COYOTE FORAGING PATTERNS IN THE CENTRAL MOJAVE DESERT: IMPLICATIONS FOR PREDATION ON DESERT TORTOISES

FINAL REPORT

PREPARED FOR U.S. FISH AND WILDLIFE SERVICE

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TABLE OF CONTENTS

Executive summary **2**
Introduction **3**
Study Area **5**
Methods **6**
Coyote foraging patterns 6
Prey abundance 6
Coyote abundance 8
Results **9**
Coyote foraging patterns 9
Prey abundance 18
Effects of item use and availability on use of tortoises 21
Coyote abundance and distribution 24
Discussion **26**
Coyote foraging patterns 26
Effects of item use and availability on use of tortoises 27
Coyote abundance and distribution 28
Conclusions and recommendations 29
Literature Cited **33**
Appendix A **36**

LIST OF TABLES

Table 1. Frequency of occurrence of food items found in coyote scats for 5 years and all years combined on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 10
Table 2. Frequency of occurrence of food items found in coyote scats collected in three study area segments in the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 11
Table 3. Seasonal frequency of occurrence of food items found in coyote scats collected in the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 12
Table 4. Annual coyote detection rates on camera stations in 3 study area segments on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 25
Table 5. Species detected on automated cameras in 3 study area segments for 3 years combined (2012-2014) on the Desert Tortoise Translocation Area, San Bernardino County, California. 25

LIST OF FIGURES

Figure 1. Coyote foraging ecology study area depicting the West, Central, and East portions of the study area in San Bernardino County, California. 5
Figure 2. Fresh (left) and old (right) rabbit pellets. 7
Figure 3. Example of large rodent burrow. 8
Figure 4. Proportional item occurrences by food category for coyote scats collected in 5 years and for all years combined on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 13
Figure 5. Proportional item occurrences by food category for coyote scats collected in 3 study area segments on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 14
Figure 6. Proportional item occurrences by food category among seasons for coyote scats collected in the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 14
Figure 7. Frequency of occurrence of desert tortoise remains found in coyote scats for each year and all years combined on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 15
Figure 8. Frequency of occurrence of desert tortoise remains found in coyote scats collected in 3 study area segments on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 15
Figure 9. Seasonal frequency of occurrence of desert tortoise remains found in coyote scats collected on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 16
Figure 10. Frequency of occurrence of anthropogenic items in coyote scats for each year on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 16
Figure 11. Frequency of occurrence of anthropogenic items in coyote scats collected in 3 study area segments on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 17
Figure 12. Seasonal frequency of occurrence of anthropogenic items in coyote scats collected on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 17
Figure 13. Mean annual rabbit pellet counts for 3 study area segments and annual precipitation on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 18
Figure 14. Annual mean rabbit pellet counts, precipitation, and use of rabbits by coyotes on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 19
Figure 15. Mean annual large burrow counts for 3 study area segments and annual precipitation on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 19
Figure 16. Annual mean large burrow counts, precipitation, and use of kangaroo rats by coyotes on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 20
Figure 17. Mean annual small burrow counts for 3 study area segments and annual precipitation on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 20
Figure 18. Annual mean small burrow counts, precipitation, and use of pocket mice by coyotes on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 21
Figure 19. Use of desert tortoises by coyotes among years relative to use of other food items and annual precipitation on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. To better compare trends, the percent frequency of occurrence of desert tortoise in coyote scats was multiplied by 10. 22
Figure 20. Use of desert tortoises by coyotes among study area segments relative to use of other food items on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. To better compare trends, the percent frequency of occurrence of desert tortoise in coyote scats was multiplied by 10. 22
Figure 21. Use of desert tortoises by coyotes among years relative to prey availability indices and annual precipitation on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. To better compare trends, the percent frequency of occurrence of desert tortoise in coyote scats was multiplied by 10. 23
Figure 22. Use of desert tortoises by coyotes among study area segments relative to use of other food items on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 23
Figure 23. Locations of automated camera stations in 3 study area segments on the Desert Tortoise Translocation Area, San Bernardino County, California. 24
Figure 24. Locations of coyote scats collected on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. 26

EXECUTIVE SUMMARY

Coyotes (*Canis latrans*) are ubiquitous and able to exploit a wide variety of food resources that sometimes include sensitive or rare species. Desert tortoises (*Gopherus agassizii*) occur in the Mojave Desert of California, and are federally and state listed as Threatened due to numerous threats including habitat loss and direct mortality from humans, predators, and disease. Coyotes occasionally prey on desert tortoises, but the extent to which they do so and how this predation might be affected by other factors is unknown. We investigated food item use by coyotes relative to annual availability of select items and also examined coyote abundance patterns in a region of the Mojave Desert where desert tortoises were being translocated. Specific objectives were to (1) quantify seasonal and annual use of food items by coyotes, (2) assess annual abundance of primary food items, (3) assess spatial variation in food item use and availability, (4) assess relative coyote abundance and distribution, and (5) assess the implications of our results with regards to predation on desert tortoises.

We collected and analyzed 3,246 coyote scats over a 5-year period from fall 2009 to summer 2014 on a ca. 1500 km^2 area near Barstow, CA. We also indexed primary prey abundance annually using transect surveys. Automated camera stations were deployed during the latter 3 years of the project to index abundance and distribution of coyotes and other species. Coyote foraging patterns exhibited some temporal and spatial variation. Annual variation in use of items appeared strongly influenced by fluctuations in item availability associated with variation in annual precipitation. Seasonal variation in item use was minor. Rabbits were a primary, and possibly preferred, food item. Heteromyid rodents (e.g., kangaroo rats and pocket mice) also were primary items. Other natural items appeared to be consumed opportunistically and included birds, reptiles (snakes, lizards, and tortoises), insects, and fruit. Anthropogenic items commonly occurred in scats and included domestic animals, crops, and man-made materials. Reliance on anthropogenic foods may have increased as the abundance of natural items decreased during years with below-average annual precipitation. This in conjunction with scat collection locations provided some evidence that the coyote population on the study site is receiving at least some anthropogenic subsidization.

Coyotes in the study area consistently consume desert tortoises, although the frequency of occurrence in scats is low. Use of tortoises in the latter years of the study declined concurrent with declines in use and availability of primary items and also with declines in annual precipitation. This suggested that tortoises may be used opportunistically by coyotes. Also, coyotes did not appear to increase use of tortoises as availability and use of primary items declined.

Our data indicate that coyotes are consuming desert tortoises consistently but at a low frequency in this region, and tortoises appear to be a secondary item likely consumed opportunistically by coyotes. The implications of this for desert tortoise populations are uncertain in the absence of tortoise mortality rates or abundance trends. Coyotes in this region clearly are exploiting anthropogenic foods, and this subsidization could potentially increase predation pressure on desert tortoises.

INTRODUCTION

Coyotes (*Canis latrans*) are ubiquitous in North America, and have increased both their range and abundance, contrary to trends exhibited by many other species. Their success is a function of marked ecological plasticity, as exemplified by the diversity of habitats and food items used (Bekoff and Gese 2003). Coyotes are able to exploit a wide range of resources, and this sometimes can include species considered to be at risk of extinction. Predation pressure on these rare species is potentially exacerbated when local coyote populations are maintained at high levels due to an abundance of other foods or when low availability of primary food items results in compensatory switching to secondary items that may include rare species. Examples of at risk species impacted by coyote predation include western snowy plovers (*Charadrius alexandrinus nivosus*; Point Reyes Bird Observatory 2001), California least terns (*Sterna antillarum browni*; Butchko 1990), San Joaquin kit foxes (*Vulpes macrotis mutica*; Butchko 1990), swift foxes (*V. velox*; McGee et al. 2006), and gopher tortoises (*Gopherus polyphemus*; Moore et al. 2006).

Desert tortoises (*Gopherus agassizii*) occur in the Mojave and Sonoran deserts of the United States and Mexico. Desert tortoises in California, are federally and state listed as Threatened (U.S. Fish and Wildlife Service 2011, California Department of Fish and Game 2008) due to numerous threats including habitat loss and direct mortality from humans, predators, and disease. Coyotes are among the many predators that kill desert tortoises (Woodbury and Hardy 1948, U.S. Fish and Wildlife Service 2011, Lovich et al. 1999, Esque et al. 2010, Lovich et al. 2014).

In response to a planned expansion of the Ft. Irwin National Training Center (NTC) north of Barstow, California, almost 600 tortoises were translocated off the NTC in 2008 to release sites on nearby public lands (Esque et al. 2005, Esque et al. 2010). Release areas consisted of high quality habitat occupied by resident tortoises. To assess the effects of translocation on tortoises removed from the NTC and also any impacts to resident tortoises in the release areas, 357 of 571 translocated tortoises and a sample of resident tortoises were monitored via radio telemetry. Furthermore, a sample of animals in areas outside of release sites was monitored as a control group. All transmittered animals were usually monitored weekly to assess survival and movements, and to identify sources of mortality (Esque et al. 2010). Current plans call for additional tortoises to be translocated in the future (Esque et al. 2009).

Monitoring has revealed that mortality rates among all 3 groups of tortoises are higher than expected. Mortality at 9 monitoring sites ranged from 6.7% to 45.5%, and rates at 6 of the sites exceeded 20% (Esque et al. 2010). Predation by coyotes was identified as a primary source of tortoise mortality on these sites. Concern has been expressed among desert tortoise experts that such high mortality rates are not sustainable and could reduce population viability for desert tortoises eventually resulting in local or regional extirpations.

Coyote predation on desert tortoises has been well documented previously with reported rates of 18-30% (e.g., Turner et al. 1984, Peterson 1994). Thus, it is not completely clear what rate or range of rates is “normal”. Coyotes are foraging generalists that opportunistically exploit resources based on abundance and foraging efficiency. Therefore, predation by coyotes on desert tortoises very likely varies with availability and use of other food items. Furthermore, the availability of anthropogenic foods may subsidize coyotes in some areas resulting in enhanced predation rates on tortoises. Esque et al. (2010) hypothesized that low availability of other foods due to extended drought conditions may be responsible for elevated predation rates on tortoises, and that this effect may be enhanced in areas where coyotes are subsidized by anthropogenic foods.

Coyote foraging dynamics in the Mojave Desert have not been well documented. Ferrel et al. (1953) reported that rabbits (*Lepus californicus* and *Sylvilagus nuttallii*), rodents (primarily *Microtus* spp., *Neotoma* spp., and *Spermophilus beechyi*), deer (*Odocoileus hemionus*), and birds were the most frequently occurring items in coyote stomachs from a region that included the Mojave Desert. However, most of the stomachs were collected in areas other than the Mojave Desert. Similarly, rabbits, various species of rodents, birds, and insects are common dietary items for coyotes in other desert regions of North America (e.g., Sperry 1941; Johnson and Hansen 1977, 1979; Hernández et al. 1994; Cypher et al. 1994; Nelson et al. 2007). Use of food items by coyotes typically varies seasonally (Bekoff and Gese 2003). Furthermore, annual resource availability in arid regions can vary markedly, primarily as a function of annual precipitation, and food item use by coyotes also would be expected to vary.

The dynamics between coyote foraging patterns and both annual and seasonal variation in resource availability in the Mojave Desert have not been thoroughly investigated. Consequently, the relationship between these dynamics and coyote predation on desert tortoises is unclear. Availability of other food items, coyote abundance, or some interactive effect between these factors could affect predation rates on tortoises. Furthermore, the availability of anthropogenic food items might elevate predation rates by maintaining high coyote abundance relative to the availability of natural food items (Esque et al. 2010). However, use of and reliance on anthropogenic food items by coyotes in the Mojave Desert are unknown. Finally, coyote foraging dynamics and concomitant predation on tortoises might vary spatially if resources are heterogeneously distributed across the landscape. Understanding the interrelationships above could provide valuable information for developing and refining conservation strategies for desert tortoises.

