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Do trap-neuter-return (TNR) practices contribute to human–coyote conflicts in southern California?

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Abstract: One possible contributor to the unusually high number of conflicts between coyotes (*Canis latrans*) and people in urban southern California, USA, may be the abundance of free-roaming domestic cats (*Felis catus*; cats) subsidized by feeding and augmented by trap-neuter-return (TNR) programs. To determine if coyotes regularly prey on and consume cats, we combined visual and molecular-genetic approaches to identify prey items in stomachs of 311 coyotes from Los Angeles County and Orange County, provided to the South Coast Research and Extension Center, in Irvine, California, between June 2015 and December 2018. We detected cat remains in 35% of the stomachs of 245 coyotes with identifiable meals, making cats the most common mammalian prey item consumed and more common than reported previously. Using a geographic information systems approach, we then compared landscape characteristics associated with locations of coyotes that ate cats to public shelter records for TNR cat colonies. Cat-eating coyotes were associated with areas that were more intensively developed, had little natural or altered open space, and had higher building densities than coyotes that did not eat cats. Locations of TNR colonies had similar landscape characteristics. Coyotes associated with TNR colonies, and those that were euthanized (vs. road-killed), were also more likely to have consumed cats. The high frequency of cat remains in coyote diets and landscape characteristics associated with TNR colonies and cat-eating coyotes support the argument that high cat densities and associated supplemental feeding attracted coyotes. Effective mitigation of human–coyote conflicts may require prohibitions on outdoor feeding of free-roaming cats and wildlife and the elimination of TNR colonies.

Key words: California, *Canis latrans*, *Felis catus*, free-roaming cats, human–wildlife conflict, subsidized feeding, trap-neuter-return, TNR, urban coyotes

There are an estimated 95.6 million owned (American Pet Products Association 2014) and 30–80 million free-roaming cats (*Felis catus*; cats) in the United States (Levy and Crawford 2004, Loss et al. 2013). Free-roaming cats are defined as owned cats that are not confined in a yard or house, as well as unowned cats such as feral, stray, and abandoned cats (Jessup 2004, Levy and Crawford 2004).

Cats have been documented as effective predators of small vertebrates (Fitzgerald and Turner 2000, Dueñas et al. 2021). Where introduced onto islands, feral cats have caused the extinction of several native species (Nogales et al. 2013, Doherty et al. 2016). Cats are also considered a significant threat to wildlife populations in mainland settings (Clarke and Pacin 2002, Loss et al. 2013).

High densities of cats also spread diseases to wildlife, pets, and humans, especially when cats lack routine veterinary care (Gerhold and Jessup 2013, Thomas et al. 2016, Montoya et al. 2018). For example, prevalence of feline immunodeficiency virus is 3 times higher in feral cat populations than in pet populations (Norris et al. 2007), and aggression between cats can increase the likelihood of exposure and transmission of parasites and pathogens (Schmidt et al. 2009, Torrey

Figure 1. Feeding stations for free-roaming cats (*Felis catus*) provided by volunteer caretakers in Orange County, California, USA (*photos courtesy of D. Bucklin*).

Figure 2. Coyote (*Canis latrans*) carrying a domestic cat (*Felis catus*) through a road underpass in the eastern Los Angeles basin (western San Bernardino County), California, USA (*photo courtesy of K. Crooks, Colorado State University and U.S. Geological Survey*).

and Yolken 2013, Cummings et al. 2016).

Although the negative environmental, nuisance, and public health impacts of free-roaming cats are well established, cat advocates have influenced laws and regulations regarding cat management and have increasingly gained support from other nonprofit organizations and advocates for "no-kill" shelters (Longcore et al. 2009). Trap-neuter-return (TNR) programs attempt to manage free-roaming cat populations by capturing, sterilizing, vaccinating, and then re-releasing cats, usually at or near the capture location (Levy and Crawford 2004). Cats may also continue to be provided with food and water (Figure 1), which can lead to the establishment of large numbers of cats (colonies) at some locations.

The underlying goal of most TNR programs is to reduce the number of unowned cats via eventual attrition through natural mortality (Levy and Crawford 2004, Slater 2007). But cats remaining in the environment can continue to prey on wildlife and constitute a public nuisance and health risk. Feeding colonies attract unsterilized cats and encourage the dumping of others, and the health and well-being of the cats themselves has been questioned (Crawford et al. 2019). The level of sterilization and adoption effort required to eliminate or meaningfully reduce the size of a cat colony may be unsustainable except under the most controlled conditions. For example, for TNR to successfully control a free-roaming cat population, it has been estimated that at least 75% of the colony must be sterilized (Andersen et. al 2004). Immigration, including cat abandonment, can hinder the success or slow the rate of population decline in TNR colonies (Foley et al. 2005, Robertson 2008, Schmidt et al. 2009, Swarbrick and Rand 2018).

Despite the paucity of evidence of the long-term effectiveness of TNR programs, some local governments have promoted or tacitly adopted these practices (Holtz 2013), including municipalities in southern California, USA (Cummings et al. 2016). One aspect of the application of TNR that has not been sufficiently explored is the potential effects of cat colonies as a source of prey for local wildlife populations. For instance, coyotes (*Canis latrans*) are among the most successful carnivores in cities because of their generalized diet and high tolerance of humans (Bekoff 1977, Gehrt et al. 2011).

