroduction into the wild), additional actions are necessary for the long-term protection and security of the populations. Actions in-progress to achieve this goal include golden eagle removal, bald eagle (*Haliaeetus leucocephalus*) restoration, feral animal removal, epidemiological monitoring and prophylaxis, and habitat restoration. The purpose of restoration activities is to improve the quality of habitats degraded by feral animals, military training activities, and invasion by non-native plants (US Fish and Wildlife Service, 2012). Habitat restoration can increase available cover and could provide even greater benefit to island foxes if such restoration also increases the abundance of preferred foods.

Typical of many canids, island foxes are considered “generalists” with regard to foraging patterns. They feed on a wide variety of food items, including rodents, birds, insects, carrion, and fruits (Cypher, 2003; Moore and Collins, 1995). Prior investigations of island fox food habits usually were not conducted in a manner that captured seasonal variations in use of items or permitted among-island comparisons unbiased by annual variation in resource availability. Also, preferences among items have not been determined. The recent low population levels on several of the islands provided an opportunity to evaluate item preferences. Due to these low levels, resource abundance was presumably high relative to fox population size and intra-specific competition for resources was relatively low. Thus, foxes were better able to express foraging preferences. By identifying item preferences, it may be possible to conduct habitat restoration or manage habitats in a manner that enhances the availability of preferred foods for foxes.

The goal of this project was to examine seasonal and spatial patterns of resource exploitation by island foxes. Specific objectives were to (1) examine seasonal food item use on all 6 inhabited islands, (2) compare item use among islands, (3) determine use of non-native items by foxes, and (4) use these results to develop recommendations for the management and conservation of island fox populations.

2. Methods

2.1. Study area

Island foxes occur on the islands of San Miguel, Santa Rosa, Santa Cruz, Santa Catalina, San Nicolas, and San Clemente off the coast of southern California (Fig. 1). These islands range in size from 37–249 km² (Table 1). The islands are primarily volcanic in origin with sedimentary components as well (Schoenherr et al., 1999). The diversity of habitats and biota on the islands (Table 1) varies with island size, terrain complexity, and distance from the mainland. In general, diversity increases with island size and terrain complexity, and decreases with distance from the mainland (Schoenherr et al., 1999). As biotic diversity increases, the number of food items potentially available to island foxes also is higher. More detailed descriptions of the biotic and abiotic attributes of each island can be found in Schoenherr et al. (1999).

Table 1

Attributes and island fox population size for the 6 Channel Islands occupied by foxes.

Source: Island attribute data modified from Schoenherr et al. (1999).

Island	Area km ² (mi ²)	Elevation m (ft)	Distance to mainland km (mi)	Estimated 2009 fox population ^a
San Miguel	37 (14)	253 (830)	42 (26)	318
San Nicolas	58 (22)	277 (910)	98 (61)	500
San Clemente	145 (56)	599 (1965)	79 (49)	1094
Santa Catalina	194 (76)	648 (2125)	32 (20)	947
Santa Rosa	217 (84)	484 (1589)	44 (27)	389
Santa Cruz	249 (96)	753 (2470)	30 (19)	1000+

^a T. Coonan, National Park Service, unpublished data.

2.2. Diet analysis

Island fox scats (feces) were collected from all 6 islands in 2009. Scats were collected during each of 4 seasons: Winter (January–March), Spring (April–June), Summer (July–September), and Fall (October–December). Scat collections were conducted by biologists based on each island and included staff from the National Park Service (San Miguel and Santa Rosa), The Nature Conservancy (Santa Cruz), Catalina Island Conservancy (Santa Catalina), Institute for Wildlife Studies (San Nicolas), and the US Navy (San Clemente). Attempts were made to collect scats from as many areas on each island as was feasible. Factors such as lack of trail and road access or presence of unexploded ordnance precluded collections from limited portions of some islands. All scats were collected into paper bags and allowed to air-dry. Bags were labeled with the date and location of collection.

Analysis of scats was conducted at the California State University-Stanislaus, Endangered Species Recovery Program office in Bakersfield, CA. Prior to analysis, scats were placed in a drying oven at 24 °C for at least 24 h to remove remaining moisture and to destroy any eggs or cysts of zoonotic parasites. Contents of each scat were then carefully separated and individual food items within the samples were identified to the lowest taxonomic level possible. Mammalian remains were identified based on bone and dental fragments and guard hair characteristics. Birds were identified based on feather and foot characteristics. Insects were identified based on exoskeleton characteristics. Fruits were identified based on seed and exocarp characteristics. Identification of items was based on comparison of remains with characteristics in established guides (e.g., Glass, 1981; Moore et al., 1974; Roest, 1986; Young and Young, 1992) or by comparison with reference collections.

Frequency of occurrence of items was determined for each island and season. However, many items only occurred at low frequencies (<10%) suggesting that such items were opportunistically encountered and consumed, and were not important to the overall diet of island foxes. Thus, to facilitate statistical analysis, items were grouped into 5 broad categories: Deer mouse (*Peromyscus maniculatus*), Insect, Native fruit, Non-native fruit, and Other. Using these categories, annual use of items was compared among islands and seasonal use of items was compared for each island using contingency table analyses employing a χ^2 statistic. *P*-values ≤ 0.05 were considered significant.

Shannon diversity indices (H') were calculated for annual diets on each island using the equation:

$$H' = (N \log N - \sum n_i \log n_i) / N$$

where N is the total number of occurrences of all items and n_i is the number of occurrences of item i (Brower and Zar, 1984). To further compare annual fox diets among islands, Horn's Index of Similarity (R_o) was calculated for each pair-wise comparison of islands using the Shannon diversity indices (Brower and Zar, 1984).

3. Results

3.1. Annual foraging patterns

During January–December 2009, a total of 2643 island fox scats was collected and analyzed. Over 40 different food items were identified in island fox scats collected from the 6 islands. Also found were a number of non-food items, many of which likely were ingested incidentally along with food items. Non-food items included grass, twigs, pieces of other vegetation, soil, pebbles, and anthropogenic items such as pieces of plastic and fibers from burlap used to cover fox traps. Island fox hairs were occasionally found in scats in small quantities and were presumed to have been ingested during self- or allo-grooming.