The goal of this investigation was to examine food item use by coyotes relative to annual availability of select items and also examine coyote abundance patterns in the region of the Mojave Desert where desert tortoises were being translocated. Specific objectives of this investigation were to:

1. quantify seasonal and annual use of food items by coyotes,
2. assess annual abundance of primary food items,
3. assess spatial variation in food item use and availability
4. assess relative coyote abundance and distribution, and
5. collaborate with desert tortoise researchers in an effort to determine whether item use, item availability, or coyote abundance correlate with observed temporal and spatial variation in coyote predation rates on tortoises.

Field work for this project was conducted over a 5-year period from fall 2009 to summer 2014.

STUDY AREA

This investigation was conducted in the Desert Tortoise Translocation Area, which encompasses approximately 1,500 km^2 north of Barstow, California (Figure 1). The area is bounded on the north by Fort Irwin and the China Lake Naval Air Weapons Station, and on the south by Interstate 15 and State Route 58. It extends from about the town of Hinkley on west to Afton Road on the east. The study area was within the Western Mojave Recovery Unit of Critical Habitat for desert tortoises (USFWS 1994). The study area was characterized as typical Mojave Desert scrub vegetation (Turner 1994) dominated primarily by creosote bush (*Larrea tridentata*) and with perennial plant cover ranging from 1 to 29% (Esque et al. 2010). Elevation ranged from 500 to 900 m, and the varied terrain included flat dry lake beds, gentle alluvial fans, and steep, rugged hills. Mean annual precipitation for Barstow, California was 13.4 cm (U.S. Climate Data 2014). Much of this area comprises public lands managed by the U.S. Bureau of Land Management with interspersed private lands. Human densities and influences were greatest around Barstow, Hinkley, and Harvard, and declined with distance from these towns.

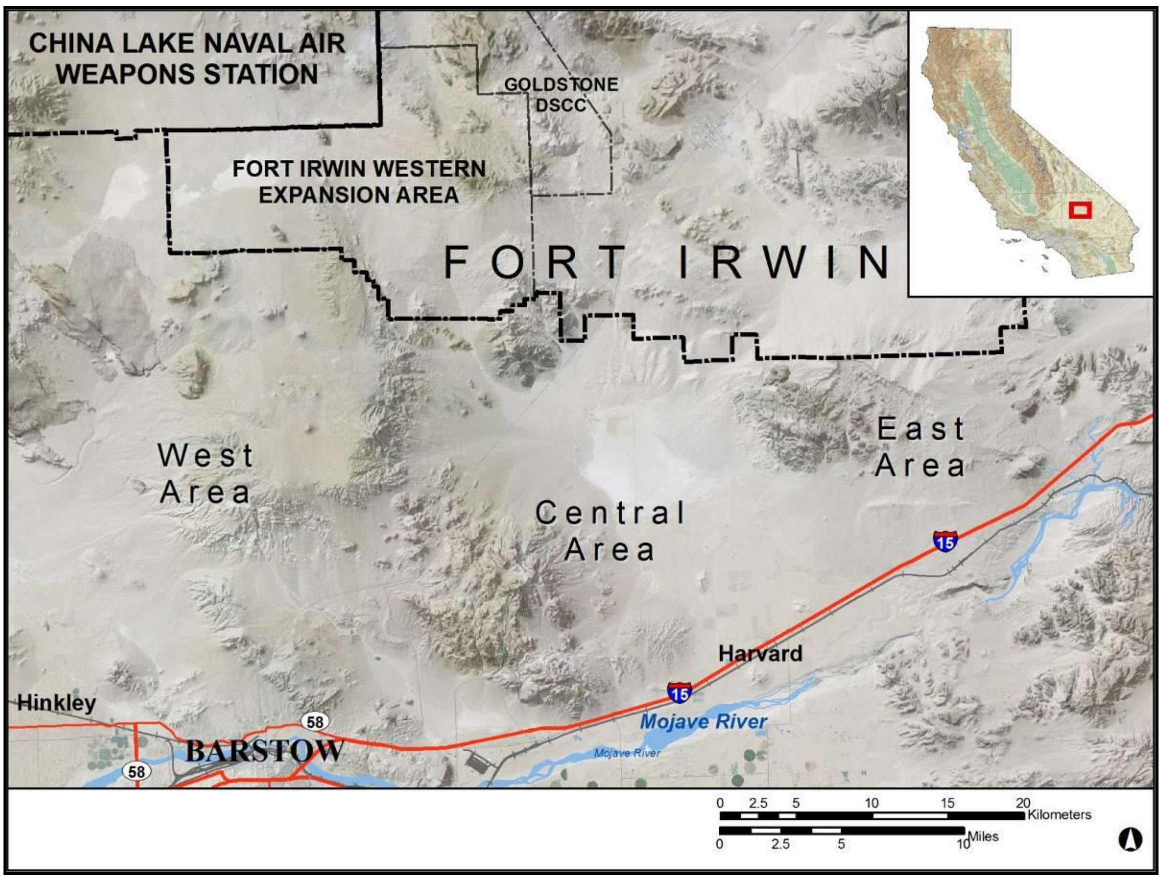

Figure 1. Coyote foraging ecology study area depicting the West, Central, and East portions of the study area in San Bernardino County, California.

METHODS

COYOTE FORAGING PATTERNS

Food item use by coyotes was determined by examining scat (fecal) samples. To collect scats, each portion of the study area was visited at least 1 day each season. Unpaved roads were traveled at slow speed (i.e., 5-15 kph) while observers searched for coyote scats on and alongside the road. Scats also were collected when encountered along prey assessment transects (see below). All scats found were placed in a separate paper bag, and the collection date and location (UTM coordinates) were recorded.

Scats were air-dried and then stored in insect-proof storage containers. To destroy any zoonotic parasites (e.g., hydatid tapeworm; *Echinococcus multilocularis*), all scats were placed in a drying oven at 60°C for ≥ 24 hr prior to analysis. Scats then were placed in nylon pouches, washed in a washing machine to remove soluble material, and dried in a tumble dryer. The remaining undigested material was examined to identify items consumed by coyotes. Mammalian remains were identified by examining macroscopic (e.g., length, texture, color, banding patterns) and microscopic (e.g., cuticular scale patterns) characteristics of hairs (Moore et al. 1974), and by comparing teeth and bone fragments to published guides (Glass 1981, Roest 1986) and reference specimens. Attempts were made to identify other vertebrate (i.e., bird, reptile) and all invertebrate (e.g., insects, arachnids) remains at least to order based on feathers, scales, and exoskeletons. Any fleshy fruits consumed were identified at least to genus based on seed characteristics (Young and Young 1992). Anthropogenic items were identified based on the presence of domestic animal remains or incidentally ingested items (e.g., plastic, paper, cloth). Frequency of occurrence of food items in scats was determined by season, geographic area, and year. Food items also were combined into broader categories: rabbit, rodent, domestic animal, bird, reptile, invertebrate, and fruit.

The annual availability of natural foods, particularly in arid environments, generally fluctuate with precipitation abundance received during the wet-season that occurs from late fall through spring. Thus, to better pair coyote foraging patterns with annual prey availability, years were defined as October to September. We determined annual precipitation totals for these same intervals using data from U.S. Climate Data (2014). Seasons were defined as fall (Oct-Dec), winter (Jan-Mar), spring (Apr-Jun), and summer (Jul-Aug).

PREY ABUNDANCE

Leporids (primarily black-tailed jackrabbits; *Lepus californicus*) and rodents (primarily kangaroo rats [*Dipodomys* spp.], pocket mice [*Perognathus spp*. and *Chaetodipus spp.*], squirrels [*Spermophilus* spp. and *Ammospermophilus leucurus*], and desert woodrats [*Neotoma lepida*]) were expected to constitute primary prey items for coyotes in the study area. To assess relative prey abundance among years and sections of the study area, 20 1-km transects were established in each section for a total of 60 transects. The transects were established on public lands (U.S. Bureau of Land Management or California Department of Fish and Game). Transects began approximately 25 m from an unpaved road and were oriented approximately perpendicular to the road. To increase sampling efficiency, transects were established in pairs with the transects in each pair oriented parallel to each and separated by 250 m. Pairs of transects were spaced at least 2 km apart. Transects were established in areas that appeared to have typical habitat conditions for each section of the study area.

Relative abundance of rabbits and rodents was assessed by counting fresh rabbit pellets and active rodent burrows along each transect. Fresh pellets were characterized by a golden to dark brown color and a smooth surface (Figure 2) whereas old pellets were characterized by a gray color and surface roughed by weathering. Rodent burrows were characterized as "large" (burrow opening ≥ 3 cm) or "small" (burrow opening < 3 cm). Large burrows are typical of those used by kangaroo rats or ground squirrels (Figure 3) while small burrows are typical of those used by pocket mice or other mice. Burrows with openings obstructed by vegetation or spider webs are not considered active and were not counted.

Figure 2. Fresh (left) and old (right) rabbit pellets.

Figure 3. Example of large rodent burrow.

Prey abundance assessments were conducted once each year in the spring. Assessments were conducted by 2 observers slowly walking along each transect. The first observer acts as orienteer and counted all active burrows within 1 m of either side of the transect. The second observer counted all fresh rabbit pellets within 1 m of either side of the transect and recorded data.

COYOTE ABUNDANCE

Automated digital field cameras (Cuddeback Digital Attack IR, Model 1156, Non Typical Inc. Green Bay, WI; Stealth Cam 3.0 MP Digital Scouting Cameras, Model STC-AD2/AD2RT, Stealth Cam LLC, Bedford, TX) were deployed in an effort to detect the presence and relative abundance of coyotes across the study areas. The cameras were secured to 1.2-m (3-ft) U-posts with zip ties and duct tape. A can of cat food was staked to the ground approximately 2 m in front of each camera using 30-cm nails. A scent lure (Carman's Canine Call Lure, Russ Carman, New Milford, PA) was dripped on the can and vegetation near the camera as an extra attractant for carnivores. Camera stations were deployed near each pair of prey abundance transects in early December and were left to run for 8-10 weeks. Each year, the number of cameras recording visits by coyotes and the minimum number of coyotes visiting cameras was recorded for each portion of the study area.

RESULTS

COYOTE FORAGING PATTERNS

Over the 5 years of the study, 3,246 scat samples were collected and analyzed (range 474-801 per year). Approximately 50 different items were identified in coyote scats (see Appendix A for a complete list of food items and scientific names). Rabbits, kangaroo rats and pocket mice appeared to be primary food items for coyotes. The rabbit in scats likely was primarily black-tailed jackrabbit, which was the species most frequently observed in the study area. Desert cottontails also are present in the area but appeared to have a more localized distribution particularly near water sources. Kangaroo rat species potentially occurring in the study area included desert (*D. deserti*), Merriam's (*D. merriami*), and chisel-tooth (*D. microps*) kangaroo rats. Potential pocket mouse species included desert (*C. pencillatus*), long-tailed (*C. formosus*), and little pocket mice (*P. longimembris*). Squirrels in the study area include round-tailed (*S. tereticaudus*), Mohave ground squirrel (*S. mohavensis*), and white-tailed antelope squirrel (*A. leucurus*). Birds and snakes and insects also were commonly consumed but usually could not be identified to species. Anthropogenic remains identified in scats included cat, dog, livestock, gut piles, domestic animal waste, and various crops including walnuts, almonds, pistachios, olives, pumpkin, melon, corn, and beans. Other non-food anthropogenic items included pieces of cloth, paper, plastic, leather, cartridge casings, and other materials. A number of other items appeared to be ingested incidentally and included twigs, grass, other vegetation, pebbles, and soil.

For all years combined (Table 1), rabbit was the primary item found in coyote scats. Other items occurring in ≥ 10% of scats included kangaroo rat, snake, pocket mouse, and bird. Rabbit also was the most frequently occurring item in each year (Table 1), study area segment (Table 2), and season (Table 3). Other items occurring at frequencies ≥ 10% in annual, seasonal and area samples typically included kangaroo rat, snake, pocket mouse, and bird. Less typical items included squirrels in Year 3 and Fall; Coleopterans in Year 2, Summer, and the West area; insect larvae in Year 5; and pistachios in the East area.

Table 1. Frequency of occurrence of food items found in coyote scats for 5 years and all years combined on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. Years are defined as October-September.

