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Do Coyotes Eat Mesocarnivores in Southern California? A Molecular Genetic Analysis

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ABSTRACT: Urban coyotes are commonly exposed to rodenticides used to control non-native commensal rodents, but these rodents are rare in published accounts of their diets. An alternative source of rodenticide exposure is through the consumption of mesocarnivores that have themselves eaten either toxic bait directly or poisoned rodents or invertebrates. Carcasses of 311 nuisance and road-killed coyotes from suburban and urban areas of southern California were collected from 2016-2018. Stomachs were dissected and prey items were identified visually. Stomach contents containing tissue from suspected mammalian prey (N = 178) were homogenized and DNA was extracted. Genus-specific primers (123-366 bp) were designed for Virginia opossums, raccoons, and striped skunks, regionally common species that are known to be consumed by coyotes. PCR was performed for each primer pair, and presence of PCR products of particular amplicon lengths were determined by gel electrophoresis. Coyote stomachs containing a PCR product of the appropriate size were considered to contain that prey item. Land use data were used to assess landscape factors that are associated with the consumption of mesocarnivores. Combining both techniques, mesocarnivores were detected at low frequencies: opossums (8%) were more common than raccoons (2%) and skunks (2%). Some 72% of meso-carnivores present in stomachs were detected by molecular methods, while 66% were identified by morphological methods. Opossums were associated with increased development and anthropogenic land use, while skunks were associated with large natural areas, and raccoons used all habitat types. The extent to which mesocarnivores themselves eat poisoned prey remains unknown, although they may be a potential source of exposure for coyotes. Additionally, landscape factors do not appear to be related to raccoon consumption but may influence presence, and therefore consumption, of skunks and opossums.

KEY WORDS: *Canis latrans*, coyote, *Didelphis virginiana*, *Mephitis mephitis*, mesocarnivores, molecular genetics, opossum, *Procyon lotor*, raccoon, rodenticide, striped skunk, urban carnivores

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INTRODUCTION

The coyote (*Canis latrans*) is a common urban dweller in southern California and across North America that has adapted well to life among people (Morey et al. 2007). Unhabituated coyotes often attempt to avoid contact with people, shifting from their natural crepuscular state to nocturnal behavior in more developed areas (Grinder and Krausman 2001, Timm et al. 2004). Urban coyotes tend to have smaller home ranges (Quinn 1997) and higher densities (Fedriani et al. 2001) than their rural counterparts, perhaps as a result of abundant food and fragmented habitat. However, as coyotes become more habituated to the presence of humans, they may become increasingly bold, approaching people and their pets during daylight hours (Baker 2007). Urban-adapted coyotes tend to show more exploratory behaviors than rural counterparts, potentially making them more likely to approach and interact with human-created objects, though individual responses vary (Breck et al. 2019).

Coyotes are opportunistic omnivores (Bowyer et al. 1983). Urban coyotes typically consume rodents, rabbits, and road-killed ungulates (Bekoff and Wells 1981, Morey et al. 2007, Garwood et al. 2015, Larson et al. 2015, Poessel et al. 2017). Plant parts (Cunningham et al. 2006) can also make up large portions of their diet. The diet of urban coyotes is more diverse than those from rural areas (Morey et al. 2007). In southern California, coyotes eat mainly native rodents and rabbits (Fedriani et al. 2001, Larson et al. 2015). Coyotes occasionally consume cats and other anthropogenic foods in urban areas (MacCracken 1982). However, there is little evidence that coyotes eat significant numbers of commensal rodents, the mice (*Mus musculus*) and rats (*Rattus* spp.) that are associated with disturbed urban and suburban landscapes (Larson et al. 2015) and are commonly targeted for extermination using anticoagulant rodenticides (Cypher et al. 2014). Nevertheless, urban coyotes are exposed to rodenticides (Poessel et al. 2015) and have a higher rate of mortality from rodenticides than coyotes found in natural areas (Riley et al. 2003). Tertiary exposure via consumption of wild mesocarnivores that have eaten poisoned prey, such as raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), and skunks (*Mephitis mephitis*), is one possible route of exposure of urban coyotes. Consumption of mesocarnivores by coyotes may have important top-down effects on native prey populations in southern California (Crooks and Soulé 1999).

In urban environments, opossums are associated with high-density housing and streams (Klinkowski-Clark et al. 2010) and native California plant communities (Crooks 2002). Raccoon presence is often positively correlated with developed land, including commercial and industrial development and streams in these areas (Broadfoot et al. 2001, Klinkowski-Clark et al. 2010). They tend to have the most extensive home range of the three mesocarnivores (Crooks 2002) but occur at higher densities than their rural counterparts (Gehrt 2012). Skunks tend to be less common in urban areas than raccoons and opossums and are often associated with anthropogenic open spaces or low-density development or habitat fragments (Crooks 2002, Klinkowski-Clark et al. 2010), rarely in industrial zones (Broadfoot et al. 2001). Skunks tend to achieve similar population densities in urban and rural areas, suggesting that they cannot take advantage of anthropogenic resources (Gehrt 2012).

