



REVIEW

A review of the diet of the common vampire bat (*Desmodus rotundus*) in the context of anthropogenic change

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Abstract

The common vampire bat (*Desmodus rotundus*) maintains a diverse, sanguivorous diet, utilizing a broad range of prey taxa. As anthropogenic change alters the distribution of this species, shifts in predator–prey interactions are expected. Understanding prey richness and patterns of prey selection is, thus, increasingly informative from ecological, epidemiological, and economic perspectives. We reviewed *D. rotundus* diet and assessed the geographical, taxonomical, and behavioral features to find 63 vertebrate species within 21 orders and 45 families constitute prey, including suitable host species in regions of invasion outside *D. rotundus*' range. Rodentia contained the largest number of species utilized by *D. rotundus*, though cattle were the most commonly reported prey source, likely linked to the high availability of livestock and visibility of bite wounds compared to wildlife. Additionally, there was tendency to predate upon species with diurnal activity and social behavior, potentially facilitating convenient and nocturnal predation. Our review highlights the dietary heterogeneity of *D. rotundus* across its distribution. We define *D. rotundus* as a generalist predator, or parasite, depending on the ecological definition of its symbiont roles in an ecosystem (i.e., lethal vs. non-lethal blood consumption). In view of the eminent role of *D. rotundus* in rabies virus transmission and its range expansion, an understanding of its ecology would benefit public health, wildlife management, and agriculture.

Keywords Anthropogenic · Common vampire bat · *Desmodus rotundus* · Diet · Predator · Prey · Rabies

Introduction

It is widely recognized that human modification of natural landscapes continues to transform ecosystems at an immense rate (Barlow et al. 2016; Ellis et al. 2010; Grantham et al. 2020). Anthropogenic disturbances such as

land-use change, exploitation of natural resources, climate anomalies, and agricultural expansion continue to alter biodiversity assemblages (Bengtsson et al. 2005; Bellard et al. 2012; Chaudhary and Mooers 2018; Hooper et al. 2012). In Latin America, this phenomenon remains disproportionately significant, given the abundant ecosystem services provided by this region (Nobre et al. 2016; Salazar et al. 2015). Deforestation remains the dominant land-use trend in this expanse, driven by a demand for cattle production and export-oriented monoculture agriculture (Dros 2004; Grau and Aide 2008). Moreover, climate projections anticipate substantial change in both precipitation and temperature in subtropical Latin America in the coming years, further altering ecosystem structure and function (Cabr   et al. 2016; Nu  ez et al. 2009).

Facing the constraints of the Anthropocene epoch and in response to increasingly unsuitable habitats, wildlife populations in Latin America are undergoing major geographic redistribution (Ancillotto et al. 2016; McCracken et al. 2018; Osland et al. 2021). Wildlife is significantly impacted by the diminished forests that occur secondary to land-use changes as well as the climate alterations that further relegate the

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amount of wild landscapes that meet their ecological needs (Grantham et al. 2020; Willmott et al. 2022). Movement of non-native taxa into novel regions is, thus, increasingly common as species are driven to seek refuge elsewhere (Pech et al. 2017; Willmott et al. 2022). Changes in the distribution and abundance of wildlife linked to land cover change have already been documented in Latin America for several taxa, including amphibians (Vieira et al. 2018), rodents (Campos-Krauer and Wisely 2011), birds (Hayes et al. 2018), artiodactyls such as peccaries (Altrichter and Boaglio 2004) and tapirs (Reyna-Hurtado et al. 2019), marsupials (Loyola et al. 2012), and numerous bat species (Barquez et al. 2013; LaVal 2004).

Historically, the common vampire bat, *Desmodus rotundus*, has been confined to tropical and subtropical regions of Latin America, spanning southward from Mexico to northern Argentina, central Chile, and southern Uruguay (Greenhall 1988; Zarza et al. 2017). This phyllostomid species can be found at sea level to over 3500 m of altitude (Greenhall et al. 1983; Greenhall 1988). *Desmodus rotundus* occupies diverse habitats ranging from rainforests to deserts, where it maintains an exclusively hematophagous diet and feeds on the blood of numerous vertebrate species (Greenhall 1972, 1988; McNab 1973). Rising temperatures, habitat fragmentation, and agricultural activities have altered the dispersal and driven this Neotropical sanguivore both northward and into higher altitudes (Botto Nuñez et al. 2020; Camargo et al. 2018; Rojas-Sereno et al. 2022). *Desmodus rotundus* has recently been documented close to the United States–Mexico border, a novel region for the species (Bodenchuck and Bergman 2020; Hayes and Piaggio 2018) and at higher elevations in Costa Rica than previously noted (LaVal 2004). Climate models have suggested potential range expansion of *D. rotundus* in Colombia, French Guyana, Suriname, Venezuela, Mexico, and at greater altitudes such as those maintained in the Andes Mountains of Chile (Lee et al. 2012; Mistry and Moreno-Valdez 2009; Zarza et al. 2017). In time, *D. rotundus* may enter the United States through the southern borders of Texas or Arizona (Hayes and Piaggio 2018; Mistry and Moreno-Valdez 2009).

As with any non-native taxa, the expansion of *D. rotundus* populations into novel regions holds potential for cascading repercussions (Andersen and Shwiff 2014; Borremans et al. 2019; Clavero and García-Berthou 2005; Paini et al. 2016). Through evolutionary time, wildlife has reliably adapted to utilize novel prey species upon migration, including livestock, igniting changes in the trophic structure and introducing pathogens into naïve populations and regions (El-Sabaawi 2018; Plowright et al. 2015). Known for their robust adaptive capacity, range expansion of *D. rotundus* is particularly important given that the species (i) feeds on a diverse repertoire of prey, (ii) has demonstrated considerable plasticity in adapting to novel landscapes and diet

sources, and (iii) maintains a strictly sanguivorous (i.e., whole blood) diet, providing opportunities for rapid transmission of pathogens in which the species acts as a reservoir for (Bobrowiec et al. 2015; Greenhall 1988; Mayen 2003; Streicker and Allgeier 2016). These attributes suggest that distributional shifts of *D. rotundus* into new territories may result in establishment of the species as invasive, generating novel ecologic, epidemiologic, and economic human–wildlife conflicts (Acha and Alba 1988; Delpietro and Russo 1996; Ingala et al. 2019; Mayen 2003).

Importance of understanding prey richness

Ecologic

Changes in predator–prey dynamics and disruptions in trophic structure are an unavoidable and expected consequence of changes to biodiversity (Gámez et al. 2022; Guiden et al. 2019; Murphy et al. 2021). When wildlife migrates to novel regions or changes in abundance, interspecific interactions change correspondingly (Fleming and Bateman 2018; Guiden et al. 2019). For example, when the ranges of predators increasingly overlap and prey populations decline, predators often switch to generalist diets or utilize new taxa as sources of prey (Ballejo et al. 2018; Fleming and Bateman 2018; Murray et al. 2015; Rodewald et al. 2011; Wolfe et al. 2018). This may include livestock in landscapes subject to agricultural conversion, should natural prey become scarce or less accessible relative to domestic herbivores (Cardinale et al. 2006; Green et al. 2022; Michalski et al. 2006; Murphy et al. 2021; Patten et al. 2019). Novel landscape conditions may likewise promote phenological shifts such as changes in temporal patterns (Lebbin et al. 2007; Mandel and Bildstein 2007; Rich and Longcore 2013), behavioral adaptations related to sensory processes (Chan et al. 2010; Eisenbeis et al. 2009; Siemers and Schaub 2011; Simpson et al. 2016), and alterations in feeding (Grabruker and Grabruker 2010; Stafford-Bell et al. 2012; Valeix et al. 2012; Weir and Kacelnik 2006).

The ability of *D. rotundus* to readily adapt to new landscapes and novel prey sources is documented in both wild and captive settings (Bolívar-Cimé et al. 2019; Greenhall 1988). Experimentally, *D. rotundus* has been offered and readily accepted a variety of non-natural diets including both live prey and extracted blood. The bats have attacked species such as armadillos and porcupines and demonstrated successful location of vulnerable areas for biting (Greenhall 1988). In the wild, studies have detailed *D. rotundus* feeding on invasive feral swine and other taxa which did not co-evolve as not part of their diet (Calfayan et al. 2019; Galetti et al. 2016; Grotta-Neto et al. 2021; Hernández-Pérez et al. 2019; Pereira et al. 2016). The prey consumed by *D.*

rotundus is suggested as largely dependent on surrounding fauna of the bats, that is, based on availability (Gonçalves et al. 2021). The success of this species in geographic regions with sparse wildlife or poor species richness has been achieved through the utilization of livestock on multiple accounts (Bobrowiec et al. 2015; Botto Nuñez et al. 2020; Delpietro et al. 1992; Voigt and Kelm 2006). The absence of native or abundance of introduced prey, or alternatively, the establishment of *D. rotundus* in alien regions may provide ample opportunity for dietary shifts and novel interspecific interactions (Gonçalves et al. 2021; Streicker and Allgeier 2016).