Across all 6 islands, 16 items occurred with a frequency $\geq 10\%$ in annual fox diets (Table 2). These items were deer mice, birds (comprising multiple species), lizards, beetles (comprising multiple species), beetle larvae, Jerusalem crickets (*Stenopalmatus* spp.), silk-spinning sand crickets (*Cnemotettix* spp.), grasshoppers, earwigs (*Forficula auricularia*), terrestrial snails, and fruits of toyon (*Heteromeles arbutifolia*), manzanita (*Arctostaphylos* spp.), prickly pear cactus (*Opuntia* spp.), ice plant (*Carpobrotus* spp., *Mesembryanthemum crystallinum*), summer holly (*Comarostaphylis diversifolia*), and Australian saltbush (*Atriplex semibaccata*). The number of items with a frequency $\geq 10\%$ ranged from 5 on Catalina to 9 on San Miguel. Annual dietary diversity was highest on San Miguel and lowest on Santa Rosa, based on the Shannon index (Table 2). Of the 16 items above, beetles were primary foods in annual diets on all 6 islands while 4 items were primary foods on just 1 island

Table 2

Food items occurring with a frequency $\geq 10\%$ and Shannon diversity indices (H') for annual diets of island foxes during 2009 on each of the Channel Islands with foxes.

Food items/Frequency of occurrence (%)											
San Clemente	San Nicolas		Santa Catalina		San Miguel		Santa Rosa		Santa Cruz		
Beetle	62.6	Beetle	64.3	Toyon	60.1	Beetle	68.6	Deer mouse	64.0	Manzanita	48.4
Beetle larva	33.9	Snail	45.2	Prickly pear	33.5	Jer. cricket	60.1	Jer. cricket	51.5	Jer. cricket	35.6
Deer mouse	30.3	Ice plant	35.0	Jer. cricket	24.7	Deer mouse	54.2	Beetle	50.7	Beetle	30.6
Snail	20.1	Earwig	32.5	Beetle	24.5	Ice plant	41.8	Earwig	30.7	Toyon	30.6
Prickly pear	17.8	Aus. saltbush	21.1	Deer mouse	18.6	Sand cricket	26.5	Beetle larva	14.5	Earwig	25.6
Lizard	11.8	Sand cricket	18.9			Lizard	17.3	Grasshopper	13.7	Sum. holly	17.2
		Deer mouse	12.0			Grasshopper	17.2	Toyon	13.3		
		Beetle larva	10.7			Beetle larva	12.0	Bird	10.1		
						Earwig	10.2				
H'	0.64		0.73		0.66		0.79		0.59		0.69
Scats	433		560		388		577		505		180

Table 3

Horn's index of similarity for pair-wise comparisons of annual island fox diets between islands during 2009.

	Horn's similarity index				
	San Nicolas	Santa Catalina	San Miguel	Santa Rosa	Santa Cruz
San Clemente	0.51	0.52	0.50	0.55	0.24
San Nicolas	–	0.20	0.52	0.44	0.37
Santa Catalina	–	–	0.49	0.56	0.59
San Miguel	–	–	–	0.74	0.41
Santa Rosa	–	–	–	–	0.58

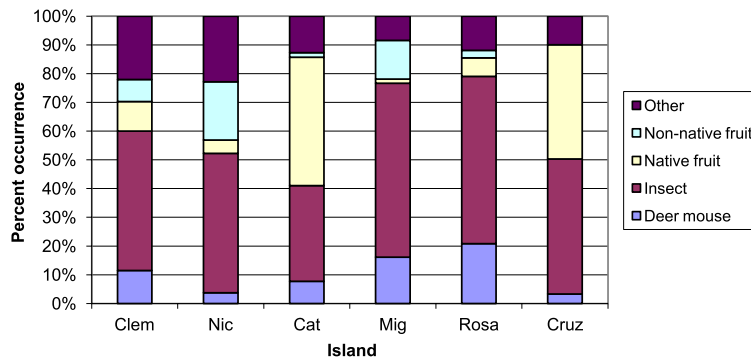


Fig. 2. Annual use of food items (grouped into 5 categories) by island foxes on each island during 2009.

each (birds on Santa Rosa; manzanita and summer holly on Santa Cruz; Australian saltbush on San Nicolas). Based on the use of items occurring with a frequency $\geq 10\%$, annual diets were most similar ($R_o = 0.74$) between San Miguel and Santa Rosa, and least similar ($R_o = 0.20$) between San Nicolas and Santa Catalina (Table 3).

For food items grouped into 5 categories (Fig. 2), annual fox diets differed significantly among islands ($\chi^2 = 2450$, 20 df, $P < 0.0001$). Insects clearly were important foods on all islands. Native fruits were important foods on Santa Catalina (toyon and prickly pear cactus) and Santa Cruz (manzanita and toyon) while non-native fruits were important foods on San Nicolas (ice plant and Australian saltbush) and San Miguel (ice plant). Deer mice were important foods on Santa Rosa and San Miguel whereas other items (e.g., terrestrial snails but other items as well) were important foods on San Nicolas and San Clemente.

3.2. Seasonal foraging patterns

On San Clemente, 11 items occurred with a frequency $\geq 10\%$ in seasonal fox diets (Table 4) and ranged from 4 in winter to 8 in fall. Deer mice, beetles, and beetle larvae were primary foods in all 4 seasons while earwigs, Australian saltbush, and sand crickets were primary foods in just 1 season each. For food items grouped into 5 categories (Fig. 3), fox diet on San Clemente differed significantly among seasons ($\chi^2 = 142.7$, 12 df, $P < 0.0001$). Insects, especially beetles, were clearly important foods in all seasons. Native fruits were important foods in winter and fall (prickly pear cactus) while non-native fruits (ice plant) were important foods in summer. Deer mice were important foods in winter and spring whereas other items collectively were important foods in all 4 seasons.

Table 4

Food items occurring with a frequency $\geq 10\%$ for seasonal diets of island foxes during 2009 on each of the Channel Islands with foxes.

