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RESEARCH ARTICLE

Patterns of exposure of coyotes to anticoagulant rodenticides in California, USA

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Abstract

Secondary exposure to anticoagulant rodenticides (ARs) causes the death of mammalian predators and scavengers directly and indirectly through sublethal effects that reduce fitness. Poisoning by ARs has been proposed to be a significant source of mortality for coyotes (*Canis latrans*), a medium-sized canid that thrives at the urban–wildland interface and may prey upon species targeted by pest control efforts. However, only 1 study, with a relatively small sample size, documented the prevalence of AR exposure in a free-roaming coyote population. We quantified AR exposure in carcasses of 365 urban and suburban coyotes in southern California, USA, and compared AR prevalence and hepatic residue concentrations to those of 120 rural coyotes collected elsewhere in the state. For urban coyotes, we also examined demographic (sex, age, body mass, cause of death) and environmental factors (season, degree of urbanization, diet) that could influence the number of AR compounds and residue concentrations. Nearly all urban coyotes (98.1%) were exposed to at least 1 AR, compared to 41.7% of rural coyotes, and most individuals had residues of both first-generation (FGAR) and the more potent second-generation (SGAR) compounds, often at concentrations exceeding thresholds considered lethal in other mammals. Anticoagulant rodenticide exposure of urban coyotes did not vary by sex or season, but the number of compounds detected increased with mass, and adults tended to have residues of more compounds and at higher concentrations than juveniles, suggesting repeated and chronic exposure. Livers of road-killed coyotes had higher SGAR concentrations than those euthanized as nuisance animals, which had lower SGAR

concentrations in intensively urbanized areas. Concentrations of SGAR and FGAR residues were highest in suburban areas with natural open space and lower intensity development, and stable isotope values suggested that these coyotes were exposed to ARs by consuming commensal rodents and possibly mesocarnivores. In contrast, coyotes from urbanized areas had lower AR concentrations possibly because less AR is applied in these settings or because coyotes consumed foods with less AR, such as domestic cats and anthropogenic resources. Although some coyotes showed evidence of internal bleeding consistent with AR toxicosis and were in poorer body condition, there was no clear relationship between the extent of hemorrhaging and AR exposure. Despite statewide legislation to restrict their use and mitigate non-target impacts, AR exposure remains ubiquitous in southern California and represents another stressor of urban life to which coyotes have successfully adjusted, making them a potential sentinel of environmental contamination.

KEYWORDS

anticoagulant rodenticide, California, *Canis latrans*, exposure pathways, lethal nuisance control, roadkill, rural exposure, stable isotope analysis, sublethal effects, urbanization

Commensal and pest rodents cause hundreds of millions of dollars of economic damage annually and risk human health through the spread of diseases and allergens and poor sanitation (Meerburg et al. 2009, Ahluwalia et al. 2013, Diagne et al. 2023). These rodents are also invasive in many natural systems, especially islands, where they contribute to declines and extinction of native species (Howald et al. 2007). Chemical toxicants, particularly anticoagulant rodenticides (ARs), are commonly used to control rodent pests. Although appropriate baiting strategies can reduce broader contamination (Jacob and Buckle 2018), exposure and subsequent mortality of non-target species continue to be major environmental concerns. Wild granivorous and omnivorous species (e.g., rodents, songbirds) may consume poisoned baits directly (primary exposure), whereas predatory and scavenging mammals and birds are exposed secondarily by eating contaminated invertebrates or dead and moribund prey, resulting in accumulation of ARs in their tissues (Rattner et al. 2014).

Anticoagulant rodenticides act by binding to and inactivating vitamin K epoxide reductase (VKOR), impairing blood clotting, and resulting in fatal hemorrhaging and toxicosis (Rattner et al. 2014). These are typically classified as first-generation (FGARs) or second-generation (SGARs) compounds, which differ in their potency and persistence, both in the body and the environment (Erickson and Urban 2004). First-generation compounds include warfarin and coumatetralyl and are often grouped with intermediate-generation compounds such as diphacinone and chlorophacinone (Rattner and Mastrota 2018). Second-generation compounds, including brodifacoum, bromadiolone, difethialone, and difenacoum, were developed in response to decreasing effectiveness of FGARs, in part due to development of genetic resistance (Jacob and Buckle 2018). In general, FGARs are considered to be less toxic, requiring multiple feedings to deliver a lethal dose, whereas SGARs are more toxic, with lower LD_{50} values and longer half-lives in the liver, the organ where VKOR expression is greatest and that is usually tested for AR residues (Rattner and Harvey 2021). Although a single meal of SGAR-laden bait may be fatal, the time lag between

consumption and toxicosis may cause an individual rodent to consume multiple meals, resulting in a super-lethal concentration of ARs in its body. Predatory and scavenging wildlife that consume these dead and dying prey or that consume many poisoned individuals may be exposed to large quantities of ARs (López-Perea and Mateo 2018), causing or contributing to mortality in raptors, owls, and mammalian carnivores (Rattner et al. 2014, Elliott et al. 2016). However, the extent to which ARs are metabolized and accumulate in tissues and cause systemic effects and mortality varies considerably within and among species that have been studied in captivity, and are unknown for most non-target species in the wild (Rattner and Harvey 2021).

In the United States, application of ARs has been restricted to reduce risk of non-target exposure, with FGARs used in rural and agricultural settings and urban and suburban areas, and SGARs largely restricted to control of commensal rodents in and near buildings and to protect infrastructure and public health and safety (Rattner et al. 2014), although both are used for invasive species eradication. California is one of the most restrictive states in terms of legal use of ARs, with recent legislation to ban most uses of SGARs in 2021 (California Assembly Bill [AB] 1788) and diphacinone (AB1322), effective in 2024. Recent restrictions have been spurred by evidence of AR exposure of raptorial birds and, especially, top predators such as mountain lions (*Puma concolor*) and bobcats (*Lynx rufus*) in southern California (Riley et al. 2007, Serieys et al. 2015), although population impacts are not known.

Coyotes (*Canis latrans*) are the most common, medium-sized carnivore throughout much of North America and as habitat and dietary generalists that are tolerant of human development, have successfully adjusted to urban and suburban environments (Gehrt and Riley 2010). Despite the great potential for coyotes to be exposed to ARs, only a single study has estimated the prevalence of AR exposure in a free-roaming coyote population, and the few other unpublished incident reports are scattered and based on small sample sizes. Summarizing research from the Santa Monica Mountains in southern California, Moriarty et al. (2012) reported that livers of 83% (20) of 24 coyotes tested between 1996 and 2004 contained residues of ≥1 AR. They attributed 14 fatalities to AR toxicosis (representing 30% of known-cause mortalities); all were exposed to SGARs and 4 were exposed to both SGARs and FGARs. Erickson and Urban (2004) reported liver residue concentrations in 22 coyotes that were exposed to ARs, including many of the coyotes tested for the Santa Monica Mountains study referenced above, 10 coyotes from northern California (also summarized in Hosea [2000]), and 1 from New York. Poessel et al. (2015) found SGAR residues in the livers of all 5 coyotes tested from outside Denver, Colorado, and attributed the deaths of at least 2 individuals to AR poisoning. Way et al. (2006) described an instance in which 3 coyotes were intentionally poisoned with brodifacoum (an SGAR) in Massachusetts, indicating primary exposure is also possible.

We marshaled data and evidence from a variety of sources to investigate patterns and pathways of AR exposure in 365 coyotes in southern California and 120 coyotes collected in rural and agricultural areas of the state. We predicted that because of the wide variety of AR compounds used in urban and suburban settings and the mix of professional and private rodent control efforts, urban coyotes would be exposed to more AR compounds and have higher liver SGAR residues than coyotes from rural areas. We also predicted that adult coyotes would be exposed to more AR compounds and have higher residue concentrations than juveniles because they have consumed more prey over their lives, including prey exposed to ARs. We also expected that AR exposure would be inversely related to the intensity of urban development, reflecting higher use of rodenticides in suburban areas with single-family homes and larger yards that are closer to open space (Morzillo and Schwartz 2011). Finally, we predicted that AR exposure would be higher in coyotes consuming prey that are the targets of rodenticide applications versus those dependent on natural or human-provisioned foods.

STUDY AREA

We opportunistically obtained carcasses of coyotes from urban and rural areas of California, USA. We collected urban carcasses from Los Angeles County and Orange County, in locations that were characterized as urban or suburban, although coyotes regularly moved between areas of human development and more natural areas,

including private and government-owned parks, water conveyance infrastructure, and protected open space (Riley et al. 2003). The Los Angeles-Long Beach-Anaheim metropolitan statistical area (12,580 km^2) had a population of 13.2 million people (2020 Census; www.census.gov). The basin has a Mediterranean climate, with warm, dry summers and mild, wet winters (Cleland et al. 2016). Most of the 46 cm of average annual precipitation falls as rain between November and April, although there is much inter-annual variability. The natural vegetation is characterized as coastal sage scrub and chaparral mixed with riparian woodlands and grasslands, although most areas have been transformed by human development and landscaped with ornamental plants and turf.

