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REVIEW

Global review of anticoagulant rodenticide exposure in wild mammalian carnivores

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Abstract

Anticoagulant rodenticides (ARs) are an effective tool used to suppress rodent populations in urban and agricultural settings to reduce human disease risk and economic loss, but widespread use has resulted in adverse effects on predators globally. Attention has largely been focused on impacts of ARs on raptors, although there is increasing evidence that mammalian carnivores are also impacted. We conducted a literature review to assess the extent to which ARs have been documented in wild mammalian carnivores globally and identify potential overlap with imperiled carnivores. We found a small but growing body of literature documenting exposure to ARs in 8 Carnivora families, with Mustelidae (64% of studies), Canidae (44%) and Felidae (23%) most represented. At least 11 different AR compounds were documented in carnivores, and authors claimed that exposure caused mortality of at least one individual in 33.9% of species studied. ARs were listed as a threat for 2% of Red List carnivores, although we found that 19% of Red List carnivores had ranges that overlap countries that have documented AR exposure in carnivores. Collectively, our review highlights the need to prioritize conservation attention on the potential role of ARs on global carnivore declines. We suggest (1) expanding AR monitoring and research outside of the northern hemisphere, (2) supporting long-term AR monitoring to understand the spatial and temporal variation of AR use and exposure risk, (3) expanding research across trophic levels and across the urban–wildland gradient and 4) research to further our understanding of the point at which morbidity and mortality occur.

Introduction

Terrestrial carnivore populations are declining globally due to various threats, particularly increasing interactions with humans (Ripple *et al*., 2014, Marneweck *et al*., 2021). The leading threats to carnivores are habitat loss and degradation resulting from human land use change (Ceballos & Ehrlich, 2002), followed by persecution due to human–wildlife conflict (Woodroffe, Thirgood, & Rabinowitz, 2005), unregulated harvest for traditional medicine, furs or other goods (Alves *et al*., 2013; Hiller & Vantassel, 2022) and depletion of prey (Ripple *et al*., 2014; IUCN, 2022). Humans can also indirectly threaten carnivores through introduction of domestic or invasive carnivores, facilitating spread of disease (e.g., between domestic and wild animals) and pollution (Wilcove & Master, 2005; Ripple *et al*., 2014; IUCN, 2022). An increasingly realized threat to carnivores globally is non-target exposure to pesticides (e.g., Thompson *et al*., 2014; Lohr & Davis, 2018; Rudd *et al*., 2018).

Anticoagulant rodenticides (ARs) are pesticides used to suppress rodent populations in urban and agricultural settings and though effective in reducing human disease risk and economic loss (Watt, Bradberry, & Vale, 2005; Battersby, 2015), widespread use has resulted in adverse effects for non-target wildlife globally (Nakayama *et al*., 2019). These pesticides inhibit vitamin K epoxide reductase, an important enzyme in the production of blood clotting factors (Rattner *et al*., 2014). Exposed animals typically experience prolonged blood clotting time, which can lead to lethal hemorrhaging and interference with organ function (Eason *et al.*, 2002; Fraser *et al.*, 2018). ARs are categorized as either first-generation (chlorophacinone, coumachlor, coumatetralyl, diphacinone, pindone, and warfarin) or second-generation (brodifacoum, bromadiolone, difenacoum, difethialone, and flocoumafen) based on chemical structure (Rattner & Mastrota, 2018). Second-generation ARs require less exposure encounters for effective poisoning (i.e., the dose required to kill 50% of a population, or LD50, is lower for second-generation ARs), have a higher chance of overdosing the target species, and may have a higher chance of bioaccumulating in non-target species than first-generation compounds due to longer half-lives of these compounds (Eason *et al.*, 2002; Watt, Bradberry, & Vale, 2005). Routes of exposure in wildlife include ingestion of bait (primary or direct exposure), consumption of poisoned target species (secondary exposure), and consumption of secondarily poisoned prey (tertiary exposure) (Fig. 1a) (López-Perea & Mateo, 2018; Nakayama *et al.*, 2019). Terrestrial species are most commonly reported; however, it has been surmised that aquatic species may face exposure risk via direct exposure or ingestion of poisoned carcasses that end up in aquatic environments (Regnery *et al.*, 2019).

AR exposure in mammalian carnivores can lead to several type of morbidity, including decreased body condition (Elmeros, Christensen, & Lassen, 2011), immune dysregulation (Fraser *et al.*, 2018; Serieys *et al.*, 2018), susceptibility to disease and ectoparasites such as mange (Riley *et al.*, 2007; Serieys *et al.*, 2013, 2015; Riley, Serieys, & Moriarty, 2014), and behavioral changes (Salim *et al.*, 2014; Parli *et al.*, 2020). ARs can also cause acute mortality (Murray, 2011; Thomas *et al.*, 2011; Serieys *et al.*, 2015; Niedringhaus *et al.*, 2021) or make species more susceptible to other means of mortality (Vidal *et al.*, 2009; Riley, Serieys, & Moriarty, 2014; Serieys *et al.*, 2015; Carrera *et al.*, 2023). AR-induced morbidity and mortality can even cause population-level declines, but research on this topic is relatively sparse (Salim *et al.*, 2014; Nogeire-McRae *et al.*, 2019; Rodríguez-Estival & Mateo, 2019). Currently, most ecological studies on non-target AR exposure are regional (Eason *et al.*, 2002; Thompson *et al.*, 2014; Weir, Thomas, & Blauch, 2018; Thornton *et al.*, 2022), exclusively examine raptors (e.g., Gomez, Hindmarch, & Smith, 2021), focus on one species or taxonomic family (e.g., Herring & Eagles-Smith, 2017), or are primarily aimed at identifying the pathways to exposure (e.g., Hindmarch & Elliott, 2018). While multiple reviews exist of AR detections in non-target species (e.g., Laakso, Suomalainen, & Koivisto, 2010; López-Perea & Mateo, 2018; Nakayama *et al.*, 2019), few