Food items/Frequency of occurrence (%)							
Winter		Spring		Summer		Fall	
<i>San Clemente</i>							
<i>n</i> = 133		<i>n</i> = 107		<i>n</i> = 86		<i>n</i> = 107	
Deer mouse	54.1	Beetle	54.2	Beetle	98.8	Beetle	75.7
Beetle	35.3	Beetle larva	38.2	Beetle larva	57.0	Snail	38.3
Beetle larva	20.3	Deer mouse	30.4	Snail	41.9	Prickly pear	43.9
Lizard	15.8	Lizard	22.4	Ice plant	39.5	Beetle larva	28.0
		Aus. Saltbush	15.9	Crustacean	19.8	Ice plant	25.2
		Earwig	15.0	Prickly pear	14.0	Crustacean	22.4
				Deer mouse	10.5	Deer mouse	15.9
						Sand cricket	12.2
<i>San Nicolas</i>							
<i>n</i> = 139		<i>n</i> = 144		<i>n</i> = 148		<i>n</i> = 129	
Beetle	84.9	Beetle	67.4	Ice plant	56.1	Snail	57.4
Snail	35.3	Snail	47.9	Beetle	48.0	Beetle	57.4
Beetle larva	29.5	Earwig	47.2	Snail	41.2	Earwig	55.8
Ice plant	10.1	Ice plant	31.9	Sand cricket	31.8	Aus. saltbush	46.5
		Deer mouse	19.4	Aus. saltbush	31.8	Ice plant	57.4
		Lizard	16.7	Myoporum	22.3	Sand cricket	39.5
				Earwig	21.6	Prickly pear	27.1
				Grasshopper	18.9	Jer. cricket	18.6
				Deer mouse	12.2		
<i>Santa Catalina</i>							
<i>n</i> = 99		<i>n</i> = 93		<i>n</i> = 102		<i>n</i> = 94	
Toyon	87.9	Toyon	92.5	Toyon	48.0	Prickly pear	88.3
Jer. cricket	31.3	Jer. cricket	22.6	Prickly pear	29.4	Beetle	36.2
Beetle	18.2	Beetle	21.5	Beetle	22.6	Jer. cricket	29.8
Deer mouse	17.2	Deer mouse	18.3	Deer mouse	22.6	Earwig	17.0
Earwig	16.2			Manzanita	21.6	Deer mouse	16.0
Prickly pear	14.1			Jer. cricket	15.7	Lizard	15.1
				ls. redberry	12.8	Toyon	11.7
<i>San Miguel</i>							
<i>n</i> = 141		<i>n</i> = 150		<i>n</i> = 146		<i>n</i> = 140	
Jer. cricket	63.1	Beetle	67.3	Beetle	80.8	Jer. cricket	75.0
Beetle	58.2	Deer mouse	58.0	Ice plant	80.8	Beetle	67.9
Deer mouse	54.6	Jer. cricket	56.0	Deer mouse	47.3	Deer mouse	57.1
Sand cricket	31.2	Ice plant	56.0	Jer. cricket	47.3	Sand cricket	47.9
Earwig	14.9	Beetle larva	28.7	Lizard	26.7	Grasshopper	36.4
		Lizard	27.3	Grasshopper	20.6	Ice plant	25.0
		Sand cricket	16.0	Sand cricket	11.6	Earwig	12.1
		Earwig	12.0				
		Grasshopper	10.7				
<i>Santa Rosa</i>							
<i>n</i> = 54		<i>n</i> = 150		<i>n</i> = 151		<i>n</i> = 150	
Deer mouse	66.7	Deer mouse	66.0	Deer mouse	68.2	Jer. cricket	72.0
Beetle	64.8	Beetle	54.0	Jer. cricket	55.0	Deer mouse	56.7
Jer. cricket	31.5	Jer. cricket	34.7	Beetle	38.4	Beetle	54.7
Toyon	29.6	Beetle larva	34.7	Lizard	16.6	Earwig	51.3
Ungulate	20.4	Earwig	33.3	Earwig	13.9	Grasshopper	26.0
Bird	20.4	Toyon	26.7	Crustacean	11.9	Aus. saltbush	10.7
Earwig	13.0	Bird	12.7	Beetle larva	11.3		
		Lizard	10.0	Grasshopper	10.6		
				Manzanita	10.6		

(continued on next page)

On San Nicolas, 13 items occurred with a frequency $\geq 10\%$ in seasonal fox diets (Table 4) and ranged from 4 in winter to 9 in summer. Beetles, snails, and ice plant fruits were primary foods in all 4 seasons while lizards, beetle larvae, grasshoppers, Jerusalem crickets, myoporum (*Myoporum spp.*) fruits, and prickly pear cactus fruits were primary foods in 1 season each. For food items grouped into 5 categories (Fig. 3), fox diet on San Nicolas differed significantly among seasons ($\chi^2 = 155.0$, 12 df, $P < 0.0001$). Insects were important foods in all seasons. Native fruits collectively were used in low frequencies while non-native fruits, particularly ice plant and Australian saltbush, were important foods in spring, summer, and fall. Deer mice also

Table 4 (continued)

Food items/Frequency of occurrence (%)							
Winter	Spring		Summer		Fall		
<i>Santa Cruz</i>							
<i>n</i> = 28	<i>n</i> = 35		<i>n</i> = 86		<i>n</i> = 31		
Toyon	71.4	Jer. cricket	51.4	Manzanita	44.2	Earwig	58.1
Jer. cricket	50.0	Beetle	40.0	Jer. cricket	27.9	Beetle	32.3
Earwig	42.9	Manzanita	40.0	Summer holly	27.9	Manzanita	29.0
Beetle	35.7	Toyon	37.1	Beetle	24.4	Jer. cricket	25.8
Manzanita	10.7	Earwig	31.4	Toyon	19.8	Summer holly	19.4
		Lizard	25.7	Grasshopper	11.6	Toyon	16.1
		Deer mouse	20.0				
		Acorn	14.3				