We collected carcasses of coyotes from rural and agricultural areas of 19 other California counties. Climate and vegetation varied greatly across these counties, which spanned the length of the state and nearly 10° of latitude. Most coyotes were from agricultural counties in the Central Valley or the surrounding foothills, in areas dominated by irrigated cropland, non-native grasslands, or oak or mixed-conifer woodlands. Some were from desert scrubland areas in the southern part of the state. Coyotes were subjectively characterized as rural by the individuals who collected them (see below).

METHODS

Our sample of urban coyotes consisted of 501 coyotes killed by vehicles (roadkill) or by professional trappers and animal control agents (euthanized). We took liver samples from 365 of these coyotes (256 euthanized, 109 roadkill), killed between July 2015 and January 2020 (Figure 1). We also obtained liver samples from 120 coyotes euthanized between March 2019 and August 2021. Sample size differed among the 19 rural counties: we collected between 7–20 individuals from 8 counties (Madera [7], Amador [9], Sonoma [10], Fresno [10], Modoc [12], San Diego [13], El Dorado [14], Kern [20]) and between 1–5 individuals from 11 counties (San Luis, Riverside, Kings, Colusa, Butte, Placer, Humboldt, Solano, Imperial, Calaveras, Mendicino). We recorded sex, age class (adult and juvenile, including young-of-year), and evidence of conspicuous sarcoptic mange (*Sarcoptes scabiei*) infestation (hair loss, skin lesions). For urban coyotes, we also recorded body mass (in kg), cause of death (roadkill, euthanized), season of collection (wet: Nov–Apr; dry: May–Oct), and location (latitude, longitude). When precise location information was not available, we used the intersection of the nearest cross streets. We did not have specific location data for rural coyotes.

Sample processing

We sent livers to the Texas A&M Veterinary Medical Diagnostic Laboratory (College Station, Texas) to test for residues of 7 ARs using a dispersive solid-phase extraction procedure (QuEChERS method; Vudathala et al. 2010), with chemical analysis using liquid chromatography-mass spectrometry (LC-MS). The lab analyzed extractions for the residues of 3 FGARs (diphacinone, chlorophacinone, warfarin) and 4 SGARs (brodifacoum, bromadiolone, difethialone, difenacoum). Because liver samples were analyzed at different times, the limits of detection (LOD) and quantitation (LOQ) varied. Limit-of-quantitation values were 5 or 10 ng/g for all compounds except chlorophacinone, for which quantitation limits were 5, 10, or 20 ng/g. We assigned samples with concentrations between the LOD and LOQ a residue value of half the quantitation limit. Although this method of addressing left-censored data has been criticized and alternatives have been proposed (Helsel 2009, Zoffoli et al. 2013), we took this approach because relatively few detections were below the LOQ ($\bar{x}$ = 7.3%) and because of its simplicity. Moreover, Zoffoli et al. (2013) reported that this approach had low bias for datasets with high geometric standard deviations (GSD close to or >3.0), which was the case for our concentration values ($\bar{x}$ GSD = 3.4; range = 2.6–4.0).

We used 2 sets of variables to describe exposure to ARs: counts of the numbers of FGARs, SGARs, and total AR compounds detected in each coyote; and summed concentrations of FGAR and SGAR compounds (ΣFGAR, ΣSGAR)

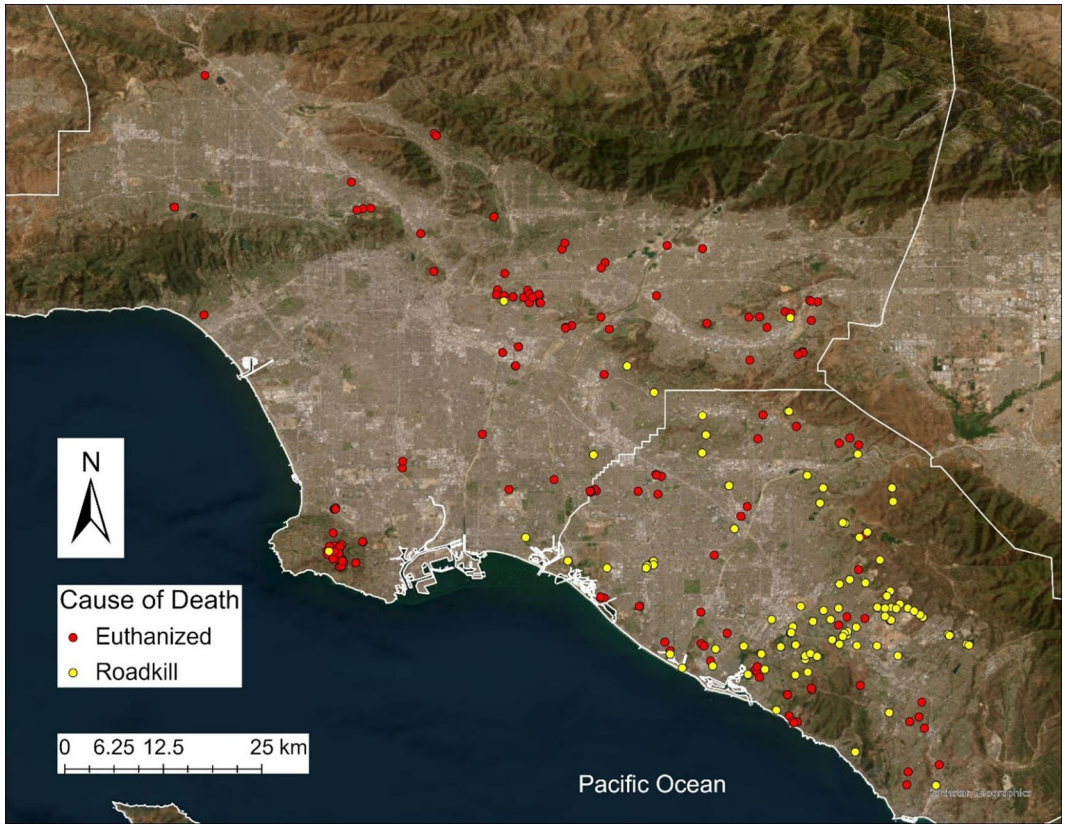

FIGURE 1 Locations of euthanized and road-killed coyotes tested for exposure to anticoagulant rodenticides in Los Angeles County and Orange County, California, USA, 2015–2020. Locations of 2 coyotes from the Antelope Valley, north of the San Gabriel Mountains at the top of the image, are not shown. White lines show the county borders. Map created in ArcGIS Pro (version 3.3; Esri).

for coyotes with measurable residues (≥LOQ). We included detections of warfarin (24 coyotes) and difenacoum (5 coyotes) in counts of the number of FGAR and SGAR compounds, respectively, and in the total number of ARs but did not include warfarin or difenacoum residues in ΣFGAR and ΣSGAR values because concentrations were consistently very low (20/24 warfarin and 4/5 difenacoum concentrations were below the LOQ). For both FGARs and SGARs, the individual compounds have similar molecular weights and roughly similar potency (Rattner and Harvey 2021), making summing them reasonable. In laboratory rodents, hepatic half-lives of the FGARs we included range from 3 days to 35.4 days, whereas those of SGARs vary from 28.5 days to 350 days (Horak et al. 2018); there are no comparable persistence data for dogs or other canids.

Ecological correlates of rodenticide exposure

Following Bucklin et al. (2023), to investigate landscape characteristics around urban coyote locations, we generated 1,500-m-radius buffers (7-km^2) around GPS coordinates using ArcGIS Pro (version 3.3; Esri, Redlands, California, USA). We used the 2016 National Land Cover Database to estimate percent cover of 6 land cover variables (high-, medium-, and low-intensity development, altered open space, shrub, grass) in buffers. We also estimated building density (buildings/km^2) using county building footprint data. We transformed all variables to a

uniform mean and standard deviation (z-score) prior to analysis. We used principal components analysis (PCA) to reduce the number of variables and create composite variables that described the extent and type of urbanization in the landscape around coyote locations.

We collected muscle tissue of 149 coyotes from Los Angeles and Orange County, 130 of which were tested for ARs, to assess long-term, assimilated diet using stable carbon (C) and nitrogen (N) isotope analysis. In terrestrial systems, variation in the ratio of heavy and light C stable isotopes reflects relative dietary contributions of C_3 and C_4 or crassulacean acid metabolism (CAM) plants and the consumers that feed upon them (Ben-David and Fleharty 2012). Anthropogenic food sources derived from corn, a C_4 plant, also tend to have higher (enriched) C isotope ratios, making the C isotope ratio a potentially useful measure of consumption of human-associated foods in C_3 plant-dominated ecosystems (Newsome et al. 2015). In addition to providing dietary source information, the N isotope ratio typically increases with trophic level, with carnivores usually having more enriched N isotope ratios than omnivores and herbivores in the same system (Ben-David and Fleharty 2012).