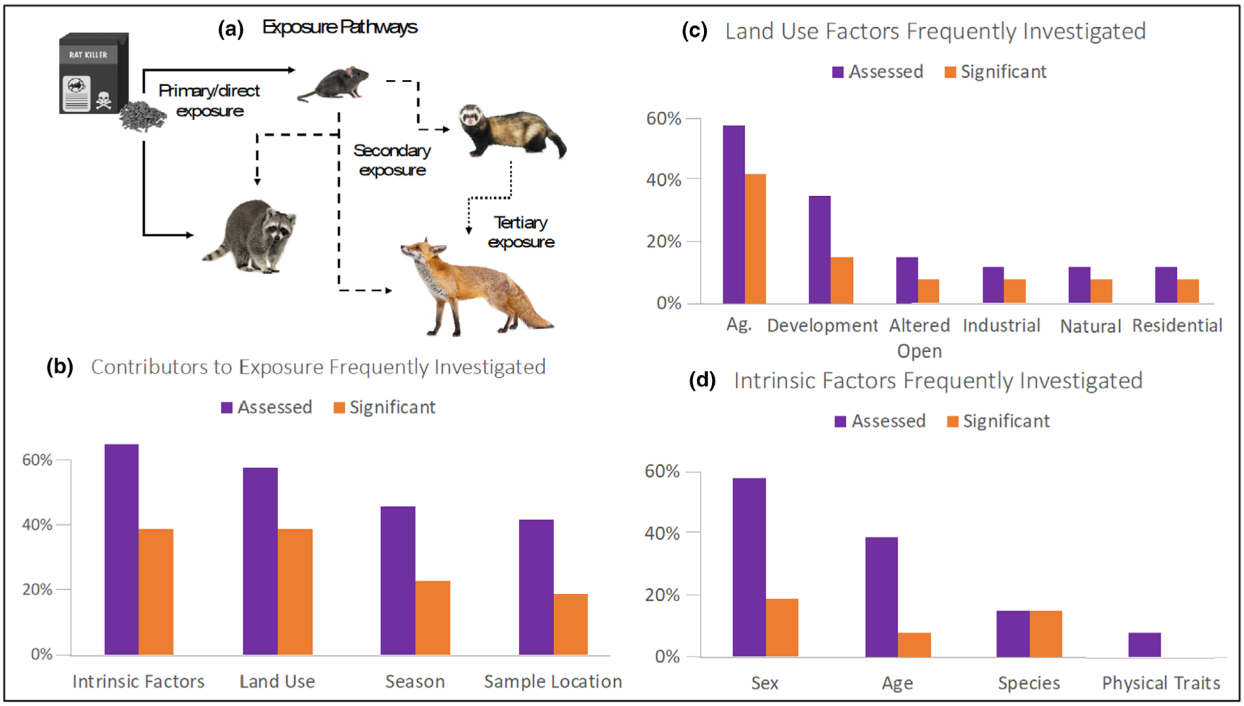

Figure 1 Diagram of primary (or direct), secondary and tertiary exposure pathways (a) by which carnivores are likely exposed to anticoagulant rodenticides (ARs). Summary of factors often investigated as contributing to AR exposure across 26 studies in our review (b). Intrinsic factors contributing to AR exposure were most frequently investigated and within that category species sex and age were commonly investigated (c). Land use was the second-most frequently investigated factor, with exposure most frequently found related to agriculture (including livestock) and development (d). Natural areas were negatively associated with exposure in all cases, and though Agriculture was always positively associated with exposure, some forms of agriculture, such as less productive farms, were less strongly positive. In one case, altered open areas were positively associated with second-generation ARs but negatively associated with first-generation ARs.

have been conducted recently and none focus exclusively on mammalian carnivores. Thus, a current review of AR exposure in mammalian carnivores is warranted.

We examined the literature to assess the extent to which ARs have been documented in wild mammalian carnivores globally. Our first objective was to summarize current AR research on mammalian carnivores. We recorded which species were monitored for ARs, which species have documented exposure, the percent of individuals documented to be exposed to ARs within studies, and where studies have taken place. We predicted that species with rodent-dependent diets would be more represented in studies than carnivores with more generalist diets and those that prefer larger-bodied prey, such as big cats. We also predicted that similar to meta-analyses of raptor exposure to ARs (e.g., Nakayama *et al*., 2019; Gomez, Hindmarch, & Smith, 2021), studies documenting AR exposure in mammalian carnivores would be concentrated in the northern hemisphere (Hickisch *et al*., 2019). We summarized which compounds have been detected and the biological samples used along with how often AR exposure is linked to morbidity, or ill effects, and mortality in the literature. Finally, to gain an understanding of where risk of exposure is greatest, we examined intrinsic (e.g., sex and age) and extrinsic (i.e., land use and season) factors investigated in predictive analyses of exposure within studies and summarized how often they had a significant effect on AR exposure.

Our second objective was to investigate how often ARs are a threat to terrestrial or semi-aquatic carnivores threatened with extinction. First, we examined species accounts for each International Union for the Conservation of Nature (IUCN) Red List mammalian carnivore and tallied the number of species that listed rodenticides as a threat. Given the relatively recent rise in concerns over ARs in carnivores and that the Red List status is infrequently updated for many mammalian carnivore species (Marneweck *et al*., 2021), we anticipated that species accounts might not reflect the actual risk of AR exposure to those species. Accordingly, we attempted to coarsely assess the potential for AR exposure in at-risk species by overlapping the range of Red List carnivore species with the location of studies that have documented AR exposure in mammalian carnivores.

Materials and methods

We conducted a literature search in September 2022 for publications on terrestrial or semi-aquatic mammals in the order Carnivora, excluding marine mammalian carnivores, families Phocidae (true seals), Otariidae (eared seals), Odobenidae (walrus), and feral domesticated species such as cats (*Felis catus*), dogs (*Canis familiaris*), and ferrets (*Mustela furo*). First, we searched the Web of Science database using the search term "*TS=*'*anticoagulant rodenticide$' AND TS=(*predator* OR *carnivore*)*." We limited our search to relevant papers that reported exposure data on wild animals, not laboratory animals, and publications classified as journal articles, academic theses, academic dissertations, academic reports, agency reports, or conference proceedings. To assess relevance, we scanned publication titles. If the relevancy was ambiguous, we scanned abstracts and downloaded potentially relevant publications for further review. We additionally used a "snowball" approach to examine the literature cited sections of relevant publications for additional papers that met our inclusion criteria (Prugh & Sivy, 2020). Finally, we searched the Google Scholar database using the search term "'*anticoagulant rodenticide' [predator OR predatory OR carnivore OR carnivorous]*." We examined the first 300 papers as sorted by "*Relevance*" and included any new relevant papers found. When new relevant papers were found, we reviewed the next 100 papers, repeating this process until no new relevant papers were found. We also documented whether the data were unique to the publication, which we considered to be data that were not reported elsewhere, and if data were published in two different formats we used the most recent journal article. We also conducted a second literature search using Web of Science and the search term "TS=(carnivore NOT marine)." Results from this search were only used to compare trends in publication rate over time (Appendix S1) and not used in subsequent analyses discussed.