We used a combination of visual morphological methods and molecular genetic methods (polymerase chain reaction, PCR) to determine consumption of wild mesocarnivores by coyotes in southern California. Most diet studies of carnivores, including coyotes, are based on visual analyses of scat contents. These methods, however, may not accurately describe diet (Newsome et al. 2015). Scats may be incorrectly identified if multiple carnivore species are present (Morin et al. 2016), and visual analysis can be difficult, time-consuming, and can miss highly digestible items (Zarzoso-Lacoste et al. 2016). In a direct comparison, molecular genetics methods detected more prey items than traditional morphological methods (Mumma et al. 2016). Molecular methods can yield precise measurements of carnivore diet, identifying more prey items per predator and achieving greater taxonomic resolution than morphological studies (Zarzoso-Lacoste et al. 2016).

Based on Crooks and Soulé (1999), we hypothesized that urban coyotes in southern California will consume wild mesocarnivores and represent a potential route of secondary exposure to rodenticides in the absence of significant evidence of consumption of commensal rodents. We also hypothesized that consumption of different species of mesocarnivores by coyotes will reflect the different habitat associations of these species in urban and suburban southern California.

METHODS

Study Site

A total of 311 coyote carcasses were obtained from urban areas of Los Angeles and Orange Counties in southern California. Of these, 200 were nuisance coyotes removed by agency or private trappers, 100 were road-killed individuals, and 11 were of unknown origin. Stomachs were obtained from carcasses necropsied at the University of California South Coast Research and Extension Center in Irvine, CA. Most stomachs (245) contained some sort of identifiable food item; stomachs that were empty or contained small amounts of wood or unidentifiable items were not included in our analysis.

Visual Morphological Analysis

The contents of each coyote stomach were rinsed thoroughly with deionized water. Contents were identified visually to the highest taxonomic level achievable using keys and reference sample; in some cases, mammals were identified using microscopic examination of hair. Following dissection, stomach contents were placed in 95% ethanol in a sealed Whirl-pak® (Whirl-pak, Madison, WI).

Morphological analysis of stomach contents identified 178 coyotes as having likely consumed mammals and containing enough mammalian tissue (approximately 0.5 ml) for DNA extraction (22 of the 200 stomachs contained mammalian hair or bone fragments only and were not tested). Stomach contents of the 178 coyotes were homogenized in an industrial blender in 95% ethanol following removal of bones, hair, and hard plant matter. Following homogenization, six 1.25-mL samples of homogenate were taken, dried at room temperature for 72 hours to remove all ethanol, and further homogenized by chopping with a razor blade. DNA was extracted from two 5-10 mg samples per stomach using the Qiagen DNEasy Blood and Tissue Kit (Qiagen, Germantown, MD). The number of samples per coyote was determined using a species accumulation curve produced by taking five samples from each of five coyotes known to have consumed three or more mammals. For samples with too little tissue to homogenize (<0.5 mL), a sample was taken from each piece of tissue and air-dried for 30-45 minutes before extraction. The equipment used for homogenization and extraction was cleaned in 10% bleach for 10 minutes and then rinsed thoroughly with deionized water between samples.

Molecular Analysis

PCR Primer Design

Although present in southern California, bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), and spotted skunks (*Spilogale gracilis*) are reportedly uncommon in the diet of coyotes and thus were not screened for. Using GenBank, sequences of the cytochrome oxidase b (cytb) and cytochrome oxidase subunit I (COI) genes were obtained for genera likely to be in the diets of coyotes. Based on the alignments, primers for *Procyon* (113 bp) and *Mephitis* (176 bp) were constructed from the cytb alignment and COI was used for *Didelphis* (366 bp). Sequences were aligned in GENEIOUS vR11 (Kearse et al. 2012). A consensus sequence was created for each genus, and consensus sequences for each gene were aligned. Primers were designed such that each genus differed from other genera in the same region by 18-24 base pairs. PCR primers were tested with tissue samples obtained from frozen specimens of target genera. Each primer was tested against all other possible prey items in the study, as well as coyote DNA, to ensure a lack of non-specific binding that would result in false positives. *Mephitis* and *Didelphis* samples were obtained from Orange County Vector Control; *Procyon* samples were obtained from the California Department of Fish and Wildlife and salvaged tissue donated to California State University, Fullerton.