Epidemiologic

In general, bats are important pathogen reservoirs in emerging infectious disease (Plowright et al. 2015), as noted by outbreaks of Hendra virus (Halpin et al. 2000), Nipah virus (Yob et al. 2001), SARS (Wang et al. 2006), and other coronaviruses (Burki 2020; Hernández-Aguilar et al. 2021). Given their unique behavioral and ecological traits, as well as the plethora of pathogens harbored by the species, *D. rotundus* may be a key Chiropteran in heterospecific disease transmission (Johnson et al. 2014; Wray et al. 2016).

Desmodus rotundus is a known host for many viral pathogens, most notably as the primary rabies virus (RABV) reservoir in Latin America (Benavides et al. 2020a; Cárdenas-Canales et al. 2020; Johnson et al. 2014; Streicker et al. 2012). Several additional viral agents have been detected in the species, including adenoviruses, herpesviruses, vesiculoviruses, and coronaviruses, among others (Bergner et al. 2019; Wray et al. 2016). Recent metagenomic sequencing of *D. rotundus* fecal and saliva samples identified over 58 viral families, 17 of which are known to infect mammalian species (Bergner et al. 2021a). *Alphacoronaviruses*, a viral genus significant to mammal health, have been detected in *D. rotundus* subjects in Argentina (Arteaga et al. 2022), Brazil (Alves et al. 2021; Asano et al. 2016), and Peru (Bergner et al. 2020). A *Betacoronavirus* related to MERS-CoV was found in *D. rotundus* in Belize (Neely et al. 2020). The presence of deltaviruses, originally associated with hepatitis B co-infections in humans, has been confirmed in the saliva of *D. rotundus* as well. Phylogenetic analysis suggests that bat deltaviruses arose from other mammalian deltaviruses, and therefore hold potential for cross-species transmission (Bergner et al. 2021b). The viral agent responsible for foot and mouth disease, one of the most economically important diseases of livestock and greatest biosecurity threat to many nations, was successfully inoculated and recovered from *D. rotundus* in experimental settings (Lord et al. 1986).

Desmodus rotundus also hosts a variety of other pathogens, including *Leptospira* spp. (Ballados-González et al. 2018) and *Bartonella* spp. (Wray et al. 2016), both zoonotic

bacteria agents. Urination during feeding and flying has been noted as a possible means of leptospirosis transmission (Greenhall 1964). In addition, *D. rotundus* has recently also been implicated in fecal carriage of multidrug-resistant extended-spectrum beta-lactamase-producing *Escherichia coli* to livestock (Benavides et al. 2022). Numerous endoparasites have also been found on *D. rotundus*, such as *Toxoplasma gondii* (Zetun et al. 2009) and various trypanosomes including *Trypanosoma cruzi* (Quiroga et al. 2022). Ectoparasites include ixodid and argasid ticks (*Ixodes*, *Amblyomma*, and *Ornithodoros* sp.), trombiculid or spider mites (*Euschoengastia* spp.), mange mites (*Sarcoptes* sp.), Siphonapterid fleas, and numerous bat flies (Anciaux de Faveaux 1971; Greenhall et al. 1983; Rojas et al. 2008; Tamsitt and Fox 1970; Wenzel and Tipton 1966).

Distributional shifts of *D. rotundus* into novel regions may provide new opportunities for pathogen spillover when suitable hosts are available (Altizer et al. 2011; Borremans et al. 2019; Streicker et al. 2016). The nature of an obligate sanguivorous diet alone implies easy and robust transmission of saliva and blood-borne pathogens between prey and *D. rotundus* (Dunn 1932; Gupta 2005; Rocha and Dias 2020). Likewise, wide geographic ranges, prolonged exposure to prey during feeding, co-species roosting, and social behavior such as sharing blood meals and allogrooming have numerous implications for disease transmission (Rocha et al. 2020; Wray et al. 2016). Studies have hypothesized that emergence of vampire bat rabies in Uruguay resulted from a combination of land-use change and *D. rotundus* migration, leading to increased viral persistence and transmission to cattle (Nuñez et al. 2019). The potential for pathogen emergence is especially notable given the wide array of species *D. rotundus* has been documented to feed upon and their ability to utilize novel prey (Bobrowiec et al. 2015; Greenhall 1988; Herrera et al. 1998; Voigt and Kelm 2006). Furthermore, *Desmodus rotundus* bites can increase the susceptibility of prey species to secondary infections in the wound, even if pathogens were not directly transmitted by the bats (Johnson et al. 2014). Following a blood meal, prey may have residual hemorrhage for several hours, depending on the prey species and duration of *D. rotundus* feeding, leaving animals vulnerable to other pathogens and blood loss during this period of time (Greenhall et al. 1969).

Economic

In addition to infectious disease and ecologic concerns, *D. rotundus* causes massive economic loss to the livestock industry, primarily through the transmission and propagation of rabies. Although to a considerably less degree, *D. rotundus* may negatively impact livestock through means other than rabies, including production loss via decreased milk output, poor or diminished weight gain, anemia,

myiasis (fly strike), and damaged hides attributable to bite wounds following attack (Thompson et al. 1977; Acha and Alba 1988; Greenhall 1988; Mayen 2003). Nevertheless, this financial impact has been largely overlooked and is a rarely focused area of research compared to that of rabies, which occurs directly through the deaths of thousands of cattle and indirectly through the cost of rabies prevention and control measures (Acha and Alba 1988; Meltzer and Rupprecht 1998; Schmidt and Badger 1979).

In the 1960s, there were an estimated 90,000–100,000 rabies-related cattle deaths per year in Mexico (Acha 1967). Presently, there are over 400 deaths per 100,000 cattle head in Peru (Benavides et al. 2017) and 100,000–500,000 cattle deaths in Latin America annually (Mello et al. 2019). In the 1980s, livestock losses due to rabies, mostly ascribed to *D. rotundus*, were estimated to be around US\$50 million annually in Latin America (Acha and Szyfres 1986). In Brazil alone, this value is estimated at over US\$17 million (Horta et al. 2022). Currently, *D. rotundus* continues to be the principal RABV reservoir in the Latin American region (Constantine and Bleher 2009; Horta et al. 2022). Should *D. rotundus* spread to southern Texas in the United States, a livestock-dense portion of the country, the economic impact via rabies in cattle, swine, sheep, and goats is estimated to be between US\$7 million and US\$9.2 million annually (Anderson and Shwiff 2014).

Additionally, *D. rotundus* may transmit RABV to non-livestock species, including both wildlife and companion animals in captive and free-range settings (Gonçalves et al. 2021; Schneider et al. 2009). *Desmodus rotundus* has historically been implicated in rabies cases found in free-ranging capybaras, deer, foxes, non-sanguivorous bat species, and other mammals known to play a role in both sylvatic and urban cycles of the disease (Delpietro et al. 2009; Gonçalves et al. 2021; Favoretto et al. 2002; Kobayashi et al. 2005). In captive settings, *D. rotundus* has been documented to prey on animals housed in zoos, farms, and residential sites (Benavides et al. 2020a, 2020b; Constantine 1979; Valderama et al. 2006). A zoologic institution in Brazil recently reported a case of rabies encephalitis in a lowland tapir (*Tapirus terrestris*), with suspicions of *D. rotundus* involvement described (Pereira et al. 2022). Similarly, and also suspected to be incited by *D. rotundus*, a fatal infection was described for a captive white-tailed deer in Mexico (Franco-Molina et al. 2021). Both cases involved economic loss to the respective organizations, through the cost of employees' post-exposure prophylaxis, confirmatory diagnostics for the case itself, and preemptive testing, post-exposure vaccination, and quarantine of other animals on site (Franco-Molina et al. 2021; Pereira et al. 2022).

The prevalence and incidence of livestock, companion animal, and human rabies caused by *D. rotundus* continues to wax and wane throughout Latin America, with

anthropogenic features described as a key driving force (Botto Nuñez et al. 2020; Dos Santos et al. 2022; Hutter et al. 2018; Ribeiro et al. 2021; Rojas-Sereno et al. 2022; Streicker et al. 2012). For example, a relationship between artificial shelters (i.e., abandoned houses, manholes) and higher concentrations of bovine rabies has been reported in Brazil (Mantovan et al. 2022). Given this close association with human environments and their owned animals, significant funding continues to be poured into serologic studies, vaccination campaigns, and surveillance measures focused on *D. rotundus* in Latin America (León et al. 2021; Megid et al. 2021; Mello et al. 2019; Ribeiro et al. 2021).