For each publication, we recorded the year of publication, time period of data collection, the species assessed, the general location (i.e., country, province and/or state) of the study, the proportion of the individual species exposed to ARs, and the AR compounds and amounts, if listed. We also documented the methods for monitoring AR exposure and the potential vectors for exposure, if listed. We documented how often authors claimed exposure caused (a) morbidity and (b) mortality for at least one individual of a species by splitting publications into separate "species records" (one or more individuals of a species that were tested) if multiple carnivore species were assessed. To summarize the accounts of morbidity and mortality, we excluded data obtained from feces and data where multiple species were lumped together or only the genus was listed. For the mortality percentage, we also excluded species records where no AR residue was detected and records where the cause of death was known for all individuals at the time of sample collection (e.g., roadkilled, trapped or shot). Lastly, for papers that involved predicting exposure risk, we summarized support for factors predicted to impact AR exposure. We identified which covariates were used in each study and recorded whether or not the authors found a covariate to have a statistically significant effect on some metric of exposure. For covariates that were unique to one study (e.g., irrigation canals, horse ranches), we grouped variables as "other land use" and recorded whether the authors found at least one variable within that group to be statistically significant.

We downloaded species accounts of all Red List terrestrial and freshwater mammalian carnivores that are either extinct, critically endangered, endangered, vulnerable, or near-threatened as of November 2022 and searched for the term "rodenticide" (IUCN, 2022). To estimate the potential risk of AR exposure in imperiled mammalian carnivores, we downloaded the total range map (including sub-populations and subspecies) shapefiles for each carnivore species

(IUCN, 2022), and overlaid the range maps with our records of countries with documented AR exposure in carnivores (QGIS Development Team, 2022). We did not include any enclaves, territories, or overseas departments in our country borders.

Results

Literature search

Through our Web of Science search, we identified 334 potentially appropriate publications, of which 45 were determined to be relevant for our review (Appendix S2). The "snowball" and Google Scholar approaches resulted in the inclusion of 30 and 3 additional relevant publications, respectively. Thus, we evaluated a total of 78 publications for our review, of which 70.5% ($n = 55$) appeared to report completely unique exposure data, 20.5% ($n = 16$) appeared to have a combination of unique and repeat exposure data, and 9% ($n = 7$) appeared to not provide any unique exposure data and instead only report data from a previous publication in a different language or format. The latter were removed from the literature review as they added no new information, so from the remaining 71 publications, we defined 167 individual species records of exposure.

Trends in AR and mammalian carnivore research

We observed a small increase in AR-related publication rate (0.06 ± 0.04 papers per year) beginning in 1996, with never more than 7 publications in a given year (Appendix S2). In comparison, we saw a publication rate on terrestrial carnivores in general that was 200% larger (33.56 ± 1.76 papers per year) over the same period (Appendix S2). In 2022, there were over 1200 publications on terrestrial carnivores and only 2 of those investigated ARs. Of the 8 Carnivora families reported across the 78 publications in our literature search, Mustelidae was the most represented and was included in 64% of publications, followed by Canidae (44%) and Felidae (23%) (Fig. 2). The most represented species from each family consisted of the western polecat ($n = 16$ studies; *Mustela putorius*) and stoat ($n = 15$; *M. erminea*), red fox ($n = 23$; *Vulpes vulpes*), and bobcat ($n = 11$; *Lynx rufus*), respectively (Fig. 2). Of the 19 countries that produced publications, all but two were located in the northern hemisphere (Fig. 3). The US ($n = 24$), the UK ($n = 11$), France ($n = 8$) and New Zealand ($n = 8$) accounted for the majority of publications. Within the US, California accounted for nearly 80% ($n = 19$) of publications.

Of the 11 AR compounds reported in these studies, brodifacoum and bromadiolone (both second-generation ARs) were most frequently reported and were documented in over 66% of studies, in over 80% of study species, and in over 81% of study locations (Table 1). Across studies and compounds, percent exposure ranged from 0 to 100%, with an average of 32.77% (Appendix S3). The largest range of mean concentrations was reported for diphacinone (0.03–55 mg/kg), which included the highest reported mean concentration of any compound (Table 1, Appendix S3). However, excluding this outlier the largest range of mean concentrations were reported for bromadiolone (0.009–

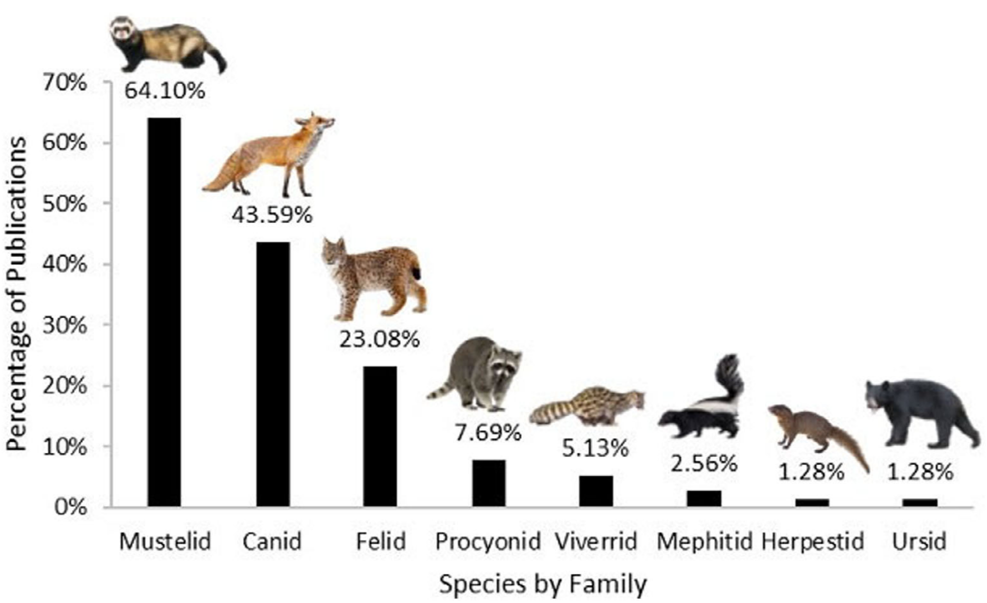

Figure 2 The percentage of publications (1988–2022) that included species belonging to Mustelidae, Canidae, Felidae, Procyonidae, Viverridae, Mephitidae, Herpestidae or Ursidae, respectively. The most reported species within each family is pictured, represented by the western polecat (*Mustela putorius*), red fox (*Vulpes vulpes*), bobcat (*Lynx rufus*), raccoon (*Procyon lotor*), common genet (*Genetta genetta*), striped skunk (*Mephitis mephitis*), water mongoose (*Atilax paludinosus*), and American black bear (*Ursus americanus*), respectively. Mustelidae was also highly represented by stoats (*Mustela erminea*), which had one less species record than western polecats.