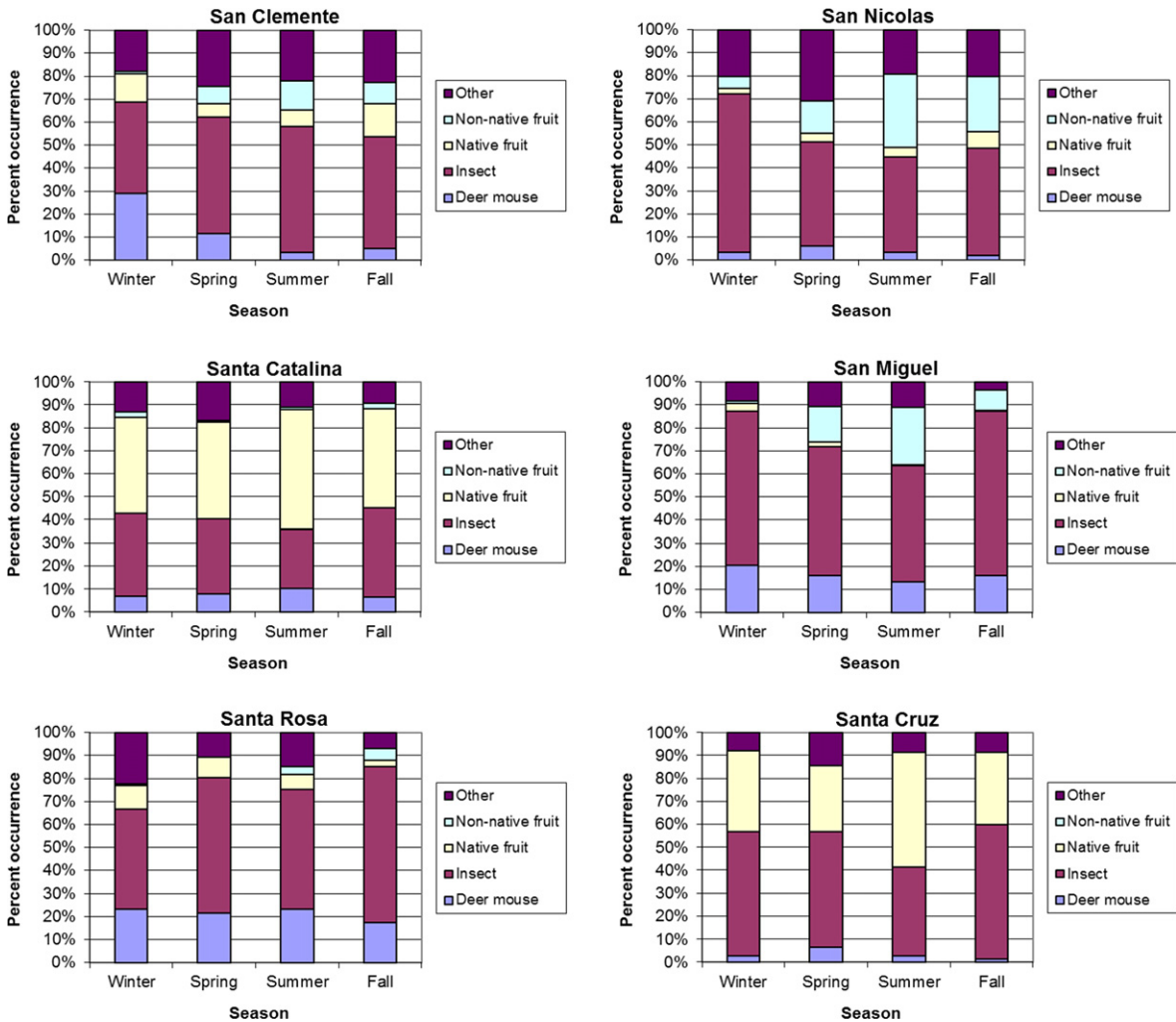


Fig. 3. Seasonal use of food items (grouped into 5 categories) by island foxes on each island during 2009.

were used in relatively low frequencies in all seasons whereas other items, particularly terrestrial snails, were important foods in all 4 seasons.

On Santa Catalina, 9 items occurred with a frequency $\geq 10\%$ in seasonal fox diets (Table 4) and ranged from 4 in spring to 7 in summer and fall. Deer mice, beetles, Jerusalem crickets, and toyon fruits were primary foods in all 4 seasons while manzanita fruits, island redberry (*Rhamnus pirifolia*) fruits, and lizards were primary foods in just 1 season each. For food items grouped into 5 categories (Fig. 3), differences among seasonal fox diets on Santa Catalina were marginally significant ($\chi^2 = 21.11, 12 \text{ df}, P = 0.0501$). Collectively, native fruits were important foods in all seasons, as were insects. Deer mice

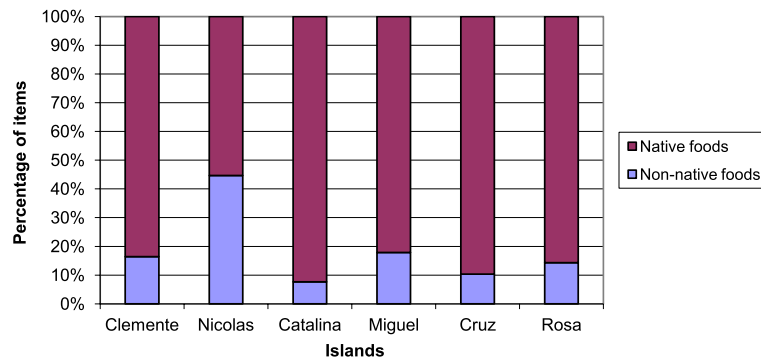


Fig. 4. Proportional use of native and non-native foods in annual diets of island foxes on each island in 2009.

were most important in summer. Non-native fruits were used very infrequently, and other items collectively were important foods in all 4 seasons.

On San Miguel, 9 items occurred with a frequency $\geq 10\%$ in seasonal fox diets (Table 4) and ranged from 5 in winter to 9 in spring. Deer mice, beetles, Jerusalem crickets, and sand crickets were primary foods in all 4 seasons while beetle larvae were a primary food in just 1 season. For food items grouped into 5 categories (Fig. 3), fox diet on San Miguel differed significantly among seasons ($\chi^2 = 155.0$, 12 df, $P < 0.0001$). Insects were important foods in all seasons, as were deer mice. Native fruits collectively were used in low frequencies while non-native fruits, particularly ice plant, were important foods in spring and summer. Other items (e.g., lizards) were important foods in spring and summer, and snails occurred in scats at a low frequency (2.1%–9.9%) in all seasons.

