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Research article

The importance of livestock in the diet of Mexican wolf *Canis lupus baileyi* in northwestern Mexico

Jorge L. Reyes-Díaz[1,2], Nalleli E. Lara-Díaz[2], María Gabriela Camargo-Aguilera[1], Laura L. Saldívar-Burrola[1] and Carlos A. López González[1]

[1]Laboratorio de Zoología, Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, México
[2]Laboratorio de Ecología Animal, División de Ciencias Biológicas y de la Salud, Universidad Autónoma Metropolitana Unidad Iztapalapa, Ciudad de México, México

Correspondence: Nalleli E. Lara-Díaz (lara.nalleli@gmail.com), Carlos A. López González (cats4mex@gmail.com)

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The reintroduction of the Mexican wolf in the wilds of northwestern Mexico has allowed us to address its trophic ecology and elucidate conflicts with livestock producers: their main mortality factor. Our objective was to determine the feeding habits of wolves in Mexico, as well as the quantity and frequency of livestock predation in relation to seasonal and individual variables, through the analysis of genetically identified scats. During 2012–2022 we collected 1171 Mexican wolf scats. We extracted and sequenced DNAm and identified individuals and their sex using microsatellite analysis. We washed the scat and separated the undigested components for taxonomic identification. We estimated the frequency of prey items, the biomass it contributed to the diet, and compared prey consumption between sexes and between the birth and dispersal seasons. We constructed generalized linear models to identify the relationship between livestock presence in the diet and dietary prey richness with respect to environmental and individual variables. We identified 68 wolves that had consumed 30 species of vertebrates. Of these, white-tailed deer (36.12%), diversionary feeding (22.79%), and cattle (25.56%) had the highest contribution to biomass. The ingestion of items was independent of the sex of the wolves but was dependent on the season. The presence of deer and diversionary feeding decreased the likelihood of cattle being ingested but also decreased the richness of items of wild species in the wolf diet. Wolves in northwestern Mexico fed mainly on large prey available in the reintroduction area, including livestock. As wolves consume livestock, it increases the risk of retaliatory actions from ranchers. Our results serve as a basis for the implementation of strategies to reduce human–wolf conflicts and set a baseline for coexistence in northwestern Mexico.

Keywords: cattle consumption, Chihuahua, coexistence, diet, white-tailed deer

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Introduction

The Mexican wolf (*Canis lupus baileyi*) was extirpated from the wild in the mid-20th century as part of a campaign to mitigate conflict with livestock in the USA and Mexico (McBride 1980, Brown 1983). Wolves were considered pests that had to be fought with hunting, trapping, and poisoned meat (De la Peña 1947, Brown 1983). A captive breeding program for Mexican wolves implemented in the late 1970s allowed for the reintroduction of the subspecies in Arizona and New Mexico, USA, in 1998 (USFWS 2017). The reintroduction in Mexico took place in 2011 in the State of Sonora and in 2012 in Chihuahua (Lara-Díaz et al. 2015, Siminski 2016). During 2014, the first wild-born litter of Mexican wolves was recorded in Mexico after more than three decades of absence (Lara-Díaz et al. 2015). The occurrence of reproduction and a small population in the wild promoted in 2019 the reclassification of the subspecies by the Mexican authorities from 'Likely extinct in the wild' to 'Endangered with extinction' (SEMARNAT 2019). Twenty-five years after the first release of Mexican wolves into the wild, the population grew to a size that allows ecological studies that have helped to understand its historical distribution (Heffelfinger et al. 2017), suitable habitat (Martínez-Meyer et al. 2021), kill rates on native ungulate prey (Smith et al. 2023), and feeding habits of the subspecies (Reed et al. 2006, Carrera et al. 2008, Merkle et al. 2009).

The gray wolf *C. lupus* is one of the mammals with the widest historical distribution in the world (Mech and Boitani 2003), derived from its feeding habits that are plastic enough to adapt to the search and hunting of various prey species in a variety of habitats and ecosystems (Mech and Boitani 2003, Newsome et al. 2016, Roffler et al. 2021). In general, the diet of wolves is mainly carnivorous and is dominated by medium- and large-sized ungulates in North America, and medium-sized ungulates and various domestic species dominate in European and Asian countries (Newsome et al. 2016, Ferretti et al. 2019, Lippitsch et al. 2024). The consumption of small mammals, birds, and fish, as well as arthropods, berries, and even garbage, has been recorded as well (Paquet and Carbyn 2003, Tourani et al. 2014, Gable et al. 2017, Barton et al. 2019).

Prior to extirpation of the Mexican wolf from the wild, Ligon (1918) and McBride (1980) described the first reports on its diet based on the stomach contents of wolves killed after capture, and on scats. Both Ligon (1918) and McBride (1980) identified multiple remains of domestic fauna (i.e. cows, horses, sheep, goats, and donkeys) in addition to wild fauna (deer, skunks, and rodents). However, 60% of the items could not be identified to lower taxa (Ligon 1918, McBride 1980). In the Mexican wolf Eexperimental population area (MWEPA) 16 species comprise the Mexican wolf diet, where elk *Cervus canadensis* was the most commonly consumed species (Reed et al. 2006, Carrera et al. 2008, Merkle et al. 2009). As elk are not naturally distributed in Mexico (Carrera and Ballard 2003), the natural diet of the Mexican wolf remained incomplete and was not useful for management decisions.

In Mexico, the diet of free-roaming Mexican wolves has been documented to include white-tailed deer *Odocoileus virginianus couesi*, rabbits *Sylvilagus* spp., skunks *Mephitis* spp., squirrels *Otospermophilus variegatus*, and other small rodents (Saldívar Burrola 2015, Reyes Díaz 2021, Reyes-Díaz et al. 2022). In addition, livestock *Bos taurus* are also part of their diet; therefore, to alleviate depredation pressure and ingestion of domestic fauna, the reintroduction program in Mexico provides diversionary feeding to released Mexican wolves that consist of domestic pig *Sus scrofa domesticus* (López-González et al. 2021, Lara-Díaz et al. 2022). This item thus is expected to occur frequently in the diet of naively released Mexican wolves (Saldívar Burrola 2015, Reyes Díaz 2021).