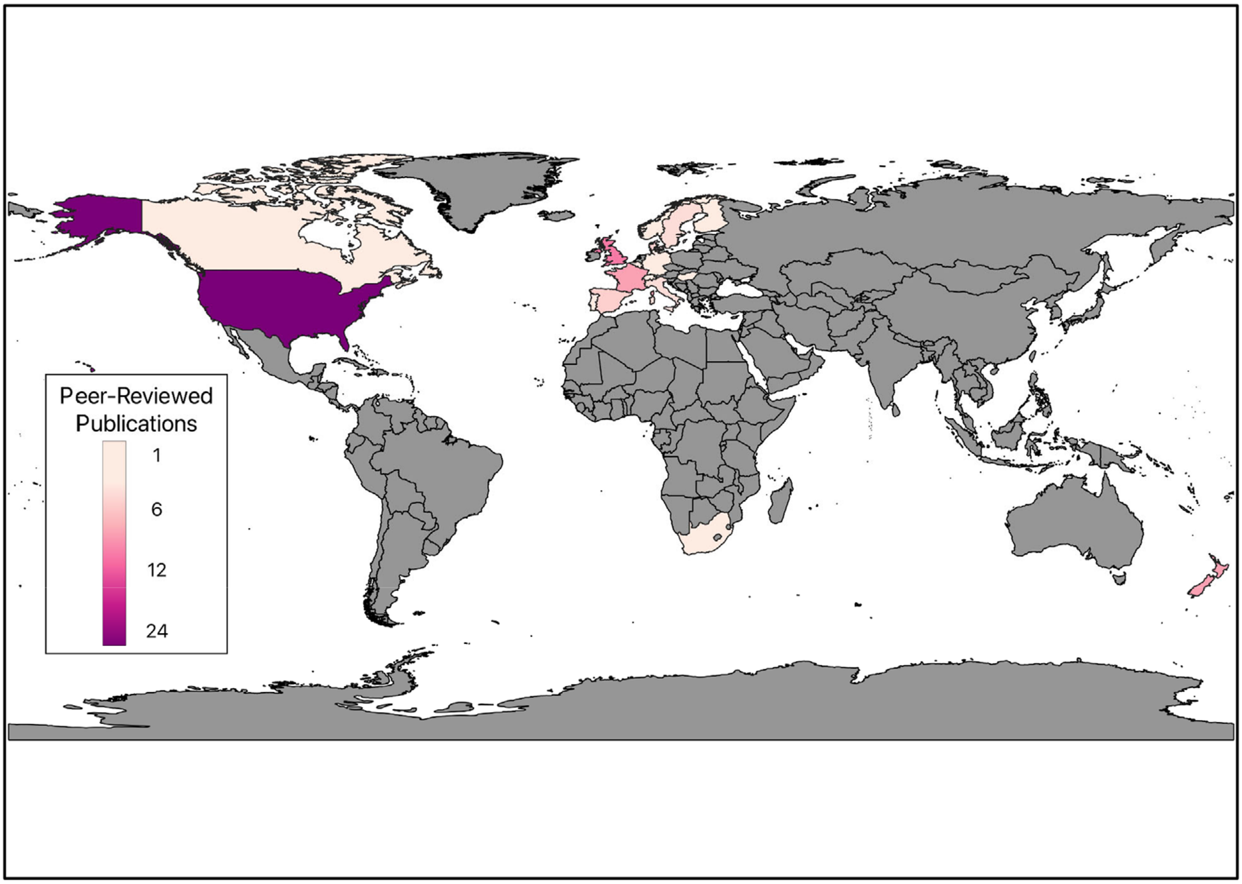

Figure 3 Countries with publications that met our inclusion criteria. Publication frequency varies from 1 to 24 as represented by the light to dark color scale. The majority of publications are limited to the northern hemisphere, specifically North America and Western Europe.

Table 1 The reported range of mean concentrations of anticoagulant rodenticide (AR) compounds found in our review of mammalian carnivore literature, along with the number of studies that reported those compounds in an animal belonging to a Carnivoran family and by country between 1988 and 2022. The specified families represent the most studied families and the countries represent the top four countries by number of confirmed cases in our review

Compound	Mean conc. range (mg/kg)	Family					Country					
		Mustelid	Canid	Felid	Other	Total	U.S.	U.K.	France	New Zealand	Other	Total
Brodifacoum	0.002–2.93	40	24	11	9	84	33	8	0	12	31	84
Bromadiolone	0.009–6.6	41	27	11	11	90	25	14	12	0	39	90
Difenacoum	0.003–0.85	27	14	2	4	47	3	12	1	0	31	47
Difethialone	0.001–5.7	13	5	8	2	28	10	1	1	0	16	28
Flocoumafen	0.0002–0.35	12	6	0	1	19	0	2	0	1	16	19
Chlorophacinone	0.013–5.5	6	9	4	2	21	14	0	4	0	3	21
Coumachlor	Not reported	0	1	0	0	1	0	0	0	0	1	1
Coumatetralyl	0.0018–0.68	14	13	0	0	27	2	5	1	0	19	27
Diphacinone	0.03–55[a]	1	4	8	5	18	18	0	0	0	0	18
Pindone	6.93[b]	0	1	0	0	1	1	0	0	0	0	1
Warfarin	0.001–0.37	4	6	3	0	13	4	1	1	1	6	13
Unspecified AR	Not reported	12	7	4	0	23	7	0	8	0	8	23

[a] These high concentrations were reported in Littrell (1988).

[b] Only one concentration reported (Erickson & Urban, 2004).