Urban coyotes are subsidized by anthropogenic resources and have been reported to kill and eat pets (Figure 2). Diet studies elsewhere suggest that cats are not common prey (Quinn 1997, Morey et al. 2007, Murray et al. 2015, Poessel et al. 2017*b*). However, if coyotes increasingly perceive cats as food and are attracted to TNR colonies, this may explain high encounter rates reported between people and coyotes in southern California, which often result in the death of pets and injuries to people (Baker and Timm 2017).

We examined the potential relationship between coyotes and TNR colonies by first determining the extent to which southern California coyotes feed on cats. We combined visual analysis of stomach contents with a molecular-genetics approach (polymerase chain reaction [PCR], followed by gel electrophoresis), which allowed us to identify prey remains at a fine taxonomic resolution and in degraded samples (Zarzoso-Lacoste et al. 2016). We then used these results to determine if consumption of cats by coyotes could be related to the presence of free-roaming cats associated with TNR colonies. We used a geographic information systems (GIS) approach to compare the landscape characteristics around locations of coyotes that ate cats with those associated with locations of known TNR colonies in Los Angeles and Orange County, California. We predicted that if coyotes that ate cats tended to occur in the same types of areas where TNR colonies were routinely established, this would provide evidence that colonies may attract coyotes.

Study area

The Los Angeles-Long Beach-Anaheim California Metropolitan Statistical Area has a human population of nearly 13 million, making it the second most populous metropolitan region in the United States (2021 data; U.S. Census Bureau 2022). The area (12,561 km^2) consists of the Los Angeles basin, the foothills of the surrounding mountain ranges, and the eastern Mojave Desert. The climate is semi-arid, with hot, dry summers and mild, wet winters, and a strong maritime influence. The native vegetation consists of coastal sage scrub, chaparral, oak woodlands, and desert scrubland, with pine-oak forests at higher elevations (Avolio et al. 2020). However, most low-lying areas have been developed for human uses and are covered by buildings, transportation, water, and energy infrastructure, and other impervious surfaces. Native plant communities have been replaced by cultivated and irrigated landscapes and are dominated by exotic and invasive species, although areas of natural open space remain adjacent to large tracts of public lands and as small fragments interspersed among development (Pataki et al. 2016). These wildland/urban interfaces provide habitat for a wide range of introduced and native wildlife species, which vary in their tolerance for anthropogenic disturbance (Crooks and Soulé 1999, Tigas et al. 2002).

Methods

To complete this study, we examined carcasses of 311 coyotes collected between June 2015 and December 2018 (Figure 3) and delivered to the South Coast Research and Extension Center, in Irvine, California. Coyotes had either been euthanized as nuisance animals by public agencies or private pest control operators, or they were collected as roadkill (e.g., a few carcasses for which the cause of death was not reported were combined with roadkills). Carcasses were collected opportunistically (i.e., in all cases, coyote mortality was completely outside of our control). Carcasses collected between May and October in a given year were considered to represent the "dry" season, whereas those collected between November and April were considered "wet" season samples, based on the timing of most precipitation in the region.

Diet determination

Most diet studies of coyotes have examined scat contents, which may underestimate consumption of highly digestible food items and cryptic prey (Reynolds and Aebischer 1991, Pires et al. 2011) and overemphasize the diet of particular individuals whose scats are readily collected. Moreover, in areas where multiple canid species occur, including domestic dogs (*C. familiaris*), it also may be difficult to identify scats correctly (Morin et al. 2016). Thus, we used a combination of traditional visual and molecular-genetic methods (e.g., PCR to investigate consumption of cats by coyotes (Bucklin 2021).

In brief, visual analysis involved the removal and dissection of stomach contents, followed by identification of prey remains by hand and using a dissecting microscope, with the aid of