Mexican wolf releases come from a variety of sources including animals which have been under human care, and some individuals have been transferred from the southwestern US population (López-González et al. 2021, Lara-Díaz et al. 2022). In addition, wild-born individuals have been recorded on the Mexican landscape since 2014 (Lara-Díaz et al. 2015). In order to reduce the number of conflicts of these reintroduced Mexican wolves with livestock producers, we implemented a diversionary feeding technique. We provided meat for Mexican wolves under the assumption that a food supplement would allow wolves time to habituate to their natural surroundings and increase survival (Miller 2017). This initial feeding technique was predicted to reduce predation of cattle, the most available and easy prey item to consume in the region (Kubasiewicz et al. 2016, Garshelis et al. 2017). We provided the meat in the form of domestic pigs *Sus scrofa*, which were obtained from local farmed enclosures. In addition, the area where wolves were reintroduced do not have invasive wild boars (Álvarez-Romero and Medellín 2005).

The wolf's predatory behavior results in a conflict with humans, stemming from attacks on domestic animals and competition for wild ungulates of importance for hunting (Naughton-Treves et al. 2003). The prey selection of wolves is driven by availability and abundance of prey species (Janeiro-Otero et al. 2020, Guimarães et al. 2022, Mayer et al. 2022, Smith et al. 2023). When wild prey in natural habitats are overhunted and then replaced with an overabundance of domestic animals, the opportunities for coexistence between ranchers and wolves is reduced. This is a scenario that ultimately threatens the survival of entire wolf populations (McBride 1980, Hartman 1995, Laliberte and Ripple 2004).

Human–wildlife coexistence studies in Mexico are beginning to develop (Flores-Armillas et al. 2020) but are scarce in northern Mexico (Bueno-Cabrera et al. 2005, Rosas-Rosas et al. 2008, 2010, Peña-Mondragón and Castillo 2013, Durán-Antonio et al. 2020). As part of these coexistence alternatives, it is necessary to understand the trophic dynamics of a species that has been absent from its native ecosystems for almost half a century (Smith et al. 2023). Furthermore, study of the diet of the Mexican wolf will help us to elucidate the potential severity of conflicts with livestock producers, whose historical aversion has hindered the full establishment of wild Mexican wolves (López-González et al. 2021, Lara-Díaz et al. 2022).

In the evaluation of diet, scat analysis is the most common and effective technique for studying the trophic ecology of carnivores (Klare et al. 2011). It allows for a representative number of samples to provide greater objectivity in the analysis (Gallina-Tessaro 2011, Nilsen et al. 2012, Morin et al. 2019), in addition to being a noninvasive and relatively economical method to assess food habits (Monterroso et al. 2019, Morin et al. 2019). Genetic identification also provides valuable demographic information, such as precise identification of the predator species and identification of individuals and their sex (López-Bao et al. 2018). This makes it possible to address intraspecific variation in the consumption of items derived from different scenarios.

We wanted to test sex-related differences in items consumed, under the assumption of the division of responsibilities during capture, handling, or acquisition of consumed items between individuals of different sexes during the pup-rearing or dispersal seasons (Mech 1974, Packard et al. 1992, Mech et al. 1999, Roffler et al. 2022). This seasonal effect would also be present as dispersing juveniles search for open space or mates and form a new pack (Gese and Mech 1991, Mech et al. 1998, Mech 1999). We would expect Mexican wolves to consume smaller-sized items during dispersal (October–April, when settling into a different region than the natal area) than during the pup-rearing season (May–September, central feeding limited to den site fidelity). There is a documented size dimorphism in Mexican wolves (Brown 1983, Nowak 2003), consequently we would expect a difference in the items consumed by females and males. There should be a trend for larger males to consume larger-sized items than females.

Furthermore, the high availability of livestock and relative ease of capture increases the likelihood presence in the diet of wolves, particularly during low productivity when resources are scarce (Rosas-Rosas et al. 2008, Anaya-Zamora et al. 2017). We expect a reduction in the consumption of livestock by wolves as the availability of diversionary feeding increases (Kubasiewicz et al. 2016, Miller 2017). Furthermore, we expect a reduction in livestock consumption will occur when a broader diversity of wild items are consumed (Meriggi et al. 2011, Ferretti et al. 2019, Barja et al. 2023).

The objective of this study was to determine the diet and the diversity of items consumed by reintroduced Mexican wolves in Mexico, as well as the importance of domestic and wild fauna ingested in relation to season and sex, based on the genetical analysis of collected wolf scats.

Material and methods

Study area

The study area included seven municipalities in the northwest of the state of Chihuahua and two municipalities in the northeast of Sonora, Mexico, where we collected samples of Mexican wolf scat (Fig. 1). The study site has an area of 18732.8 km^2 and is between 1204 and 2627 m a.s.l. (USGS 2012). A temperate semi-arid climate predominates, with temperatures ranging between −17.5 and 41.5°C (Cuervo-Robayo et al. 2019). The total annual precipitation ranges from 300 to 400 mm, with a relative humidity of 50% (Cuervo-Robayo et al. 2014). Despite the large extensions of land used for grazing for livestock and agriculture (32.99 and 9.02%, respectively), 32% of the area has forests of oak *Quercus* spp., pine *Pinus* spp., oak–pine, pine–oak, and junipers *Juniperus* spp. The rest of the land is desert and xerophytic vegetation (25.33%), as well as minimal urban construction and wetland (0.62%; CCRS et al. 2023). Land ownership is divided into private properties; communal lands (both ejido and colonias), whichare mainly used for agriculture; livestock; and forestry activities (García et al. 2009, RAN 2017). Two natural protected areas exist in the region: the Janos Biosphere Reserve (5000.00 km^2) and the Campo Verde Flora and Fauna Protection Area (1080.69 km^2, CONANP 2023). As land in both protected areas are privately owned, management decisions belong to the landowner. Once a privately owned parcel is incorporated under a protected area status, the Natural Commission of Protected Areas (CONANP, Latargére 2009) attempts to restrict land use. Local management actions, such as predator control, continue to occur despite a level of protection.