		Frequency of Occurrence (%)					
	Food Item	**Year 1 (*n* = 625)**	**Year 2 (*n* = 474)**	**Year 3 (*n* = 631)**	**Year 4 (*n* = 801)**	**Year 5 (*n* = 715)**	**All Years (*n* = 3,246)**
Natural Items	Rabbit	48.3	42.0	58.2	67.5	41.4	52.5
	Kangaroo Rat	32.6	26.2	23.3	14.9	9.9	20.5
	Pocket Mouse	19.2	35.4	5.4	3.1	8.0	12.4
	Deer mouse	0.0	0.0	0.5	0.0	0.6	0.2
	House Mouse	0.0	0.4	0.0	0.1	1.7	0.5
	Squirrel	7.2	7.8	16.0	8.2	3.4	8.4
	Woodrat	2.1	8.2	7.9	2.1	1.0	3.9
	Gopher	0.2	0.0	0.0	0.1	1.4	0.4
	Unknown Rodent	7.2	3.8	2.7	2.5	5.3	4.2
	Unknown Mammal	0.5	0.2	2.5	3.5	6.9	3.0
	Bird	10.1	7.2	12.8	10.7	18.6	12.2
	Eggshell	0.3	0.6	0.0	0.4	0.4	0.3
	Snake	13.0	19.4	13.3	12.0	12.9	13.7
	Lizard	6.6	5.1	3.2	4.0	8.8	5.5
	Desert Tortoise	5.9	5.3	2.5	2.6	2.4	3.6
	Unknown Reptile	1.4	0.4	1.3	0.5	0.6	0.8
	Orthopteran	3.4	1.7	0.3	1.4	3.1	2.0
	Coleopteran	8.3	11.2	8.1	9.9	9.2	9.3
	Insect Larva	2.1	0.4	0.6	2.1	10.5	3.4
	Ant	0.0	0.4	1.0	0.5	0.0	0.4
	Caterpillar	0.2	0.0	0.0	0.0	0.0	0.0
	Jerusalem Cricket	0.0	0.2	0.8	0.4	0.4	0.4
	Earwig	0.3	0.2	0.3	0.0	0.0	0.2
	Unknown Insect	2.6	4.0	7.1	8.5	5.6	5.8
	Scorpion	0.8	1.5	0.3	1.9	1.3	1.2
	Unknown Invertebrate	0.0	0.0	0.0	0.1	0.0	0.0
	Unknown Animal	0.0	0.0	0.0	.0	1.3	0.3
	Screwbean Mesquite	3.4	0.6	5.5	1.9	0.1	1.7
	Mesquite spp.	0.0	0.0	0.0	2.6	3.5	1.4
	Boxthorn spp.	0.0	0.0	0.0	0.1	1.0	0.2
	Cucurbit spp.	0.2	0.0	0.6	0.4	0.0	0.2
	Cactus spp.	0.0	0.0	0.0	0.1	0.0	0.0
Anthropogenic Items	Domestic Dog	0.6	0.0	0.6	0.2	0.1	0.3
	Domestic Cat	0.5	0.6	1.4	0.4	0.4	0.6
	Cow	0.0	0.4	1.3	0.6	0.0	0.5
	Sheep	0.3	0.0	0.0	0.0	0.0	0.1
	Goat	0.2	0.0	0.2	0.1	0.1	0.1
	Domestic Animal	2.9	2.5	4.1	3.9	9.7	4.8
	Domestic Animal Gut Pile	0.0	0.0	0.2	1.5	0.1	0.4
	Domestic Animal Waste	0.0	0.0	0.0	0.0	4.3	1.0
	Pistachio	0.5	0.0	1.0	2.0	7.6	2.4
	Walnut	0.0	0.0	0.0	0.1	0.4	0.1
	Almond	0.0	0.0	0.0	0.0	0.3	0.1
	Cherry spp.	0.0	0.0	0.0	0.0	0.4	0.1
	Olive spp.	0.2	0.0	0.0	1.9	1.7	0.9
	Palm spp.	0.0	0.0	0.0	0.1	0.7	0.2
	Rose spp.	0.0	0.0	0.0	0.0	0.3	0.1
	Bean	0.0	0.0	0.0	0.0	0.1	0.1
	Pumpkin	0.0	0.0	0.0	0.0	0.3	0.1
	Melon	0.0	0.0	0.0	0.0	0.3	0.1
	Corn	0.0	0.0	0.2	0.2	0.3	0.2
	Sunflower Seed	0.0	0.0	0.2	0.0	0.0	0.0
	Man-made Material	2.2	4.0	6.8	5.0	6.3	5.0

Table 2. Frequency of occurrence of food items found in coyote scats collected in three study area segments in the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

	Food Item	Frequency of Occurrence (%)		
		West (*n* = 1435)	**Central (*n* = 1218)**	**East (*n* = 593)**
Natural Items	Rabbit	45.5	57.6	59.2
	Kangaroo Rat	32.2	11.1	11.5
	Pocket Mouse	19.4	7.3	6.2
	Deer mouse	0.3	0.1	0.3
	House Mouse	0.1	0.3	1.7
	Squirrel	9.8	8.1	5.7
	Woodrat	3.6	5.0	2.4
	Gopher	0.8	0.0	0.2
	Unknown Rodent	5.3	3.5	3.2
	Bird	7.3	16.8	14.7
	Eggshell	0.1	0.7	0.3
	Snake	17.6	11.0	9.8
	Lizard	5.1	5.2	7.4
	Desert Tortoise	3.8	4.1	1.9
	Unknown Reptile	1.0	0.6	0.8
	Orthopteran	3.0	1.4	0.7
	Coleopteran	11.4	7.7	7.4
	Insect Larva	3.4	2.9	4.6
	Ant	0.3	0.3	0.7
	Caterpillar	0.0	0.1	0.0
	Jerusalem Cricket	0.4	0.3	0.3
	Earwig	0.1	0.2	0.0
	Unknown Insect	5.9	5.1	6.9
	Scorpion	1.7	0.6	1.2
	Unknown Invertebrate	0.0	0.1	0.0
	Unknown Animal	0.0	0.2	1.0
	Screwbean Mesquite	0.0	4.5	0.2
	Mesquite spp.	0.3	3.0	1.0
	Boxthorn spp.	0.0	0.2	1.0
	Cucurbit spp.	0.2	0.2	0.3
	Cactus spp.	0.0	0.1	0.0
Anthropogenic Items	Domestic Dog	0.3	0.3	0.5
	Domestic Cat	0.5	0.3	1.7
	Cow	0.6	0.2	0.5
	Sheep	0.0	0.2	0.0
	Goat	0.3	0.0	0.0
	Domestic Animal	4.2	4.9	6.1
	Domestic Animal Gut Pile	0.2	0.8	0.2
	Domestic Animal Waste	0.3	1.1	2.2
	Unknown Mammal	2.4	3.0	4.2
	Pistachio	0.0	0.9	11.5
	Walnut	0.3	0.0	0.0
	Almond	0.0	0.0	0.3
	Cherry spp.	0.0	0.2	0.0
	Olive spp.	0.0	1.5	1.7
	Palm spp.	0.2	0.2	0.2
	Rose spp.	0.0	0.1	0.2
	Bean	0.0	0.1	0.0
	Pumpkin	0.0	0.0	0.3
	Melon	0.1	0.1	0.0
	Corn	0.0	0.2	0.3
	Sunflower Seed	0.0	0.1	0.0
	Man-made Material	2.5	6.2	8.3

Table 3. Seasonal frequency of occurrence of food items found in coyote scats collected in the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

		Frequency of Occurrence (%)			
	Food Item	**Fall (*n* = 845)**	**Winter (*n* = 834)**	**Spring (*n* = 738)**	**Summer (*n* = 829)**
Natural Items	Rabbit	46.7	54.2	52.2	57.1
	Kangaroo Rat	28.0	18.1	17.8	17.6
	Pocket Mouse	14.3	9.0	12.1	14.4
	Deer mouse	0.4	0.1	0.0	0.4
	House Mouse	0.4	0.6	0.3	0.6
	Squirrel	10.3	7.2	9.8	6.5
	Woodrat	5.7	2.0	3.3	4.5
	Gopher	0.2	0.2	0.7	0.4
	Unknown Rodent	4.7	5.2	2.8	4.1
	Unknown Mammal	2.4	3.4	3.8	2.5
	Bird	11.4	10.1	14.0	13.8
	Eggshell	0.4	0.2	0.7	0.1
	Snake	13.7	9.1	13.8	18.2
	Lizard	3.9	2.6	7.9	8.1
	Desert Tortoise	4.4	3.5	4.9	1.7
	Unknown Reptile	1.2	0.4	0.9	0.8
	Orthopteran	2.5	2.0	2.0	1.3
	Coleopteran	9.2	8.2	7.7	11.8
	Insect Larva	1.9	1.7	5.7	4.7
	Ant	0.5	0.0	0.1	0.8
	Caterpillar	0.1	0.0	0.0	0.0
	Jerusalem Cricket	1.1	0.1	0.1	0.1
	Earwig	0.2	0.1	0.3	0.0
	Unknown Insect	3.3	4.6	7.7	7.8
	Scorpion	0.8	0.8	0.7	2.3
	Unknown Invertebrate	0.0	0.0	0.0	0.1
	Unknown Animal	0.0	0.6	0.0	0.5
	Screwbean Mesquite	2.4	1.0	2.6	1.1
	Mesquite spp.	1.1	1.3	0.5	2.7
	Boxthorn spp.	0.1	0.7	0.1	0.0
	Cucurbit spp.	0.5	0.0	0.3	0.2
	Cactus spp.	0.1	0.0	0.0	0.0
Anthropogenic Items	Domestic Dog	0.4	0.2	0.4	0.4
	Domestic Cat	0.4	0.4	1.1	0.8
	Cow	0.4	0.5	0.4	0.6
	Sheep	0.2	0.0	0.0	0.0
	Goat	0.1	0.2	0.1	0.0
	Domestic Animal	3.7	6.4	3.1	5.9
	Domestic Animal Gut Pile	0.1	0.2	1.2	0.2
	Domestic Animal Waste	0.0	1.2	0.9	1.7
	Pistachio	2.5	4.1	1.5	1.6
	Walnut	0.2	0.0	0.3	0.0
	Almond	0.0	0.0	0.1	0.1
	Cherry spp.	0.0	0.0	0.0	0.4
	Olive spp.	1.1	0.2	0.3	1.8
	Palm spp.	0.1	0.1	0.4	0.1
	Rose spp.	0.0	0.0	0.1	0.1
	Bean	0.0	0.1	0.0	0.0
	Pumpkin	0.0	0.2	0.0	0.0
	Melon	0.0	0.2	0.0	0.0
	Corn	0.1	0.2	0.3	0.0
	Sunflower Seed	0.0	0.0	0.0	0.1
	Man-made Material	3.8	4.8	5.8	5.5

When items were grouped into broader food categories, rodents comprised the largest proportion of items in Years 1 and 2, and rabbits comprised the largest proportion in Years 3, 4, and 5 (Figure 4). Proportional occurrence of birds, reptiles, invertebrates, and vegetation in coyote scats was relatively consistent among years. The proportion of anthropogenic items also was relatively consistent except for Year 5 when it about doubled.

Among study area segments, rabbits comprised the largest proportion of items in the East and Central areas, but rodents comprised the largest proportion in the West area (Figure 5). The proportions of other item categories were generally consistent among areas except for anthropogenic items. For these items, the proportion was lowest in the West area, higher in the Central area and highest in the East area where they comprised the second largest category of items consumed by coyotes.

Among seasons, the proportions comprised by each food item category were relatively consistent (Figure 6). Rabbits and rodents consistently were the 2 largest categories with rodents being a bit larger in the Fall and rabbits being a bit larger in the other seasons.

Frequency of desert tortoise remains in coyote scats was 3.6% for all years combined, and varied from 2.4% to 5.8% for individual years (Figure 7). Tortoise occurrence in scats was approximately twice as high in the Central and West areas compared to the East area (Figure 8). Tortoise was present in scats during all seasons, and was highest in Spring and lowest in Summer (Figure 9).