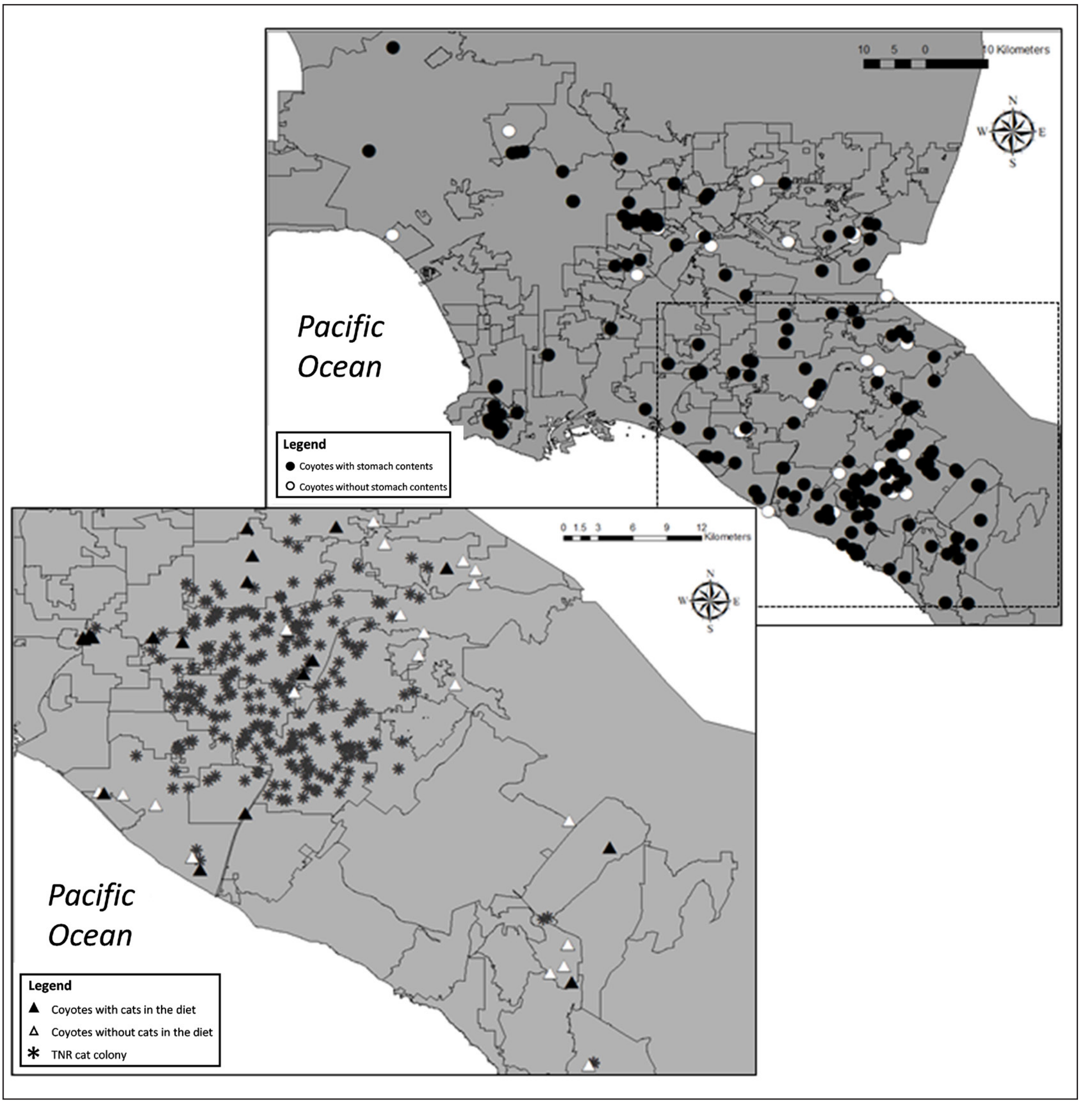

Figure 3. Map showing locations of 311 coyote (*Canis latrans*) carcasses that were collected in Los Angeles and Orange Counties, southern California, USA, between 2015 and 2018. Filled circles show locations of coyotes with identifiable meals (n = 245). Inset (area bounded by dashed lines): locations of coyote carcasses in Orange County cities and neighboring areas where Orange County Animal Care (OCAC) was contracted to perform animal services. Filled triangles show locations of coyotes that ate cats (*Felis catus*); empty triangles show those that did not. Asterisks show trap-neuter-return (TNR) cat colonies (i.e., locations where 5 or more cats were released in a given year between 2015 and 2018). Source: ArcGIS 10.7.1.

a reference collection and keys (Martin et al. 2001, Broughton and Miller 2016). We used a compound microscope to identify mammal hair based on morphological traits, using reference slides and keys (Mayer 1952, Moore et al. 1974, Debelica and Thies 2009). The remaining contents were then rinsed with 95% ethanol, placed in Whirl-Paks® (Nasco Sampling, Madison, Wisconsin, USA) containing 95% ethanol, and then stored at -20°C. All the sample processing and visual identification was completed by the same researcher to reduce inter-observer bias.

For PCR analysis, stomach contents were removed from the freezer, rinsed in distilled water, and homogenized in an industrial blender. Large chunks of tissue were dissected manually and then blended and included in the homogenate. Six portions of approximately 1.25 mL were taken from the contents of each stomach and dried on filter paper at room temperature for 72 hours to remove ethanol. These were then finely diced and mixed, and then 2 sub-samples of 5–10 mg of the mixture were placed into separate 1.7-mL centrifuge tubes. We extracted DNA from each sub-sample using a Qiagen DNEasy™ Blood and Tissue Kit (Qiagen, Germantown, Maryland, USA). We constructed a primer sequence (96 base pairs) of the cytochrome oxidase subunit I gene that targeted the genus *Felis* using GenBank. The primer was tested against frozen cat tissue samples to ensure that it amplified cat DNA and against frozen tissue samples of coyotes and other likely prey genera to ensure that it would not bind to DNA of other mammalian prey. The PCR was performed on sample volumes of 25 µL. Each PCR batch contained a positive control, a negative control, and ~16 stomach content samples.

We visualized the results by gel electrophoresis on a 2% agarose gel within 24 hours. We compared band locations to a standardized DNA fragment length ladder and to the positive control for *Felis*. Each lane served as a presence/absence test: if a correctly sized band was present in either of the 2 sub-samples, we concluded that the coyote had eaten at least 1 cat. One of the authors (J. M. Shedden) did all the PCR and gel electrophoresis to reduce interobserver bias.