Livestock landscape

Northwestern Mexico dedicates more than 70% of its area to livestock production, making it one of the main economic activities (SEMARNAT 2023). Production in tons of live cattle represented an average of 4.27% of the national production between 2012 and 2022, while the study area contributed between 3.98 and 5.18% of the annual state production (SIAP 2023). In addition, the area is one of the main exporters of cattle to the USA, ranking second nationally from 2012 to 2016 and first from 2017 to 2022 (SENASICA 2023). Livestock production is extensive, with calf production year-round and little to no husbandry practices by landowners. The occurrence of coexistence techniques within the region is limited to those producers that have a favorable attitude toward predator presence (Lara-Diaz et al. 2022).

Sample collection

During 2012–2022, we collected scats opportunistically along trails, forest roads, and within areas known to have been used by Mexican wolves through satellite locations. Radiotelemetry was not used to search for scats but to determine Mexican wolf presence. We identified canid scats using diameter, sign, and odor (Reed et al. 2004). All scats were collected on private ranches or communal lands. Scat search included both protected and unprotected landscapes, without differentiation. We collected scats using latex gloves to prevent DNA contamination, and placed them in paper bags labeled with date, locality, coordinates, and additional observations. All samples were air-dried and placed directly under sunlight to avoid fungal contamination.

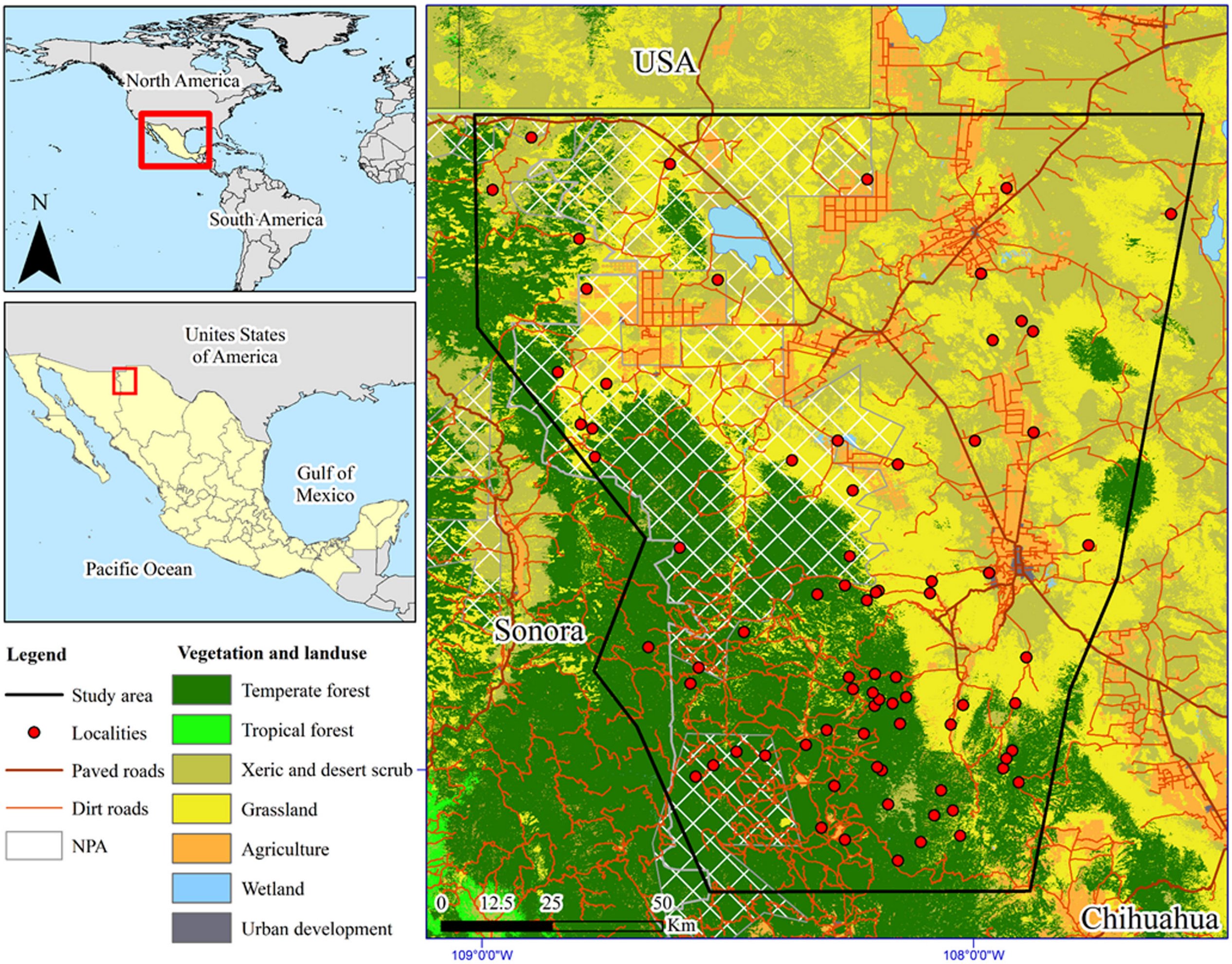

Figure 1. Mexican gray wolf scat sampling polygon within the reintroduction area in Mexico. We indicate the types of vegetation present, paved roads, dirt roads, and natural protected areas (NPA).