We removed a sample of masseter (jaw) muscle from each carcass, placed it in a vial with 95% ethanol, and kept it in a conventional laboratory freezer (−20°C) until preparation. We dried, homogenized, and shipped samples to the University of California Davis (UCD) Stable Isotope Facility (Plant Sciences). The lab analyzed samples using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope-ratio mass spectrometer (Sercon, Cheshire, United Kingdom). They calculated stable isotope ratios, expressed using delta (δ) notation in parts per mille (‰) as:

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1{,}000,$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio of heavy ^{13}C to light ^{12}C or ^{15}N to ^{14}N. The $R_{standard}$ values are based on international standards for $\delta^{13}C$ (Vienna PeeDee Belemnite [VPDB]) and $\delta^{15}N$ (atmospheric N_2). The long-term standard deviation at the facility is 0.2‰ for ^{13}C and 0.3‰ for ^{15}N.

We compared $\delta^{13}C$ and $\delta^{15}N$ values of coyotes to those of potential food items collected from the region. We collected all prey samples opportunistically in suburban and urban areas in Los Angeles County and Orange County area between May 2017 and January 2024. We collected plant samples by hand. For domestic cats, clinics conducting spay and neuter programs donated ear tissue. We obtained commensal rodents through trapping and from pest control operators that donated carcasses. For all other mammals, we took muscle tissue from carcasses (usually masseter) of roadkills or those donated from pest control operators and agencies. We obtained 3°C_4 and CAM plant samples: seeds of unidentified cactus species, unidentified cholla species, and commercial silo millet. We collected 19°C_3 plants: fruits, berries, and seeds of ornamental plants including avocado, lime, orange, fig, palm, Japanese mock orange, unidentified ornamental shrubs, and sunflower seeds. We obtained 22 anthropogenic food samples: dry and wet cat and dog food (11 samples) and retail fast food, including beef hamburger, chicken, hot dog, french-fried potatoes, and corn tortilla (11 samples). We obtained 67 samples of commensal rodents: (roof rat [*Rattus rattus*] and house mouse [*Mus musculus*]), 14 samples of wild rodents (fox squirrel [*Sciurus niger*], California ground squirrel [*Otospermophilus beecheyi*], valley pocket gopher [*Thomomys bottae*], California vole [*Microtus californicus*], western harvest mouse [*Reithrodontomys megalotis*], woodrats [*Neotoma* spp.], deer mice [*Peromyscus* spp.]), 6 samples of desert cottontails (*Sylvilagus audubonii*), 6 samples of mesocarnivores (striped skunk [*Mephitis mephitis*], Virginia opossum [*Didelphis virginiana*], raccoon [*Procyon lotor*]), and 343 samples of domestic cats (*Felis catus*). We dried plant samples (seeds, fruits) and stored animal tissues (muscle) in 95% ethanol in a conventional freezer. We prepared prey samples as described above for coyote muscle samples and sent them for analysis at the UCD facility.

Necropsies and body condition

For a subset of 50 coyote carcasses collected in 2019, we conducted detailed necropsies to seek evidence of internal and subcutaneous hemorrhaging and poor body condition that might be indicative of coagulopathy related

to AR exposure. We used 3 measures to assess body condition. First, to describe external condition visually, we assigned each coyote a whole-number rating on a 5-point body condition score (BCS) developed for domestic dogs (American Animal Hospital Association, Lakewood, CO, USA, https://www.aaha.org/wp-content/uploads/globalassets/02-guidelines/weight-management/weightmgmt_bodyconditionscoring.pdf), with each rating point associated with key, palpable changes in fat stores and prominence of bony structures. Second, we calculated the kidney fat index (KFI), an index of total body fat, by removing the right kidney and the surrounding (perirenal) fat and then dividing the mass of the perirenal fat by the mass of the fat-free kidney, expressed as a percentage (Finger et al. 1981). Lastly, we counted the number of helminths in the digestive tract, under the premise that animals in poorer health might have high parasite loads. We removed the intestinal tract and stored it at −80°C for at least 72 hours to kill any infectious eggs and then stored it at −20°C. We then thawed and dissected the intestines and suspended their contents in warm water (40°C) for 30 minutes. After a series of sedimentation and clearing steps to remove excess debris, we washed the final sediment in a 106-µm sieve and removed all helminths. We fixed helminths in alcohol-formalin-acetic acid for 3 days, then placed them in a mixture of 70% ethanol and 5% glycerine for storage. We categorized helminths into major groups using a dissection microscope. For consistency, one author (AM) conducted all necropsies, which were completed prior to AR residue testing.

Because 16 of these coyotes were killed by vehicles and thus suffered injuries that likely caused or contributed to internal bleeding, we restricted our analyses of relationships between evidence of hemorrhaging and AR exposure to the 34 euthanized coyotes. In consultation with a wildlife veterinarian, we developed a 6-point, whole-number qualitative rating to describe the intensity of subcutaneous and internal (pulmonary, thoracic, coelomic) hemorrhaging observed during necropsy that could not be attributed to injury.

Data analysis

We used contingency table analyses and non-parametric tests for univariate and bivariate comparisons. We used generalized linear multiple regression to investigate relationships between measures of AR exposure and demographic and environmental variables. We conducted analyses in R (version 4.2.2; R Core Team 2022) implemented through RStudio (version 2024.4.2.764; RStudio Team 2024) and GraphPad Prism (version 10.2.3; GraphPad Software, Boston, Massachusetts, USA). *A priori*, we constructed a base model consisting of additive main effects of sex, season, cause of death, body mass (in kg; a continuous proxy for age), and the first 2 landscape principal components (PC1, PC2). We used a negative binomial distribution to model counts of the number of AR compounds and quantile regression to identify significant predictors of ΣFGAR and ΣSGAR concentrations. We $\log_{10}$-transformed ΣFGAR prior to analysis and square-root-transformed ΣSGAR and mass. After initial runs of the base model, we removed variables with weak or no evidence of an effect ($P > 0.05$) and re-ran models using only the remaining variables. We investigated interactions between continuous and categorical variables in these subsequent runs to identify evidence of an effect. Because stable isotope data were only available for 36% of coyotes tested for AR exposure, we explored the potential contributions of $\delta^{13}C$ and $\delta^{15}N$ by examining Spearman rank correlations with other factors and by including $\delta^{13}C$ and $\delta^{15}N$ as additive main effects in the final median models for ΣFGAR and ΣSGAR concentrations.

RESULTS

Patterns of exposure

All but 7 of the 365 urban coyotes (98.1%) had detectable liver residues of at least 1 AR (Table 1): 97.3% were exposed to SGARs, 67.4% were exposed to FGARs, and 66.6% were exposed to both AR classes. Diphacinone was

TABLE 1 Frequency of detection (%) and summed concentrations of anticoagulant rodenticide (AR) residues in livers (ng/g) of 365 coyotes from urban Los Angeles County and Orange County compared to 120 coyotes from rural areas of California, USA, 2015–2021.

AR compound type	Urban (n = 365)	Rural (n = 120)
First-generation (FGAR)		
Diphacinone (%)	65.5	22.5
Chlorophacinone (%)	6.6	7.5
Warfarin (%)	6.6	0.8
All FGAR frequency (%)	67.4	25.8
Median Σ concentration (ng/g)	45.8	41.0
Maximum Σ concentration (ng/g)	1,752.3	1,527.6
Second-generation (SGAR)		
Brodifacoum (%)	95.1	12.5
Bromadiolone (%)	83.3	24.2
Difethialone (%)	72.9	5.0
Difenacoum (%)	1.4	2.5
All SGAR frequency (%)	97.3	30.0
Median Σ concentration (ng/g)	803.2	60.0
Maximum Σ concentration (ng/g)	3,276.2	1,355.3
Both FGAR and SGAR compounds (%)	66.6	13.3
All AR frequency (%)	98.1	41.7

the only commonly detected FGAR (65.5%), whereas 3 SGARs (brodifacoum, bromadiolone, difethialone) were present in most urban coyotes. In contrast, fewer rural coyotes (41.7%) were exposed to ARs ($\chi^2_1 = 215.2$, $P < 0.001$), with FGAR and SGAR compounds detected in similar frequencies (25.8%, 30.0%, respectively; Table 1). Only 13.3% of rural coyotes were exposed to both AR classes. Diphacinone (22.5%) was the most common FGAR in rural coyotes, whereas bromadiolone (24.2%) was the only SGAR detected regularly. Exposure to the number of FGAR compounds, the number of SGAR compounds, and both types of compounds were higher for urban coyotes than for rural ones (chi-square tests, $P < 0.001$). In the 8 counties with ≥7 individuals sampled, prevalence of SGARs ranged from 10.0–70.0% ($\bar{x}$ = 32.8%) and FGARs ranged from 0 to 71.4% ($\bar{x}$ = 25.5%), with the highest combined AR prevalence in 2 Central Valley agricultural counties, Madera (85.7%) and Fresno (70.0%; average AR prevalence in the other 6 rural counties was 33.3%). Coyotes from Modoc (41.7%) and San Diego (38.5%) counties also had relatively high SGAR exposure among rural counties sampled.