6.6 mg/kg), difethialone (0.001–5.7 mg/kg), and chlorophacinone (0.013–5.5 mg/kg), respectively (Table 1, Appendix S3). Liver was the most commonly tested tissue, appearing in 88.73% ($n = 63$) of the 71 publications included in our review. Alternative samples included blood (11.27%, $n = 8$), other organs or tissues (8.45%, $n = 6$), feces (4.23%, $n = 3$), digestive contents (2.82%, $n = 2$), and thoracic and abdominal fluid (1.41%, $n = 1$). Further, we found that authors claimed exposure caused morbidity for at least one individual in 33 of 161 (20.49%) applicable species records (Table 2); however, these records only included canids, felids, mephitids, mustelids and procyonids. Abdominal or thoracic cavity hemorrhages ($n = 31$ reports) were the most frequently reported symptoms and accounted for over half (52%) of reported symptoms, most of which were canids ($n = 11$) or mustelids ($n = 17$, Table 2). Pulmonary hemorrhages ($n = 6$) and edema ($n = 5$) were the only symptoms reported in all five families, though at low rates (Table 2). We found that authors claimed exposure caused mortality for at least one individual in 40 of 118 (33.90%) applicable species records. Exposure vectors were rarely conclusively identified, but often linked to rodents.

We found that 26 studies conducted analyses across 24 covariates to assess potential contributors to AR exposure (Appendix S4). Intrinsic factors were assessed in 62% ($n = 16$) of studies and were the most frequently included covariates (Fig. 1b). These factors included sex (54% of studies, $n = 14$), age (38%, $n = 10$), species (15%, $n = 4$), and physical traits (12%, $n = 3$) (Fig. 1c). Land use was also frequently included and accounted for in 58% ($n = 15$) of studies (Fig. 1b). Within those 15 studies, land use was most often broken into agriculture or livestock (73% of studies, $n = 11$), human development (60%, $n = 9$), natural or forested areas (33%, $n = 5$), altered open space (27%, $n = 4$), industrial (20%, $n = 3$), and residential (20%, $n = 3$, Fig. 1d). Other common covariates were season, included in 42% of studies, sample collection location (i.e., course scale area, region or sub-population range; 42%) and time period of sample collection (i.e., before and after some treatment; 31%). Statistically significant variables most often fell into time period (63% of studies that included this covariate), agriculture (69%), season (55%), sample collection location (55%), and sex (36%, Fig. 1).

The potential threat of ARs to threatened carnivores

Only 3 of the 34 species covered in our literature review that had evidence of AR exposure are of global conservation concern: the African clawless (*Aonyx capensis*) and Eurasian (*Lutra lutra*) otters, both near-threatened, and the critically endangered European mink (*Mustela lutreola*). Within the US, 3 species that had evidence of AR exposure are listed under the Endangered Species Act: the threatened Pacific

Table 2 Tally of reported symptoms from 33 individuals across 19 publications that reported morbidity in one or more individuals within Canidae, Felidae, Mephitidae, Mustelidae and Procyonidae

	Symptom	Canidae	Felidae	Mephitidae	Mustelidae	Procyonidae	Select literature
Hemorrhaging	Abdominal or thoracic cavity	11	2		17	1	Riley et al. (2007), Gabriel et al. (2012), Cypher et al. (2014), Poessel, Breck, Fox, & Gese (2015), Serieys et al. (2019)
	Gastrointestinal tract		1		1	1	Littrell (1988), Ruder et al. (2011)
	Inter/ intramuscular					1	Stone, Okoniewski, & Stedelin (1999)
	Intrauterine					1	Stone, Okoniewski, & Stedelin (1999)
	Lungs	1	2	1	1	1	Stone, Okoniewski, & Stedelin (1999)
	Nasal/oral		1		1	1	Littrell (1988), Alterio, Brown, & Moller (1997)
	Stomach				1		Martin, Delheimer, Gabriel, Wengert, & Moriarty (2022)
Poor body condition	Emaciation	1					Way, Cifuni, Eatough, & Strauss (2006)
	Low blood volume in major vessels					1	Stone, Okoniewski, & Stedelin (1999)
	Lesions	1			3		Fournier-Chambrillon et al. (2004)
	Observed weakness		1				Littrell (1988)
	Pallor of tissues or organs	1					Stone, Okoniewski, & Stedelin (1999)
Excess fluid	Edema	1	1	1	1	1	Littrell (1988), Stone, Okoniewski, & Stedelin (1999), Ruder et al. (2011)
	Hyperemia				1		Fernandez-de-Simon *et al.* (2022)

Abdominal or thoracic cavity hemorrhages were most frequently reported. Representative citations are included.

marten (*Martes caurina*), the Pacific fisher (*Pekania pennanti*), and the San Joaquin kit fox (*Vulpes macrotis mutica*), both endangered (U.S. Fish and Wildlife Service, 2022). In our review of Red List species accounts, the term "rodenticide" was only listed as a threat for the vulnerable marbled polecat (*Vormela peregusna*) and the endangered dhole (*Cuon alpinus*; IUCN, 2022).

We found that 18% of Red List imperiled mammalian carnivore species have range overlap with countries that documented AR exposure in mammalian carnivores. Of the 17 Red List species with ranges overlapping countries with AR exposure, 14 were not represented in our literature review (Table 3). Species range overlaps ranged between 1.8% (African Wild Dog [*Lycaon pictus*]) and 100% (black-footed ferret [*Mustela nigripes*], Iberian lynx [*Lynx pardinus*], island fox [*Urocyon littoralis*] and red wolf [*Canis rufus*]) with a mean range overlap of 38.26% (Table 3). Of the species with ranges overlapping AR-exposed carnivores, the red wolf is critically endangered and the African wild dog, black-footed ferret, Iberian lynx, and sea otter (*Enhydra lutris*) are endangered (Table 3).

Table 3 Percent range overlap of IUCN Red List carnivores and countries with documented AR exposure

Species	Common name	IUCN designation	Percent overlap
Canis rufus	Red Wolf	CR	100
Lynx pardinus	Iberian Lynx	EN	100
Mustela nigripes	Black-footed Ferret	EN	100
Urocyon littoralis	Island Fox	NT	100
Spilogale putorius	Eastern Spotted Skunk	VU	99.1
Felis nigripes	Black-footed Cat	VU	49.9
Parahyaena brunnea	Brown Hyena	NT	33.9
Ursus maritimus	Polar Bear	VU	17.7
Mustela lutreola[a]	European Mink	CR	12.4
Lutra lutra[a]	Eurasian Otter	NT	9.5
Aonyx capensis[a]	African Clawless Otter	NT	8.8
Hydrictis maculicollis	Spotted-necked Otter	NT	4.8
Panthera pardus	Leopard	VU	4.4
Acinonyx jubatus	Cheetah	VU	3.1
Enhydra lutris	Sea Otter	EN	2.6
Panthera leo	Lion	VU	2.4
Lycaon pictus	African Wild Dog	EN	1.8

Percent overlap was calculated by overlapping total species range distributions, including sub-populations and subspecies, with the boundaries of countries that have documented anticoagulant exposure. IUCN designations refer to near threatened (NT), vulnerable (VU), endangered (EN) and critically endangered (CR).