On Santa Rosa, 13 items occurred with a frequency $\geq 10\%$ in seasonal fox diets (Table 4) and ranged from 6 in fall to 9 in summer. Deer mice, beetles, Jerusalem crickets, and earwigs were primary foods in all 4 seasons while ungulates, marine crustaceans, manzanita fruits, and Australian saltbush fruits were primary foods in just 1 season each. For food items grouped into 5 categories (Fig. 3), fox diet on Santa Rosa differed significantly among seasons ($\chi^2 = 94.35$, 12 df, $P < 0.0001$). Insects were important foods in all seasons, as were deer mice. In comparison, fruits were less important and their use was greatest in winter and spring. Other items collectively were important foods in winter, spring, and summer.

On Santa Cruz, 10 items occurred with a frequency $\geq 10\%$ in seasonal fox diets (Table 4) and ranged from 5 in winter to 8 in spring. Beetles, Jerusalem crickets, toyon fruits, and manzanita fruits were primary foods in all 4 seasons while lizards, deer mice, acorns, and grasshoppers were primary foods in just 1 season each. For food items grouped into 5 categories (Fig. 3), fox diet on Santa Cruz differed significantly among seasons ($\chi^2 = 24.9$, 12 df, $P = 0.0037$). Insects and native fruits were important foods in all seasons. Deer mice and other items were not particularly important in any season, and both were used the most in spring.

3.3. Use of non-native items

Foxes consumed non-native food items on all islands, although the contribution of these items to annual diets varied considerably among islands (Fig. 4). The proportion of non-native food item occurrences ranged from 7.6% on Santa Catalina to 44.7% on San Nicolas. Non-native food items included mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), rats (*Rattus spp.*), house mice (*Mus musculus*), European earwigs, European garden snails, and fruits of ice plant, Australian saltbush, myoporium, pepper tree (*Schinus molle*), carob tree (*Ceratonia siliqua*), and palm (Palmeaceae). Additionally, evidence of anthropogenic foods (e.g., food wrappers) was found in 2 scats from Santa Catalina and 1 scat each from San Clemente and Santa Rosa.

Among annual diets, 4 of the 8 primary items consumed by foxes on San Nicolas were non-native (Table 2). In contrast, no primary items were non-native on Santa Catalina, while 1 or 2 were non-native on each of the other 4 islands. Among seasonal diets, non-native foods were the most frequently occurring items in summer (ice plant fruits) and fall (snails) on San Nicolas, and in fall (earwigs) on Santa Cruz. Non-native foods were primary items (frequency $\geq 10\%$) in 2 seasons on Santa Catalina, 3 seasons on San Clemente and Santa Cruz, and 4 seasons on San Nicolas, San Miguel, and Santa Rosa (Table 4).

4. Discussion

4.1. Food items

Island foxes exhibit euryphagus, omnivorous, and opportunistic foraging patterns (Coonan et al., 2010; Moore and Collins, 1995; Roemer, 1999). These general patterns are consistent with those of many other fox species, particularly closely related gray foxes (*Urocyon cinereoargenteus*; Cypher, 2003). Island foxes exploit a wide variety of food items including vertebrates, invertebrates, and fruits. The dietary differences observed among islands and seasons reflect a functional response on the

part of foxes to spatial and temporal variation in food item availability. Variation among islands and seasons also was reported by Laughrin (1977). This response is consistent with an opportunistic, generalist foraging strategy (Stephens and Krebs, 1986).

Among all of the North American foxes, island foxes consume the least amount of vertebrate prey, probably due to depauperate rodent communities on the Channel Islands (Wenner and Johnson, 1980). Deer mice were consumed by foxes on all islands, and were a particularly important food item on Santa Rosa, San Miguel, San Clemente, and Santa Catalina. Deer mice also were found to be important island fox foods in previous studies (Collins, 1980; Laughrin, 1977). Deer mice are fairly ubiquitous with regard to habitat (Schwemm, 2008) and generally are available throughout each island.

Other mammals generally occurred only infrequently in fox diets. Introduced deer and elk were present on Santa Rosa while introduced deer are present on Santa Catalina. The ungulates were harvested on both islands during this study. Ungulate remains were present in fox scats in all seasons on both islands. Remains sometimes consisted of hair and bone, and other times consisted of a black, tar-like substance, which is indicative of foxes consuming “gut piles” resulting from hunters dressing out harvested animals. Additionally, ungulates mortally wounded during harvests that were not subsequently recovered by hunters also served as a potential food source for foxes. Consequently, ungulate remains generally occurred most frequently in the fall and winter, concomitant with harvest seasons. Ungulates even constituted a primary item in fox diets in winter on Santa Rosa (Table 4). Ungulate carcasses and organ remains constitute an energy dense food source with relatively low associated capture or handling costs, and therefore it is not surprising that foxes would readily exploit this resource. Similarly, Laughrin (1973, 1977) reported use of livestock carrion by foxes when livestock (e.g., goats, cows, sheep, pigs) were still present on some islands.

Other mammals consumed by foxes included Catalina California ground squirrels (*Otospermophilus beecheyi nesioticus*), pinnipeds, island spotted skunks (*Spilogale gracilis amphiala*), rats, house mice, and a bat (*Myotis spp.*). Use of California ground squirrels, harvest mice (*Reithrodontomys megalotis*), California voles (*Microtus californicus*), rats, and house mice has been reported previously (Laughrin, 1973; von Bloeker, 1967). Ground squirrels are only present on Santa Catalina, but are abundant and were consumed in all seasons. This consistent use suggests that the squirrels were more than just incidental items in the diet. Pinnipeds occur on all islands, but are particularly abundant on San Nicolas and San Miguel where large, multi-species rookeries have been established. Pinnipeds were detected in scats from San Nicolas, San Miguel, San Clemente, and Santa Catalina, although the number of occurrences in any season never exceeded 5. Predation on pinnipeds by foxes is unlikely. Instead, foxes probably scavenged dead pinnipeds or consumed pieces of molted pelts. Laughrin (1977) also reported use of marine mammals by foxes. Island spotted skunks only occur on Santa Rosa and Santa Cruz. Skunks occurred in 3 scats from Santa Cruz and 7 scats from Santa Rosa. Skunks may be consumed more as a result of competitive interactions than direct predation (Jones et al., 2008). Similarly, the low occurrences of rat, house mouse, and bat indicate that these also were opportunistically consumed items.