Urban coyotes were exposed to many more AR compounds than their rural counterparts. Whereas most rural coyotes (58.3%) were exposed to no ARs and only 19% had residues of 2 or more compounds, livers of urban coyotes usually contained residues of 3 or 4 ARs (71.2%), and 8.8% contained 5 or 6 compounds (Figure 2). Most urban coyotes had residues of 1 (57.6%) or no FGAR compounds (32.6%), whereas 88.8% were exposed to 2 or more SGARs. Combining the lowest (0-1) and highest counts (4-6) to ensure sufficient cell frequencies for analyses, the distribution of total AR compounds across the 4 bins differed between urban and rural coyotes ($\chi^2_3 = 261.7$, $P < 0.001$). We observed similar results for FGAR and SGAR compounds examined separately. Liver ΣFGAR concentrations were similar between urban and rural coyotes (Mann-Whitney U = 4,261, $P = 0.834$), but ΣSGAR

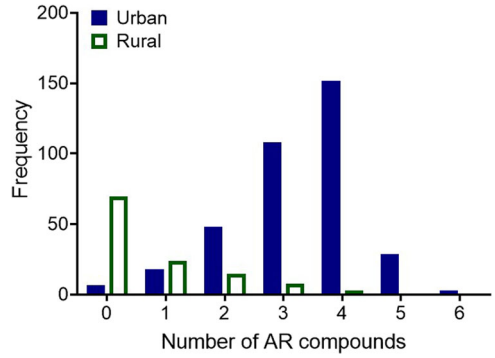

FIGURE 2 Frequency distribution of counts of the number of urban and rural coyotes in California, USA, exposed to different numbers of anticoagulant rodenticide (AR) compounds (first-generation and second-generation ARs combined) in 2015–2021.

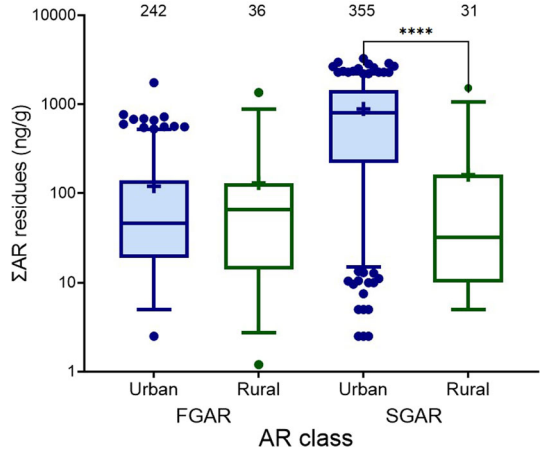

FIGURE 3 Summed residue concentrations (ng/g) of 2 first-generation (FGAR) and 3 second-generation (SGAR) anticoagulant rodenticide (AR) compounds in livers of urban and rural coyotes in California, USA, 2015–2021. Box shows median and 25% and 75% quartiles, whiskers show 5% and 95% confidence limits, and + indicates the mean. Numbers above whiskers are sample sizes. **** denotes a difference between urban and rural coyotes in a Mann-Whitney test, with $P < 0.001$. Only coyotes exposed to FGAR or SGAR are included.

concentrations were much higher in urban coyotes ($U = 1687$, $P < 0.001$; Figure 3). Of the 355 urban coyotes exposed to SGARs, 76.3% had ΣSGAR concentrations >200 ng/g, and 40.8% (145) had ΣSGAR concentrations >1,000 ng/g (Figure S1, available in Supporting Information), compared to 13.9% (5) and 2.8% (1), respectively, of the 36 exposed rural coyotes.

Pooling urban coyotes with low (0-1) and very high (4-6) numbers of ARs, we found no evidence for differences in the number of ARs between males and females ($\chi^2_3 = 4.99$, $P = 0.173$), between wet and dry seasons ($\chi^2_3 = 1.75$, $P = 0.627$), or between euthanized and roadkill coyotes ($\chi^2_3 = 5.03$, $P = 0.170$; Figure 4). Juveniles tended to be overrepresented among urban coyotes with few ARs and underrepresented among those most heavily exposed (Figure 4), and we found only weak evidence for a difference in the number of ARs between juveniles and adults ($\chi^2_3 = 7.30$, $P = 0.063$). We did not find evidence that the number of AR compounds in rural coyotes differed between sexes ($\chi^2_2 = 0.38$, $P = 0.829$; bins of 0, 1, ≥2 ARs) or seasons ($\chi^2_2 = 0.71$, $P = 0.703$). There were too few juvenile rural coyotes (12) to compare ages.

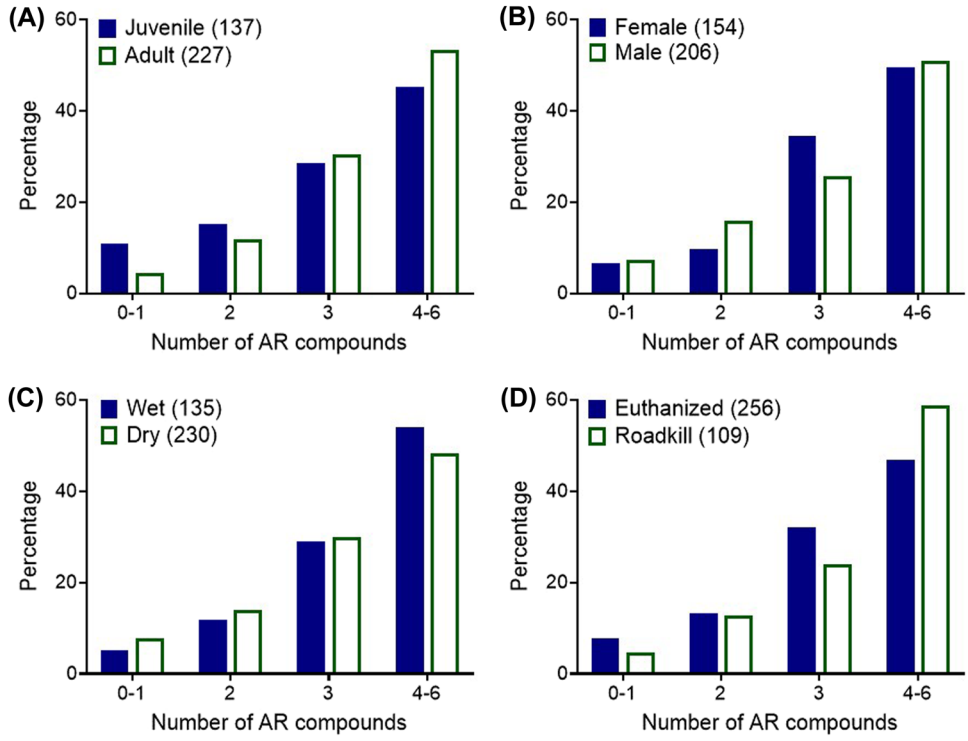

FIGURE 4 Differences in frequency distributions (%) of the number of anticoagulant rodenticide (AR) compounds detected in urban coyotes in southern California, USA, 2015–2020, between A) ages, B) sexes, C) seasons of collection, and D) cause of death. Values in parentheses are sample sizes.

Univariate tests of differences in summed residue concentrations (ΣFGAR, ΣSGAR) between sexes and seasons yielded similar results for urban and rural coyotes: no evidence for an effect (Mann-Whitney tests, $P > 0.117$). The ΣFGAR concentrations of urban coyotes also did not differ between age classes ($U = 6593$, $P = 0.682$) or cause of death ($U = 5710$, $P = 0.317$), but roadkill coyotes had higher ΣSGAR concentrations (median = 1,030.1 ng/g) than euthanized ones (median = 669.0 ng/g; $U = 9{,}476$, $P < 0.001$) and adults tended to have higher ΣSGAR concentrations (median = 749.2 ng/g) than juveniles (623.2 ng/g; $U = 1{,}2903$, $P = 0.058$).