Species, individual, and sex identification

In a sterile environment generated by a Bunsen burner (Sanders 2012), we scraped the surface of each scat with a single-edge razor to obtain epithelial cells from the canine digestive system and deposited 0.3–0.5 g in Eppendorf tubes. We purified the DNA using the QIAmp ®DNA Stool Mini Kit following the manufacturer's protocol (Qiagen Inc., Valencia, California) with adjustments in the lysis step and DNA elution: we used 1.8 ml of ASL buffer, and incubated it at 70°C for 30 min. During DNA elution, we added 100 µl of buffer AE to the Qiagen column, centrifuged, washed it with 100 µl of PCR water, and centrifuged again at a final volume of 200 µl (Montana et al. 2017). We amplified the extracted DNA following the general PCR protocol for the identification of each sample (Rinkevich 2012), where we used universal primers (mcb398 and mcb869) and a final concentration of 15 µl: 9 µl green taq (PROMEGA Corp), 0.2 µl BSA 7.5% (Sigma-Aldrich, St. Louis, MO, USA), 0.2 µl $MgCl_2$ (Qiagen Inc., Valencia, California), 0.3 µl of each primer, 5 µl of DNA, and 0.3 µl of PCR water (Montana et al. 2017). We performed agarose gel electrophoresis to verify the amplification and assess the presence of the DNA of interest. After DNA extraction, a measurement of the concentration and purity of the DNA obtained through spectrophotometry was made and only those samples between 260 nm/280 nm were used (Lucena-Aguilar et al. 2016). The resulting PCR products were purified using ExoSAP-IT (USB Corporation, Cleveland, OH, USA) and sequenced. We used the mtDNA control region (D-loop) canid specific primers to separate Mexican wolf from coyote scats. Mexican wolves present the Mva1 specific restriction site while the coyotes do not (Reed et al. 2004). We aligned and reviewed the obtained sequences (i.e. forward and reverse) in the MEGA X software (Kumar et al. 2018). We compared them with the sequences contained in the Gen Bank database (Benson et al. 2018) using the remote software BLAST (Altschul et al. 1990) from the National Center for Biotechnology and Information (NCBI), where we selected the samples with a compatibility equal or greater than 99% with the sequences of the subspecies *C. l. baileyi*.

We performed a PCR amplifying the DBY-F (5′ GCAAATTTGGTTTGTAGTCACA-3′) and DBY-R

(5′-CCATCTCAACATCGCTGAAC-3′) fragments to determine the sex of the samples, whose total volume was 15 µl: 2 µl of DNA, 9 µl green taq master mix (PROMEGA Corp), 0.2 µl $MgCl_2$ (Qiagen Inc., Valencia, California), 0.3 µl BSA 7.5% (Sigma-Aldrich, St Louis, MO, USA), 0.3 µl of each primer, and 3.2 µl of water (Piaggio et al. 2016, Montana et al. 2017). We performed 2% agarose gel electrophoresis stained with an ethidium bromide finger with a 200 bp ladder to visualize the fragments obtained, where one fragment indicates a female individual and two fragments indicate a male individual (Sastre et al. 2009).

Diet components

We placed the scats inside nylon hosiery and separated each sample with a knot to avoid the loss of undigested parts. They were washed with hot water while manually separating the undigested parts of the organic material from the scat until completely clean. We allowed them to air dry and then separated the undigested parts. The components of the samples included guard hairs, bones, teeth, feathers, claws, scales, arthropods, and vegetal remains, which were placed inside small plastic bags to identify the prey items when possible. Guard hairs were used to identify potential prey by observing the characteristics of the hair including cuticular scales and medulla pattern using an optical microscope with the assistance of hair identification guides (Moore et al. 1977, Monroy-Vilchis and Rubio-Rodríguez 2003). We developed a reference hair collection from mammals that inhabit the study area and identified dental pieces using reference materials and identification guides (Elbroch 2006). We clustered the detected species into 10 categories: birds (unable to identify lower taxonomical levels), leporids, squirrels (terrestrial and arboreal), small rodents (mice, rats, and gophers), carnivores and marsupials, wild ungulates, livestock, diversionary feeding (domestic pig), arthropods, and plant matter.

Prey consumed species richness and seasonality

We estimated Simpson's true diversity index and built an accumulation curve of species using the Jackknife 1 estimator (Moreno et al. 2011). We determined the frequency of occurrence ($FO = (Fs/n) \times 100$) of each prey species and the relative biomass consumed by Mexican wolves ($RBC = ((FO \times Y)/\Sigma(FO \times Y)) \times 100$), where Fs is the number of scats where prey species appear, n is the number of scats analyzed, Ft is the sum of occurrences of all prey species, and Y is the correction factor of Weaver (1993; $Y = 0.439 + 0.008X$), where X is the mass of the prey in vivo (Supporting information; Anderson 1972, Ackerman et al. 1984, Galindo-Leal and Weber 1998, Hakkinen 2001, Marceau 2001, McCullough 2001, Siciliano Martina 2013, Clement 2015, Goldverg and Ravagnolo 2015, Rowe 2017, Lara-Díaz et al. 2022, Benson 2023). In addition, we performed a χ^2 test to evaluate the dependence of the Mexican wolf diet in relation to the sex of the individuals or pup-rearing season (April–October) and the dispersal of young individuals (November–March, Brown 1983). We performed an analysis of similarities (ANOSIM), a multilevel pattern analysis, and a non-metric multidimensional scaling (NMDS) to assess prey consumption differences between sexes and seasons, where we used the libraries 'tidyr' (Wickham et al. 2023), 'vegan' (Oksanen et al. 2022), 'indicspecies' (De Cáceres et al. 2023), and 'simEd' (Lawson et al. 2021) in the software R ver. 4.3.1 (www.r-project.org).