PCR was performed at a sample volume of 25 μL. Samples were tested against one genus-specific primer set at a time, as multiplexing proved ineffective. Each PCR batch contained a positive control, a negative control, and 16 samples of coyote stomach content DNA. PCR was performed using 18.4-19.9 μL water, 2.5 μL 10× buffer, 0.5 μL (*Didelphis*) or 1 μL (*Mephitis*, *Procyon*) 50 mM $MgCl_2$, 0.5 μL dNTPs, 0.5 μL each of forward and reverse primers, and 0.1-0.25 μL TAC polymerase per 1.0 μL DNA.

PCR conditions consisted of an initial denaturation at 95°C for 4 min, followed by 31 cycles at 95°C for 30 sec, genus-specific annealing temperature (52°C *Didelphis*, 53°C *Procyon*, 55°C *Mephitis*) for 30 sec, and 72°C for 1 min. Results were visualized by gel electrophoresis on a 2% agarose gel. Band locations were compared to a standardized DNA fragment length ladder and the positive control. Each lane served as a presence/absence test: if a correctly sized band, as compared to the ladder and positive control, was visualized, the targeted genera was assumed to be in the coyote's diet. Results from molecular analysis were compared to those from morphological analysis.

GIS Analysis

The address, nearest cross streets, or mileage markers of each coyote carcass location were recorded and converted to GPS locations, which were mapped in ARCMAP 10.6.1 (ESRI 2018). Land use data were obtained from the NCLD 2011 survey (MRLC 2011). Past urban and suburban coyote home range studies (Shargo 1988, Grinder and Krausman 2001, Tigas et al. 2002, Riley et al. 2003, Grubbs and Krausman 2009, Poessel et al. 2016) were used to estimate average home range size estimate of coyotes. Coyotes in urban areas had an average home range size of 8.47 km^2, whereas ones in urban southern California had an average home range size of 3.55 km^2. To account for an apparent smaller home range size in southern California but potential inexact carcass locations, a circular buffer with a radius of 1.5 km and a total area of 7 km^2 was created around each coyote location. If a home range contained water or beachfront, only the land area was included. The area of each land use type was tabulated inside the buffer and calculated as a percentage of total land area inside the buffer. The percentage land cover variables examined were as follows: open space, low-density development, mid-density development, high-density development, grassland, and shrub/scrub.

Distance to the nearest natural area was also measured for each coyote. Natural area was defined as any land containing wild-growing vegetation with an area of greater than 2 ha, typically nature reserves or other undeveloped lands. The distance from the coyote's location to the nearest natural area was measured in ARCMAP 10.6.1 (ESRI 2018), using the GAP/LANDFIRE Natural Terrestrial Ecosystems data to locate and measure the size of natural areas and the satellite imagery basemap to confirm vegetation cover type as needed. Housing density was determined using building footprints from the Los Angeles and Orange County data portals. Confidence intervals (95%) were created to compare the differences between these variables among coyotes that consumed prey of each genus.

RESULTS

Based on both visual morphological analysis and PCR, opossums were the most common mesocarnivore consumed (N = 19; 7.8% of 245 stomachs), followed by raccoons (N = 7; 2.9%) and skunks (N = 4, 1.6%; Figure 1). Of the 30 mesocarnivores detected in the stomachs, most were detected by PCR alone (N=14) or by both PCR and morphological methods (N = 7; Figure 1). Three opossums were detected visually in stomachs that not analyzed using PCR. The age or sex of a coyote did not seem to affect the likelihood that it consumed a meso-carnivore; proportions of male, female, juvenile, and adult coyotes were roughly equivalent among mesocarnivore-eaters and the overall population of coyotes examined.

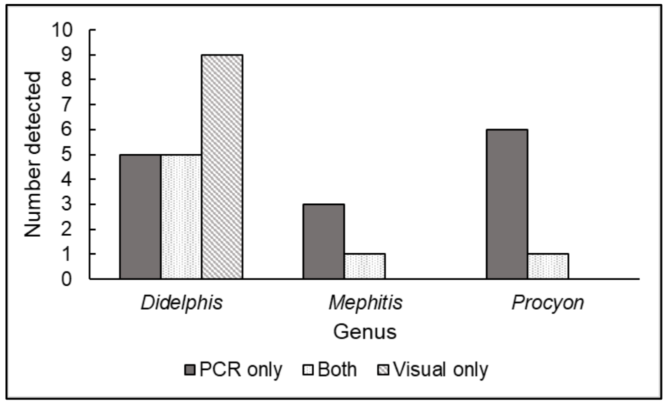

Figure 1. Number of wild mesocarnivores detected in coyote stomachs by visual morphological compared to PCR molecular methods.

Landscape factors were related to the consumption of different mesocarnivore species, though not consistently. Distance to natural area was greater for coyotes that consumed opossums (Table 1), though only significantly different from skunk-eating coyotes, with raccoon-eating coyotes found at an intermediate distance. Coyotes that ate raccoons or skunks were found further from natural areas than the average coyote in the sample. All four skunks were consumed by coyotes found within 0.2 km of a natural area. Of land cover variables, only high-density housing differed between coyotes eating different meso-predators, again with opossum-eaters in the most urbanized areas (Table 1). Grassland cover was significantly lower for the locations of opossum-eating coyotes than coyotes that consumed either other species (Table 1).