[a] Represented in our literature review.

Discussion

Anticoagulant rodenticides have been documented in an increasingly wide diversity of carnivores at multiple trophic levels, ranging from large apex carnivores to small mesocarnivores (Appendix S3). AR exposure has been linked to morbidity, individual mortality, and even population-level declines in mammalian carnivores. For example, in coyotes (*Canis latrans*) in southern California, non-target exposure to ARs was the second-leading source of mortality (Riley *et al*., 2003; Gehrt & Riley, 2010). In western Europe, least weasel (*Mustela nivalis*) and stoat (*M. erminea*) populations declined at sites treated with ARs (Fernandez-de-Simon *et al*., 2019). However, relative to other topics, research on ARs only represents 0.5% of all carnivore-related research. This is despite the projected increase of AR use globally into the future (Grand View Research, 2021; Market & Market, 2022). Thus, research on ARs in mammalian carnivores is a small but gradually growing body of research that deserves additional attention as an emerging threat to declining carnivore populations globally.

Anticoagulant rodenticide detection is widespread across a diversity of mammalian carnivore families and trophic levels. As predicted, members of Mustelidae are the most represented in the literature, accounting for over 52% of species records found in our literature review. Many Mustelids are highly carnivorous rodent specialists and may be studied more frequently because of their direct link to rodents and potential exposure to ARs (McDonald *et al*., 1998; Rodríguez-Estival & Mateo, 2019), high level of endangerment and conservation concern (Dobson & Lyles, 2000; Fournier-Chambrillon *et al*., 2004), or monitoring through investigations into Mustelid control efforts (Alterio & Moller, 2000). Nevertheless, a wide variety of species with different dietary habits and at different trophic levels are documented as having AR exposure. Canidae, the second-leading family documented in the literature, represents a set of species (Padilla & Hilton, 2014), which we predicted would be less represented in the literature. Felidae, the third-leading family, was represented in part by Eurasian lynx (*Lynx lynx*) and mountain lion (*Puma concolor*), both of which primarily consume ungulates (Moriarty *et al*., 2012; Khorozyan & Heurich, 2023), suggesting that a direct link to rodent predation is not the only pathway to exposure (Riley *et al*., 2007; Rudd *et al*., 2018). This is supported by research by Jacquot (2013), Serieys *et al*. (2019), and Fernandez-de-Simon *et al*. (2022), who found that diet was not a significant factor in exposure risk, and by Gabriel *et al*. (2012) and Serieys *et al*. (2015) which documented exposure in fetal or nursing individuals. The documentation of AR exposure in Eurasian (*Lutra lutra*; Fournier-Chambrillon *et al*., 2004, Lemarchand, Rosoux, & Berny, 2010, and others) and African clawless otters (*Aonyx capensis*, Serieys *et al*., 2019) identified in our review, along with more recent research on Eurasian (Regnery *et al*., 2024) and North American river (*Lontra canadensis*; Facka *et al*., 2023) otters, suggests that ARs may also be a threat to those primarily aquatic and piscivorous species. The wide variety of species representation in our review supports the notion that ARs are not limited to any one trophic level and are cascading up the food chain (Littrell, 1988; Riley *et al*., 2007).

We found numerous AR compounds documented in the literature, but perhaps most concerning is the dominance of brodifacoum and bromadiolone. Second-generation ARs, such as brodifacoum and bromadiolone, are far more potent than first-generation compounds and have high liver retention rates (e.g., as long as 100–300 days; Vandenbroucke *et al*., 2008), which may affect the frequency in which they are detected (Eason *et al*., 2002; Erickson & Urban, 2004; Watt, Bradberry, & Vale, 2005; Wobeser, 2005) and the duration over which prey may remain toxic to predators (Eason *et al*., 2002). Brodifacoum and bromadiolone have the longest half-lives in the liver, followed by two other second-generation ARs, difethialone and difenacoum (Vandenbroucke *et al*., 2008; Herring & Eagles-Smith, 2017), and together represent the most-detected compounds in the mammalian carnivore literature. We were unable to find LD50 values for mammalian carnivores, but research into avian toxicity suggests that brodifacoum and difethialone have the lowest LD50 (i.e., highly toxic) in avian raptors, while bromadiolone has the highest LD50 in avian raptors (i.e., moderately toxic) (Erickson & Urban, 2004; Herring & Eagles-Smith, 2017). First-generation ARs such as chlorophacinone, diphacinone, and warfarin are considered slightly to moderately toxic in the avian raptor literature but are much less represented in our literature review (Herring & Eagles-Smith, 2017). The most detected first-generation AR was coumatetralyl, which has reportedly high liver retention in mammals (Crowell *et al*., 2013), suggesting that liver retention rates affect detection more than potency. While it is not possible to translate lethal dose equivalents to unstudied mammalian carnivores, many of our reported mean concentrations far exceed any LD50 values reported in the avian literature. Despite a lack of research on lethal doses in mammalian carnivores, mortality has been strongly linked to wildlife in the currently extant literature across both first- and second-generation compounds (Riley *et al*., 2003; Gabriel *et al*., 2012; Serieys *et al*., 2019). Further, multiple-compound exposure could lead to increased vulnerability to acute toxicity by both first- and second-generation compounds (Rattner *et al*., 2020). The underrepresentation of first-generation ARs in our review should not be interpreted as an indication that they are used less or that they are not a threat to wildlife. Further, additional research into the threshold of ill-effects of AR compounds is warranted, but it is not the only information needed to interpret the current threat to wildlife.