In view of the ecologic, epidemiologic, and economic points described, a thorough understanding of the diet of *D. rotundus* is, therefore, critical in preparing for latitudinal and altitudinal expansion of the species' distribution (Bodenchuck and Bergman 2020; Hayes and Piaggio 2018; Mayen 2003; Schneider et al. 2009). The aim of this paper is, thus, to revise the diet of *D. rotundus* to identify major prey consumption trends in light of ongoing anthropogenic change. Here, we expand a previous contribution by Carter et al. (2021) on the taxonomic breadth of *D. rotundus* prey and account for species-level characteristics relevant to prey selection, provide an updated record of recognized prey taxa, and discuss these findings in the context of *D. rotundus* range expansion. Moreover, we discuss the relevance of *D. rotundus* prey presently occurring in the United States. Ultimately, this information may be used to anticipate pathogen emergence in new species, identify at-risk populations of domestic and wildlife taxa, and critically evaluate mitigation methods in specific localities.

Materials and methods

A literature search was conducted using Web of Science Core Collection (WoS), Scopus, and Science Direct databases to identify recorded prey species of *D. rotundus*. The search strategy used the following search terms in all fields: *Desmodus* or vampire bat* and prey or predation* or attack* or diet* or bite* or feeding* and was restricted to papers in English, Spanish, and Portuguese. Duplicates were removed, retrieving a total of 360 results. Inclusion criteria for study selection included a documented occurrence of *D. rotundus* feeding on an identifiable vertebrate species in a known geographical location. Although humans are a recognized prey species of *D. rotundus*, these reports were excluded from assessment, given the scope of the review and number of existing publications focusing on the public health components of *D. rotundus*. Prey detection methods utilized were extracted for each study included in the review. Taxonomic information of prey was standardized using the Integrated Taxonomic Information System (<https://www.itis.gov/>) for a

more accurate categorization of species. Information on the geographic, temporal, and social behavior was pulled from a variety of literature sources (Supplementary Table S3). Data were analyzed and visualized using JMP Pro 16.0.0 (SAS Institute Inc, Cary, NC) statistical software and QGIS (Bioalowieza Version 3.22.7; Open Source Geospatial Foundation, OR).

Literature trends

Desmodus rotundus diet has been studied over the last century with existing literature scattered across the scientific disciplines, from ecology and animal behavior to physiology and epidemiology (Arellano 1988; Freitas et al. 2003; Greenhall et al. 1971; Souza et al. 1997). Carter et al. (2021) summarized the diet of the three known vampire bat species, including *D. rotundus*, and revealed the broad array of species predated upon. From our literature review, we recovered a total of 67 publications containing 214 reports of *D. rotundus* feeding on prey during the period 1931–2020. There was an apparent rise in publications of *D. rotundus* between 1970 and 1979 and a later increase in the 2010's (Fig. 1A). The number of prey species documented each year has likewise continued to grow (Fig. 1B).

The liquid nature of *D. rotundus*' diet has limited the implementation of standard fecal analysis based on detritus in feces as a means of prey identification (Bobrowiec et al. 2015). Other attempts have been made to quantify target species, including using direct observation, camera traps, genomics, stable isotope analysis, and experimental studies (Greenhall et al. 1969; Greenhall 1988; Hernández-Pérez et al. 2019; Voigt and Kelm 2006). Methods for *D. rotundus* prey documentation from the articles reviewed included anecdotal evidence (57%), molecular and chemical techniques (49%), experiments performed in captivity (32%), bite wound visualization (27%), camera traps (24%), and live field observations of attack (22%). Anecdotal evidence includes interviews, authors' personal accounts, or any reports from community members, producers, and other individuals where *D. rotundus* is claimed to have bitten specific prey species within the publication, though attacks or wounds were not necessarily witnessed. Bite wound analysis comprises reports or studies that involve documented visualization of insults. Anecdotal reports and bite wound analysis were most common in literature dating before 1980. This lack of field-based methodology utilized in older research and the resultant uncertainty in data credibility and species identification is a major limitation when assessing the diet

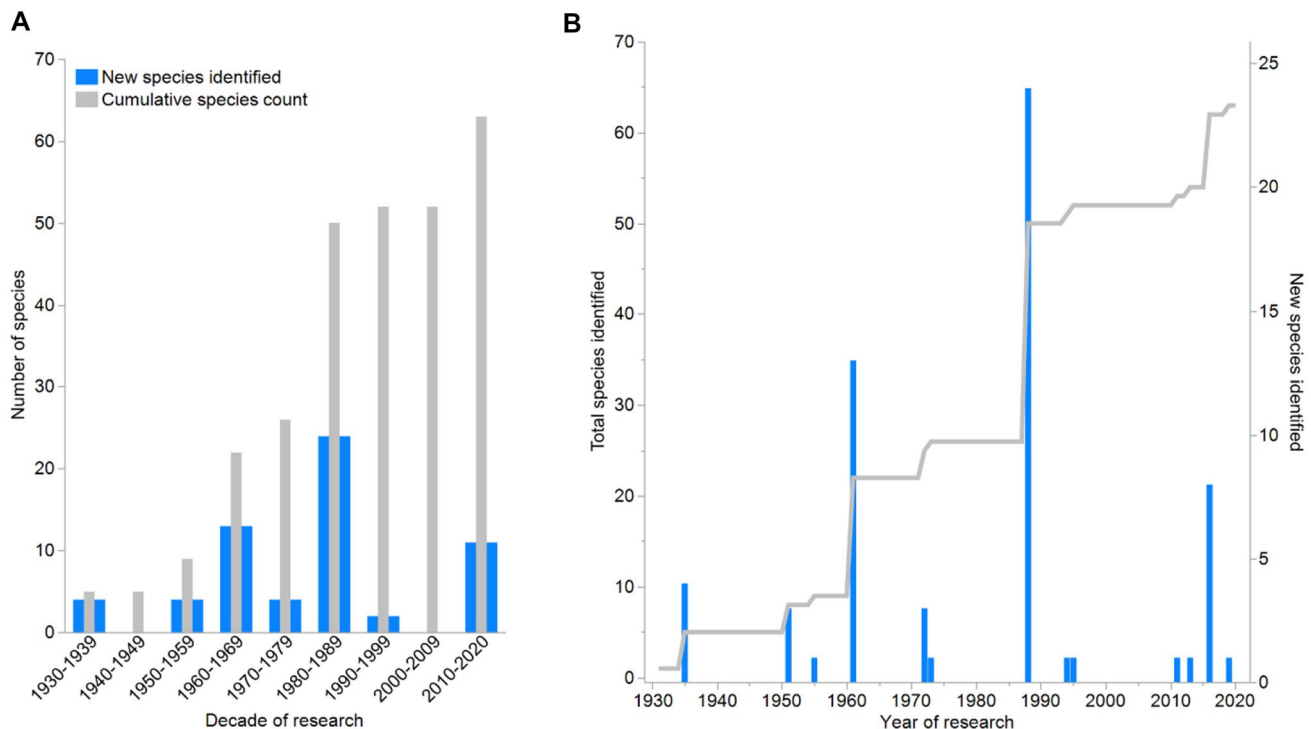


Fig. 1 *Desmodus rotundus* literature on prey species published between 1930 and 2020. **A** Decadal number of prey species. The number of new species discovered over the course of each decade (blue) and the cumulative number of *D. rotundus* prey species documented by the end of each decade (gray). No new species were

reported as *D. rotundus* prey between 1940–1949 and 2000–2009. Research throughout the last decade has resulted in documentation of 11 new prey species. **B** Cumulative number of prey species (gray) and new species reported annually (blue)

of *D. rotundus*. Today, ecological and genomic technology is increasingly utilized as a means to document predation. In the last decade, 35% of occurrences were documented via camera traps and 35% via molecular techniques. Contrarily, live field observations have become a less common methodology and were only used to document 2.8% of all occurrences between 2010 and 2020.