Generalized linear models

We built a generalized linear model (GLM) with binomial error structure to predict if the presence of cattle in the diet (0 or 1) was related with the presence (0 or 1) of other large-sized items (diversionary feeding, white-tailed deer), and richness of ingested items (number of items of wild prey found in each scat excluding white-tailed deer). We also constructed a GLM with a Poisson error structure to evaluate the relationship between the numbers of items consumed (range 0–4) with large-sized items (cattle, white-tailed deer). We used season, individual, and sex in both models (Supporting information). The seasons correspond to pup rearing (April–October) or dispersal (November–March; Brown 1983). The individuals and sex correspond to those uniquely genetically wolves in the study (n = 68, 26F:42M). We selected the best model considering the lowest Akaike information criteria (AIC; Akaike 1973), in addition to having an AIC weight equal to 1. If no model met this last requirement, we selected models that had a combined value ≈ 1, and averaged them (Burnham and Anderson 2002). We selected variables with significant contributions to the model based on p values ≤ 0.157 (Sutherland et al. 2023). The GLMs were built using the libraries 'plyr' (Wickham 2011), 'gmodels' (Warnes et al. 2018), and 'AICcmodavg' (Mazerolle 2019) in the software R ver. 4.3.1. (www.r-project.org).

Results

Genetic identification

We collected 2254 canid scats from 75 properties (including privately owned ranches and communal lands), of which 1171 belonged to the Mexican wolf and the remaining to the coyote.

We identified 41.4% female and 58.6% male Mexican wolves which were detected in 1145 scats. Additionally, a total of 26 samples did not amplify the primers for sex identification. These samples were included for prey diversity analyses but not for the rest of the analyses and tests.

Prey diversity

We found 1320 different items in the scats, and we identified 30 vertebrate items consumed by Mexican wolves (Table 1); although Simpson's true diversity index obtained a value of 5.34 effective items, indicating that the wolves' diet consisted of five to six items with the same theoretical abundance.

Table 1. Species consumed by wolves in the Mexican gray wolf reintroduction area in Mexico. No. – number of occurrences, FO – frequency occurrence, Y – correction factor, RBC – relative biomass consumed.

Wild ungulates		No.	FO (%)	Y (kg)	RBC (%)
White-tailed deer	*Odocoileus virginianus couesi*	408	34.84	0.90	36.12
Collared peccary	*Dicotyles tajacu*	6	0.51	0.67	0.39
Diversionary feeding					
Domestic pig	*Sus scrofa domesticus*	305	26.05	0.76	22.79
Livestock					
Cattle	*Bos taurus*	232	19.81	1.12	25.56
Horse	*Equus caballus*	7	0.60	2.12	1.46
Squirrels					
Rock squirrel	*Otospermophilus variegatus*	71	6.06	0.72	5.00
Squirrel	Sciuridae	12	1.02	0.68	0.80
Mexican fox squirrel	*Sciurus nayaritensis*	11	0.94	0.81	0.88
Leporids					
Eastern cottontail	*Sylvilagus floridanus*	56	4.78	0.45	2.47
Dessert cottontail	*Sylvilagus audubonii*	7	0.60	0.73	0.50
Black-tailed jackrabbit	*Lepus californicus*	3	0.26	0.46	0.14
Carnivores and marsupials					
Striped skunk	*Mephitis macroura/mephitis*	43	3.67	0.45	1.90
Virginia opossum	*Didelphis virginiana*	6	0.51	0.47	0.28
White-nosed coati	*Nasua narica*	5	0.43	0.47	0.23
Spotted skunk	*Spilogale gracilis leucoparia*	3	0.26	0.47	0.14
Small rodents					
Yellow-nosed cotton rat	*Sigmodon ochrognathus*	36	3.07	0.07	0.25
Rodents	Rodentia	18	1.54	–	–
White-throated woodrat	*Neotoma albigula*	14	1.20	0.20	0.27
Deermouse	*Peromyscus* sp.	13	1.11	0.03	0.03
Cotton rat	*Sigmodon* sp.	12	1.02	0.09	0.10
Mexican woodrat	*Neotoma mexicana*	10	0.85	0.19	0.19
Beach vole	*Microtus pennsylvanicus*	5	0.43	0.04	0.02
Botta's pocket gopher	*Thomomys* aff. *bottae*	3	0.26	0.15	0.04
Harvest mouse	*Reithrodontomys* sp.	3	0.26	0.01	0.003
Kangaroo rat	*Dipodomys* sp.	2	0.17	0.05	0.01
Tawny-bellied cotton rat	*Sigmodon* aff. *fulviventer*	1	0.09	0.11	0.01
Grasshopper mouse	*Onychomys* sp.	1	0.09	0.03	0.003
Southern rock deermouse	*Peromyscus* aff. *difficilis*	1	0.09	0.03	0.003
Birds					
Birds	Aves	18	1.54	–	–
Common turkey	*Meleagris gallopavo*	8	0.68	0.50	0.39
Arthropods					
Beetles	Coleoptera	25	–	–	–
Grasshoppers	Orthoptera	13	–	–	–
Vegetal remains					
Grasses	Poaceae	95	–	–	–
Juniper seeds	*Juniperus* spp.	48	–	–	–

According to the Jackknife 1 estimator, the detection of prey in the Mexican wolf diet reached 90.9% (Obs = 31 / Exp = 33, with a standard deviation of 1.73). Additionally, we identified 179 items as arthropods (i.e. Coleoptera and Orthoptera) and vegetal remains such as grasses (Poaceae) and juniper seeds *Juniperus* spp. (Table 1).

Prey consumption

White-tailed deer was the most frequent wild prey in the Mexican wolf diet in Mexico, with 34.84% of occurrence, followed by diversionary feeding and cattle with 26.05 and 19.81%, respectively. Additional relevant wild prey in the wolf diet were rock squirrels, cottontail rabbits, and striped skunks, which together had a 15.11% frequency of occurrence, while the rest of the consumed items represented less than 5% (Table 1).