Mammalian carnivore and AR research was primarily produced in the US, followed by the UK, France and New Zealand. While not unexpected given the global northern predominance in research production (Hickisch *et al*., 2019), this pattern is likely not representative of non-target AR exposure risk. For example, only one publication was produced on the subject in South Africa despite ARs being readily available at a non-commercial level and unrestricted in residential use (Serieys *et al*., 2019). We found no research on AR exposure in mammalian carnivores in South America where ARs such as bromadiolone are used in at least some regions of the continent (León, Fraschina, & Busch, 2020). ARs are also commonly used in Asia, with over 30 years of documented residential and agricultural use in China (Ma *et al*., 2018) and southeast Asia (Ravindran, Noor, & Salim, 2022), and with documentation of non-target AR exposure in raptors in both Taiwan (Hong *et al*., 2019) and Malaysia (Naim *et al*., 2010). While we did not find research on mammalian carnivores and ARs in southeast Asia, common palm civets (*Paradoxurus hermaphroditus*), leopard cats (*Prionailurus begalensis*), and, to a lesser extent, Malay civets (*Viverra tangalunga*) have been documented in palm oil plantations in Indonesia where ARs are frequently used, and all three species are frequent or occasional predators of rodents (Jennings *et al*., 2015; Ravindran, Noor, & Salim, 2022). Given Africa and Asia are home to over half of all Red List carnivore species (IUCN, 2022), we encourage particular attention to the potential threat of ARs to imperiled carnivores in these regions.

Accounts of morbidity or mortality were not documented for each species record, likely because most sampling was often via deceased, unmarked animals. Additionally, it is difficult to directly link AR exposure to morbidity or mortality in wild populations (López-Perea & Mateo, 2018). Our findings of higher reported mortality rate than morbidity rate is likely an artifact of how ARs are typically evaluated through analysis of liver tissue, where toxins and toxicants accumulate and persist, potentially revealing a history of exposure rather than just recent exposure (Imran *et al*., 2015), and where the animal has been found dead or killed. However, liver sampling typically requires finding a dead animal before the carcass begins to decay, which is difficult in individuals that have not been harvested or marked for radio telemetry studies, such that much of the evidence of rodenticide exposure likely goes undiscovered by researchers. Further, a lack of non-invasive or live sampling may lead to missed morbid symptoms. For example, hemorrhaging was the most frequently reported exposure symptom in the literature, and included bleeding from the nose (Alterio, Brown, & Moller, 1997), in abdominal or thoracic cavities (Riley *et al*., 2007; Uzal *et al*., 2007; Gabriel *et al*., 2012; Poessel *et al*., 2015; Serieys *et al*., 2019), gastrointestinal tracts (Littrell, 1988; Ruder *et al*., 2011), lungs (Stone, Okoniewski, & Stedelin, 1999), and stomachs (Martin *et al*., 2022), most of which occur internally and may otherwise go unnoticed. Symptoms like immune dysregulation occur at the genome- and cellular-level and require specialized investigation, thereby likely going undetected through most post-mortem investigations (Fraser *et al*., 2018; Serieys *et al*., 2018). Other examples of morbidity reported in the literature include edema (Littrell, 1988; Stone, Okoniewski, & Stedelin, 1999; Ruder *et al*., 2011), emaciation (Way *et al*., 2006), hemothorax (Ruder *et al*., 2011), hyperemia (Fernandez-de-Simon *et al*., 2022), lesions (Fournier-Chambrillon *et al*., 2004), low blood volume in major vessels (Stone, Okoniewski, & Stedelin, 1999), pallor of tissues or organs

(Stone, Okoniewski, & Stedelin, 1999), and observed weakness in live animals (Littrell, 1988). Without lethal sampling, these morbidity symptoms would be unlikely to be linked to AR exposure and our reported morbidity levels are likely conservative. The development and use of non-invasive AR sampling, such as via fecal tests (Seljetun *et al.*, 2019, 2020), could allow managers to passively monitor AR exposure levels in wildlife populations and better link exposure with behavioral monitoring and assessments of animal health, such as signs of morbidity. Additionally, prothrombin time testing via simple blood draws (e.g., in wildlife captured for radio-collar studies) could be informative for widespread assessments of exposure (Hindmarch, Rattner, & Elliot, 2019), however it should be noted that this is not effective for all taxa, particularly felids (Fraser *et al.*, 2018, Serieys *et al.*, 2018). More so, many non-invasive and antemortem sample techniques can produce false negatives where compounds are present but undetected and different tissue types can produce different exposure concentrations (Serieys *et al.*, 2015; Rached *et al.*, 2023). Finally, conclusively linking AR exposure to morbidity and mortality is difficult without strong experimental design (e.g., Serieys *et al.*, 2018; Fernandez-de-Simon *et al.*, 2019), which itself is difficult to achieve in a field setting, however such monitoring is an important first step in better understanding the non-lethal impacts of ARs in wildlife.

Contributors of exposure, when identified, included spatial, demographic and temporal factors. Across studies, there was nuance to every variable with the exception of physical attributes (i.e., weight, length), which were consistently found to be insignificant in predicting exposure (Sainsbury *et al.*, 2018; Fernandez-de-Simon *et al.*, 2022). Several studies positively correlated exposure with human development (Riley *et al.*, 2007; Geduhn *et al.*, 2015; Elmeros *et al.*, 2018), but not all (Thompson *et al.*, 2014; Lestrade *et al.*, 2021; Fernandez-de-Simon *et al.*, 2022). In some cases, this variable was further specified as residential, commercial, and industrial areas (Cypher *et al.*, 2014; Serieys *et al.*, 2015), but these variables differed in their ability to explain variation in AR exposure across studies. In one example, San Joaquin kit foxes (*Vulpes macrotis mutica*) that spent time on golf courses were more likely to test positive for second-generation ARs than those that spent time in commercial areas, but were less likely to test positive for first-generation ARs than those in industrial areas (Cypher *et al.*, 2014). Further, the method for assessing the influence of land use types can lead to different results. For example, in the same study area, Serieys *et al.* (2015) found a negative correlation between natural areas and AR exposure, but Riley *et al.* (2003) found it to be insignificant in predicting exposure. There was also relatively little agreement about the significance of sex, and when it was found to be significant it was different for males and females across studies (Elmeros, Christensen, & Lassen, 2011 found female least weasels to be more likely to be exposed while Gabriel *et al.*, 2015 found male Pacific fishers to be more likely to be exposed). Similarly, when season was identified as a significant contributor to exposure, it was often different seasons across studies (Elmeros, Christensen, & Lassen, 2011; Serieys *et al.*, 2015; Elmeros *et al.*, 2018; Seljetun *et al.*, 2019). While covariates were not consistently measured across individual studies, taken together, it is evident that contributors to exposure are context-dependent and variable across the urban– and agricultural–wildland interface.