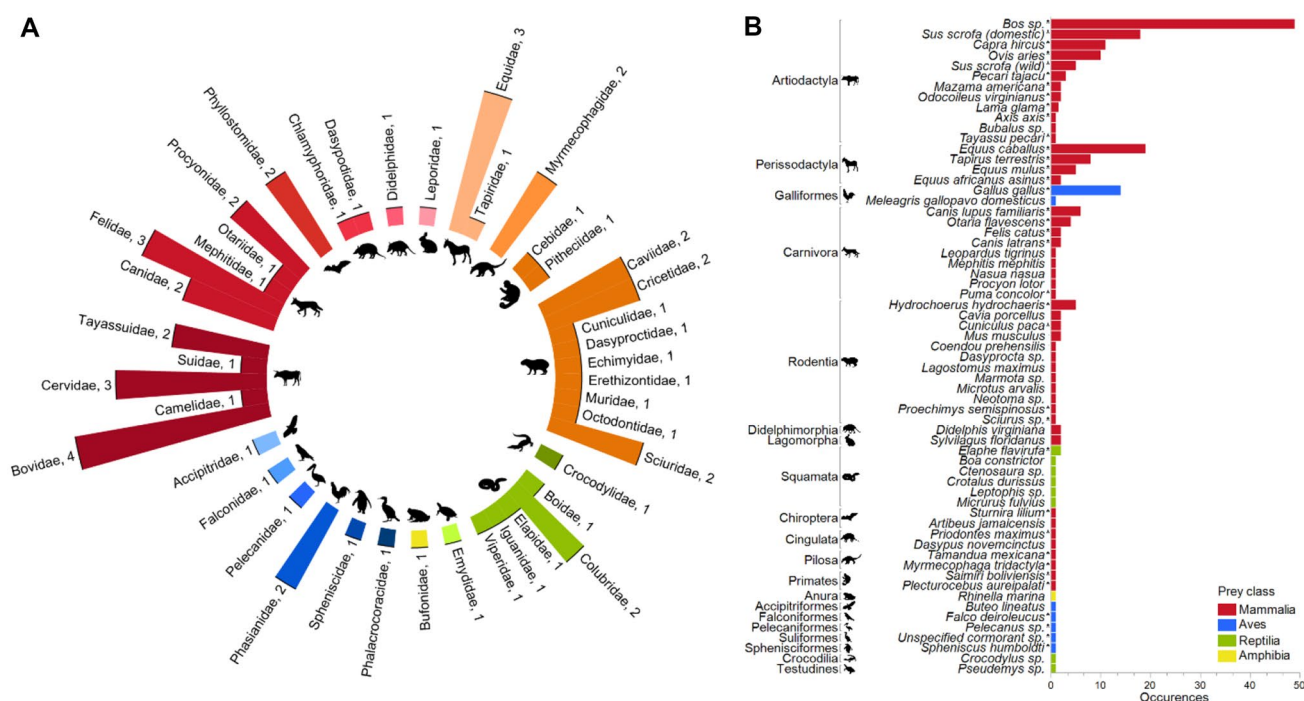
Prey diversity

Cumulatively, all existing literature supports the notion that *D. rotundus* is able to feed on a diverse collection of species, including those in the classes Mammalia, Reptilia, Aves, Amphibia, and Insecta (Bobrowiec et al. 2015; Greenhall 1988; Herrera et al. 1998; Voigt and Kelm 2006). A total of 63 prey species within 5 classes, 21 orders, and 45 families were recovered from the literature by 2020 and used to create a comprehensive dataset (Fig. 2, Supplementary Table S1). Note that these species include those documented under all conditions, including experiments performed in captivity. Insecta was documented as a prey class but for unspecified

taxa (Arata et al. 1967; Rouk and Glass 1970; Bohmann et al. 2018) and was, thus, excluded from our assessment.

Prey data were then examined in terms of taxonomic richness (i.e., number of species) (Fig. 2A) and number of publications (Fig. 2B). Most of the prey were mammals (75.4%) with 47 species documented, though several species from other taxa were identified, including 7 avian, 8 reptilian, and 1 amphibian species. Species were characterized as wildlife (i.e., free-ranging and undomesticated) or domestic (i.e., bred and raised for companionship or production/vocational purposes). Domestic species were further divided into those that function as livestock and those that act primarily as companion animals. Swine (*Sus scrofa*) were counted in both livestock and wildlife groups as there are reports of *D. rotundus* preying on both feral and domestic pigs.

The order Rodentia contained the largest number of *D. rotundus* prey species ($n = 12$), followed by Artiodactyla ($n = 11$) and Carnivora ($n = 9$) (Fig. 2). Rodent species include those of the families Caviidae ($n = 2$), Cricetidae ($n = 2$), Sciuridae ($n = 2$), Cuniculidae ($n = 1$), Dasypodidae ($n = 1$), Echimyidae ($n = 1$), Erethizontidae ($n = 1$), Muridae ($n = 1$), Octodontidae ($n = 1$), and



($n=1$), and Octodontidae ($n=1$). Artiodactyl species include Bovidae ($n=4$), Cervidae ($n=3$), Camelidae ($n=1$), Suidae ($n=1$), and Tayassuidae ($n=2$). Bovidae contained the most Artiodactyl species ($n=4$). Families within Carnivora include Felidae ($n=3$), Canidae ($n=2$), Procyonidae ($n=2$), Mephitidae ($n=1$), and Otariidae ($n=1$). Other prey orders identified include Accipitriformes, Anura, Chiroptera, Cingulata, Crocrodilia, Didelphimorphia, Falconiformes, Galliformes, Lagomorpha, Pelecaniformes, Perissodactyla, Pilosa, Primates, Sphenisciformes, Squamata, Suliformes, and Testudines.

Regarding methodology, 56% of all species were documented in a non-captive setting (i.e., via camera trap, field observation, chemical and molecular analysis, bite wound visualization). The remaining 33% were identified as *D. rotundus* prey in captive experiments and 10% via anecdotal evidence only. Anecdotally identified prey includes the turkey (*Meleagris gallopavo domesticus*), guanaco (*Lama glama*), Virginia opossum (*Didelphis virginiana*), agouti (*Dasyprocta* sp.), Argentine plains viscacha (*Lagostomus maximus*), and marmot (*Marmota* sp.). Species only identified under experimental conditions are described in the proceeding sections. The methods used to identify *D. rotundus* prey is a major limitation in the accuracy of these data, especially for wild settings, but could provide signal of prey use.

Wildlife as *D. rotundus* prey

Historically, *Desmodus rotundus* is described to prey on medium-to-large-bodied terrestrial mammals, particularly ungulates, although there are reports of the bat preying on small mammals, marine mammals, birds, and reptiles as well (Bobrowiec et al. 2015; Greenhall 1988; Voigt and Kelm 2006). Commonly discussed wildlife prey includes peccaries (Voigt and Kelm 2006), deer (Sánchez-Cordero et al. 2011), tapirs (Gnocchi et al. 2017), and capybaras (Gonçalves et al. 2021). Our review supported these claims, identifying a total of 52 wildlife species as *D. rotundus* prey. The South American tapir (*Tapirus terrestris*) ($n=8$), capybara (*Hydrochoerus hydrochaeris*) ($n=5$), feral pig (*Sus scrofa*) ($n=5$), and South American sea lion (*Otaria flavescens*) ($n=4$) were the most commonly reported wild mammals attacked by *D. rotundus*.

Of these 52 species, 27 were observed in non-captive settings, while the remaining 25 were documented under experimental conditions. Mammalian species observed as *D. rotundus* prey in field settings include the puma (*Puma concolor*), coyote (*Canis latrans*), chital deer (*Axis axis*), South American red brocket (*Mazama americana*), white-tailed deer (*Odocoileus virginianus*), wild pig (*Sus scrofa*), collared peccary (*Pecari tajacu*), white-lipped peccary (*Tayassu pecari*), South American sea lion (*Otaria flavescens*), little yellow-shouldered bat (*Sturnira lilium*), giant

armadillo (*Priodontes maximus*), South American tapir (*Tapirus terrestris*), giant anteater (*Myrmecophaga tridactyla*), Northern tamandua (*Tamandua mexicana*), madidi titi (*Plecturocebus aureipalati*), black-capped squirrel monkey (*Saimiri boliviensis*), lowland paca (*Cuniculus paca*), capybara (*Hydrochoerus hydrochaeris*), spiny rat (*Proechimys semispinosus*), squirrel (*Sciurus* sp.), and rat snake (*Elaphe flavirufa*).

Desmodus rotundus was reported to predate upon one amphibian species, a cane toad (*Rhinella marina*), which was only documented in a captive setting (Greenhall 1988). Similarly, the majority of literature on *D. rotundus* predating on eight reptilian species was done in captivity, with the exception of the rat snake (*Elaphe flavirufa*) (Greenhall 1988). Six avian species were identified as *D. rotundus* prey in wild settings, including the orange-breasted falcon (*Falco deiroleucus*), Humboldt penguin (*Spheniscus humboldti*), pelican (*Pelicanus* sp.), cormorant (Suliformes), and domestic chicken (*Gallus gallus*). *Desmodus rotundus* was also documented to feed on the red-shouldered hawk (*Buteo lineatus*) in captivity.

Livestock as *D. rotundus* prey

Despite the research efforts devoted to predation on native species, the general consensus in the literature is that *D. rotundus* selects livestock as prey over free-ranging wildlife when provided the opportunity (Voigt and Kelm 2006). There is inconsistency regarding which livestock species are most commonly targeted, with some reports suggesting a tendency to feed on cattle (Bohmann et al. 2018; Goodwin and Greenhall 1961), horses (Mialhe 2014; Turner 1975), or swine (Bobrowiec et al. 2015). Poultry is described as a possible second choice (Bobrowiec et al. 2015) and small ruminants (sheep and goats) as uncommon prey choices, although the reason for a plausible distaste is unknown (Turner 1975; Mialhe 2014). Our review revealed that cattle were the most commonly reported prey species across all publications ($n=49$). There were 26 reports documenting *D. rotundus* feeding on equine (*Equus* spp.), 18 on domestic swine (*Sus scrofa*), 14 on chickens, 11 on goats (*Capra hircus*), 10 on sheep (*Ovis aries*), 2 on llamas (*Lama glama*), and 1 on turkeys. *Desmodus rotundus* did predate upon livestock species more often than others in this review, with 121 total occurrences, compared to 80 for wildlife and 10 for companion animals.