Birds were consistently consumed by foxes on all islands and in all seasons. Remains commonly consisted of non-descript feathers and therefore species identification was not possible. Foxes may prey on ground-dwelling birds or nestlings in ground or arboreal nests (island foxes are excellent climbers; Coonan et al., 2010), or scavenged dead birds washed up on shorelines. Remains of ground nesting birds have been reported in scats from San Miguel, Santa Cruz, and San Nicolas and included horned larks (*Eremophila alpestris insularis*), western meadowlarks (*Sturnella neglecta*), and chukars (*Alectoris chukar*) (Collins, 1980; Laughrin, 1977; Moore and Collins, 1995). It is unclear whether birds were consumed opportunistically as encountered or specifically hunted. However, birds were primary items in winter and spring on Santa Rosa (Table 4), and occurred in >5% of scats in at least 1 season on all islands except San Clemente suggesting that foxes may have specifically hunted birds. On San Clemente, foxes were determined to be a significant predator on nests of endangered San Clemente loggerhead shrikes (*Lanius ludovicianus mearnsi*) resulting in nest protection strategies, including lethal removal of foxes (Cooper et al., 2005).

Lizards occurred in fox scats from all islands and most seasons. Indeed, lizards were primary items in fox diets in 1 or more seasons on all islands, and therefore constituted an important food item for foxes. At least 2 lizard species occur on each island with 5 occurring on Santa Catalina (Schoenherr et al., 1999). Low frequency use of reptiles by island foxes has been reported previously (Crowell, 2001; Moore and Collins, 1995), including consumption of snakes. However, only lizard remains were detected in the current study.

Insects were extremely important food items for foxes on all islands and in all seasons. When using frequency of occurrence of items in scats, the contributions of small food items like insects can be over-estimated in canid diets if such items occur frequently but comprise a relatively small proportion of scat contents (e.g., Cypher, 1991). However, that generally was not the case in the island fox scats where insect parts commonly comprised a significant proportion of each scat. Insects occur in apparent abundance on all islands, involve low foraging costs, and are highly nutritious. Thus, energetically, selective feeding on insects constitutes an optimal foraging strategy for island foxes.

Beetles and beetle larvae were frequently consumed. Beetles were not identified to species, but darkling beetles (Family Tenebrionidae) and ten-lined June beetles (*Polyphylla decemlineata*) were commonly detected. Doyen (1974) identified at least 9 different beetle species in fox scats collected in spring on San Clemente. Jerusalem crickets, silk-spinning sand crickets, and grasshoppers also were frequently consumed on most islands. These Orthopterans appear to be particularly important foods, as has been reported previously (Collins, 1980; Crowell, 2001; Laughrin, 1977). Non-native European earwigs are now ubiquitous and abundant throughout North America, including the Channel Islands (Langston and Powell, 1975). Earwigs occurred commonly in scats from all islands and appear to be a relatively important food for island foxes.

Other insects detected included cockroaches, fly larvae (i.e., maggots—probably from carrion), dragon flies, Lepidopteran larvae (i.e., caterpillars), wasps, and ants (ants likely were consumed incidentally with other foods). All of these other insects were only infrequently detected and therefore were likely consumed opportunistically as encountered.

Other invertebrates also were detected in fox diets. Crustaceans, including beach hoppers (*Orchestoidea californiana*) and mole crabs (*Emerita analoga*) as well as other unidentified crabs, were frequently consumed by foxes and indicate that foxes may commonly forage along shorelines. European garden snails are present on most islands and commonly occur in association with ice plant. Indeed, these snails were primarily found in scats from the 3 islands where ice plant fruits also were frequently consumed—San Nicolas, San Clemente, and San Miguel. The snails constituted particularly important food items on San Nicolas and San Clemente. [Garcelon and Hudgens \(2008\)](#) suggested that snails might be particularly important for older foxes.

Fruits from a number of plant species were consumed in abundance on all islands and in most seasons. Thus, fruit constitutes a significant component of fox diets, as has been reported previously ([Crowell, 2001](#); [Laughrin, 1977](#); [Moore and Collins, 1995](#)). The species of fruit consumed varied depending upon the species present on each island, and included both native and non-native species. Among native species, prickly pear cactus, toyon, and manzanita fruits were important foods for foxes on 3 islands each. Island redberry, summer holly, and acorns (*Quercus spp.*) each were important foods on 1 island. One or more native fruits were important foods on all islands except San Miguel, where no native fruits were detected in island fox scats. Lemonade berry (*Rhus integrifolia*) was occasionally detected in scats from San Clemente, Santa Cruz, San Nicolas, and Santa Rosa.

Island foxes commonly exploited non-native fruits on all islands except Santa Cruz and Santa Catalina. Australian saltbush fruit constituted an important food on 3 islands (San Clemente, San Nicolas, and Santa Rosa). Likewise, ice plant fruit was an important food on 3 islands (San Clemente, San Nicolas, and San Miguel). Myoporum was an important seasonal food on San Nicolas. Australian saltbush was detected at low frequencies in scats on Santa Cruz while palm, carob, ice plant, and pepper tree were detected at low frequencies on Santa Catalina.

4.2. Islands

Island-specific availability of food items strongly influenced foraging patterns by foxes. Use of specific foods probably is mediated by their relative abundance on each island and by their abundance relative to that of other food items. Some items, such as deer mice, lizards, Jerusalem crickets, beetles, and earwigs, are ubiquitous and abundant on all or most of the islands ([Schoenherr et al., 1999](#)), and these were routinely exploited by foxes. Other items were only present in abundance on 2 or 3 islands, but were readily exploited where available. These items mostly were fruits and included toyon and manzanita on Santa Catalina, Santa Rosa, and Santa Cruz; prickly pear cactus on San Clemente and Santa Catalina; ice plant on San Clemente, San Nicolas, and San Miguel; and Australian saltbush on San Clemente, San Nicolas, and Santa Rosa. Similarly, European snails were commonly consumed in abundance on San Clemente and San Nicolas where ice plant is abundant.