White-tailed deer, cattle, and diversionary feeding had the highest biomass contribution to the wolves' diet (Table 1), whose pooled values represented a range between 67.33 and 91.71% per year (Fig. 2). The remaining consumed items represented 15.43% of the relative biomass consumed by the wolves (Table 1). The biomass contribution of large-sized items to the diet of wolves showed no meaningful variation over time (average large items consumed per year was 84.99 ± 7.14). During 2018 the consumption of small- and medium-sized items was higher compared to the rest of the years analyzed. Thereafter, we observed an increase in cattle

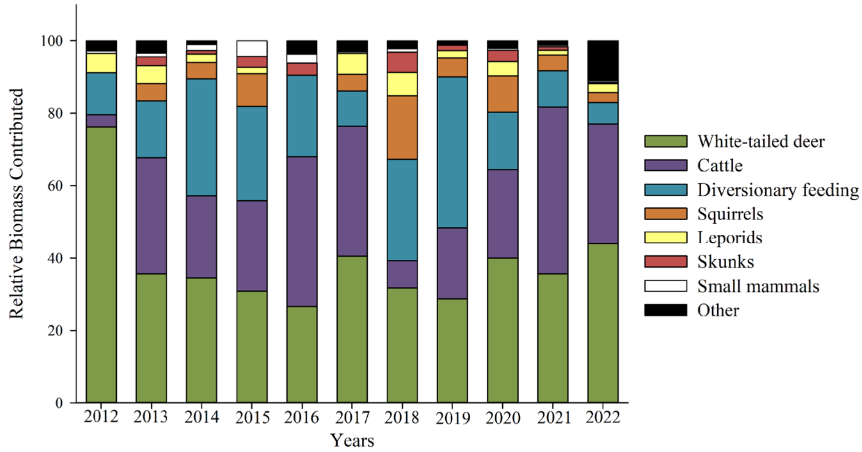

Figure 2. Biomass contribution of different ingested items to the diet of the Mexican wolf in northwestern Mexico from 2012 to 2022. The biomass contributed by white-tailed deer, cattle, and diversionary feeding stood out throughout this period.

consumption and a decrease in the diversionary feeding consumption. The highest cattle intake (46.03%) was recorded in 2021 (Fig. 2).

Differences in prey consumption

The χ^2 test indicated that prey consumption was independent of the sex of the wolves ($X^2 = 28.724$, df = 28, $p > 0.05$), in addition to the fact that the dissimilarity index was null (ANOSIM = 0.03909; significance = 0.26; Fig. 3a), and there was no specific prey consumption associated with the sex of the individuals. However, we found that the frequency of prey consumption was dependent on the wolf breeding and dispersal season ($X^2 = 57.555$, df = 28, $p < 0.05$), even though the dissimilarity index was null (ANOSIM = 0.00157; significance = 0.43; Fig. 3b).

Multilevel pattern analysis did not associate the consumption of any of the prey groups with the sex of the wolves. However, the non-metric multidimensional scaling (NMDS) placed squirrels and carnivores within the female polygon, while diversionary feeding and livestock were closer to the male polygon; leporids were found within the polygons of both sexes, and wild ungulates were found on their limits (Fig. 4a). In terms of season, almost all prey groups were found within or close to the birth and dispersal season polygons (Fig. 4b). In addition, the multilevel pattern analysis was associated with wild ungulates ($r_{pb} = 0.317$, $p = 0.0017$), leporids ($r_{pb} = 0.263$, $p = 0.0104$), and small rodents ($r_{pb} = 0.197$, $p = 0.0133$) during the dispersal season.

The best model to predict cattle presence in scats included diversionary feeding and white-tailed deer variables, with the lowest AIC value and weight of 1 (Table 2). The model indicated that white-tailed deer consumption was the variable with the highest weight, and cattle consumption decreased, followed by a high consumption of diversionary feeding (Table 3). In addition, the richness of ingested items was related to all variables. However, the consumption of diversionary feeding, cattle, and white-tailed deer had the greatest influence on the richness of ingested items according to the average of the eight models with a weight of AIC equal to 1 (Table 2). This indicated that the consumption of ungulates decreased the richness of ingested items per sample and was therefore consumed by wolves (Table 3).

Discussion and conclusions

Since 2011, the reintroduction of the Mexican wolf into the wild in Mexico has provided a valuable opportunity to understand the process of reintegration into the ecosystems of northwestern Mexico, including the study of its trophic ecology. The genetic analyses allowed us to identify that close to 50% of the samples collected belonged to coyotes and highlighted the importance of not only considering the morphometric characteristics of the scats to identify the target species (Reed et al. 2004). Furthermore, accuracy in species identification using molecular scatology prevents the generation of erroneous information regarding feeding habits (Jensen et al. 2022). The female-to-male ratio (0.71:1) may be skewed due to collection site accessibility. Contrasting with a previous female-biased study (Pletscher et al. 1997), Mexico's data suggest a male-driven population, consistent with high-density, low-nutrition environments (Mech 1975).

In Mexico, females usually frequent steep sites with vegetation cover that probably provides them with resting places with privacy and the ease of hiding their burrows and cubs (Packard 2003, Trapp 2004). Males, for their part, tend to move greater distances through open terrain with moderate relief (López-González et al. 2021, Lara-Díaz et al. 2022).

The Mexican wolf, like the rest of the wolves in the world, is a facultative carnivore that tend to feed almost exclusively on mammals (Newsome et al. 2016), except for wild turkeys and some unidentified birds that were consumed infrequently (0.04–2.22%; Reed et al. 2006, Carrera et al. 2008). Arthropods and juniper berries (i.e. *Juniperus* spp.) were also occasionally ingested, likely a byproduct of the capture of a prey item.