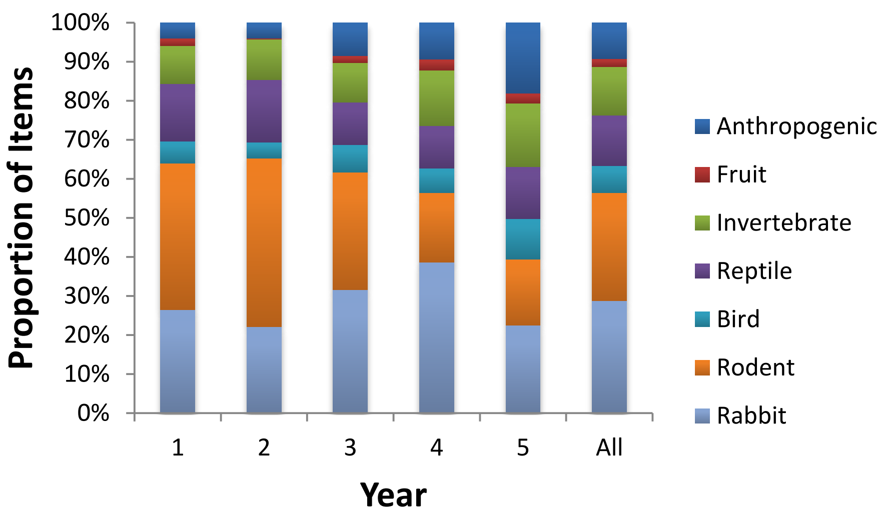

Figure 4. Proportional item occurrences by food category for coyote scats collected in 5 years and for all years combined on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

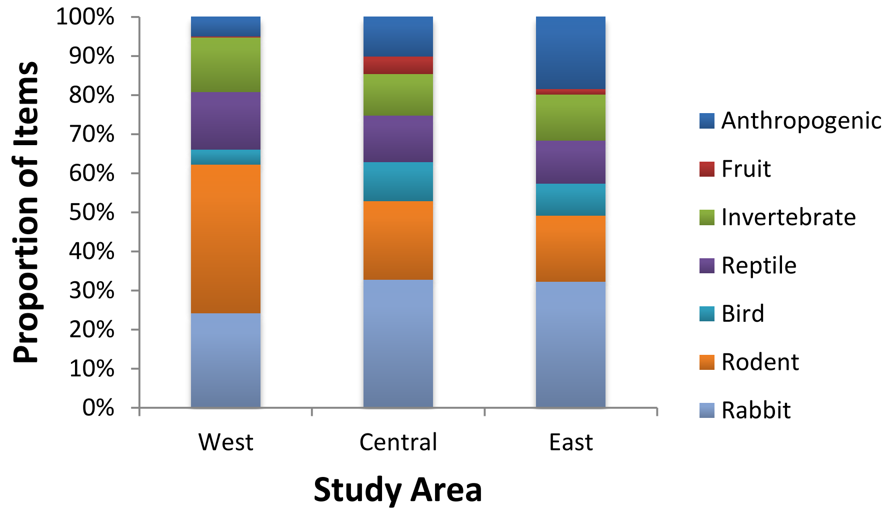

Figure 5. Proportional item occurrences by food category for coyote scats collected in 3 study area segments on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

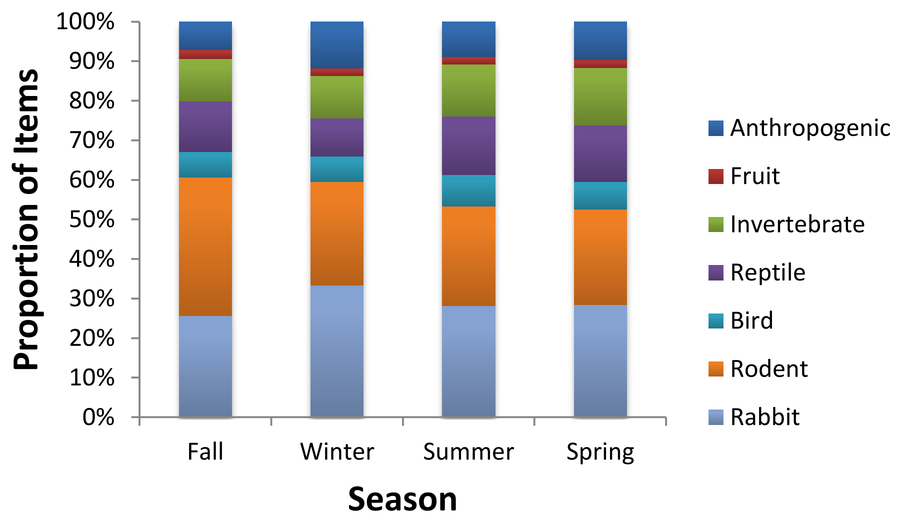

Figure 6. Proportional item occurrences by food category among seasons for coyote scats collected in the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

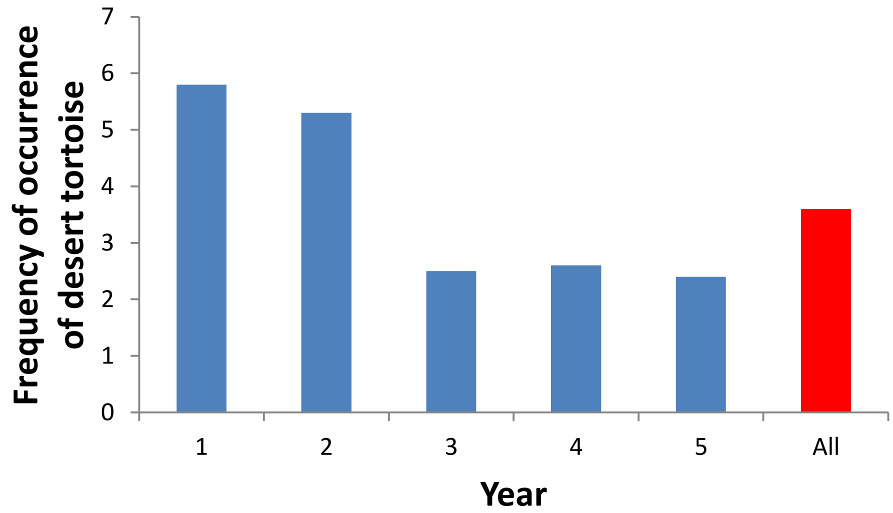

Figure 7. Frequency of occurrence of desert tortoise remains found in coyote scats for each year and all years combined on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

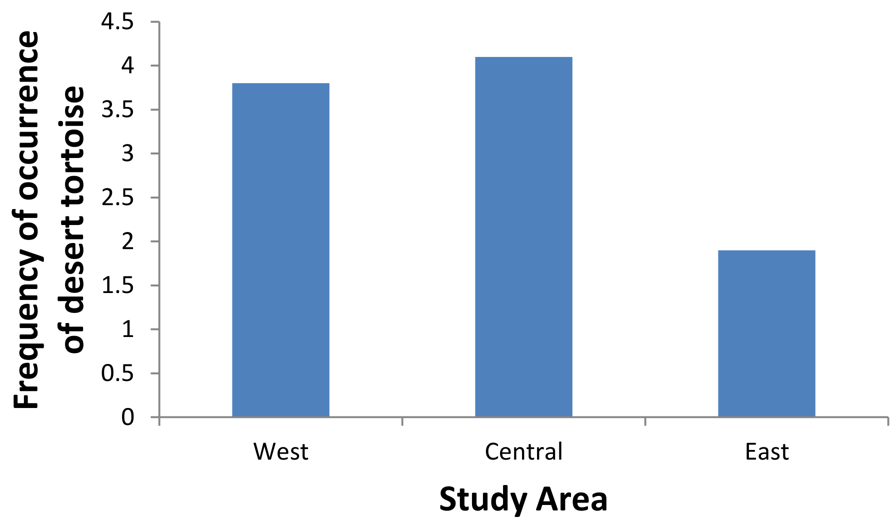

Figure 8. Frequency of occurrence of desert tortoise remains found in coyote scats collected in 3 study area segments on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

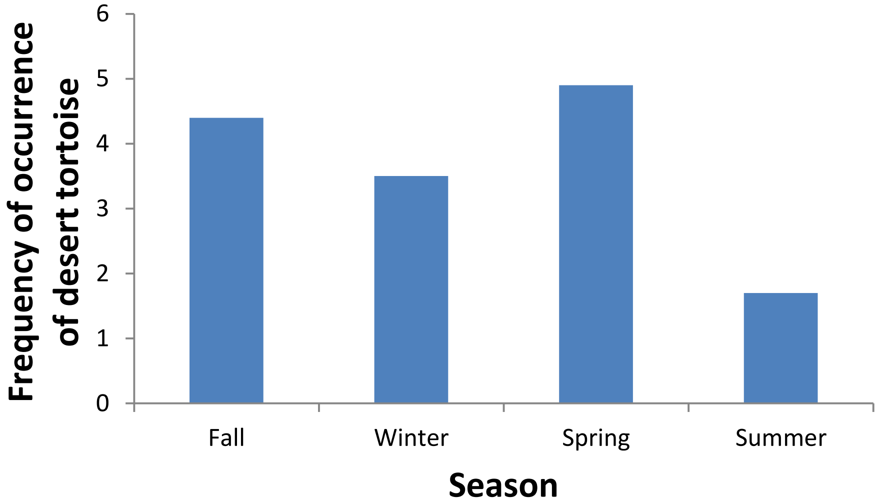

Figure 9. Seasonal frequency of occurrence of desert tortoise remains found in coyote scats collected on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

Use of anthropogenic items increased during the 5 years of the study (Figure 10). By Year 5, the occurrence of anthropogenic items was almost double compared to the previous 2 years. Use these items was highest in the East area and lowest in the west (Figure 11), and use was fairly consistent across seasons (Figure 12).

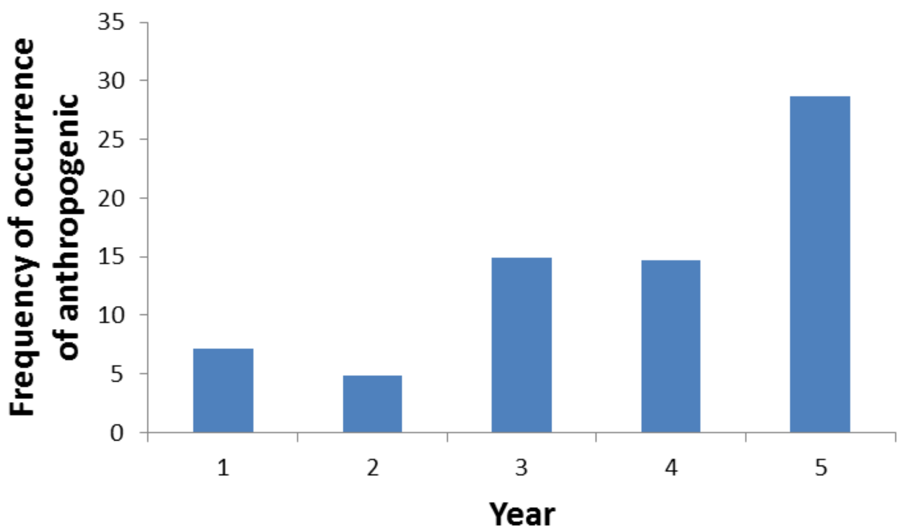

Figure 10. Frequency of occurrence of anthropogenic items in coyote scats for each year on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