Ecological correlates of rodenticide exposure

Principal components analysis reduced the 7 landscape variables to 2 composite axes with eigenvalues >1, which collectively explained 70.9% of the total variance (Figure 5). The first component (PC1) was positively correlated to percent cover of medium- and high-intensity development and building density ($r > 0.37$) and negatively correlated to cover of altered open space and shrub cover ($r < -0.39$). The second (PC2) was strongly and positively related to cover of grasses and shrubs and high-intensity development ($r > 0.30$), and negatively related to cover of low-intensity development, altered open space, and building density ($r < -0.32$). Thus, we interpreted PC1 to reflect a gradient from low- to moderate- and high-intensity development with high building densities, whereas PC2 distinguished between locations based on whether the surrounding open space was altered and dominated by low-intensity development versus natural open space adjacent to high-intensity development.

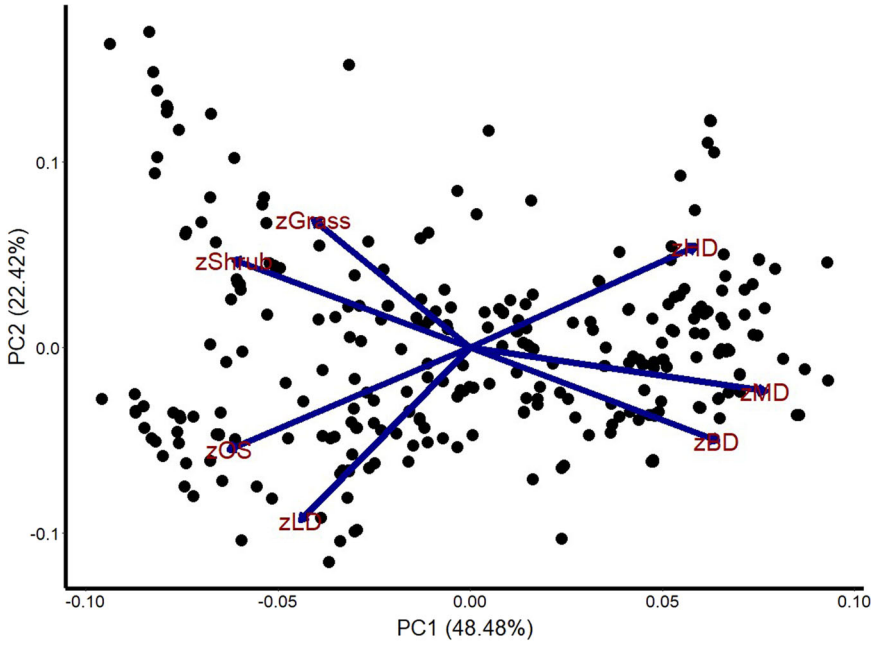

FIGURE 5 Results of principal components (PC) analysis of 7-km^2 buffers around collection locations of urban coyotes in southern California, USA, 2015–2020. Variables were building density (BD); percentage cover of high- (HD), medium- (MD), and low-intensity (LD) development; altered open space (OS); and grass and shrub cover types. We converted measurements to z-scores before analysis.

Of the 6 factors in the base negative binomial model, body mass was the only supported predictor of the number of AR compounds detected (intercept: $\beta_0 = 0.566$, SE = 0.202, $P = 0.005$; √mass: $\beta_1 = 0.194$, SE = 0.061, $P = 0.001$; $\chi^2_{358} = 151.7$, $P = 1.000$; pseudo-$R^2 = 0.07$), with larger coyotes exposed to more compounds (Figure S2, available in Supporting Information). Mean mass of coyotes with ≤2 AR compounds was 9.2 ± 4.0 kg, whereas coyotes with ≥5 AR compounds weighed, on average, 11.1 ± 3.2 kg. Body mass was also the only predictor with evidence for an effect in separate regression models of the number of FGAR and SGAR compounds (results not shown). However, ΣFGAR and ΣSGAR residue concentrations were not correlated with mass ($P \geq 0.542$; Figure S2).

Based on quantile regression, none of the 6 factors included in the initial model were supported predictors of low levels (quantiles 0.1 and 0.3) of ΣFGAR. At higher ΣFGAR concentrations (quantiles 0.5, 0.7, and 0.9), the only variable with strong evidence of an effect in the final models was PC2 (Table 2; Figure 6), which suggests that ΣFGAR concentrations increased with increasing cover of shrub and grass vegetation. At the lowest levels (quantiles 0.1 and 0.3), ΣSGAR concentrations increased with body mass (Table 2) and ΣSGAR was also lower during the wet season than the dry season at the lowest quantile (0.1). At higher quantiles, evidence did not indicate a relationship with mass, but ΣSGAR concentrations were consistently higher in roadkill coyotes than euthanized ones and, overall, decreased with the intensity of human development (PC1). Interactions between PC1 and cause of death, however, revealed a negative relationship between ΣSGAR and PC1 for euthanized coyotes but not for roadkill coyotes (Table 2; Figure 6).

Including all 130 coyotes with both AR residue and stable isotope values, ΣSGAR was negatively correlated with $\delta^{13}C$ (Spearman $r = -0.36$, $P < 0.001$) and positively correlated with $\delta^{15}N$ ($r = 0.23$, $P = 0.010$; Figure 7). Summed residues of first-generation compounds (ΣFGAR) were also positively correlated with $\delta^{15}N$ ($r = 0.33$, $P = 0.001$) but not $\delta^{13}C$ ($r = -0.02$, $P = 0.866$). Analysis revealed $\delta^{13}C$ was positively correlated with PC1 ($r = 0.54$, $P < 0.001$) and negatively correlated with PC2 ($r = -0.22$, $P = 0.009$), but $\delta^{15}N$ was not related to either landscape variable ($P \geq 0.340$). When we added $\delta^{13}C$ and $\delta^{15}N$ to the final median regression model of ΣSGAR, $\delta^{13}C$ was the

TABLE 2 Summary of quantile regression analyses to fit summed first-generation (ΣFGAR) and second-generation (ΣSGAR) anticoagulant rodenticide residue concentrations in livers of urban coyotes in southern California, USA, 2015–2020, as a function of demographic (sex, square-root (sqrt) of mass, cause) and environmental (season, principal components PC1 and PC2) factors. Results shown are the final models containing only variables with $P < 0.05$. Cause (RK) and season(wet) refer to coefficients for roadkill coyotes and wet season samples, which are compared to euthanized coyotes and dry season samples, the reference levels for these categorical variables. The quantile (τ) column shows the percentile of the response variable that was tested in a given model. The last row shows results of regression analysis of ΣSGAR that included the final median model (intercept, cause, PC1, PC1×cause) and stable isotope values ($\delta^{13}C$, $\delta^{15}N$) for 130 coyotes, with $\delta^{13}C$ the only factor remaining with $P < 0.05$. For ΣFGAR, there were no variables in models of quantiles 0.1 and 0.3 with $P < 0.05$ and neither $\delta^{13}C$ nor $\delta^{15}N$ were significant predictors of ΣFGAR when included in the final median regression (intercept, PC2).

Response	Quantile (τ)	GOF[a]	Residual df	Factors	Coefficient	[95%LCL, 95%UCL]	*P*
logΣFGAR	0.5	0.046	235	Intercept	1.69	[1.55, 1.74]	<0.001
				PC2	0.13	[0.025, 0.185]	0.003
	0.7	0.036	235	Intercept	1.99	[1.86, 2.13]	<0.001
				PC2	0.13	[0.035, 0.209]	0.019
	0.9	0.035	235	Intercept	2.54	[2.41, 2.61]	<0.001
				PC2	0.11	[0.020, 0.292]	0.014
sqrtΣSGAR	0.1	0.071	347	Intercept	−8.48	[−15.0, −5.84]	0.002
				Season(wet)	−4.79	[−8.11, −0.56]	0.002
				Sqrt(mass)	5.65	[4.46, 7.76]	<0.001
	0.3	0.077	347	Intercept	−6.70	[−12.60, 6.16]	0.316
				Cause(RK)	11.60	[7.03, 16.70]	<0.001
				Sqrt(mass)	6.28	[2.16, 8.13]	0.002
	0.5	0.082	345	Intercept	25.9	[22.5, 27.9]	<0.001
				Cause(RK)	7.12	[3.56, 11.20]	0.003
				PC1	−2.68	[−3.79, −1.33]	0.001
				PC1 × cause(RK)	4.05	[1.50, 6.32]	0.006
	0.7	0.072	345	Intercept	32.3	[31.1, 35.2]	<0.001
				Cause(RK)	8.21	[2.60, 10.9]	<0.001
				PC1	−1.90	[−2.77,−0.97]	0.001
				PC1 × cause(RK)	3.16	[0.65, 5.24]	0.015
	0.9	0.078	345	Intercept	41.4	[39.1, 43.6]	<0.001
				Cause(RK)	5.24	[3.30, 7.25]	0.001
				PC1	−2.13	[−3.27, −0.42]	0.002
				PC1 × cause(RK)	2.89	[1.75, 4.68]	0.001
sqrtΣSGAR	0.5	0.671	126	Intercept	−37.7	[−78.4, −0.4]	0.035
				$\delta^{13}C$	−3.29	[−5.16, −1.57]	<0.001

[a]The goodness-of-fit (GOF) measure (Koenker and Machado 1999) was estimated as 1 minus the ratio between the sum of absolute deviations in the fully parameterized models and the sum of absolute deviations in the null quantile model (intercept only). The GOF values are lower than coefficients of determination (R^2) from linear regression, which are based on the variance of squared deviations.