Landscape characteristics around locations of coyotes and TNR colonies

We plotted all spatial data in the North American Datum 1983 coordinate system in ArcMap 10.7.1 (ESRI 2019). We entered coyote carcass collection locations into a GIS layer based on geographic positioning system coordinates at the carcass location or the nearest cross streets. Within ArcMap, we placed a 7-km^2 buffer around each carcass location, an area intended to represent the approximate home range of a coyote in a highly urbanized city (Shargo 1988, Grinder and Krausman 2001, Tigas et al. 2002, Riley et al. 2003, Grubbs and Krausman 2009, Poessel et al. 2017*a*), with the caveat that this required us to assume that the animal was killed at the center of its range.

We obtained information on cat release sites between 2015 and 2018 through a public records request to Orange County Animal Care (OCAC) Services. Records were provided as fixed-image digital files (PDFs) of scanned, word-processed documents, which had to then be re-entered by hand into a spreadsheet. We conservatively defined a cat colony as a location where 5 or more cats were released at a single location within a single year; Levy and Crawford (2014) defined a colony as 4 or more cats. Colony locations were entered into a GIS layer, and we created buffers of 1.8 km^2 around each location to approximate the average home range size of a free-roaming cat (Guttilla and Stapp 2010, Horn et al. 2011).

To determine if TNR locations differed from areas where there were no colonies, we generated 90 random locations in cities in Orange County where OCAC was contracted to provide TNR services. We considered these generated points to be non-TNR colony locations because there were no OCAC records of sterilized cat releases at these locations. We placed buffers of 1.8 km^2 around non-colony locations for spatial analyses.

We compared landscape characteristics within buffers around locations of coyotes with cat remains in their stomachs to those of coyotes that had not eaten cats. We also compared habitat characteristics within buffers around known OCAC colony locations and non-colony locations. We harvested data on 8 spatial landscape variables from public databases. Land cover type was estimated from a 30-m raster layer obtained from the National Land Cover Database 2011. We focused on 6 major land cover types that were present in our study area, expressed as a percentage of a given area, that reflected gradients in urbanization: non-natural developed open space (e.g., lawns, parks); low-, medium-, and high-intensity development; shrub or scrub cover; and grassland or herbaceous cover. Building density was calculated from the building footprints in parcel data maps from Orange and Los Angeles counties. Lastly, distance to the nearest natural area ≥2 ha in area was estimated from the 30-m raster layer downloaded from the U.S. Geological Survey GAP/LANDFIRE National Terrestrial Ecosystems 2011 database, which provides thematically detailed estimates of vegetation cover.

We completed data statistical analyses in R studio version 4.0.0. We used Mann-Whitney *U*-tests to identify significant differences in land variables between coyotes with cats in their stomachs compared to those without, as well as for known OCAC TNR cat colonies and locations without known cat colonies.

We used principal components analysis (PCA) to reduce dimensionality and eliminate multi-collinearity among landscape variables (Singh et al. 2008). Although the same 8 variables were included, separate PCAs were performed to examine differences among coyotes and among colony and non-colony locations. We used squared-cosine analysis (cos2) to visualize the strength of the relationship between a given variable and the major PCA axes. Separate logistic regressions were then fitted to predict the probability of whether a coyote ate a cat (Miller et al. 2013), based on its scores on the major PCA axes, and to predict whether a given location had a TNR cat colony. We assessed the reliability of the predictions by examining residual deviance values.

Results

Of the 311 coyote stomachs examined, 245 had identifiable contents, 200 contained mammal remains, and 178 had sufficient tissue for PCR analysis. A detailed description of the diet of the coyotes in our study is provided in Bucklin (2021). Based on frequency of occurrence (*n* = 245 stomachs), coyotes commonly ate rodents (49%), rabbits (*Sylvilagus* spp.; 29%), fruits and seeds (34%), and anthropogenic foods (33%). However, domestic cats were the single most common genus of mammalian prey we detected, with cat remains found in 35% (86) of stomachs. The frequency of cat consumption did not differ between dry and wet seasons (χ^2 = 0.15, *P* = 0.696). Most (67%; 165) of the 245 coyotes had been euthanized rather than roadkills; 39% (64) of the euthanized coyotes had eaten cats, compared to 26% (22) of roadkills (χ^2 = 4.09, *P* = 0.043).

Over the 4-year period covered by the public records request, OCAC released 5,956 cats, across a mean of 721 different release locations per year (SD = 75, range = 630–814). Colony size ranged from 5–26 cats ($\bar{x}$ = 7.2 cats, SD = 3.0, *n* = 251). Focusing just on OCAC-contracted cities and adjacent areas in Orange County, 7-km^2 buffers around 26 coyotes contained at least 1 TNR colony. Eighteen (69%) of these 26 coyotes had eaten a cat.