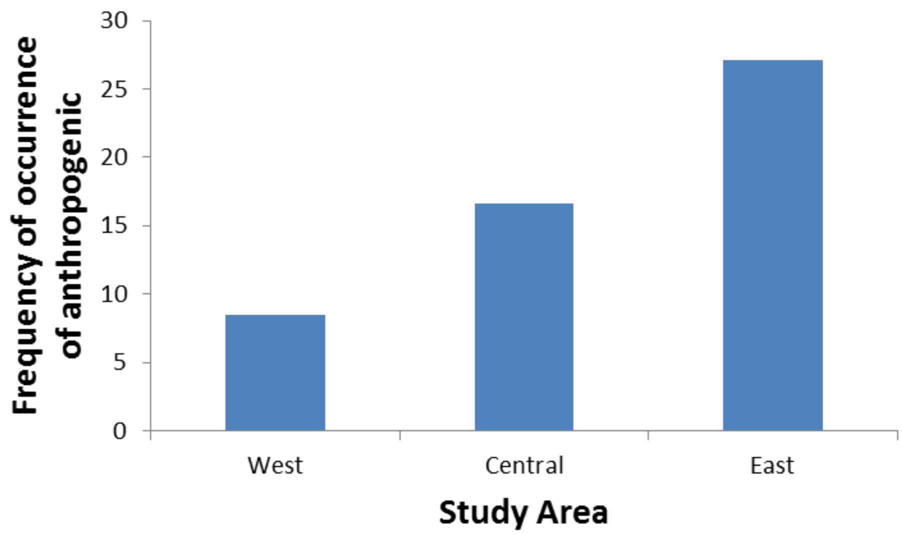

Figure 11. Frequency of occurrence of anthropogenic items in coyote scats collected in 3 study area segments on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

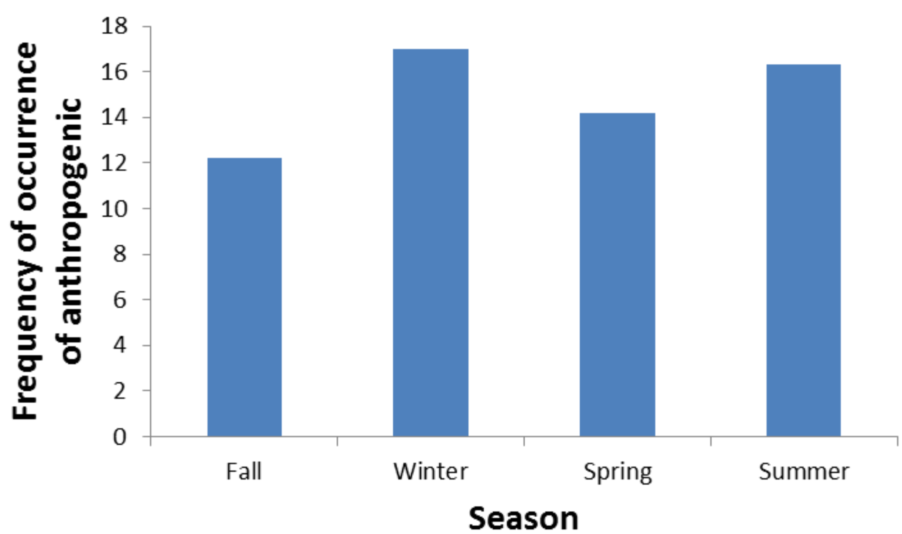

Figure 12. Seasonal frequency of occurrence of anthropogenic items in coyote scats collected on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

PREY ABUNDANCE

Annual precipitation totals for Years 1-5 were 16.9 cm, 28.2 cm, 7.3 cm, 7.5 cm, and 8.0 cm, respectively. Average annual precipitation for the region is approximately 13.2 cm. Prey availability assessments were conducted during March-May annually. The mean annual number of rabbit pellets per transect exhibited similar trends across the 3 study area segments (Figure 13). Most notably, the numbers on all 3 areas exhibited a pronounced spike in Year 3, which followed 2 years of above average precipitation. Across the entire study area, trends in use of rabbits by coyotes generally reflected trends in rabbit pellet counts, but exhibited a 1-year lag (Figure 14). The mean annual number of large burrows also exhibited somewhat similar trends across the three areas; higher in the earlier years of the study and lower in the later years (Figure 15). Across the entire study area, large burrow counts and use of kangaroo rats by coyotes both exhibited declining trends (Figure 16). These trends only weakly tracked annual precipitation. The mean number of small burrows was more variable among areas and did not closely track annual precipitation (Figure 17). Similarly, across the entire study area, small burrow abundance generally declined over the course of the study probably reflecting lower precipitation in the latter years (Figure 18). However, use of pocket mice by coyotes very closely tracked annual precipitation trends.

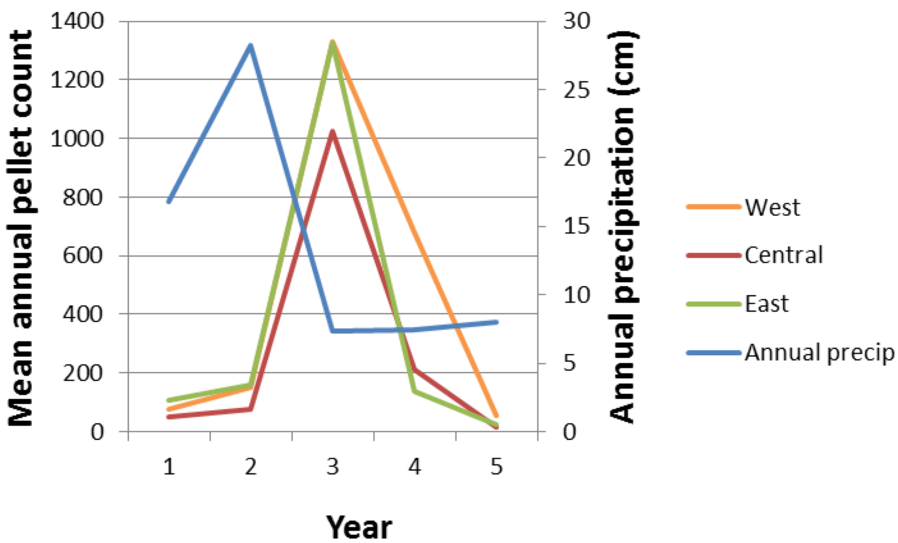

Figure 13. Mean annual rabbit pellet counts for 3 study area segments and annual precipitation on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

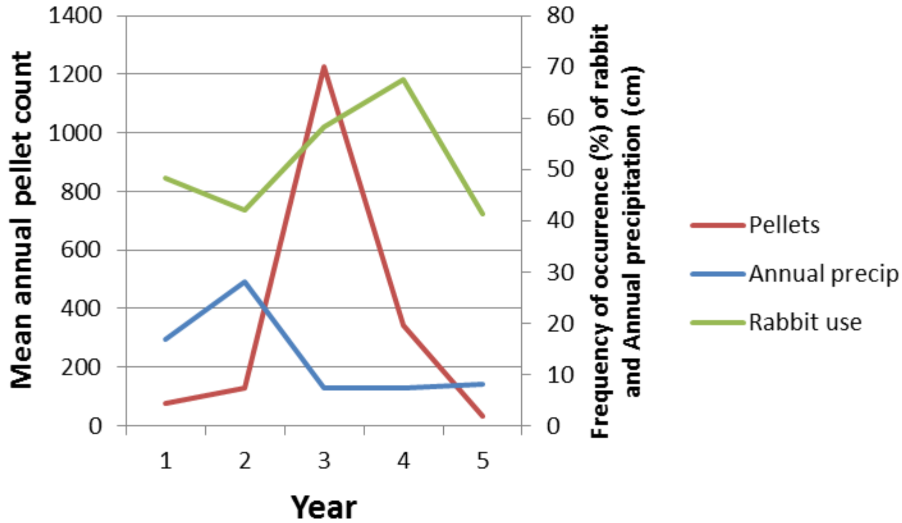

Figure 14. Annual mean rabbit pellet counts, precipitation, and use of rabbits by coyotes on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

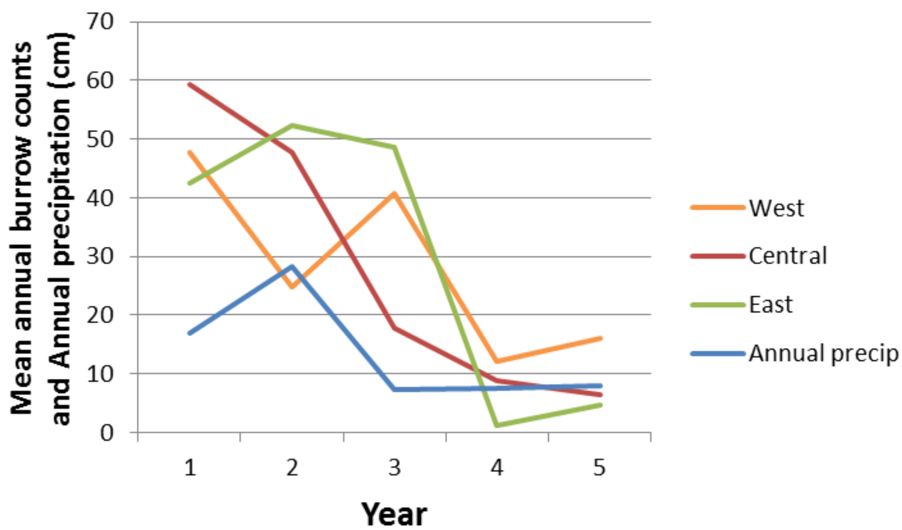

Figure 15. Mean annual large burrow counts for 3 study area segments and annual precipitation on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

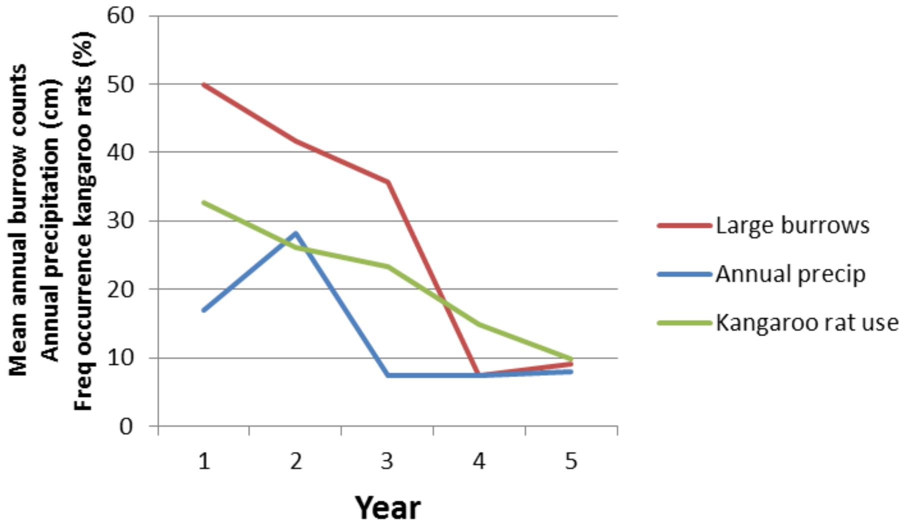

Figure 16. Annual mean large burrow counts, precipitation, and use of kangaroo rats by coyotes on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

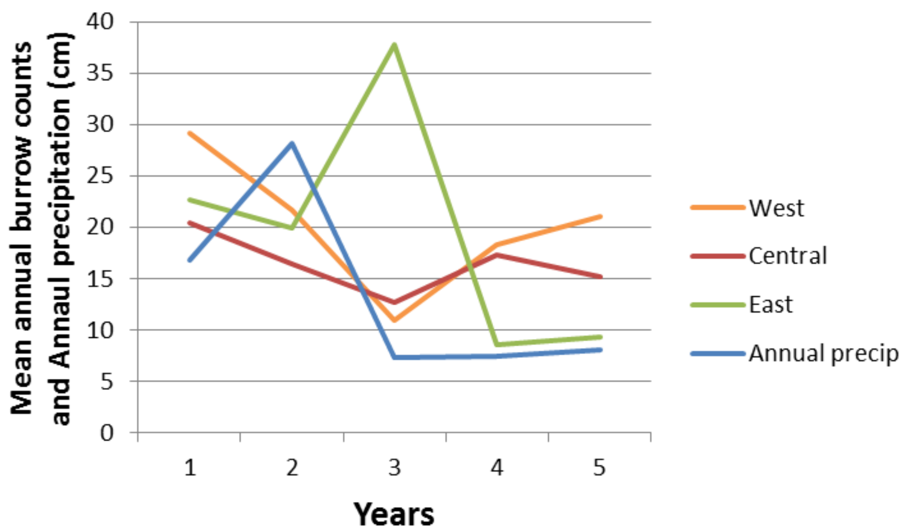

Figure 17. Mean annual small burrow counts for 3 study area segments and annual precipitation on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