While few IUCN Red List threatened species list ARs as a current threat, species range distributions suggest ARs could be an unrecognized threat for at least 18% of Red List terrestrial carnivore species. The ranges of the endangered black-footed ferret, endangered Iberian lynx, near-threatened island fox, and critically endangered red wolf, for example, do not list ARs as a threat despite having range entirely within countries where documented carnivore AR exposure has occurred, highlighting the need for AR monitoring in these carnivores (Table 3). Further, each of these species has a limited range and feeds either primarily (black-footed ferret) or partially (Iberian lynx, island fox, and red wolf) on rodents (McVey *et al.*, 2013; Brickner *et al.*, 2014; Boscaini *et al.*, 2015), which could potentially indicate a larger risk of non-target AR exposure for these species (Lestrade *et al.*, 2021). For species without entire range overlaps with documented AR exposure, a reevaluation of the unrecognized threat of ARs seems prudent. The range of the black-footed cat (*Felis nigripes*) overlaps with South Africa by nearly half (49.9%), a country with documented AR exposure in carnivores and little regulation of AR compounds, and preys almost exclusively upon rodents (Renard *et al.*, 2015; Serieys *et al.*, 2019). Nearly a third (33.9%) of the range of brown hyenas (*Parahyaena brunnea*) also overlaps with South Africa and they are known to hunt small mammals when their primary food source, carrion, is not readily available (Slater & Muller, 2014). We also note that while predators that generally shy away from human development are expected to have relatively low risk of exposure, illegal human activity in or around protected or wildland areas can be a source of AR exposure (e.g., Thompson *et al.*, 2014; Franklin *et al.*, 2018). We identified several other species ranges which overlapped with documented AR exposure by a third or less (Table 3), indicating a potential for localized population effects of ARs in these regions. While our use of range overlap is simplistic given the known contribution of land use, species life history, and temporal factors that can contribute to exposure (see above), we believe it is still informative in highlighting the potential for AR exposure risk in many imperiled carnivore populations globally.

Despite the threat ARs pose on populations of carnivores and other species, globally, there are few regulations limiting the use of ARs, and existing regulations and requirements for registration appear variable between nations and regions (Jacob & Buckle, 2018). There are no formal restrictions in Africa or Central and South America that we are aware of, but there have been recent efforts requiring the registration of chemicals in Côte d'Ivoire, Ghana, Kenya, Nigeria, Rwanda, and South Africa (Yordas Group, 2023) and efforts to regulate appropriate use in Brazil, Chile, Colombia, and Costa Rica (Acta, 2023). Within Asia, formal regulatory legislation has been enacted in China, Japan, and South Korea (Enhesa, 2023) and the latter works closely with the United States Environmental Protection Agency to research the environmental effects of pesticide use and to discuss chemical restrictions (Thomas & Pan-Jei, 1987). All 11 compounds found in our literature search are registered and approved for use under the European Union Registration, Evaluation, Authorization and Restriction of Chemicals, which oversees chemical use in Denmark, France, Italy, Spain, Sweden, and the UK, as well as other European Union nations (European Chemical Agency, 2023). Individual nations within the European Union can implement stronger regulations, however, so while we did not find any specific laws within the nations represented in our review, they may exist in some form. Similarly, members of the Eurasian Economic Union must register chemicals according to Technical Regulation chemical framework, although it is unclear which rodenticides, if any, are restricted (Eurasian Economic Union, 2023). Australia is one of few nations where use is restricted, and second-generation ARs are only approved for use in residential and commercial areas, not in agricultural areas (Australian Pesticides & Veterinary Medicines Authority, 2023). Legislation restricting any use of brodifacoum, bromadiolone, difenacoum, and difethialone is currently pending in the US as of 2022, but these compounds are approved for all use outside of California, which implemented a residential-use moratorium in 2020 and a subsequent ban was formalized in 2023 (U.S. Environmental Protection Agency, 2022; California Department of Pesticide Regulation, 2023). Coumatetralyl has never been approved for use in the US and has never been marketed, but chlorophacinone, diphacinone, flocoumafen, and warfarin are currently approved for use within the US (U.S. Environmental Protection Agency, 2022). The production of coumachlor has been discontinued, and it is no longer registered in the US (U.S. Environmental Protection Agency, 2022). Despite the differences in regulation across countries with documented AR exposure in carnivores, the trend of compound detection appears similar across countries (Table 1).

Overall, our review suggests there is need for more attention on ARs in mammalian carnivores and we suggest that there are at least four priority areas for research to address this emerging threat. First, given ARs are known to be used in most countries globally, expanding the breadth of research through the initiation of studies in areas that currently lack research (e.g., greater coverage of the global north, initiation of studies in the global south). Such baseline information will provide insights into the potential threat ARs pose to carnivore species and where conservation and research attention should be prioritized. Second, AR-related monitoring and research needs to be maintained over the long-term to aide in investigating how patterns of AR exposure vary spatially and temporally and how wildlife respond to mitigation measures. Third, there is a need to study species from a diversity of trophic levels, including species not known to frequently prey on rodents and across the urban to wildland gradient to understand the extent of bioaccumulation in carnivore species. Fourth, we encourage researchers to utilize novel non-invasive sampling methods and strong experimental designs to attempt to identify the point at which AR exposure leads to morbidity and mortality in free-ranging carnivores. Such information is critical to ongoing and future policy debates on these widely utilized, but largely unregulated, pesticides and their potential role in global carnivore declines.

Author contributions

D.S. Jachowski and E.A. Saldo conceived of the idea, design and experiment; M.P. Keating, E.A. Saldo, J.L. Frair, S.A. Cunningham, R. Mateo and D.S. Jachowski wrote the paper; D.S. Jachowski and E.A. Saldo developed and designed methods; M.P. Keating, D.S. Jachowski and E.A. Saldo analyzed the data.

Conflict of interest statement

All authors declare that they have no conflicts of interest.

Ethics statement

This material is the authors' own original work, which has not been previously published elsewhere. The paper is not currently being considered for publication elsewhere. The paper reflects the authors' own research and analysis in a truthful and complete manner.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. The number of publications on mammalian carnivores and anticoagulant rodenticides from 1988 to 2022 represented by blue bars. The secondary axis represents the number of publications on carnivores by year and is represented by a gray line. The secondary axis was generated from a Web of Science search using the search term "TS=(*carnivore NOT marine*)."

Appendix S2. The process of our literature search, including the number of potentially appropriate results, potentially relevant publications, and publications included in our literature review. We utilized Web of Science, Google Scholar, and a snowball approach.

Appendix S3. The reported concentrations (range and mean) by species, including the percentage of species that tested positive for each of the 11 compounds found in our review. Concentration can vary by tissue type and readers are encouraged to reference the cited literature for more details.

Appendix S4. Potential contributors to exposure investigated in our review, whether the contributor was significant, and the direction of significance, if applicable.