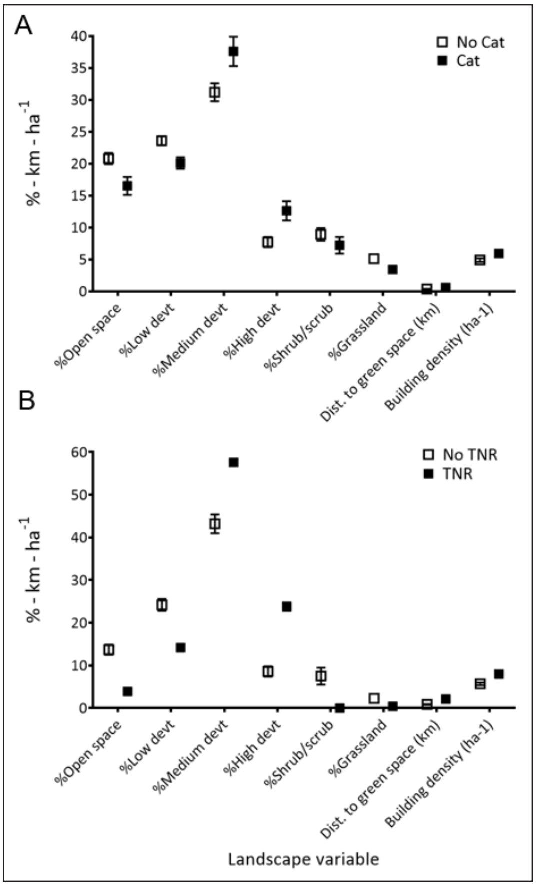

Figure 4. Means (±1 SE) of 8 landscape variables for (A) collection locations of coyotes (*Canis latrans*) that consumed cats (*Felis catus*) and coyotes that did not, and (B) locations of trap-neuter-return (TNR) cat colonies and random non-colony locations in Orange County, California, USA. Units for land-cover types are percentages (%), km for distance to nearest natural area, and ha^{-1} for building density. Some error bars were so small as to be obscured by the symbol. Mean values of landscape variables for coyotes that ate cats differed significantly from those that did not (Mann-Whitney *U*-test with Holm-Bonferroni correction, $P \leq 0.04$), except for % medium development, % shrub, building density, and distance to nearest natural area ($0.07 \leq P \leq 0.10$). Mean values of all landscape variables differed significantly between TNR colony and non-colony locations ($P < 0.001$).

Landscape characteristics around locations of coyotes that ate cats differed from those of coyotes that did not (Figure 4A). Locations of cat-eating coyotes were more intensively developed across all categories, had less grassland

Table 1. Factor loadings for the first 2 principal components (PC1, PC2) generated from separate analyses of 8 landscape variables in buffers around locations of coyote (*Canis latrans*) carcasses and locations of trap-neuter-return (TNR) cat (*Felis catus*) colonies and random non-colony areas. Values in parentheses are the amount of variance explained by PC1 and PC2 in each analysis.

	Coyotes		TNR colonies	
Landscape variable	PC1 (51%)	PC2 (19%)	PC1 (42%)	PC2 (25%)
% Developed open space	-0.398	-0.115	0.443	0.155
% Low development	-0.169	-0.631	0.240	0.482
% Medium development	0.456	-0.163	-0.419	0.353
% High development	0.382	0.372	-0.234	-0.581
% Shrub/scrub	-0.344	0.394	0.344	-0.217
% Grassland/herbaceous	-0.357	0.218	0.395	-0.064
Distance to natural area (km)	0.274	0.369	-0.340	-0.228
Building density (ha^{-1})	0.372	-0.291	-0.354	0.422

Table 2. Maximum-likelihood parameter estimates, standard errors (SE), and *z*-tests for logistic regressions examining the relationships between separate principal components (PC1, PC2) derived from 8 landscape variables and cat (*Felis catus*) consumption by coyotes (*Canis latrans*), and presence or absence of trap-neuter-return (TNR) cat colonies. The PC1 and PC2 together explained 70% of the variation in landscape variables for coyote locations and 67% of the variation in landscape variables for colony locations. Residual deviance values and associated χ^2 tests show how well each predictor (PC1, PC2) decreases residual deviance compared to the null model (intercept only), as a measure of model fit. PC1 and PC2 were the only predictors that resulted in a significant decline in residual deviance for either analysis ($P \leq 0.1$).

Parameter	Estimate	SE	*z*-value	Pr(>|*z*|)	Residual deviance	Pr(>χ^2)
Coyotes						
Intercept	-0.645	0.139	-4.65	<0.001	317.56	-
PC1	0.217	0.068	3.20	0.001	306.73	0.001
PC2	0.204	0.115	1.78	0.075	303.63	0.078
TNR colonies						
Intercept	1.314	0.186	7.07	<0.001	390.93	-
PC1	-1.162	0.177	-6.55	<0.001	241.58	<0.001
PC2	-0.355	0.153	-2.32	0.020	234.53	0.008

and shrub cover, and had higher building densities. These coyotes also tended to be farther from natural areas ($\bar{x} \pm$ SE: 0.59 km ± 0.10, n = 86), on average, than coyotes that did not consume cats (0.35 km ± 0.04, n = 158; Mann-Whitney *U*-test, $P = 0.08$). Similarly, locations of TNR colonies were more developed, had less grass and shrub cover and higher building densities, and were much farther from natural areas than non-colony locations (Figure 4B).