Nonetheless, this tendency for *D. rotundus* to predate on livestock and the interpretation as a true predation pattern may be biased. There is a large effort devoted to studying these species with regard to the potential RABV transmission from *D. rotundus* (Mayen 2003). The likelihood of witnessing predation is also much greater for livestock than wildlife, given the relative exposure of humans to domestic

species (Mialhe 2014; Voigt and Kelm 2006). Livestock is often handled at a frequent cadence and bite wounds are readily evident as producers and large animals typically seek out any lesions or form of injury that may ultimately impact production or economics (Greenhall 1972). Likewise, it may be due to the limited research on *D. rotundus* feeding in wild settings and lack of information on livestock availability for many studies that cover wildlife predation (Bobrowiec et al. 2015). Additional research examining the influence of livestock availability on the utilization of wildlife prey is, therefore, needed to better understand predation patterns across the domestic and wild prey.

Although not unanimously agreed upon, convenience is the most commonly cited driving factor for prey selection (Delpietro et al. 1992; Gonçalves et al. 2021; Voigt and Kelm 2006). Anecdotal reports suggest that livestock is targeted due to its abundant and stable availability as compared with wildlife prey (Delpietro et al. 1992; Gonçalves et al. 2021; Voigt and Kelm 2006). These claims may, again, be biased considering that *D. rotundus* roosts are often located in close proximity to humans where these studies often take place (Ribeiro et al. 2021; Rojas-Sereno et al. 2022). Likewise, studies on prey availability versus richness are, thus, limited in pristine environments where wildlife are most abundant (Bobrowiec et al. 2015). Other studies hypothesize that prey richness is influenced by various facets of convenience including large prey size for larger volumes of blood (Delpietro et al. 1992; Johnson et al. 2014), proximity to roost site (Rocha et al. 2020), ease of attack (Mialhe 2014), lack of prey reactivity (Arellano and Greenhall 1971; Delpietro 1989; Delpietro et al. 1992), and herd size (Bobrowiec et al. 2015). Nutritional composition of blood has also been described as a factor (Voigt and Kelm 2006). For cattle specifically, there is a reported inclination to feed on calves over older cows and heifers, and likewise a breed difference in Holstein predation over various others (Arellano and Greenhall 1971). This is suspected to be due to prey temperament and lack of prey reactivity that would facilitate easier feeding (Arellano and Greenhall 1971).

Companion animals and other domestic species as *D. rotundus* prey

Desmodus rotundus also feeds on anthropogenic prey with reports describing attacks on dogs and humans, although these events are much less common in the literature (Schneider et al. 2001; Streicker and Allgeier 2016; Torres et al. 2005). We retrieved six reports of *D. rotundus* predation on domestic dogs (*Canis familiaris*). Nevertheless, the literature involving cats (*Felis catus*) describes the species as a livestock guardian of sorts (Delpietro et al. 1994). The addition of barn cats was an effective means to deter *D. rotundus* from attacking livestock and it is proposed that the bats avoid

domestic cats given their reactivity (Delpietro et al. 1994). Nevertheless, this does not mean the species is immune to being predated upon. Guinea pigs (*Cavia porcellus*) were utilized as prey in two publications, but both events occurred in captive settings. Although predation events involving companion animals are less commonly observed, they are considered risk factors for RABV spillover from bats to pets to humans (Schneider et al. 2009; Valderrama et al. 2006).

Geographic trends in *D. rotundus* predation

In terms of geography, there is a need for additional research on the prey of *D. rotundus* in certain countries, and a greater focus on less commonly targeted classes such as Aves, Reptilia, and Amphibia. Blood meal or fecal sample analysis for *D. rotundus* subjects obtained from regions with unaddressed research needs may provide a valuable tool for characterization of prey taxa. The number of documented species and relatedness to prey richness for each country versus true sampling bias due to sampling effort influencing the number of species detected must likewise be distinguished. For instance, across Latin America, no literature was identified for feeding occurrences in Belize, El Salvador, Honduras, Bolivia, Paraguay, Uruguay, Guyana, Suriname, or French Guiana (Fig. 3A). Feeding events were reported in Argentina, Brazil, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Nicaragua, Peru, Trinidad and Tobago, and Venezuela. Mexico was the only country reporting prey species in more than three classes, although research on mammalian species was evenly distributed across the countries. Nevertheless, amphibian and reptilian prey sources were only documented in Mexico, and avian species in Mexico, Guatemala, Peru, Chile, Trinidad and Tobago, Argentina, and Brazil. Despite distribution of many prey species throughout most of Latin America, number of prey species was higher in Mexico ($n=32$), Peru ($n=19$), and Argentina ($n=19$). This does not necessarily correlate with the frequency of feeding events documented in each country (Fig. 3B). A total of 49 events of *D. rotundus* feeding in Mexico returned 32 different species, while 33 events in Brazil only returned 13 difference species. There was a significant positive relationship between the number of references and total species documented per country ($F_{1,11} = 113.61$, $p < 0.001$, Fig. 3C), suggesting sampling bias where more research effort returns more prey species.

Behavioral trends in predation

Prey species reported had similar solitary ($n=32$) and social behavior ($n=31$) although most prey were diurnal ($n=29$) over nocturnal ($n=19$), crepuscular ($n=9$), or cathemeral ($n=6$) (Fig. 4A). The majority of diurnal prey were social species (33%) as opposed to solitary (13%).

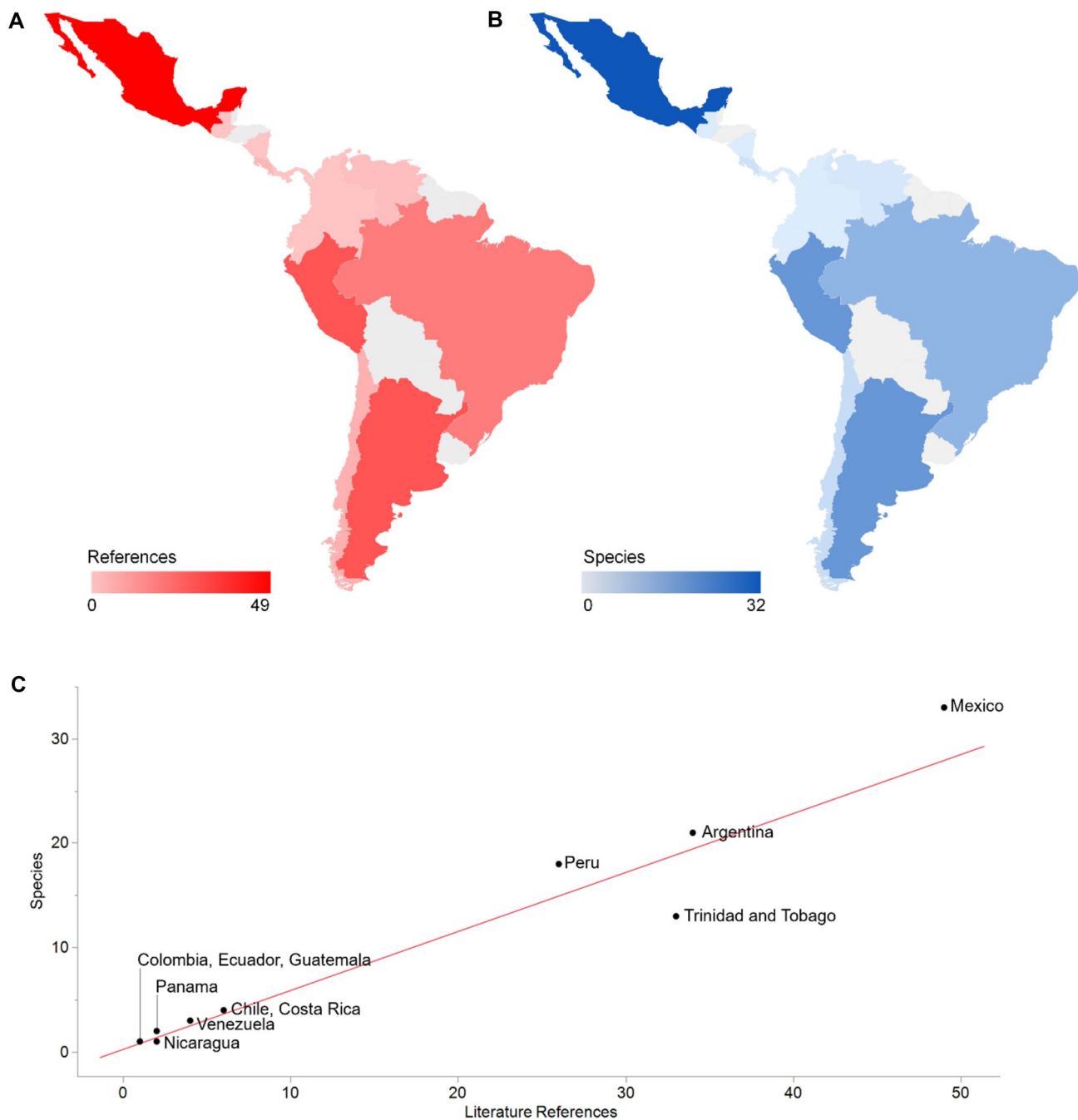


Fig. 3 Geographic distribution of *Desmodus rotundus* prey. **A** Number of references of *D. rotundus* prey per country denoting regions with none (gray), and low (light red) to high (dark red) number of publications. **B** Number of unique prey species documented in per country denoting areas with none (gray), and low (light blue) to high (dark blue) number of species detected. **C** Relationship between