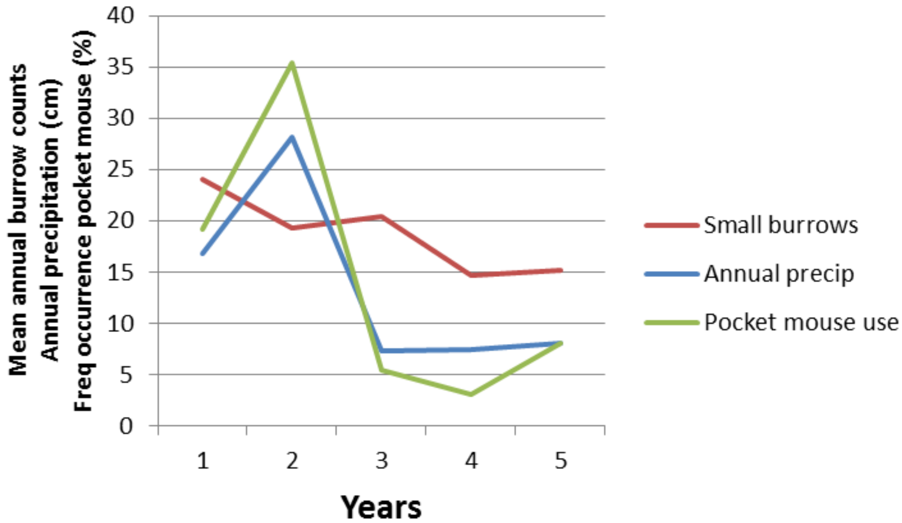

Figure 18. Annual mean small burrow counts, precipitation, and use of pocket mice by coyotes on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

EFFECTS OF ITEM USE AND AVAILABILITY ON USE OF TORTOISES

Occurrence of desert tortoise in coyote scats declined during the 5 years of the study (Figure 19). There did not appear to be a strong relationship between use of tortoise and use of other items. Annual precipitation also declined during this period, which may have resulted in lower tortoise abundance and a concomitant reduction in use by coyotes. Similarly, no relationships were apparent between use of tortoises and use of other items across the 3 study area segments (Figure 20). Furthermore, all prey availability indices also exhibited a declining trend across years similar to that of tortoise use by coyotes and likely in response to declining annual precipitation (Figure 21). As with prey item use, no relationships were apparent between prey availability indices and use of tortoises across the 3 study area segments (Figure 22).

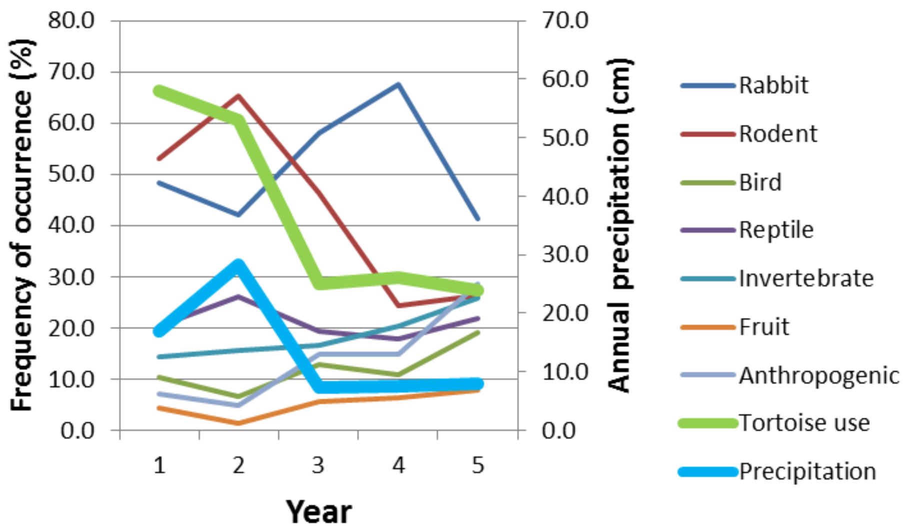

Figure 19. Use of desert tortoises by coyotes among years relative to use of other food items and annual precipitation on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. To better compare trends, the percent frequency of occurrence of desert tortoise in coyote scats was multiplied by 10.

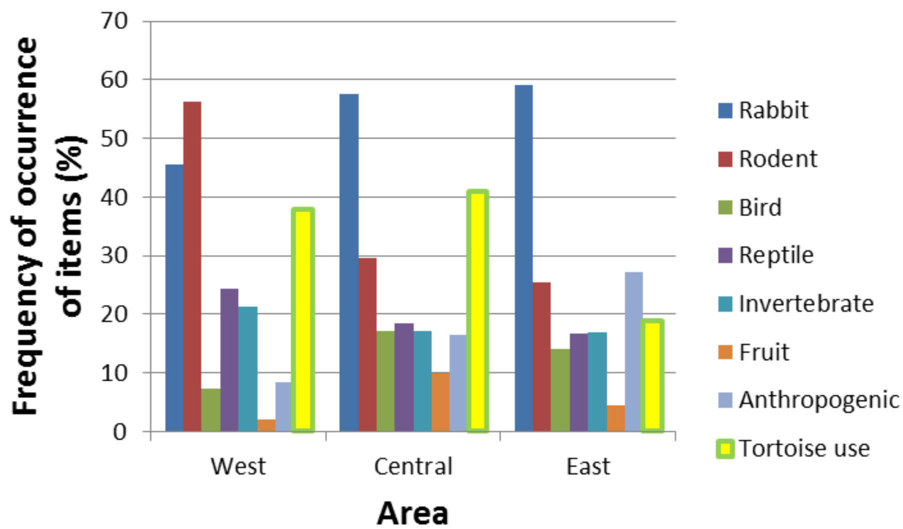

Figure 20. Use of desert tortoises by coyotes among study area segments relative to use of other food items on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. To better compare trends, the percent frequency of occurrence of desert tortoise in coyote scats was multiplied by 10.

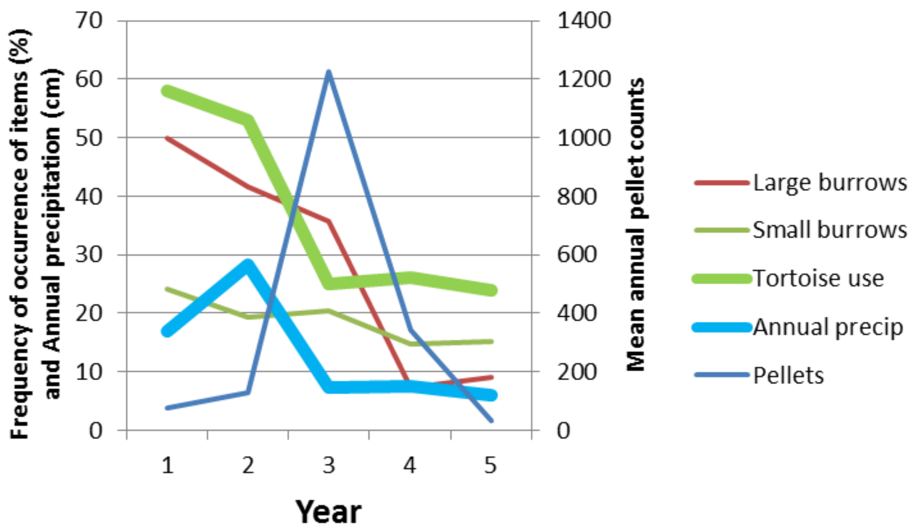

Figure 21. Use of desert tortoises by coyotes among years relative to prey availability indices and annual precipitation on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. To better compare trends, the percent frequency of occurrence of desert tortoise in coyote scats was multiplied by 10.

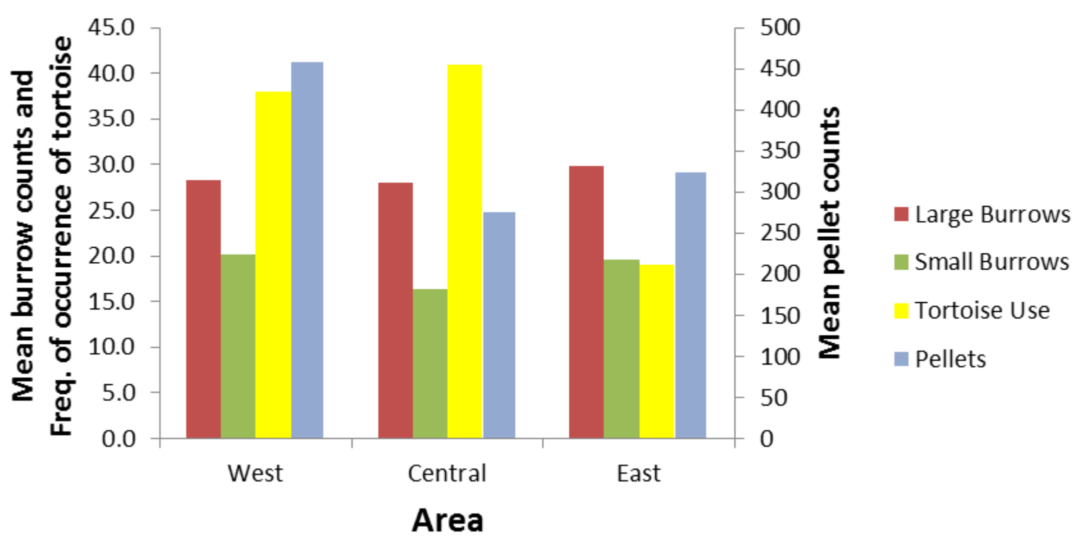

Figure 22. Use of desert tortoises by coyotes among study area segments relative to use of other food items on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014. To better compare trends, the percent frequency of occurrence of desert tortoise in coyote scats was multiplied by 10.

COYOTE ABUNDANCE AND DISTRIBUTION

Ten automated camera stations were established on each of the 3 study area segments (Figure 23) and operated for 42 nights in Year 3, 69 nights in Year 4, and 63 nights in Year 5. Camera stations were deployed in December and collected in either January or February. Coyotes were detected across the study area. They were detected on 29 of the 30 stations in one or more years. Only one station in the East area did not have a coyote detection. Coyotes may have been less abundant in the East area. Detection rates were generally were lower in the East area, although rates were similar among areas in Year 5 (Table 4). Detection rates for all areas combined did not differ markedly among years. Several other species also were detected on the cameras (Table 5). These species include other potential predators on desert tortoises, such as kit foxes (nests and hatchlings), badgers, domestic dogs, and ravens. Domestic dogs usually were detected near human inhabited areas, and in Year 5 they were detected on 9 of 28 cameras (Figure 24) indicating that they were relatively abundant.