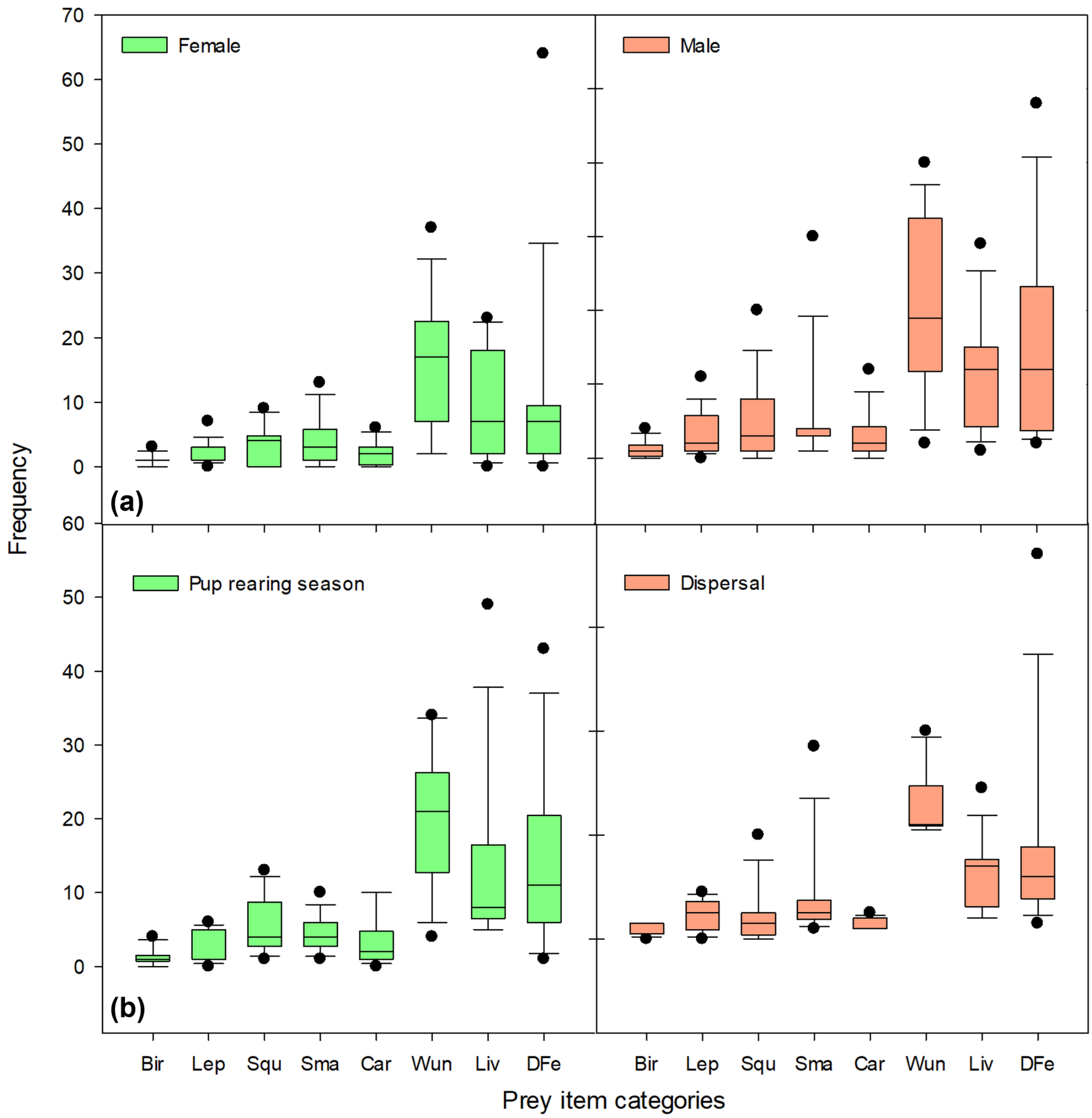

Figure 3. Analysis of boxplot similarities in the diet of Mexican wolves in northwestern Mexico between (a) sexes and (b) seasons. The similarities were based on the data of ingested items found in scats collected between 2012 and 2022.

The study area has a wealth of 77 species of wild terrestrial mammals that could be considered prey of wolves (López-González and García-Mendoza 2012). Large carnivores (i.e. jaguar *Panthera onca*, puma *Puma concolor*; Martins et al. 2020) could be fed upon if found dead, but their current numbers in the landscape surpass the abundance of wolves. In northwestern Mexico, we reported 30 vertebrate prey items consumed by Mexican wolves, of which 26 were wild mammals and represented 33.76% of the potential prey in the area. Even though the likelihood of detecting two or three new species in the diet of the Mexican wolf would require a substantial effort to collect additional scats, it is likely that such species would be small mammals (i.e. rodents, shrews) or even small and/or medium-sized carnivores.

Large ungulate species such as mule deer *Odocoileus hemionus*, pronghorn *Antilocapra americana*, or bison *Bison bison* are locally rare, either distributed in areas where wolves currently do not occur in Mexico or their populations were decimated in the early 20th century. These are currently recovering, and consequently are so small that they are unlikely to appear in the wolf diet (Leopold 1959, McBride 1980, Carreón-Hernández and Lafón-Terrazas 2018, SEMARNAT 2018, López-González et al. 2021, Lara-Díaz et al. 2022).