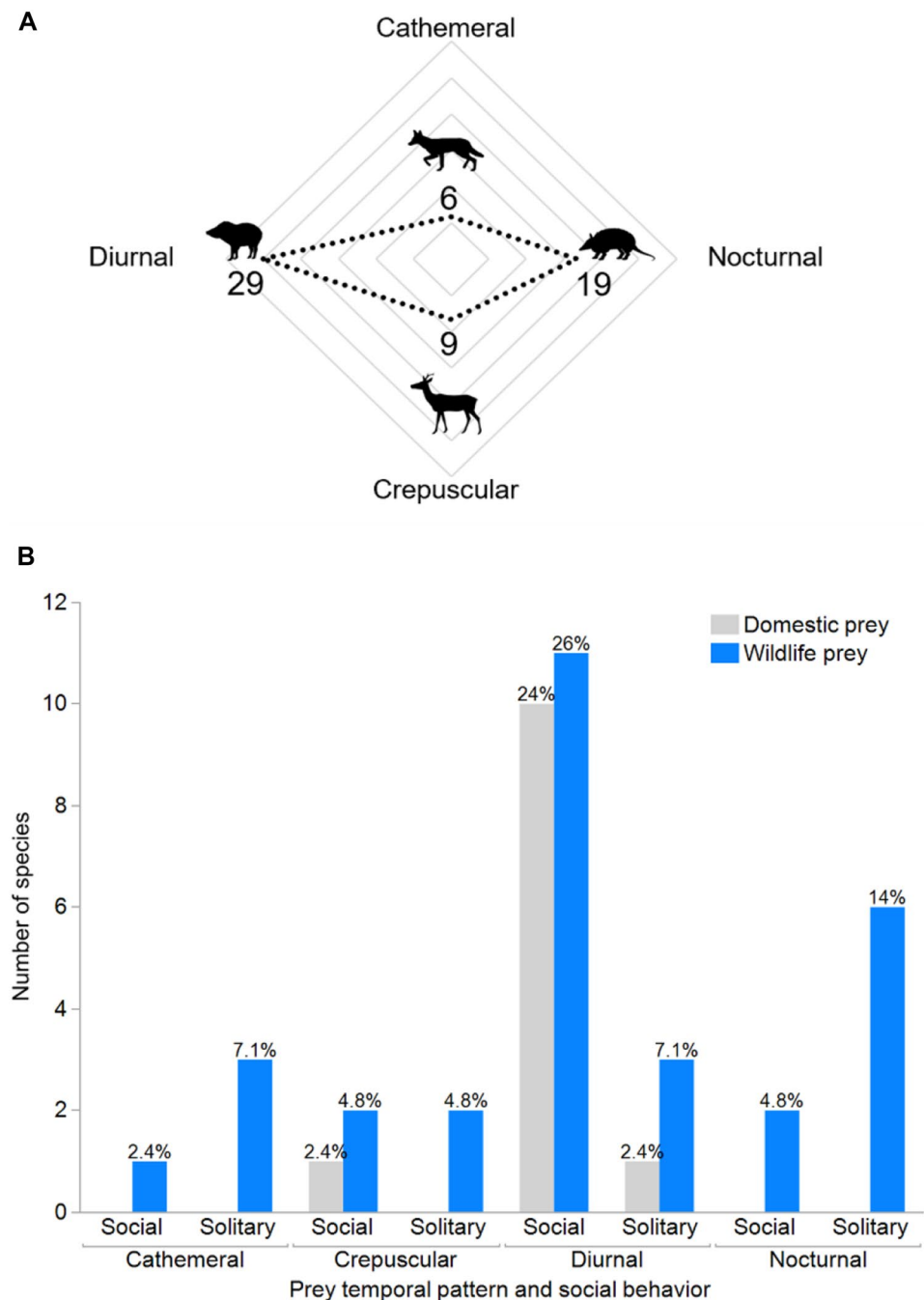
the number of reports published (x-axis) and the number of species detected (y-axis) per country suggesting a significant, positive correlation suggesting that as the research effort increases, the number of new *D. rotundus* prey species may increase. Countries with the same number of references are separated by comma

This was consistent at the prey class level (Supplementary Fig. S1), with mammalian and avian prey being primarily diurnal and social. Reptilian and amphibian prey were scattered across the temporal and behavioral patterns, but

these species were primarily studied in captive settings, and therefore the findings are less extrapolatable.

When removing species solely studied in experimental settings, findings remain similar. The majority of prey

Fig. 4 Behavioral patterns of *Desmodus rotundus* prey. **A** Number of prey species (dashed line) grouped by temporal behavior as diurnal, nocturnal, crepuscular, cathemeral (vertices). **B** Number of prey species (y-axis) grouped by prey type (i.e., wildlife or domestic prey) (blue) and temporal patterns of activity with social behavior (x-axis). Only prey species documented in non-captive settings are represented within figure



species demonstrated diurnal activity patterns (59.5%), compared to nocturnal (19.0%), crepuscular (11.9%), and cathemeral (9.5%). Prey likewise demonstrated mainly social ($n = 27$) over solitary ($n = 15$) behavior. Combined, half of all prey documented in non-captive settings demonstrated diurnal temporal patterns and social behavior, with similar distributions between wildlife ($n = 11$) and domestic ($n = 10$) species for the dual conditions (Fig. 4B). These patterns of behavior suggest that *D. rotundus* are remarkably flexible in targeting prey with very different

habits but may increasingly predate upon diurnal species that congregate in groups. Nevertheless, the temporal and behavioral characteristics for each species were classified in a general sense (i.e., predominant patterns in taxa across settings) (Supplementary Table S3). That is, there is wide variation in the true patterns behavioral demonstrated by prey species, impacted by the environment and other conditions. For instance, cattle are also odd sleepers, with frequent periods of apparent alertness throughout the night,

which could affect their vulnerability to predation (Balsch 1955; Klefot et al. 2016; Ruckebusch 1972).

Contingency analysis was likewise used to investigate temporal patterns between wild versus domestic prey species. These findings include all species detected, including those in captive settings. Temporal patterns for each species were examined in a context outside of *D. rotundus* predation events, that is, for differences in the species themselves and not between those selected by *D. rotundus* over others. Results indicated a significant difference in temporal patterns, with 93.6% of domestic and only 31.6% of wildlife species demonstrating diurnal activity ($\chi^2_{(3)} = 111.3$, $p < 0.001$). Wildlife prey were primarily nocturnal (40.5%), followed by crepuscular (17.7%) and cathemeral (10.1%; Supplementary Fig. S2A). Upon removal of species documented under experimental conditions, a larger proportion of wildlife was found to be diurnal (44%), but still remained more widely distributed across temporal conditions than domestic species ($\chi^2_{(3)} = 10.2$, $p = 0.02$). The remaining wildlife species, prey documented in field conditions, were nocturnal (28.0%), followed by crepuscular (16.0%), and cathemeral (12.0%). Domestic species continued to demonstrate primarily diurnal activity (90.9%) and to a larger degree than wildlife taxa. These patterns may, in part, explain an increased tendency to feed on for livestock, given the predominantly diurnal behavior across species, and thus lack of reactivity during *D. rotundus* prime hunting hours.

Wildlife and domestic prey also demonstrated significant differences in social behavior ($\chi^2_{(1)} = 13.79$, $p = 0.002$) (Supplementary Fig. SB). Domestic species preyed upon by *D. rotundus* in all study conditions were primarily social (88.3%), compared to solitary wildlife species (61.7%). For prey species documented only under field conditions, 90.1% of domestic animals demonstrated social behavior. Nevertheless, wild prey were more evenly distributed across the two conditions, with 56% of species considered social and 44% considered solitary ($\chi^2_{(1)} = 4.8$, $p = 0.03$).