For both coyote and TNR colony/non-colony locations, PCA reduced the number of landscape variables from 8 to 2 principal components (PC1, PC2) that, combined, explained 70% and 67%, respectively, of the variation in those variables (Table 1). In both analyses, the magnitude of the PC1 loadings were large for cover of medium- and high-intensity development and developed open space and for building density, although the directions (signs) along PC1 were reversed for analyses of coyote and colony locations. These relationships are visualized clearly by the squared-cosine analyses. Locations with medium- and high-intensity development and

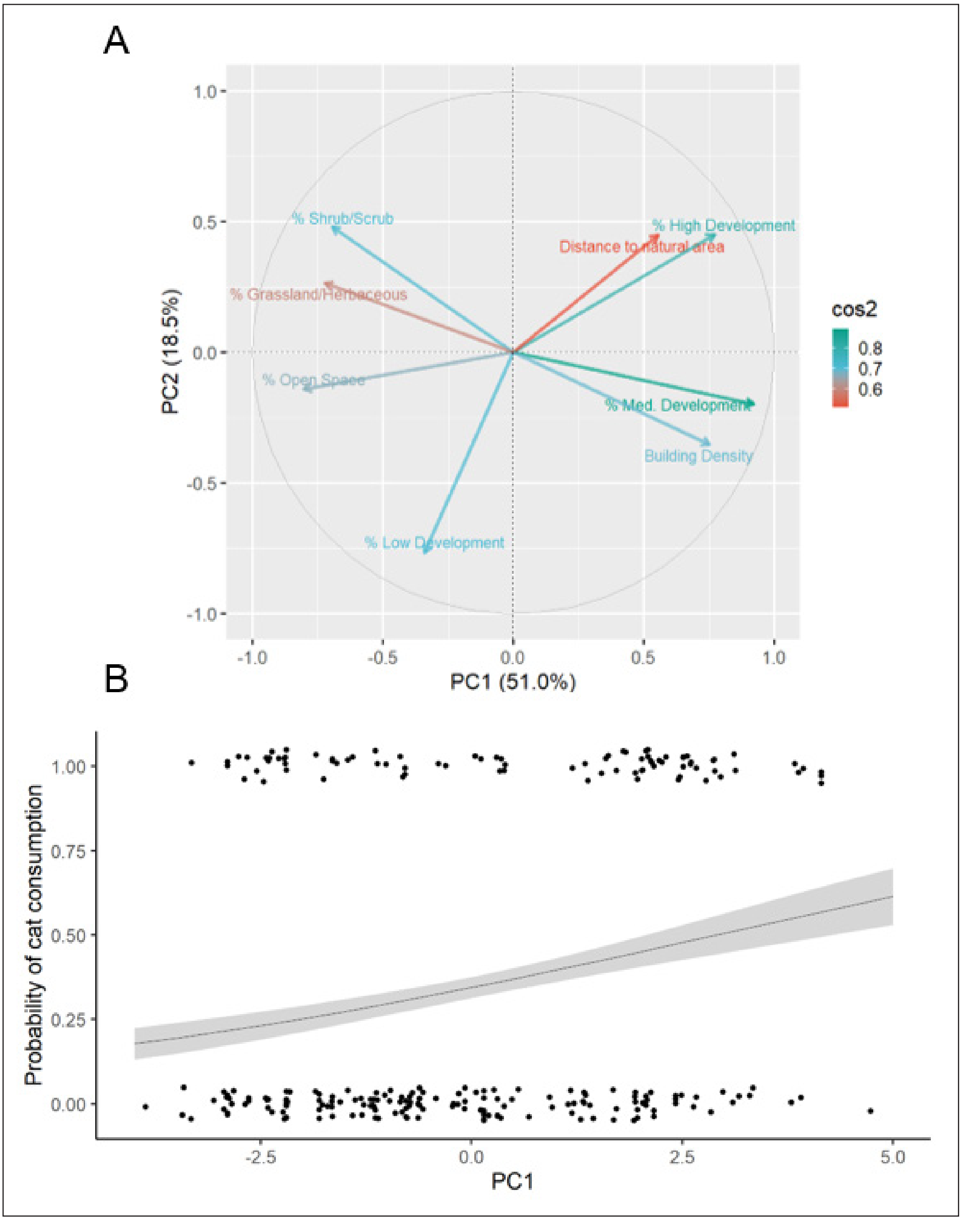

Figure 5. (A) Squared-cosine analysis (cos2) of the first 2 principal components derived from a principal components analysis (PCA) of 8 landscape variables around locations of coyote (*Canis latrans*) carcasses. A high cos2 (green) indicates that a given variable is strongly represented by the principal component, whereas a low cos2 (red) indicates a weak representation. (B) Logistic regression showing the probability of cat (*Felis catus*) consumption by coyotes as a function of principal component (PC) axis 1, which was derived from landscape variables around coyote locations. Coyotes that ate at least 1 cat were assigned a value of 1, whereas those with no cats in the stomachs were assigned a value of 0.