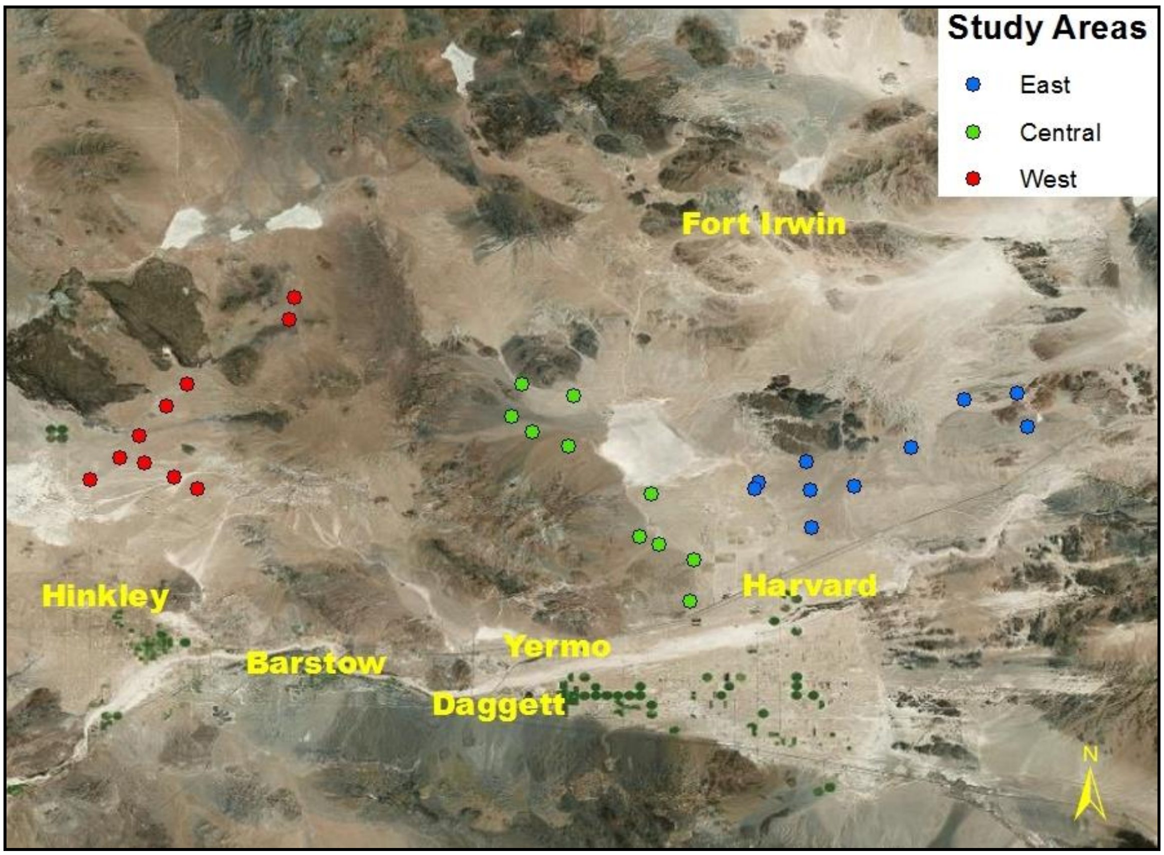

Figure 23. Locations of automated camera stations in 3 study area segments on the Desert Tortoise Translocation Area, San Bernardino County, California.

Table 4. Annual coyote detection rates on camera stations in 3 study area segments on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

	Coyote detection rates[1]			
	Study area segments			
Year	**West**	**Central**	**East**	**Total**
Year 3	1.0	0.7	0.5	0.73
Year 4	0.8	0.9	0.2	0.66
Year 5	0.7	0.7	0.8	0.71
Mean ± SE	**0.83 ± 0.09**	**0.77 ± 0.07**	**0.50 ± 0.17**	**0.70 ± 0.02**

[1] Number of cameras on which coyotes were detected/number of functional cameras. One camera malfunctioned in the East area in Year 4, and one camera malfunctioned in both the West and East areas in Year 5.

Table 5. Species detected on automated cameras in 3 study area segments for 3 years combined (2012-2014) on the Desert Tortoise Translocation Area, San Bernardino County, California.

Species		Cameras with detections[1]			
Common Name	**Scientific Name**	**West**	**Central**	**East**	**Total**
Coyote	*Canis latrans*	24	23	14	61
Desert kit fox	*Vulpes macrotis arsipis*	25	26	26	77
Domestic dog	*Canis familiaris*	4	5	2	11
Bobcat	*Lynx rufus*	5	2	2	9
American badger	*Taxidea taxus*	4	0	4	8
Spotted skunk	*Spilogale gracilis*	0	0	1	1
Black-tailed jackrabbit	*Lepus californicus*	22	20	18	60
White-tailed antelope squirrel	*Ammospermophilus leucurus*	5	2	2	9
Kangaroo rat species	*Dipodomys* spp.	3	1	0	4
Common raven	*Corvus corax*	4	1	7	12
Burrowing owl	*Athene cnunicularia*	0	1	0	1
Sage sparrow	*Amphispiza belli*	0	1	0	1
Say's Phoebe	*Sayornis saya*	0	1	0	1
Loggerhead shrike	*Lanius ludovicianus*	0	1	0	1

[1]Functional cameras over 3 years: West = 29, Central = 30, and East = 28, and Total = 87.

Coyote scats were not collected in a systematic way across the study area. However, the distribution of locations where scats were found further indicates that coyotes occurred throughout the study area (Figure 24). The pattern of locations also is consistent with camera station data that suggested lower numbers of coyotes in the East area. Indeed, particularly in the final 2 years of the investigation, most of the scats collected in the East area were found on the western side of this area close to human occupied areas.

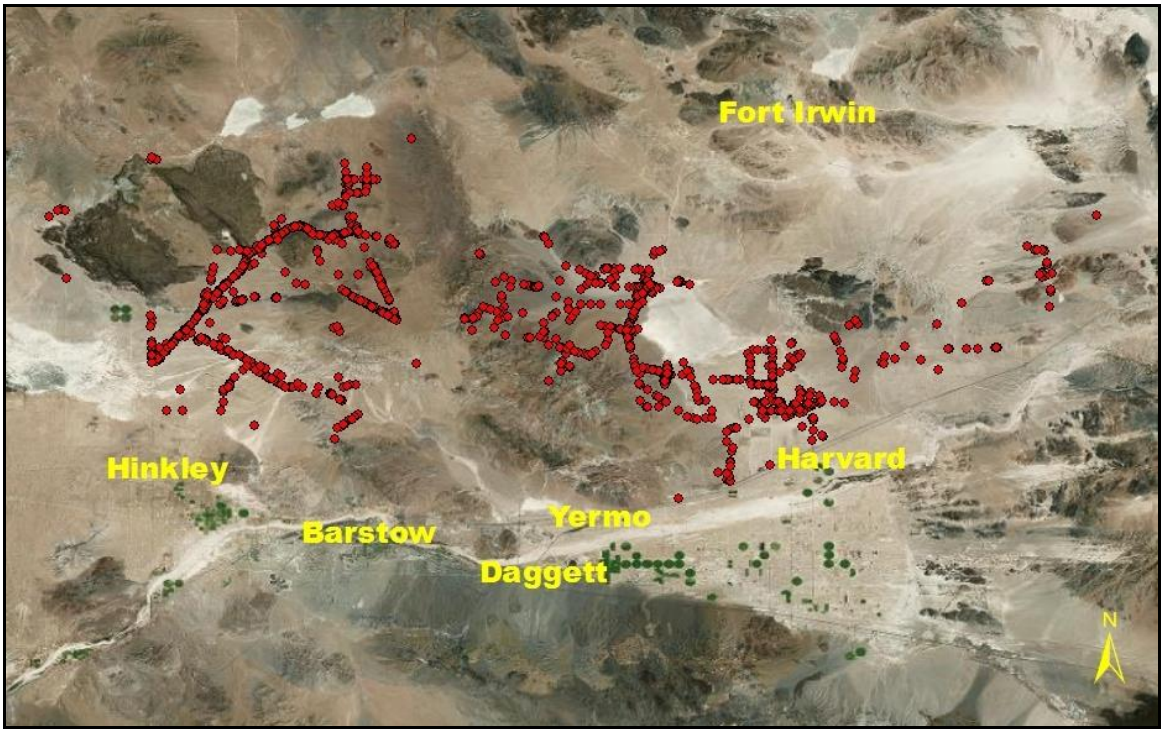

Figure 24. Locations of coyote scats collected on the Desert Tortoise Translocation Area, San Bernardino County, California during October 2009-September 2014.

DISCUSSION

COYOTE FORAGING PATTERNS

Coyotes commonly are characterized as opportunistic foraging generalists (Bekoff and Gese 2003). This is a fair generalization in a broad ecological sense, but at specific locations coyote foraging patterns may exhibit preferences (e.g., MacCracken and Hansen 1987). In this investigation, rabbits appeared to be a preferred food item on the Desert Tortoise Translocation Area. Among individual items, rabbits were the most frequently occurring item in all years, seasons, and study area segments. Based on pellet counts, rabbit abundance varied markedly during the 5 years of the study, but use by coyotes was consistently high. A preference for black-tailed jackrabbits also has been reported from other arid locations (Clark 1972, MacCracken and Hansen 1987), and rabbits commonly are a primary prey item for coyotes in California (Ferrel et al. 1953, Cypher et al. 1994).

Rodents, particularly heteromyids (e.g., kangaroo rats and pocket mice) and squirrels, also were foods commonly consumed by coyotes. Indeed, as a category, rodents were the most frequently occurring items in coyote scats in the first 2 years of the study. Use of rodents appeared to vary with their relative availability. Based on burrow counts, rodent abundance declined during the course of the study. This decline appeared to coincide with reduced precipitation in the latter years of the study. Concomitantly, use of rodents by coyotes declined as well.

Use of most other items, such as birds, reptiles, invertebrates, and fruits, likely was more opportunistic, as indicated by their relatively low frequencies of occurrence in coyote scats. Coyotes probably did not actively search for these items, but instead consumed them as they encountered them. The occurrence of these items in scats generally increased in the latter years of the study. This increase likely was associated with declining abundance of primary foods, particularly rabbits and rodents, resulting from low annual precipitation levels. Increased use of secondary food items as primary items decline is consistent with optimal foraging theory predictions for a foraging generalist (MacCracken and Hansen 1987).

Coyotes consistently consumed anthropogenic items throughout the study. Some of these items were apparently consumed for nutritional purposes (e.g., domestic animals, crops), but it is unclear why other items were consumed (e.g., cartridge casings, dog leash, rope). It is unknown whether domestic animal remains found in coyote scats resulted from depredation on live animals or scavenging on dead animals. In all 3 study area segments, we occasionally did find carcasses of domestic animals that either had gotten lost and died or that were "dumped" after death. Likewise, it is unknown whether crops in scats were a result of depredation or scavenging from garbage. As with animal carcasses, we occasionally found sites where trash had been dumped. Such dumping unfortunately appears to be common and has been well documented in areas with desert tortoises (Berry et al. 2006, Boarman et al. 2006).

The consistent presence of anthropogenic items in coyote scats suggests that this might be an important supplemental food source for coyotes, as has been reported elsewhere (Danner and Smith 1980, McClure et al. 1995, Fedriani et al. 2001). Use was consistent among seasons, but differences were evident among areas. Use was highest in the East area, although this may be somewhat of a sampling artifact. Most of the coyote scats collected in the East area were found in locations in close proximity to human habitations in the community of Harvard. Use also was higher in the Central area compared to the West area, and this is consistent with a higher number and dispersion of human habitations in the Central area. The increased use of anthropogenic items across years likely resulted from declining abundance of natural foods due to below average precipitation in the latter 3 years of the study. The frequency of occurrence of anthropogenic items increased from 7.2% and 4.9%, respectively, in the Years 1 and 2 up to 28.7% in Year 5. This trend suggests an increasing reliance on anthropogenic items to sustain coyotes, and could result in higher coyote abundance relative to carrying capacity based on natural foods alone (e.g., Fedriani et al. 2001). Such anthropogenic subsidization could result in increased pressure on remaining natural food items, including desert tortoises (Esque et al. 2010).

EFFECTS OF ITEM USE AND AVAILABILITY ON USE OF TORTOISES

The relatively low frequency of occurrence of desert tortoise remains in coyote scats suggests that tortoises are a secondary prey item. Furthermore, an important caveat is that predation could not be distinguished from scavenging. Desert tortoises can be killed by other species, such as badgers, dogs, kit foxes, ravens, and humans (Berry 1986, Berry 1990, Boarman 1992, Kristan and Boarman 2003, Esque et al. 2010, Riedle et al. 2010). Also, some tortoises die of disease (e.g., upper respiratory tract disease, shell disease) and natural causes such as starvation and dehydration (Berry et al. 2006, Peterson 1994, U.S. Fish and Wildlife Service 2011, Lovich et al. 2014). Starvation and dehydration apparently are not uncommon during periods of drought (Peterson 1994, Longshore et al. 2003, Lovich et al. 2014).

Desert tortoise remains occurred most frequently in scats collected in spring and fall, and lowest occurrence rates were in summer. These results were consistent with seasonal patterns of tortoise activity. Tortoises likely are most vulnerable to predation when they are out of their burrows and moving about seeking food or mates. Tortoises likely are less vulnerable when in their burrows although there are anecdotal reports of predators, possibly coyotes, digging tortoises out of their burrows.