Suitable prey species in areas of invasion

Given the potential for northward range expansion, species distributed in the United States were examined within the dataset. Of the 63 total species identified, 36 are currently present in the United States, including 1 amphibian, 5 avian, 6 reptilian, and 24 mammalian species. Mammals in the United States that may serve as suitable prey for *D. rotundus* include 12 domestic and 23 wild species. Wild mammalian species include the white-tailed deer, wild pig, coyote, puma, Virginia opossum, marmot, squirrel, striped skunk (*Mephitis mephitis*), northern raccoon (*Procyon lotor*), nine-banded armadillo (*Dasypus novemcinctus*), eastern cottontail (*Sylvilagus floridanus*), packrat (*Neotoma* sp.), and house mouse (*Mus musculus*).

The white-tailed deer, wild pig, coyote, puma, and squirrel have been documented as *D. rotundus* prey in non-captive settings, while opossums and marmots have been reported anecdotally. The striped skunk, northern raccoon, nine-banded armadillo, eastern cottontail, and packrat have only been studied as *D. rotundus* prey in captive settings. Wildlife of other prey classes include the rat snake (*Elaphe flavirufa*), pelican (*Pelecanus* sp.), and cormorant of unspecified species, all of which have been described as prey in non-experimental settings.

Discussion

Desmodus rotundus as a generalist predator

This article provides a comprehensive overview of the diet of *Desmodus rotundus* and reinforces the broad range of prey taxa utilized by this sanguivorous bat species. In addition to their considerably sized dietary collection, *D. rotundus* maintains the ability to utilize a variety of novel prey in the absence of natural prey sources. This is especially true in cases where wildlife is scarce and alternative food sources, such as livestock, are abundant, as *D. rotundus* will readily change their dietary reserves. It is, therefore, reasonable to characterize *D. rotundus* as a generalist predator (Hassell and May 1986; Kang and Wedekin 2013; Schutt 2008) or parasite (Combes 2001; May and Anderson 1990) given the species' dietary array and plasticity. Differentiation between the two depends on the ecological definition of its symbiont roles in an ecosystem and the taxa of prey involved (Buck 2019; Hassell 1966; Raffel et al. 2008). Range expansion of *D. rotundus* in response to anthropogenic change, therefore, holds significant risks given the dietary breadth and behavior of this species. Identifying at-risk prey, therefore, becomes critical in both preventing and mitigating these issues in ethical and efficacious ways. A clear understanding of the species at risk of *D. rotundus* predation can be used to help key stakeholders anticipate the downstream effects and plan efforts such as vaccination protocols, public health outreach and education, and resource allocation.

Regarding livestock, swine, equine, and poultry are likely at risk, with numerous reports of the *D. rotundus* feeding on these production species. Nevertheless, cattle were the most commonly cited prey throughout the literature. This observation seems to be related to intensification of livestock rearing in areas inhabited by *D. rotundus*, combined with land-use changes that reduce available wildlife prey (Lanzagorta-Valencia et al. 2020; Mantovan et al. 2022; Rojas-Sereno et al. 2022). Likewise, it may be a true pattern of predation, explained by the convenience and availability of this food source (Delpietro et al. 1992; Gonçalves et al. 2021; Voigt and Kelm 2006). As *D. rotundus* expands its geographic

range to higher latitudes and elevations, it will become increasingly crucial that members of the agricultural industry, including producers, large animal veterinarians, and public health officials, continue to stay vigilant to prepare for the potentially increased risk of RABV transmission. This includes maintaining awareness of these distribution changes and the impact *D. rotundus* may have on livestock production systems. Surveillance is particularly important in areas where livestock are abundant (i.e., Texas rangeland), as *D. rotundus* may quickly take to using these agricultural species as a primary food source (Acha and Alba 1988; Anderson and Shwiff 2014).

Dietary shifts upon range expansion are also likely to include various wildlife, as noted by *D. rotundus*' plasticity and range of suitable natural prey. Rodentia has not previously been implicated as a high-risk group for *D. rotundus* predation, but our findings demonstrate the large number of rodent species utilized by *D. rotundus*. Predation on rodents may be due to the diversity of species within this order, but the actual drivers of this association are unknown. Even-toed ungulates and carnivores may also be at risk upon *D. rotundus* invasion, given the number of species currently preyed upon in these taxonomic groups.

In the United States specifically, several wildlife taxa may serve as suitable prey for *D. rotundus*. Many of those species, such as the white-tailed deer, are widely distributed across the country and comprise ample population sizes (Johns and Kilgo 2005). The large number of rodent species identified in the review may be especially notable in semiarid regions like Texas, where numerous rodents continue to thrive (Windberg 1998; Schmidly and Bradley 2016). Novel species like the nutria (*Myocastor coypus*) may be extremely suitable species for *D. rotundus* upon invasion, given their morphologic and anatomic similarities to known *D. rotundus* prey, although additional research is needed to confirm this hypothesis (Swank and Petrides 1954). Moreover, many of the suitable wildlife species in the United States already present significant disease burdens to both domestic and livestock health. For example, the striped skunk, an identified prey source of *D. rotundus*, is the main reservoir for sylvatic rabies in Texas (Oertli et al. 2009; Wohlers et al. 2018). *Desmodus rotundus* holds the potential for interspecies RABV transmission and perpetuation of rabies in current reservoirs like the striped skunk and also for introduction of novel virus variants into novel host taxa (Favoretto et al. 2002; Kobayashi et al. 2005). It is, therefore, reasonable to describe the possible impact of *D. rotundus* on United States wildlife as considerable, particularly in regard to the economics of rabies control. Between 1989 and 2004, the United States spent over \$34 million on oral rabies vaccines for coyotes, a *D. rotundus* prey species, and gray foxes in Texas alone (Stern et al. 2009). The country continues to pour funding into efforts to control the sylvatic form

of this disease (Slate et al. 2009; Fehlner-Gardiner 2018). Range expansion of *D. rotundus* is already estimated to be a costly event (Anderson and Shwiff 2014; Zarza et al. 2017), although this estimation neglects the costs of control in the reservoir (e.g., *D. rotundus* vaccination, population control, monitoring) and may, thus, be underestimated.

While the risk of RABV transmission and occurrence of clinical disease in companion animals is lower, given the robust vaccination protocols typically used in pets (Ma et al. 2018), *D. rotundus* may predate upon domestic dogs and cats. Alternatively, dogs and cats can predate *D. rotundus* (Delpietro et al. 1994). Both events have implications for public health considering that reports of pets positive to rabies derived from *D. rotundus* are common (Badilla et al. 2003; de Mattos et al. 1996; Ito et al. 2001; Horta et al. 2022; Schaefer et al. 2002). In Latin America, domestic dogs were once RABV reservoirs of significant public health importance, causing a large number of human rabies cases (Horta et al. 2022). The number of dog-mediated human cases eventually declined in certain regions through pet vaccination campaigns, public health efforts, and widely available post-exposure prophylaxis, though their present role is non-negligible (Horta et al. 2022). Range shifts of *D. rotundus*, driven by land-use changes, led this species to surpass domestic dogs as the primary RABV reservoir in the region (Horta et al. 2022). As a result, human rabies cases have risen in recent years in some regions of Latin America (Horta et al. 2022). As *D. rotundus* expands to new ranges and potentially becomes established in areas like the United States, the risks to humans and companion animals may rise similarly to those seen in Brazil.

Mitigating the effects of *Desmodus rotundus* invasion

Although *D. rotundus* range expansion seems to be imminent due to ongoing ecosystem change, actions may be taken to mitigate the potential consequences of rabies range expansion, including a sustained availability of wildlife prey through biodiversity and habitat management. Anthropogenic change is known to be closely amalgamated with conflict and disease spread between bats, domestic animals, and humans (Stoner-Duncan et al. 2014). The relationship between diminished natural environments, declines in wildlife populations, readily available domestic species, and distribution changes of *D. rotundus* is critical to consider in mitigation attempts. As previously described, *D. rotundus* prey choice is likely attributable to convenience (Delpietro et al. 1992; Gonçalves et al. 2021; Voigt and Kelm 2006). In Latin America, land-use change not only increases the abundance of livestock, but in doing so, reduces the richness and distribution of wildlife taxa (Grau and Aide 2008; Michalski et al. 2006). Under these conditions, *D. rotundus*

readily predate upon human-supplied species such as livestock and companion animals (Acha and Alba 1988; Rojas-Sereno et al. 2022). As *D. rotundus* expands into new territories, it is reasonable to assume that domestic animal populations in invaded zones will follow similar patterns and utilize the domestic species readily available to them if wildlife is scarce or absent. An ecosystem-health approach to *D. rotundus* management, incorporating landscape, wildlife, and domestic species ecology, is, therefore, of great benefit to mitigation efforts. Conservation attempts in this context may serve as an indirect disease prevention tool and should be made not only in regard to wildlife richness, but native habitats and the larger ecological community as well. Ensuring abundant prey is available, via maintenance of suitable wildlife habitat, is especially critical in regions recently converted for agriculture use (Mayen 2003; Uhart and Milano 2002). This integrative approach to disease mitigation is an added benefit for bat population health, which must also be considered in discussions of ecological impartiality. The larger effects of bats on ecosystem health are well documented, and although less clearly defined for *D. rotundus*, conservation should be pursued when possible to avoid undue ecological damage associated with bat population declines (Kunz et al. 2011; Stoner-Duncan et al. 2014). In general, bats provide valuable ecosystem services including insect control, pollination, and seed dispersal (Kunz et al. 2011). Guano, produced by *D. rotundus* specifically, contains greater nitrogen content than that of various frugivorous and insectivorous bats (Emerson and Roark 2007; Hadas and Rosenberg 1992). Ultimately, the loss of bat species may lead to further ecologic impairment and agricultural loss (Kunz et al. 2011) and this may hold implications for *D. rotundus* itself.