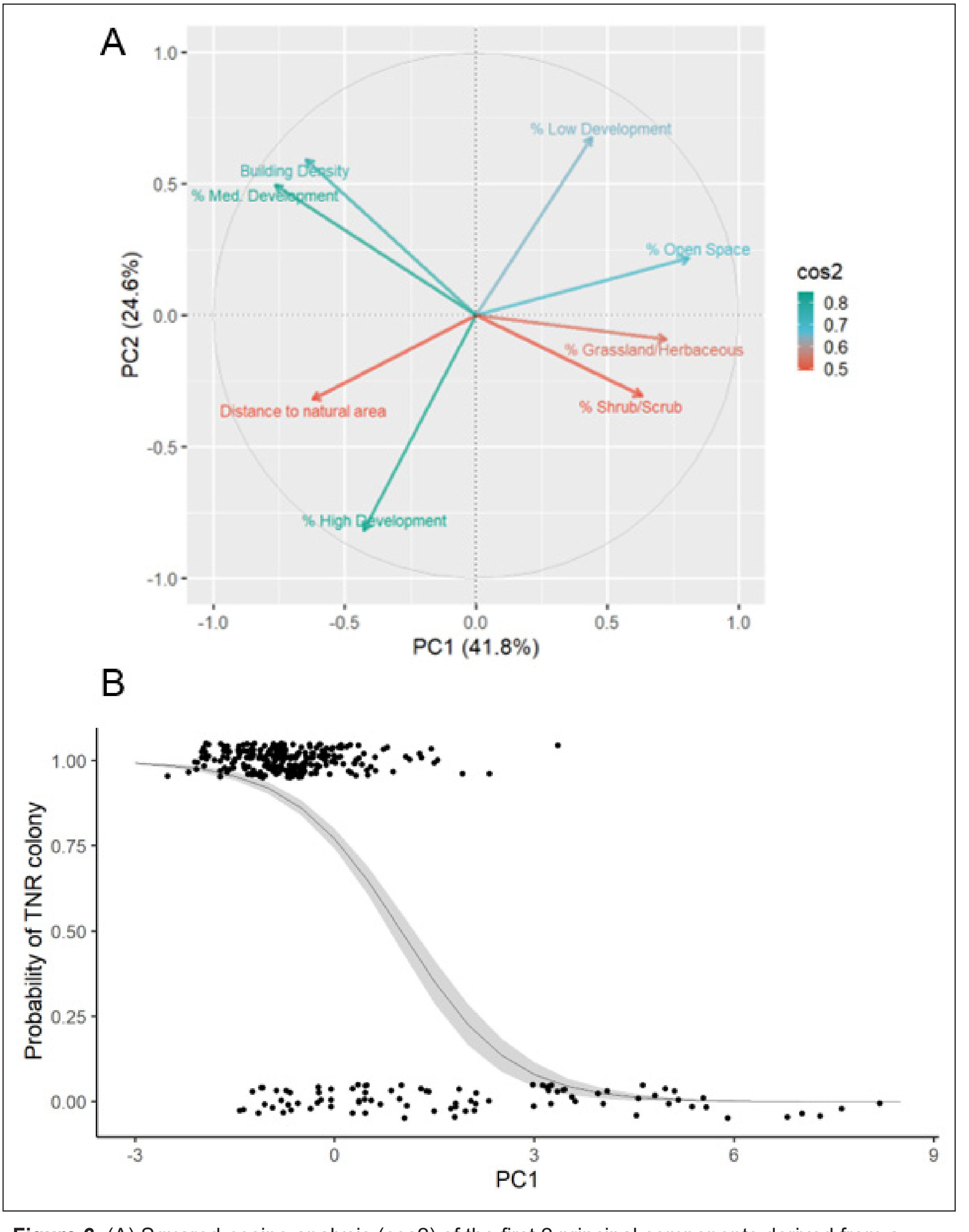

Figure 6. (A) Squared-cosine analysis (cos2) of the first 2 principal components derived from a principal components analysis (PCA) analysis of 8 landscape variables around locations of cat (*Felis catus*) trap-neuter-return (TNR) colony locations and random non-colony locations. A high cos2 (green) indicates that a given variable is strongly represented by the principal component, whereas a low cos2 (red) indicates a weak representation. (B) Logistic regression showing the probability of a given location being a TNR cat colony as a function of principal component (PC) axis 1, which was derived from landscape variables around colony and random non-colony locations. Locations with at least 1 TNR colony were assigned a value of 1, whereas non-colony locations were assigned a value of 0.

high building density have high positive cos2 scores for PC1 for coyote locations (Figure 5A) and high negative cos2 scores for PC1 for colony and non-colony locations (Figure 6A).

The PC1 was the best predictor of the probability that a coyote consumed a cat (Figure 5B; Table 2), with cat-eating coyotes associated with locations with more medium- and high-intensity development and higher building density than coyotes that did not eat cats. For colony/non-colony comparisons, PC1 was the best predictor of the probability that a location was a TNR cat colony (Figure 6B; Table 2), with colonies associated with similar landscape characteristics as those of cat-eating coyotes. The PC2, which seemed to distinguish colony and non-colony locations based on high-intensity versus medium- and low-intensity development and developed open space (Figure 6B), also was a significant predictor of the presence of a TNR colony. Colonies tended to be associated with high-intensity development (e.g., apartment complexes, row houses, and industrial and commercial areas), rather than single-family homes.

Discussion

In our study in urban and suburban southern California, more than a third of coyotes with identifiable meals in their stomachs consumed cats. Previous studies have reported consumption of cats by coyotes, including multiple studies in southern California, where frequency of occurrence values ranged from 0.4–29.0% (Crooks and Soulé 1999; Fedriani et al. 2001; Larson et al. 2015, 2020). However, our estimate, which was derived from a combination of traditional and DNA-based analyses of stomach contents rather than scats, was particularly high. Researchers in other North American cities report much less predation on cats, and some argue that coyotes and cats are spatially and temporally segregated, with coyotes preventing cats from using fragments of natural or agricultural open space (Gehrt et al. 2013, Kays et al. 2015, Poessel et al. 2017*a*). In addition to the comparatively mild climate, southern California environments and coyotes are highly urbanized, and coyotes may be bolder and more willing to venture into heavily developed areas than in other regions if food and cover are plentiful. Intentional feeding also habituates coyotes to the human environment, which may ultimately contribute to attacks on people and pets (Baker and Timm 2017).