DISCUSSION

Both methods of diet analysis revealed the presence of all three species in the diet overall but the relative frequencies of occurrence of each species differed markedly. Opossums tended to be detected more often using traditional morphological analysis, which included identification of remains based on hair alone. In contrast, all but one of the raccoons and skunks were detected by PCR only; the one raccoon and skunk detected using visual analysis was also confirmed with PCR. These results underscore the value of using both methods together to provide the most complete representation of the diet of a generalist omnivore like a coyote.

Overall, the rate of consumption of mesocarnivores in our study (2-8%, depending on species; 12.2% overall) was relatively low, but higher than that in other studies of coyote diet in urban and suburban southern California. In northwestern Los Angeles, Larson et al. (2020) found identifiable remains of these mesocarnivores in only 2.4% (N = 74) of 3,147 coyote scats, with raccoons and skunks (1%) each more than twice as common as opossums (0.4%); these results are qualitatively similar to those reported by Fedriani et al. (2001) and Shargo (1988) in the

Table 1. Means and 95% confidence limits of landscape variables within 7-km^2 buffers around carcass collection locations of coyotes that consumed wild mesocarnivores, and for all coyotes with identifiable meals.

Genus Consumed (N)	Dist. to Natural Area (km)	Open Space (%)	Low-density Develop-ment (%)	Mid-density Develop-ment (%)	High-density Develop-ment (%)	Shrub/ scrub (%)	Grass-land (%)	Building Density (units/km^2)
Opossum (19)								
Mean	0.61	14.40	23.81	41.19	13.93	2.91	1.97	710.0
95% upper limit	0.91	19.38	28.56	48.72	20.37	5.30	2.90	871.2
95% lower limit	0.31	9.42	19.05	33.65	7.50	0.52	1.04	552.7
Skunks (4)								
Mean	0.18	21.70	24.78	22.65	3.65	15.13	9.98	349.3
95% upper limit	0.05	31.22	31.72	37.03	7.81	32.45	14.15	579.8
95% lower limit	0.22	12.18	17.83	8.27	-0.51	-2.20	5.80	118.7
Racoons (7)								
Mean	0.14	28.81	24.14	21.96	3.34	10.70	6.06	372.6
95% upper limit	0.30	39.03	30.34	35.98	6.28	19.18	9.98	570.2
95% lower limit	-0.02	18.60	17.94	7.94	0.40	2.22	2.14	174.9
All coyotes (245)								
Mean	0.44	19.26	22.36	33.45	9.44	8.29	4.53	523.2
95% upper limit	0.53	20.80	23.48	35.89	10.86	9.86	9.86	568.0
95% lower limit	0.34	17.71	21.24	31.02	8.01	6.72	3.98	478.3

same general area. Mesocarnivores were more common in coyote scats in San Diego (8.4% of 119 scats; Larson et al. 2015), with the three species similarly represented (2.1-2.4% of scats). Raccoons tended to make up a higher percentage of diet of urban coyotes elsewhere (~8%; Morey et al. 2007, Poessel et al. 2017). The frequency of opossums in diet of coyotes in our study area likely reflects the suburban landscape that characterized most our study area, where opossums are very common and skunks are not (Klinkowski-Clark et al. 2010, Broadfoot et al. 2001).

Because the number of coyotes eating mesocarnivores was relatively small (N = 28), it is difficult to make solid generalizations about the landscape characteristics associated with the consumption of carnivores. Moreover, we recognize the possibility that coyotes categorized as not eating mesocarnivores may regularly consume them but not just during their final meal. Likewise, mesocarnivore-eating coyotes may not regularly consume these prey except on the occasion before they died. These caveats aside, some patterns did emerge from our analysis of landscape factors around carcass locations. For example, coyotes that ate opossums tended to be found in areas with high-density development and low grassland cover, and farther from natural areas, which matches the known urban habits of opossums. The four coyotes that ate skunks were all close to natural areas, which was much closer to natural areas than the mean for all coyotes combined (Table 1).

Lastly, although mesocarnivores are known to be exposed to rodenticide (Bautista et al. 2014), their relative scarcity in the diet of coyotes (<12%) suggests that secondary or tertiary exposure through the consumption of wild mesocarnivores probably cannot account for the recorded widespread exposure of coyotes to rodenticides (Moriarty et al. 2012). In southern California, coyotes may be more likely to ingest rodenticides by consuming small native or commensal rodents or rabbits, their typical prey, or possibly, by eating domestic cats, which can be more common in the diet of coyotes (Larson et al. 2020) and may be exposed secondarily.

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