Some spatial and temporal patterns of tortoise use by coyotes were apparent. These included markedly lower occurrence of tortoise in scats collected in the East area compared to the West and Central areas. No information is available on relative tortoise abundance among the areas, and therefore, it is not clear whether the differences in use by coyotes were attributable to differential predation rates or differences in tortoise availability. Likewise, the frequencies of occurrence of tortoise in Years 3-5 were approximately half of what they were in Years 1 and 2. Again, it is unclear whether this is attributable to differential predation rates or simply tortoise availability. Compared to Years 1 and 2, annual precipitation was substantially lower in Years 3-5, and indeed was about half of normal. Desert tortoises are herbivores and reduced primary productivity in years of lower precipitation along with lack of water potentially could result in fewer tortoises due death by starvation or dehydration (Peterson 1994, Longshore et al. 2003, Lovich et al. 2014). Also, even if tortoise abundance does not change substantially during dry years, tortoises may reduce activity in order to conserve energy and water (Duda et al. 1999). Reduced above-ground activity would reduce tortoise vulnerability to predation.

Furthermore, our data did not suggest any obvious relationships between use of tortoises and the use or availability of other food items by coyotes. Elevated predation on tortoises concurrent with declines in leporids and rodents has been reported previously (Woodbury and hardy 1948, Berry 1974, Turner et al. 1984, Peterson 1994), although prey availability on study sites was not quantified. In our study, as use of primary items such as rabbits and rodents declined across years, use of some secondary items (e.g., birds, reptiles, invertebrates, fruit, anthropogenic items) increased, but use of tortoises did not exhibit a similar increase. The lack of data on tortoise abundance in the study area makes it difficult to disentangle the effects of other item availability from tortoise availability with regards to use of tortoises by coyotes.

Another question of interest is differential predation on age classes. The tortoise remains we found in each scat sample have been passed along to a species expert to determine age class. These results will be forwarded then this analysis has been completed.

COYOTE ABUNDANCE AND DISTRIBUTION

Coyote abundance is difficult to measure. The method we used (i.e., field camera stations) only provided a very low resolution index of abundance. Coyotes are widely distributed and generally abundant throughout the Mojave Desert. Numbers likely vary spatially and temporally with food availability and anthropogenic factors (e.g., hunting).

Although we detected some spatial and temporal variation in coyote abundance indices, it is unknown whether these variations in abundance were sufficient to alter predation pressure.

The camera survey data confirmed that coyotes were well distributed across the study area, although the indices were somewhat lower in the East area during the first 2 years of the survey. Scat locations also provided some indications of area use patterns. In particular, scats from the East area were much more abundant in areas in close proximity to human residences. This suggested that coyote may have indeed been concentrating activities around such areas to exploit anthropogenic foods. It is possible that a similar effect may have been occurring in the Central and West areas. However, it was difficult to determine because the human residences in these areas were more dispersed whereas they were more concentrated in the East area. Berry et al. (2006) and Esque et al. (2010) both reported that mortality rates of transmittered desert tortoises were higher near areas that were human-occupied or anthropogenically disturbed (including the presence of trash piles). Concentrated use of such areas by coyotes could be a potential explanation for these rates.

The camera surveys also revealed the presence of other species that potentially prey on desert tortoises. Free-ranging domestic dogs were detected in all areas. Although they generally tended to be near human-occupied areas, sometimes they were detected several kilometers from the nearest residences. Bobcats and badgers also were occasionally detected. Recently, a badger gained entry into a pen with relocated desert tortoises and caused considerable injury and mortality (T. Esque, USGS, personal communication). Coyotes, dogs, badgers, and bobcats all have powerful jaws and determining which of these predators might have killed a given desert tortoise may not be possible in all instances.

Kit foxes were very frequently detected on cameras. Kit foxes likely are too small to seriously harm an adult desert tortoise, but are known predators on hatchlings and tortoise eggs (Bjurlin and Bissonette 2004). Ravens also were commonly detected and are known predators on hatchlings as well (Boarman 1992, Kristan and Boarman 2003).

CONCLUSIONS AND RECOMMENDATIONS

Coyote foraging patterns in the central Mojave Desert exhibited some temporal and spatial variation during the period fall 2009-summer 2014, and generally were consistent with expectations and previous data on coyote food habits. Annual variation in use of items appeared strongly influenced by fluctuations in item availability associated with variation in annual precipitation. Seasonal variation in item use was minor. Rabbits were a primary, and possibly preferred, food item. Heteromyid rodents (e.g., kangaroo rats and pocket mice) also were primary items. Other items appeared to be consumed opportunistically. Anthropogenic items also were readily consumed and reliance on such items may have increased as the abundance of natural items decreased in response to years with below-average annual precipitation. This in conjunction with scat collection locations provided some evidence that the coyote population on the study site is receiving at least some anthropogenic subsidization.

Coyotes in the study area consistently consume desert tortoises, although the frequency of occurrence in scats is low and it is uncertain whether tortoises were predated or scavenged. Use of tortoises in the latter years of the study declined concurrent with declines in use and availability of primary items and also with declines in annual precipitation. This suggested that tortoises may be used opportunistically by coyotes and did not provide evidence that use of tortoises is inversely related to use of primary prey items.

The issue of anthropogenic subsidization is an important one. Predator populations that are maintained at high levels, particularly during declines in primary food items, can result in inordinately high predation pressure on secondary items. This effect potentially could be catastrophic if conjoined with and additive to other population stressors. In the case of desert tortoises, populations may already be stressed by habitat loss and degradation, habitat fragmentation and direct mortality associated with expanding road systems, removal of individuals by humans, and disease. Enhanced predator populations would constitute yet another significant population stressor. Such an effect, resulting in enhanced predation on hatchling tortoises, already has been attributed to subsidized raven populations (Boarman 1992, Kristan and Boarman 2003). The anthropogenic sources that subsidize ravens (Boarman and Berry 1995, Boarman et al. 2006) also very well could subsidize coyotes.

Our data confirm that coyotes are consuming desert tortoises, this occurs at a consistent but low frequency over a large area, and tortoises appear to be a secondary item likely consumed opportunistically by coyotes. However, the implications of this for desert tortoise populations are uncertain. Again, the issue of predation versus scavenging is unresolved, although most tortoise researchers express certainty that at least some consumption of tortoises by coyotes is indeed a result of predation. Another issue is whether at least some coyote predation on tortoises is compensatory in that tortoises may have been in a morbid condition due to URDS. Finally, information on desert tortoise abundance trends or mortality rates from this area was not available. Thus, it was not possible to compare coyote foraging patterns with sympatric desert tortoise demographic trends to identify possible correlations.

Only general recommendations can be drawn from our data. Some of these are likely intuitive even in the absence of our data. However, we offer the following.

1. Coyote control is not prudent

Commonly, a natural response to a "predator problem" is to propose predator control. Control of coyote populations has been attempted on numerous occasions, and except in very limited cases involving small areas and short durations or except when toxicants were copiously dispersed over large regions (Andelt 1987), such control has typically not been successful. Due to the extensive range of desert tortoises, the indefinite duration that control would be need to be conducted, and the ecological damage and as well as illegality of dispersing non-specific toxicants across the landscape, coyote control is not likely to be effective and the cost of any such large-scale effort would be excessive. As one example, coyote control was conducted for 5 years over approximately 300 km^2 to reduce predation on endangered San Joaquin kit foxes (*Vulpes macrotis mutica*), but there was no evidence of a positive benefit to kit foxes (Cypher and Scrivner 1992). As much as 75% of all coyotes may need to be removed to achieve effective population control, and coyote numbers rapidly recover following control cessation through immigration and compensatory reproduction (Connolly and Longhurst 1975). Lethal control programs also tend to be unpopular with the public (Andelt 1987). Thus, we highly recommend against attempting coyote control. One exception might include removing problem coyotes from a focal location, such as an acclimation enclosure or some similar situation. In such situations, USDA Wildlife Services would be a logical entity to perform the removal.

2. Conduct outreach campaigns to reduce anthropogenic subsidization of coyotes

Public outreach efforts could be conducted in areas where people live in or adjacent to desert tortoise habitat. Such campaigns could emphasize appropriate disposal of domestic animal carcasses and trash the protection of live domestic animals and food crops to exclude use by coyotes. Although compliance with such requests in rural settings can be challenging, any reduction in the availability of anthropogenic resources to coyotes and other potential tortoise predators would be helpful, as was also suggested by Esque et al. (2010).

3. Create additional protected areas that include minimal or no human habitations

Desert tortoises have evolved in the presence of predation pressure from coyotes, and healthy populations in more natural landscapes likely can withstand such predation pressure without significant effects. Although some large preserves do exist, additional such preserves will benefit tortoise conservation. A key attribute of such preserves is a minimal or no human habitations that might provide supplemental foods for coyotes or ravens. This should result in more natural ecological processes and help avoid anthropogenically-induced population stressors on tortoises. Esque et al. (2010) reported that predation rates on desert tortoises were lower on sites more distant from coyote subsidization sources.

4. Conduct additional investigations to better quantify desert tortoise mortality attributable to coyotes

Additional investigations may be warranted to better quantify desert tortoise mortality attributable to coyotes, and causal factors associated with this mortality. Information of particular value would include: predation versus scavenging by coyotes; predation attributable to other predators; predation relative to tortoise health and age status; predation rates by coyotes relative to tortoise population density; predation rates relative to environmental attributes such as primary productivity and relative abundance of coyote prey species; and coyote predation rates relative to anthropogenic factors such as human habitations, habitat alteration or degradation, etc. Some of the data necessary to address these questions may already exist and could be assessed through retrospective analyses.

5. Conduct additional investigations of anthropogenic effects on predator abundance and distribution

Clearly, anthropogenic influences in the Mojave Desert affect species dispersion patterns and cause paucity or extirpation in some situations and enhanced abundance and area use in others. These perturbations have concomitant effects on the ecosystem. A better understanding of the effects of anthropogenic influences on the distribution and abundance of coyotes and other species that could adversely affect desert tortoises would provide information necessary to develop strategies to mitigate these impacts. Analyses of these effects should be conducted at landscape-level as well as local scales.

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APPENDIX A

List of items found in coyote scats in the Desert Tortoise Translocation Area, San Bernardino County, California, during fall 2009 – summer 2014.

Common name	Scientific name
Rabbit	*Lepus californicus* and *Sylvilagus audubonii*
Kangaroo rat	*Dipodomys spp.*
Pocket mouse	*Perognathus spp.* and *Chaetodipus spp.*
Deer mouse	*Peromyscus maniculatus*
House mouse	*Mus musculus*
Woodrat	*Neotoma lepida*
Gopher	*Thomomys bottae*
Squirrel	*Spermophilus tereticaudus, Spermophilus mohavensis,* and *Ammospermophilus leucurus*
Domestic dog	*Canis familiaris*
Domestic cat	*Felis cattus*
Goat	*Capra hircus*
Sheep	*Ovis aries*
Bird	Class Aves
Snake	Order Squamata
Lizard	Order Squamata
Desert tortoise	*Gopherus agassizii*
Grasshopper	Order Orthoptera
Beetle	Order Coleoptera
Caterpillar	Order Lepidoptera
Jerusalem cricket	Order Orthoptera
Ant	Order Hymenoptera
Earwig	Order Dermaptera
Scorpion	Order Scorpiones
Screwbean mesquite	*Prosopsis pubescens*
Mesquite	*Prosopis* spp.
Boxthorn	*Lycium* spp.
Cucurbit seed	Family Cucurbitaceae
Rose hips	*Rosa* spp.
Melon seeds	Family Cucurbitaceae
Walnut	*Juglans* spp.
Pistachio	*Pistacia vera*
Olive	*Elaeagnus angustifolia* and *Olea* spp.
Cherry	*Prunus* spp.
Pumpkin	*Helianthus annuus*
Almond	*Prunus dulcis*
Corn	*Zea mays*
Sunflower seed	*Helianthus annuus*
Beans	*Phaseolus vulgaris*
Date palm spp.	*Phoenix dactylifera*