One potential source of food for urban coyotes is free-roaming cats and the pet food provided to them in TNR colonies. Supplemented foods also attract other species (e.g., rats [*Rattus* spp.], opossums [*Didelphis virginiana*], raccoons [*Procyon lotor*]) that also may be preyed upon by coyotes (Gerhold and Jessup 2013). Our results demonstrated that coyotes that ate cats were found in the same types of intensively and densely developed locations where TNR colonies were established in Orange County cities. Although our study was limited to places where coyote carcasses were collected regularly and, especially, by the availability of public records of cat releases, in areas where those datasets overlapped, more than two-thirds of coyotes that overlapped with TNR colonies ate cats. Baker and Timm (1998) and Gehrt et al. (2013) also have suggested that coyotes might be attracted to cat colonies.

It is likely that our estimate of the number of cat colonies in Orange County is conservative because some of the release locations were used in multiple years but would not have necessarily been tallied as colonies within a given year. Our minimum bound of 5 cats to define a colony might also have led us to underestimate the actual number of colonies. Because of the difficulty in obtaining records of cat releases across the region, and because OCAC did not provide coyote carcasses from contracted cities until relatively late in our study, there was less overlap between the areas surveyed for coyote carcasses and records of cat releases. Therefore, it was not possible to estimate the density of or distance to TNR colonies around coyote carcass locations, or the number of coyotes killed in areas around TNR colonies, which we had originally hoped to do.

Another caveat to our findings is that we designated coyotes as cat-eating based on the presence of a cat in its stomach when it died, and not cat-eating based on the lack of evidence of cat remains. In actuality, a “cat-eating” coyote may have been killed after eating its first cat, or a coyote that regularly preyed upon cats could have been collected at one of the few times that it had not done so. That is, we assumed that the presence or absence of a cat in the stomach when it died reflected an individual coyote's overall tendency to consume cats. We also could not distinguish predation from scavenging. Moreover, there are certainly many cats outside of TNR colonies that are killed by coyotes, including free-roaming but owned pets. These sources of variability may partly explain why landscape factors related to urbanization were not as strong a predictor of cat consumption as they were for colony locations.

In some areas, coyotes are argued to benefit local wildlife by consuming mesopredators such as cats (Crooks and Soulé 1999), or by altering their habitat use or activity (Gehrt et al. 2013, Kays et al. 2015). Although we cannot account for other free-roaming cats, our results suggest that TNR colonies in Orange County tend to be in intensively developed areas, such as apartment complexes or industrial or commercial zones that are somewhat far from natural areas. While some TNR colony cats may travel to natural areas and prey upon native wildlife (Guttilla and Stapp 2010), it is conceivable that they may instead be dependent on human-provisioned food and that most wildlife they kill are nonnative, commensal, or overabundant species associated with the highly modified urban environment.

Thus, the ecological benefits of coyotes may largely be in reducing the total number of free-roaming cats in the landscape. These benefits may be outweighed, however, by the negative effects of attracting coyotes in large numbers to urban areas, subsidizing large population sizes there, and habituating coyotes to people (and people to the presence of coyotes; Bonnell and Breck 2017). Moreover, coyotes that eat cats and have little fear of humans may eventually be targeted for control, as evidenced by the relatively high frequency of cat-eating among euthanized coyotes, especially if these animals are more likely to attack pets and people. Given the highly adaptable nature of coyotes, an approach to mitigate human–coyote conflicts may be to reduce anthropogenic sources of food for coyotes as well as eliminate the human practices that could be contributing to human–coyote conflicts, such as TNR programs.

Future studies should focus on estimating the abundances of free-roaming cats as well as coyotes in urban areas, specifically in locations where conflicts between humans and coyotes are high. Improved estimates of the numbers of both the coyotes and free-roaming cats will allow us to better comprehend the relationship between these 2 species as well as assist in providing a more detailed explanation of the role free-roaming cats play in the diet of urban coyotes.

Management implications

Our study revealed that, contrary to studies from other regions of North America, cats make up a significant portion of the diet of coyotes, suggesting that reducing the availability of this food source may be an important step in reducing the likelihood of negative human–coyote encounters. Toward this end, tangible measures that could be taken include elimination of TNR programs that attract coyotes to high densities of cats and provisioned food in colonies, especially in areas in close proximity to natural areas (to protect wildlife) and to parks and schools, where those most vulnerable to coyote attacks (e.g., children, pets) are likely to encounter coyotes. In addition, initiatives and educational efforts to keep privately owned cats indoors will reduce mortality of wildlife and cats as well as coyotes if pet-killing prompts nuisance complaints that result in lethal control.

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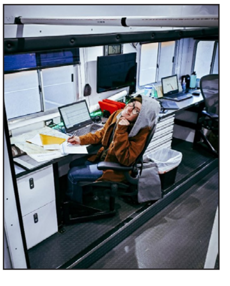

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