A conservation-minded approach to disease control is not to undermine the public and veterinary health risks associated with *D. rotundus*. Nevertheless, some form of population control is considered to be required for *D. rotundus*, given their overabundance and potential for public health and economic harm in some sites (Gonzalez and Mitchell 1976; Johnson et al. 2014; León et al. 2021). Failing to control the species through selective measures may lead to a rise in the utilization of nonselective and unethical methods (Mayen 2003; Olival 2016). For example, *D. rotundus* have historically been subjected to and targeted by campaigns fueled by fear, with little evidence-based methodology behind them (Mayen 2003). Cementing roosts closed, destroying roosts with explosives, and poisoning *D. rotundus* have all been used to as forms of population control (Gonzalez and Mitchell 1976; Greenhall 1988). Many other traditional control methods have been attempted with often limited efficacy and longevity, including both chemical and physical means of *D. rotundus* depopulation (Arellano 1988; Gonçalves et al. 2002; Johnson et al. 2014; León et al. 2021;

Thompson et al. 1972). More recently, nonselective population reduction and control methods have been highlighted as ineffective (Streicker et al. 2012), counterproductive (Viana et al. 2023), inhumane (Olival 2016), and a threat to other bat species that may be critical in maintaining ecosystem services (Mayen 2003; O'Shea et al. 2016). Research suggests that for culling to be effective, it would need to occur at a scale that is essentially not feasible (Gonçalves et al. 2021; Streicker et al. 2012) or in bat populations with absence of RABV circulation (Viana et al. 2023). Likewise, mass culling of *D. rotundus* may lead to increased disease spread via displacement of colonies in addition to the displacement already induced from habitat fragmentation itself (Streicker et al. 2012). This activity may contribute to the persistence of rabies via movement of infectious bats between colonies following frequent immunizing but non-lethal exposure (Blackwood et al. 2013). Similarly, the stress associated with culling activities may increase the likelihood of viral shedding (Olival 2016). Minimal disruption of roosts is now recommended in discussions of *D. rotundus* control (Delpietro et al. 2017; Rocha and Dias 2020; Streicker et al. 2012).

In Latin America, efforts to control *D. rotundus* have involved the administration of topical anticoagulants to cattle, ultimately causing death via hemorrhage to *D. rotundus* that feed on the bovids (Mayen 2003; Rocha and Dias 2020). Finely targeted control involves the direct application of 2% warfarin in Vaseline on the mid-dorsum of *D. rotundus* to promote intoxication of the colony during grooming (Carballo and Alejandro 1996). This solution is also applied along the walls of *D. rotundus* roosts, though this leads to indiscriminate killing of other bat species (Johnson et al. 2014). A more costly but selective variation involves the application of warfarin in paste formulation to bite wounds of cattle, targeting *D. rotundus* individuals that return to feed on cattle across multiple nights (Piccinini et al. 1998). Warfarin has also been injected directly into cattle to depopulate *D. rotundus* (Flores Crespo et al. 1979), but effects of this practice on the health of livestock and human consumers are unclear. Ultimately, no single population control strategy fits all scenarios and there is a need for continued and updated research on the topic. Sustainable and effective rabies control and prevention methods include diligent vaccination of livestock (Anderson et al. 2014) and oral vaccination of *D. rotundus* (Bakker et al. 2019). The latter is an ongoing development in terms of implementation (Delpietro et al. 2021; Sétien et al. 1998; Stoner-Duncan et al. 2014). It has more recently been under assessment in the context of *D. rotundus* social behavior, that is, utilizing social grooming as a means to introduce and spread vaccines throughout a colony (Delpietro et al. 2021; Sétien et al. 1998; Stoner-Duncan et al. 2014). The effects of rabies vaccination on *D. rotundus* and the prevalence of other bat-borne pathogens and bat demography are unknown. Reproductive drugs to sterilize bats

have also been discussed as a population control and rabies prevention tool for the species (Gonçalves et al. 2021; Ser-rano et al. 2007). Other efforts have focused on minimizing the incidence of bites and exposure of livestock to the bats (Stoner-Duncan et al. 2014). Modifications to agricultural practices that may deter *D. rotundus* establishment include netting, artificial light, and ultrasound acoustics (Arnett et al. 2013; Benavides et al. 2020a; Delpietro 1989; Gonçalves et al. 2021). Nevertheless, these interventions could also exacerbate the displacement of colonies to new areas, expanding the human–wildlife conflict. The use of repellent to selectively deter *D. rotundus* from preying on livestock has also been suggested (Mayen 2003).

Furthermore, and in regard to disease risk, much of the focus lies on *D. rotundus* as a disease reservoir and threat to domestic animal health. Given the diversity of wildlife species found in this review, it may be of value to examine the role of the different wildlife species in the transmission of RABV (Worsley-Tonks et al. 2020). This may guide decisions regarding resource allocation and target species for rabies prevention and control efforts. For example, rodents in particular may be an important prey species, but they do not play a relevant role in the epidemiology of rabies after contact with an infected *D. rotundus* (Winkler et al. 1972). Rodents, however, may serve as important reservoirs of other diseases that *D. rotundus* is known to host such as hantavirus (Sabino-Santos Jr et al. 2018) or leptospirosis (Cosson et al. 2014). As previously mentioned, certain wildlife species (i.e., those that play a role in the propagation of rabies) in at-risk regions of invasion require additional research on their interactions with *D. rotundus*. The striped skunk, a primary RABV reservoir in Texas, was demonstrated as *D. rotundus* prey, but only in captive and experimental settings. Studies to clarify whether *D. rotundus* would target this species under field conditions are needed to better characterize the species-specific risks that might present following invasion distribution changes. This is particularly important given the role of skunks as reservoir of RABV in regions of potential *D. rotundus* invasion.

Future directions

Nonrandom bias exists in study location, prey detection methods, number of samples per site, and type of *D. rotundus* prey (i.e., wildlife versus livestock), among others. These biases make interpretation of the proposed trends problematic and increase uncertainty in any extrapolations of the patterns to other areas of potential invasion. It is, therefore, difficult to infer patterns of prey selection and potential driving factors behind it, particularly without baseline data to control for species richness or density within each study location. The trends identified in this review cannot be confirmed as true biological variation

as opposed to artifacts resulting from bias in the available literature. Likewise, there are many facets of *D. rotundus* diet lacking information as a whole. For example, much research is needed on prey in countries with limited data and taxonomic groups lacking substantial literature. Carter et al. (2021) noted that variation in host species across geographic ranges is a future area of interest. Further field-based studies to accurately assess the feeding dynamics and prey utilization of *D. rotundus* in an observational setting would likewise be advantageous for its documented prey species. Camera traps have and may increasingly serve as a valuable tool in this regard, allowing monitoring and data collection without the disruption that human-led observation may pose to *D. rotundus*. In at-risk areas for invasion, robust surveillance systems, through technical or other means, are necessary to monitor trends and closely follow progression of *D. rotundus* distribution changes (Mayen 2003). These gaps must be filled as a whole to better understand trends in known prey species and to assess suitability of non-documented species as a food source.

Lastly, continuing outreach on the distributional ecology of *D. rotundus* is needed given their impending range expansion, the broad taxonomic range of suitable prey, and the magnitude of the impact that invasion of this species holds. Engagement of key stakeholders, including wildlife health professionals, researchers, veterinarians, public health officials, and producers is critical. This is particularly vital in areas of potential *D. rotundus* range expansion, such as the United States–Mexico border region and the Andes region in South America. Given the dietary adaptations of and its plasticity to use disparate prey, *D. rotundus* functions as an ideal biological model to investigate the effects of global change on predator–prey dynamics at the human–wildlife interface. The ecology of *D. rotundus* in the context of ongoing anthropogenic change is deserving of continued research attention, with significant implications for the health of humans, livestock, and wildlife alike.

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Author contributions NB and LEE devised the project, developed the proof outline, and analyzed relevant data. NB performed data collection and wrote the first draft of the manuscript in consultation with LEE. All authors approved the final version of the article.

Data availability The authors confirm that the data supporting the findings of this study are available within the article [and/or] its supplementary materials.

Declarations

Conflicts of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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