The presence and abundance of food items on each island is a function of several factors, including island size, distance from the mainland, precipitation patterns, topographic complexity, and disturbance history. Based on the principles of island biogeography, larger islands have an inherent capacity to support more species ([MacArthur and Wilson, 1967](#)), and concomitantly, a greater diversity of potential food items for foxes. Also, islands with greater topographic complexity and higher precipitation levels tend to support a greater diversity of vegetation and habitats, which again increases the number of potential food items for foxes. Finally, historic and current disturbances can reduce the number of potential food items by reducing ecosystem complexity or even completely eliminating certain habitat types and associated resources. Such disturbances include fire and introductions of invasive plants and animals, particularly larger grazing species such as goats, sheep, and pigs that can increase rapidly and significantly impact ecological communities (e.g., [Donlan et al., 2002](#)).

San Clemente is a moderately sized island with a fair amount of topographic complexity ([Table 1](#)). The island is owned and managed by the US Navy. This island has been used for live-fire exercises and these activities certainly have impacted the ecosystem. However, more significant impacts have resulted from grazing by feral goats and pigs ([Schoenherr et al., 1999](#)). Intensive grazing by these non-native animals essentially defoliated large portions of the island. The ecological communities on the island were markedly impacted and reduced, and the distribution of woodlands and shrublands was severely restricted to certain deep canyons. Consequently, island foxes on San Clemente consumed few native fruits. The exception is prickly pear cactus, which apparently was less palatable to the goats and pigs, and therefore expanded considerably in abundance and distribution with the elimination of competing vegetation.

San Nicolas is a smaller island with relatively low topographic complexity ([Table 1](#)). This island also is owned and managed by the US Navy, and is used for weapons testing, although most munitions are fired from the island to off-shore aerial or marine targets. In the 1800s, sheep were brought to the island and at one time exceeded 30,000 in number. The severe grazing by the sheep defoliated much of the island and caused severe erosion. The Navy attempted to control the erosion by aerial spreading of fertilizers and non-native grasses. As a result of all these disturbances, San Nicolas has the least diverse flora, about half of which is non-native ([Schoenherr et al., 1999](#)). Most trees and shrubs were eliminated by the sheep. Consequently, native fruits are generally unavailable to foxes. However, several non-native fruit-producing plants are well established on the island and were used extensively by the foxes, including ice plant, Australian saltbush, and myoporum. Also, European garden snails are common on the island, mostly in association with ice plant, and were used

extensively by the foxes. Thus, fox diets on San Nicolas had the largest proportion of non-native items, and the dependence of foxes on these items may be significant.

Santa Catalina is a large and topographically complex island (Table 1). Approximately 88% of the island is owned and managed by the Catalina Island Conservancy, but 2 large towns (Avalon and Two Harbors) and several smaller settlements also are present on the island. Introduced animals have included goats, pigs, horses, cattle, black-buck antelope (*Antelope cervicapra*), bison (*Bison bison*), and mule deer (Knowlton et al., 2007). These species have significantly impacted native flora, although these impacts were not as devastating as on other islands. Catalina retains high floristic diversity with many fruit-producing species. Consequently, use of fruits by foxes was highest on Santa Catalina, and most fruits used were from native species. Toyon was used extensively by the foxes, as was prickly pear cactus, which may have increased in abundance as a result of grazing by the introduced animals. Use of non-native resources was lowest on Santa Catalina.

San Miguel is a small island with relatively low topographic complexity (Table 1). The island is owned and managed by the National Park Service. Vegetation on the island has been significantly altered by past over-grazing and military activities. Due to these disturbances, along with small size and farther distance from the mainland, the island has low floristic diversity, including few trees or shrubs (Schoenherr et al., 1999). Consequently, the only fruit consumed in abundance was that of non-native ice plant. Foxes on San Miguel appear to rely extensively on insects. Habitat restoration might particularly benefit foxes on San Miguel by increasing the number of available food items.

Santa Rosa is a large and topographically complex island (Table 1). This island also is owned and managed by the National Park Service. Past grazing by cattle and sheep has altered the vegetation considerably (Schoenherr et al., 1999), and a large herd of non-native deer and elk were present on the island. Fruit use by foxes was lowest on Santa Rosa, but toyon and manzanita still were important foods seasonally, as was non-native Australian saltbush. Foxes also obviously scavenged unrecovered carcasses and gut piles of deer and elk during annual harvests. However, these ungulates have since been removed from Santa Rosa and this resource will no longer be available to foxes.

Santa Cruz is the largest of the islands, topographically complex, and floristically most diverse (Table 1). Approximately 77% of the island is owned and managed by The Nature Conservancy with the remainder owned and managed by the National Park Service. Extensive grazing and disturbance by various non-native animals (e.g., cattle, sheep, and pigs) has altered the vegetation (Schoenherr et al., 1999), but considerable native components of the ecosystem have remained intact. Consequently, a diversity of native fruits is available and is exploited by foxes, including toyon, manzanita, summer holly, and acorns. Fruit use by foxes on Santa Cruz was second only to that on Santa Catalina, and use of non-native fruits was limited to 1 occurrence of Australian saltbush. Indeed, use of non-native items was relatively low on Santa Cruz compared to most other islands, and consisted almost entirely of European earwigs. One caveat is that fewer scat samples were available for Santa Cruz relative to other islands, and thus the results for this large island may not constitute a completely accurate representation of fox diet.