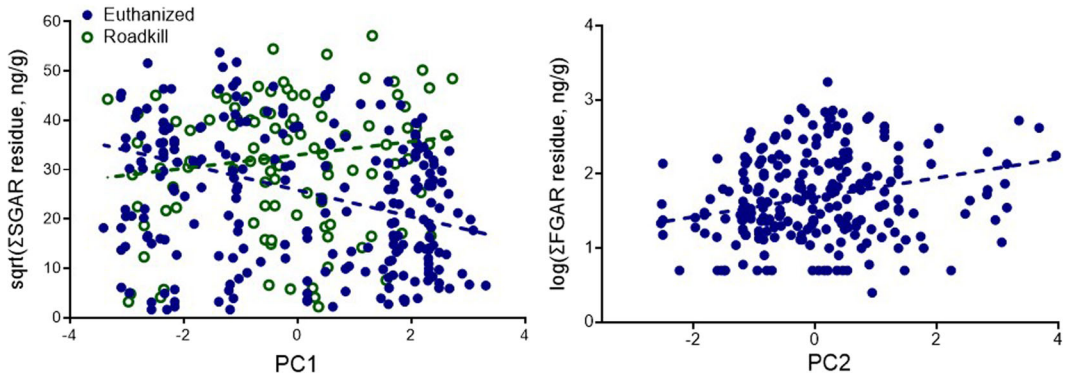

FIGURE 6 Scatterplots of the relationships between composite landscape variables (principal components PC1 and PC2) and the sum of second-generation (ΣSGAR) and first-generation anticoagulant rodenticide (ΣFGAR) concentrations in livers of coyotes from southern California, USA, 2015–2020. Dashed lines in the plot of ΣSGAR concentrations versus PC1 show predictive values of final median regressions for road-killed and euthanized coyotes separately, based on the PC1×cause interaction.

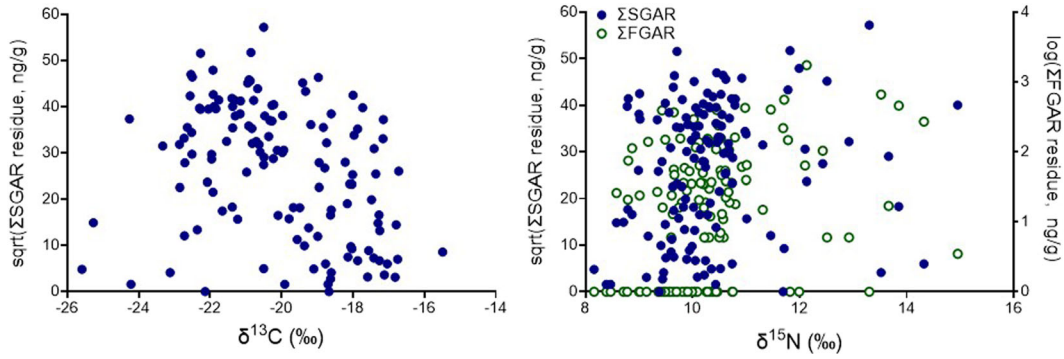

FIGURE 7 Scatterplots of liver second-generation (ΣSGAR) and first-generation anticoagulant rodenticide (ΣFGAR) residue concentrations (ng/g) and stable C and N isotope values of 129 urban coyotes from southern California, USA, 2015–2020.

only factor with evidence of an effect (Table 2). Neither $\delta^{13}C$ nor $\delta^{15}N$ had a relationship with median ΣFGAR concentration.

Domestic cats, mesocarnivores, and anthropogenic resources such as fast food and pet food tended to have more enriched $\delta^{13}C$ values compared to commensal and wild rodents and rabbits (Figure 8). Mesocarnivores, commensal rodents, and cats had higher mean $\delta^{15}N$ values than wild rodents, rabbits, and anthropogenic foods. Collectively, these results suggest that AR residue concentrations were highest for coyotes consuming primarily C_3-based prey (lower $\delta^{13}C$; e.g., rodents and rabbits) in areas with less-intensive development (lower PC1) and more natural open space (higher PC2) and increased as coyotes ate more prey from relatively higher trophic positions (higher $\delta^{15}N$), such as commensal rodents and mesocarnivores. Coyotes living in areas with more medium- and high-intensity development and higher building densities had enriched $\delta^{13}C$, suggesting that they consumed more cats and anthropogenic foods.

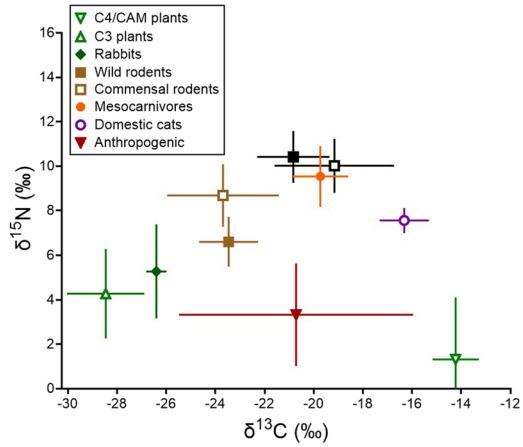

FIGURE 8 Mean (±1 SD) stable C and N isotope values of potential prey of urban coyotes in southern California, USA, 2017–2024. Samples sizes: C_4 and crassulacean acid metabolism (CAM) plants (3), mesocarnivores (6), domestic cats (343), anthropogenic foods (22), commensal rodents (67), wild rodents (14), rabbits (6), C_3 plants (19). For illustration purposes, mean isotope values of exposed coyotes are plotted as black squares, with the filled symbol showing concentrations in the upper 30% of second-generation anticoagulant rodenticide residue concentrations (ΣSGAR ≥ 1,262 ng/g, $n = 43$) and the open symbol showing concentrations in the lower 30% (ΣSGAR ≤ 279 ng/g, $n = 38$) of all ΣSGAR values. The $\delta^{13}C$ ($U = 392$, $P < 0.001$) and $\delta^{15}N$ ($U = 585$, $P = 0.028$) values differed between the 2 groups of ΣSGAR concentrations.

Necropsies and body condition

Three of 92 rural coyotes examined (3.3%) showed obvious signs of sarcoptic mange infection; 1 had a low liver diphacinone concentration (32 ng/g), whereas the other 2 had no detectable residues. Of the 501 carcasses of urban coyotes from Los Angeles County and Orange County examined, 6 (1.2%) had severe mange symptoms, 4 of which were tested for AR residues. Livers of these animals had 2 or 3 SGAR compounds, with a median ΣSGAR concentration of 364.6 ng/g (range = 99–2288 ng/g), and 1 FGAR, with a median ΣFGAR concentration of 26.1 ng/g (range = 24–368 ng/g). Overall, mange was uncommon (1.5%) in the 593 animals that we examined, and AR exposure of coyotes with mange was similar to or lower than that of the sample as a whole (Table 1).

For the 50 urban coyotes we necropsied, BCS was positively correlated with KFI (Spearman $r = 0.31$, $P = 0.030$) but we found no evidence it was related to helminth load ($r = -0.23$, $P = 0.115$; helminth prevalence = 88%, median intensity = 22.5 helminths/infested host). Summed residue of first-generation compounds (ΣFGAR) was inversely related to KFI ($r = -0.28$, $P = 0.047$) and positively correlated with helminth load ($r = 0.29$, $P = 0.039$) but did not vary with BCS ($r = -0.07$, $P = 0.623$). We did not find evidence of relationships between measures of body condition and ΣSGAR concentration ($P \geq 0.642$) or the number of AR compounds detected ($P \geq 0.140$). Of the 34 coyotes that had been euthanized, 8 had no evidence of gross internal and subcutaneous hemorrhaging (rating = 0), whereas 3 had very high levels (rating = 5). We combined euthanized coyotes with hemorrhage intensity ratings of 0 and 1 and ratings of 4 and 5 to create 4 bins of similar sample size (7–10) and permit statistical comparisons. Based on BCS values, coyotes with high levels of hemorrhaging were in visibly poorer condition than those with less hemorrhaging (Kruskal-Wallis: $H = 11.90$, $k = 4$ groups, $P = 0.008$; Table 3), but neither KFI values ($H = 1.15$, $P = 0.764$) nor helminth loads ($H = 1.00$, $P = 0.801$) differed across hemorrhage intensity groups. None of the euthanized coyotes were exposed to <2 AR compounds, and except for 1 animal with no FGAR residues, all were exposed to both FGARs and SGARs. However, the number of AR compounds detected did not vary with hemorrhage intensity ($H = 0.367$, $P = 0.943$), nor did ΣFGAR ($H = 3.32$, $P = 0.345$) or ΣSGAR ($H = 1.96$, $P = 0.580$) concentration (Table 3).