4.3. Food preferences, non-native items, and habitat restoration

Island foxes clearly are able to exploit a diversity of food items, and diets on all islands included a number of items. However, some observed dietary patterns can provide insights on preferences. The ubiquitous use of deer mice, lizards, Jerusalem crickets, beetles, and earwigs suggests some preference for these items. Such animal foods are composed of a complex of proteins, carbohydrates, and fats, and therefore comprise highly nutritious foods (Robbins, 1993). Further evidence of preference for these items might be found in the results from Santa Rosa. A diversity of food items is available on this large island. However, fox numbers were still relatively low during this study (<400; T. Coonan, National Park Service, unpublished data) compared to probable historic levels (>1700; Coonan, 2003). Consequently, available food resources on the island were not likely over-exploited by foxes and intra-specific competition for food would have been relatively low. Under these conditions, deer mice, Jerusalem crickets, beetles, and earwigs constituted the primary items in the annual diet. As further evidence of preference for deer mice, use of deer mice by foxes exhibited no detectable seasonality despite the fact that these rodents exhibit marked season variation in abundance (Drost and Fellers, 1991; Schwemm, 2008).

Certain native fruits also were used extensively by foxes on islands where available. In particular, toyon, manzanita, and prickly pear cactus fruits appeared to be preferred food items. Frequent use of prickly pear cactus and toyon fruits has been reported previously (Crowell, 2001; Moore and Collins, 1995). When abundant, fruits use is energetically efficient for foxes due to low foraging costs.

Non-native items were used extensively by foxes on some islands. Generally, use of non-native items was highest on the smaller islands: San Clemente, San Nicolas, and San Miguel. These islands also are the least diverse floristically. Thus, fewer native foods may be available on these islands resulting in foxes more frequently exploiting non-native items. Ice plant fruits were frequently consumed by foxes on San Clemente, San Nicolas, and San Miguel while Australian saltbush fruits were frequently consumed on San Clemente and San Nicolas. No native fruits were detected in scats from San Miguel, and the only native fruit consumed on San Clemente and San Nicolas was prickly pear cactus, which actually may have increased in abundance as a result of severe grazing on competing plants by non-native animals (Schoenherr et al., 1999). European snails inhabiting ice plant also were used extensively by foxes on San Clemente and San Nicolas.

Island fox foraging patterns, food preferences, and use of non-native items all have important implications for long-term fox conservation. The high dietary plasticity exhibited by foxes is advantageous, particularly given the inherent limitations on the number of available food items associated with living in an insular environment. Furthermore, habitat conditions

on all of the islands have been degraded, in some cases extensively, primarily by past land uses (e.g., grazing by domestic and feral animals, military activities). Thus, any processes or efforts that improve ecosystem integrity and habitat quality, particularly those that expand habitat diversity and complexity, have the potential to also increase food resources available to foxes. Such actions likely would increase the abundance of preferred food items, and importantly, they also would further increase the diversity of items.

Availability of specific items can vary temporally due to cyclic (e.g., precipitation, masting) or stochastic (e.g., disease) processes. For example, many island fox foods may decrease in abundance during drought periods, disease could reduce the abundance of certain prey or fruit species, and plant species produce fruit crops on multi-year cycles (P. Schuyler, personal communication). On a longer time scale, climate change could alter the abundance of various food items. Thus, as the number of available items increases, so does the likelihood that some items will remain sufficiently abundant even if other foods decline in availability. In such an event, foxes would have a greater opportunity to switch and exploit alternate resources. Increasing item diversity could help prevent or moderate food-related population declines and the associated extinction risk.

Actions that could increase food item diversity include habitat protection and restoration. Four islands are entirely or largely managed for conservation, and stringent habitat protections are being implemented on the 2 Navy-owned islands (US Fish and Wildlife Service, 2012). Many of the past ecosystem insults, particularly over-grazing by non-native animals, have been eliminated or at least mitigated on most islands. Consequently, natural ecosystem recovery is in progress on all islands, and plant and habitat diversity is increasing. On all islands, other management actions, such as fire suppression or limiting public access and uses in natural areas, are helping to prevent further habitat degradation (Coonan, 2003; US Fish and Wildlife Service, 2012). Active restoration also is being conducted or is planned on most islands. Such restoration activities include removing remaining non-native grazers (e.g., deer and elk on Santa Rosa; Griffin et al., 2009), removing invasive non-native plants (e.g., fennel (*Foeniculum vulgare*) on Santa Cruz; Erskine Ogden and Rejmánek, 2005), protecting native plants from further grazing/browsing (e.g., Santa Catalina; Ramirez et al., 2012), and planting native plants to increase their abundance and distribution (several islands).

On some islands, ecosystem restoration involving the reduction or elimination of non-native species may need to be conducted cautiously to avoid adverse impacts to food supplies for foxes. Fruits from non-native plants comprise significant proportions of fox diets on some islands, particularly San Nicolas, San Miguel, and San Clemente. On these islands, ice plant fruits are routinely consumed by foxes. Thus, any efforts to reduce or remove ice plant should be conducted gradually to allow time for foxes to switch to alternate foods. Preferably, plantings of native fruit-producing plants should be conducted concomitantly, if not well before (e.g., to allow species time to mature and produce fruit) with the removal of non-native fruit plants to avoid any reductions in overall food availability. This cautionary note may particularly apply to San Nicolas, where foxes are frequently consuming fruits from 3 non-native plants as well as non-native snails associated with 1 of the plants. Rapid removal of these 4 food items on this island could result in significantly reduced food availability for foxes.

4.4. Conclusions and recommendations

Island foxes exploit a diversity of food items with patterns strongly influenced by island-specific item availability. This ability to use numerous items likely facilitates fox persistence in the inherently space-limited environments of the islands. Non-native items are commonly used and foxes may be at least partially dependent on these items on some islands. Increasing the diversity of available food items may help to enhance the security of fox populations by ensuring more stable food supplies during resource declines associated with cyclic and stochastic events or climate change. Based on our results, we recommend (1) continuing and enhancing efforts to restore and improve habitat conditions on all islands, (2) increasing the abundance of native items in association with any removals of non-native species used by foxes, and (3) monitoring annual trends in abundance of key food items as well as periodic monitoring of item use by foxes to determine functional responses to changes in item availability. We feel that this last recommendation is particularly important because all 6 of the islands with foxes are in a state of transition as they recover from past abusive land uses, and each island is at a different point in this recovery process. Our study documented the situation at a particular point in time and provides a solid baseline for longitudinal comparisons.

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