TABLE 3 Results of necropsies of 34 euthanized coyotes (29 adults, 5 juveniles) collected in 2019 from urban Los Angeles County and Orange County, California, USA. Hemorrhage intensity was rated from 1–6 based on the relative amount of subcutaneous and internal hemorrhaging. Total anticoagulant rodenticides (ARs) shows the number of coyotes having 2–3 and 4–6 AR compounds in their livers (no necropsied coyotes had fewer than 2 ARs). We also present a veterinary body condition score (BCS) taking whole-number values from 1–5, the kidney fat index (KFI), and helminth load, which is the number of helminths in the intestines, divided by body mass in kilograms to account for size variation. We also provide summed liver concentrations of first-generation (ΣFGAR) and second-generation (ΣSGAR) AR compounds (in ng/g). For BCS, KFI, helminth load, and residue concentrations, values reported are medians (ranges).

Hemorrhage intensity rating	*n*	BCS	KFI (%)	Helminth load (count/kg)	Total ARs 2–3	Total ARs 4–6	ΣFGAR (ng/g)	ΣSGAR (ng/g)
0–1	10	3 (2–4)	15.7 (15.9–18.8)	0.5 (0.3–9.6)	2	8	52.6 (13.5–199.2)	530.0 (15.0–1,348.0)
2	9	3 (2–3)	17.4 (7.9–43.6)	2.5 (0.2–5.9)	1	8	30.2 (24.2–165.6)	1,027.0 (15.0–2,001.0)
3	8	2 (2–4)	15.3 (11.5–20.7)	2.0 (0–14.8)	2	6	58.6 (0–566.3)	641.4 (303.8–1,749.0)
4–5	7	2 (2)	15.3 (4.0–22.3)	3.6 (0–6.5)	2	5	23.9 (15.9–64.0)	421.6 (5.0–1,648.0)

DISCUSSION

Nearly all (>98%) of the 365 urban coyotes in southern California we tested were exposed to anticoagulant rodenticides, with most coyotes exposed to both SGARs and FGARs and to multiple SGAR compounds. Prevalence was much higher than that reported in large-sample studies of other North American carnivores (bobcat: 89%, Serieys et al. 2015; kit fox [*Vulpes macrotis*]: 74%, Cypher et al. 2014; fisher [*Pekania pennanti*]: 58%, Gabriel et al. 2012; 79%, Silveira et al. 2024) and European canids (e.g., red fox [*Vulpes vulpes*]: 84%, Tosh et al. 2011; grey wolf [*Canis lupus*]: 62%, Musto et al. 2024) and similar to that reported for mustelids from Europe (e.g., stone marten [*Martes foina*]: 99%; European polecat [*Mustela putorius*]: 95%, 79%; stoat [*Mustela erminea*]: 97%; least weasel [*Mustela nivalis*]: 95%; Elmeros et al. 2011, 2018; Sainsbury et al. 2018). Our data indicated that AR exposure increased with body mass and, to some degree, age, suggesting that larger and older coyotes had consumed more AR-contaminated prey in their lifetimes and consequently accumulated AR residues in their livers. Because commercial baits used to control rodent populations contain a single active AR ingredient (U.S. Environmental Protection Agency 2008), these coyotes must have been exposed repeatedly.

This result was in stark contrast to the rural coyotes that we sampled, which were exposed at a much lower frequency overall (47.1%) and usually to 1 SGAR or FGAR compound. Aside from a report of a single coyote tested from Kern County, central California, that had no detectable residues (McMillin et al. 2008), coyotes tested for AR exposure have been from urban and suburban settings. Primary and secondary poisoning of non-target wildlife by SGARs is a pressing environmental concern in agricultural areas of Europe and Asia (Hindmarch and Elliott 2018). However, in California at the time of our sampling, legal applications of SGAR compounds, the most toxic and environmentally persistent types of ARs (Hindmarch and Elliott 2018), were restricted to locations close to buildings or to protect water conveyance and on-farm transportation and would have only been available for sale by licensed dealers to certified applicators (California Department of Pesticide Regulation 2014). First-generation compounds were the only AR products legally available to kill rodents that damage field crops and rangeland, many of which are native species (e.g., California ground squirrels, deer mice, voles [*Microtus* spp.], gophers [*Thomomys* spp.]) that usually die belowground (Quinn and Baldwin 2014, Baldwin et al. 2021). Given the cost of applying rodenticides at large scales in rural and agricultural settings

and restrictions on the toxicants, baiting techniques, and timing of applications (Hueth et al. 1998, Sterner 2008), combined with the availability of alternative prey such as rabbits (*Sylvilagus* spp.), there may be relatively few AR-contaminated prey for coyotes on the rural landscape at any given time. This could explain why fewer rural coyotes were exposed to ARs and why fewer compounds were detected than in urban settings.

Liver residue concentrations of rural coyotes, notably SGARs, were also much lower than those of urban ones. Median ΣSGAR concentration of urban coyotes (802.3 ng/g) was more than 4 times the 200-ng/g potential toxicity threshold that has been used in other studies to describe lethal levels of SGAR exposure in mammals (Berny et al. 1997, Shore et al. 2003, Ruiz-Suárez et al. 2016, Elmeros et al. 2018, López-Perea et al. 2019), and is higher than SGAR concentrations of coyotes believed to have been killed by ARs. The 2 Colorado coyotes suspected by Poessel et al. (2015) of dying from AR intoxication had liver ΣSGAR concentrations of 176 and 1,205 ng/g, whereas 2 Massachusetts coyotes that were intentionally poisoned had liver brodifacoum residues of 542 and 733 ng/g (Way et al. 2006). Summarizing incident reports from across the United States (including those from Hosea [2000] and Riley et al. [2003]), Erickson and Urban (2004) described detectable ΣFGARs in 4 (median = 856 ng/g; range = 43–1,300 ng/g) and ΣSGARs in 18 (median = 280 ng/g; range = 30–930 ng/g) of 22 coyotes in California. Seven of the 34 euthanized coyotes (20.6%) we necropsied had high levels of hemorrhaging that arguably would have been fatal if the coyotes had not been killed, which is similar to the estimated fraction (23%) of coyote deaths attributed to toxicants reported by Moriarty et al. (2012). However, given the ubiquity of AR exposure in the large population of coyotes in southern California, and the high residue levels detected in animals that appeared asymptomatic and otherwise healthy, we believe it is premature to conclude that rodenticide poisoning is a significant source of mortality for coyotes compared to other causes such as vehicle strikes and targeted control, or that ARs have population-level effects.

Even if ARs are not the direct cause of many deaths, they could contribute to mortality through sublethal effects if they make coyotes susceptible to other factors (Rattner et al. 2014). For example, researchers have argued that exposure to ARs weakens the immune system of urban bobcats (Riley et al. 2007; Serieys et al. 2013, 2015, 2018), making them more vulnerable to death from notoedric mange (but see Kopanke et al. 2018). Sarcoptic mange was rare in the coyotes we sampled (1.5%), and coyotes with mange did not have unusually high levels of AR exposure. Urban coyotes with high ΣFGAR concentrations tended to be in poorer body condition, based on low kidney fat levels and high helminth loads, hinting at a possible sublethal effect of FGARs. Coyotes with the highest degree of hemorrhaging also consistently had the lowest body condition scores. Elmeros et al. (2011) similarly reported a negative correlation between body condition and liver SGAR concentrations in mustelids in Denmark. However, we found no clear connection between the intensity of hemorrhaging (as evidence of coagulopathy) and the number of ARs or liver residue concentrations in euthanized coyotes.

It has been suggested that sublethal exposure may also alter movements and behavior, making animals more susceptible to vehicle mortality (Shore et al. 2003, Sainsbury et al. 2018, Musto et al. 2021). Roadkill coyotes had higher ΣSGAR concentrations than euthanized ones, although we cannot assess whether AR exposure increased the likelihood of being struck. Necropsied roadkill coyotes had higher BCSs than euthanized ones ($U = 178.5$, $P = 0.039$) and did not differ in the other body condition measures ($P \geq 0.841$), suggesting that those killed by vehicles were not in poorer condition. Alternatively, AR exposure may simply be higher in places with a high risk of vehicle mortality, such as areas with large roads with high speed limits and traffic volumes that traverse or are adjacent to open space (Elliott 2008). We found that PC2, which reflected the type and amount of open space, was the best predictor of ΣFGAR concentration, with higher levels in locations with more grass and shrub cover. First-generation compounds such as diphacinone may be used to kill commensal and wild rodents (e.g., squirrels, mice, gophers) in larger and wilder yards farther away from structures, and in parks, golf courses, and cemeteries. The ΣSGAR concentrations of roadkill coyotes did not vary strongly with PC1, which increased with cover of medium- and high-intensity development and building density, but we also tended to have fewer roadkill coyotes in locations with high PC1 scores (Figure 6). Instead, for higher concentrations of ΣSGAR, ΣSGAR decreased with PC1 for euthanized coyotes, with those in the most heavily urbanized settings having lower ΣSGAR levels. We offer 2

possible explanations for these patterns, which are not mutually exclusive. First, coyotes living in these areas may have access to fewer AR-contaminated prey, either because AR use is lower or because coyotes select foods that are not exposed to ARs. Second, coyotes that are targeted for nuisance control may not persist in these areas long enough to accumulate high liver AR residue concentrations.

Surveys of residential landowners in southern California indicate that rodent control and use of ARs is higher in areas with single-family homes and in areas close to developed or natural open space (Morzillo and Schwartz 2011, Bartos et al. 2012). Based on reports of pests seen outdoors and damage to property or landscaping (Morzillo and Mertig 2011), rats and mice are the most common targets (Morzillo and Schwartz 2011). Landowners apply rodenticide themselves, obtain assistance from gardeners, or hire professional pest-control operators, all of whom differ in their understanding of how to use toxicants safely and diligently and of the risks of non-target exposure (Bartos et al. 2012). Although we do not have detailed information on demographic or spatial patterns of AR applications in our study area, we speculate that coyote locations with low-intensity development and altered open space (low PC1) and high cover of natural open space (high PC2) are in areas of relatively high AR use because these areas commonly have rat infestations (Burke et al. 2021). Bait stations are conspicuous and widespread in commercial, retail, and industrial settings, but we also lack specific data on AR use in these environments.

Coyotes living in more intensively urbanized areas may also be exposed to fewer ARs because they tend to consume large numbers of cats (Bucklin et al. 2023), a result that is consistent with our stable isotope analysis (Figure 8). Although stomach contents analysis may not necessarily reflect a predator's long-term diet, coyotes with cat remains in their stomachs (from Bucklin et al. 2023) had lower ΣSGAR residues and enriched $\delta^{13}C$ values compared to those with no cat remains in their stomachs (P. Stapp, California State University, Fullerton, unpublished data). Cats can be exposed to ARs (Mahjoub et al. 2022), but many cats in our study area live in small groups and colonies associated with trap-neuter-release programs and likely depend more upon provisioned pet food than potentially AR-contaminated prey. Moreover, attacking and killing pets is a major reason why these habituated coyotes are targeted for lethal control (Timm et al. 2004). More euthanized coyotes had cat remains in their stomachs than road-killed ones in a concurrent study (Bucklin et al. 2023). High population turnover and low residence times could help explain the lower ΣSGAR concentrations in euthanized coyotes from intensively urbanized settings, many of which were juveniles and exposed to fewer ARs.

Stable isotope analysis also helped elucidate pathways of secondary exposure of coyotes in less intensively developed, suburban areas. Based on their depleted $\delta^{13}C$ and enriched $\delta^{15}N$ values compared to possible food sources, these coyotes likely consumed commensal rodents and mesocarnivores. Non-native roof rats are the most widespread commensal rodent living outdoors in suburban Orange and Los Angeles County (Krueger et al. 2015). Although their diet has not been well-studied in commensal settings, these semi-arboreal rodents are known to eat fruits and seeds of native and cultivated plants, including avocados and citrus common in backyards, and small animals (Quinn 2024), which is reflected in their stable isotope signatures (Figure 8). Roof rats are a target of outdoor pest control applications in California, and although many likely die in concealed areas, carcasses are regularly seen in the open, where they may be scavenged by corvids, raptors, and mammals, including mesocarnivores and coyotes, often within 24 hours (Lotts and Stapp 2020). Virginia opossums, one of the most common mesocarnivores in urban southern California (Crooks 2002, Burke 2021), are capable of entering enclosed yards to consume rat carcasses, and juveniles enter AR bait stations and consume bait (Burke et al. 2021). Mesocarnivore remains were detected in 11% of the stomachs of coyotes from our study area (Shedden 2021), with opossums consumed most frequently (8%); however, because of their larger size, the importance of mesocarnivores may be under-represented based on stomach and scat contents studies compared to stable isotope analysis. Rodenticide residues were detected in livers of 2 euthanized raccoons from southern California, and multiple raccoons, opossums, and striped skunks from New York were exposed to SGARs (Erickson and Urban 2004), but there is remarkably little data on AR exposure of opossums and other mesocarnivores from California. Sainsbury et al. (2018) also reported that detection of SGAR compounds in European polecats in Great Britain increased with

whisker $\delta^{15}N$, which they attributed to consumption of higher trophic level prey, such as rats, that were contaminated with ARs.

Compared to our study area, AR exposure appears to be lower for coyotes in the Chicago, Illinois, area (no deaths attributed to ARs; Gehrt and Riley 2010), where the ecology of urban coyotes has been especially well-studied (Gehrt et al. 2011), which may indicate regional differences in the use of ARs for urban pest control, both by professionals and the public. Alternatively, the hospitability of the California climate and abundance of native and ornamental plants may permit roof rats to become common outdoor pests year-round (Quinn 2024). Moreover, the presence of small fragments of natural habitat in the urban and suburban matrix brings wild rodents into proximity to human development (Crooks 2002, Burke et al. 2021), where they may also be targeted for control. Coyotes in southern California differ markedly from those in other North American cities in consuming domestic cats and commensal rodents regularly (Shedden 2021), in addition to wild rodents and rabbits.

Lastly, we note that most of our sampling took place prior to the implementation of AB1788 and AB1322, which severely restricted availability and uses of SGARs and diphacinone, respectively, in California. Baits containing these compounds will likely remain in stockpiles and will continue to be applied illegally, or they may be purchased elsewhere and brought to the state. There are also exceptions to bans for protecting water infrastructure, food production and storage facilities, and public health and for removing harmful invasives on islands. A network for monitoring ARs in coyotes will aid in the assessment of the effectiveness of these new laws and identify areas of non-compliance, especially by private landowners. Our results also highlight that the risk of non-target exposure is much greater in the urban and suburban environment in California compared to agricultural and rural settings, which may warrant different mitigation strategies. It remains to be seen if the removal of ARs as a tool for commensal rodent management will result in increased use of acute toxicants such as bromethalin and cholecalciferol or a renewed emphasis on integrated pest management (trapping, exclusion, and management of waste and harborage; Quinn et al. 2019) that focuses mitigation efforts on the impact of commensal rodents as the main source of food web contamination. An enforced ban on outdoor feeding of wildlife and other animals, such as domestic cats, would significantly reduce food resources that subsidize rat populations and attract predators like coyotes, and therefore reduce opportunities for human–wildlife conflict.

MANAGEMENT IMPLICATIONS

The near-universal exposure of coyotes in southern California to ARs reflects how widespread and acceptable it is to apply rodenticides to control rodents perceived as pests. The availability of toxicants, both in retail stores and through the internet, including from out-of-state and international vendors, and their effectiveness compared to other more labor-intensive, expensive, and unsightly approaches such as landscape management and trapping, has arguably made chemical control the standard practice (Quinn et al. 2019). The ecology of commensal urban rodents remains poorly understood, and census methods are inadequate for assessing when control applications will be effective and when continuing them is counterproductive, including possibly contributing to genetic rodenticide resistance. Despite environmental awareness campaigns, many people prioritize a fast and inexpensive solution to the presence of rats and other rodents outdoors over potential risks to unseen, non-target species, and it is common practice to apply ARs prophylactically to a permanent network of bait stations, which leads to over-use. Because of their omnivorous habits and tolerance for human development, coyotes can be useful sentinels of environmental contamination from ARs and other pollutants, even if direct links between AR residue concentrations and mortality and sublethal effects at the population scale are tenuous at best. The ability to test ARs and other contaminants in samples collected less invasively (e.g., hair; Leporati et al. 2016) or scats (Sage et al. 2010, Seljetun et al. 2019), will improve monitoring capabilities, although assigning biological and environmental significance to residue concentration values, especially across different tissues, will remain a major challenge.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Mammal carcasses were obtained opportunistically (the authors had no involvement in decisions about the use and deposition of live animals) and were salvaged under valid Scientific Collecting Permits from the California Department of Fish and Wildlife. Some rodent tissue samples were collected as part of research approved under California State University Fullerton Institutional Animal Care and Use Committee protocol (#2022-1302) to P. Stapp, following ethical guidelines described by Sikes and Animal Care and Use Committee of the American Society of Mammalogists (2016). Ear tissue from domestic cats was donated by veterinarians who removed ear tips from anesthetized cats as part of trap-neuter-return sterilization programs.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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