The high diversity of prey found in our study area indicates that Mexican wolves behave as a generalist carnivore that takes advantage of the available species to which it has access. In contrast to our study area, food habits of Mexican wolves in the southwestern USA are comparable to those of gray wolves in Yellowstone National Park (Jones et al. 2021, Smith et al. 2023). Elk dominance of the landscape in the southwestern USA and their frequent consumption by wolves may reflect the lower representativeness of smaller

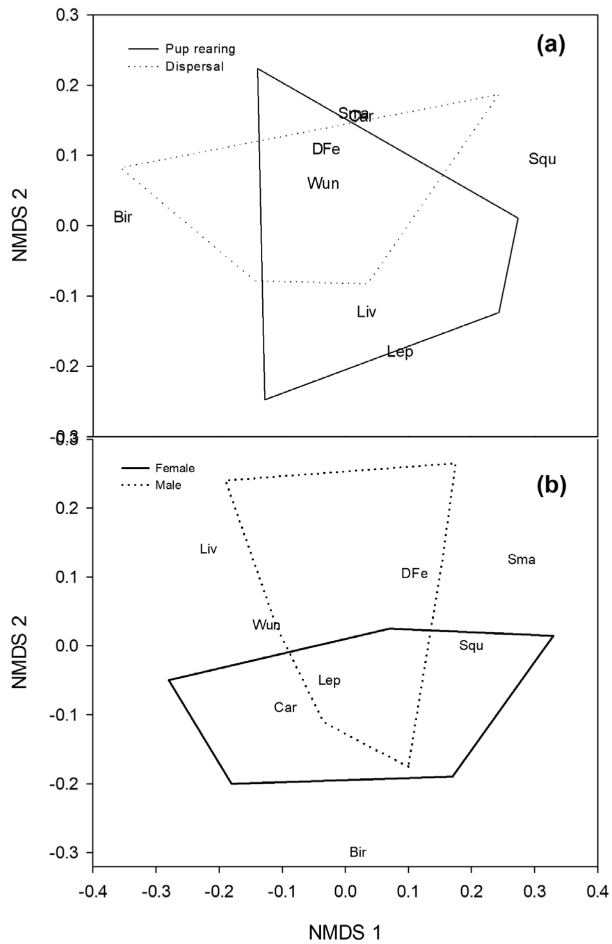

Figure 4. Non-metric multidimensional scaling of ingested items by Mexican wolves in the northwest between 2012 and 2022 according to (a) season and (b) sex. Bir – birds, Car – carnivores, DFe – diversionary feeding, Lep – leporids, Liv – livestock, Sma – small mammals, Squ – squirrels, Wun – wild ungulates.

prey items in the diet (Jones et al. 2021). Comparable-sized gray wolves in European countries exploit medium-sized ungulates (e.g. *Capreolus capreolus*, *Dama dama*, and *S. scrofa*; Mattioli et al. 2011, Nowak et al. 2011, Davis et al. 2012, Wagner et al. 2012). In Mexico, we found that white-tailed deer represents the largest wild prey consumed by wolves despite an overabundance and high availability of cattle in the region (Callejas-Juárez et al. 2014, SIAP 2023). White-tailed deer are an abundant and widely distributed species in the reintroduction area of the Mexican wolf (Lara-Díaz et al. 2011, Lara-Díaz et al. 2022). Capture of a medium-sized deer (W = 57.5 kg, Heffelfinger 2006) by a mid-sized wolf is facilitated for all behavioral social units of Mexican wolves including individuals, pairs, or packs (three to six members; McBride 1980, Brown 1983, SEMARNAT 2009, López-González et al. 2021, Lara-Díaz et al. 2022).

When other wild prey species similar in size or larger than white-tailed deer are scarce or absent, it can threaten the survival of wolf populations and other predators, as they rely on them for energetic requirements (López-Bao et al. 2013, Khorozyan et al. 2015, Parsons et al. 2022). White-tailed deer is the staple hunting trophy species throughout Mexico, with either excellent management practices or excessive unsustainable hunting practices. The white-tailed deer's resilience in Mexico is threatened by habitat loss and competition with livestock for forage, leading to conflicts with livestock owners and disrupting the ecosystem's balance (Tourani et al. 2014, Khorozyan et al. 2015, Ripple et al. 2015, Flores-Armillas et al. 2020, Chinchilla et al. 2022).

The diversionary feeding item was the second most significant component in the diet of the Mexican wolf which, like other wolves, usually takes advantage of and feeds on dead animals available in the area (Ciucci et al. 2020, Klauder et al. 2021). This management tool can reduce livestock consumption (Reyes Díaz 2021) and favor the survival of individuals that lack skills to successfully hunt wild prey due to their history under human care, experience, age, and/or social condition (e.g. solitary individuals; Wikenros et al. 2022). In addition, the consumption of the diversionary feeding requires a lower energy investment (Metz et al. 2020).

Northwestern Mexico is characterized by the widespread export of live cattle to the USA (Cortés-García et al. 2012) and production occurs in year-round extensive pastures, unguarded and with little to no husbandry practices, which generates a high availability of calves throughout the year (Callejas-Juárez et al. 2014, SIAP 2023). Our results showed that cattle represent the third most significant component of the wolves' diet in Mexico, and the frequency and biomass contributed by this item exceeded the data reported for North America (Newsome et al. 2016).

In countries such as Kyrgyzstan and India, the consumption of domestic fauna is highly significant, even though wolves feed on the wild species *Antilope cervicapra*, *Ovis ammon*, and *Capra sibirica* (Maurya et al. 2011, Jumabay-Uulu et al. 2014). Other Asian countries have shown the dominance of livestock in the diet of wolves in response to the low availability of naturally occurring wild prey (Anwar et al. 2012, Hosseini-Zavarei et al. 2013, Shabbir et al. 2013). In addition to domestic prey in some European regions, wolves have been observed scavenging for food at garbage disposal sites in areas with high levels of human activity and disturbance (Tourani et al. 2014, Ciucci et al. 2020). In our study area, while wolves do attack livestock, most depredation events on livestock have been carried out by pumas and coyotes (López-González et al. 2021, Lara-Díaz et al. 2022). In addition, as in other parts of the wolves' range, livestock carcasses occur in the landscape for other causes (e.g. extreme weather conditions, falls, and plant poisoning; Allison et al. 2016, Contreras Servín 2016, Domínguez 2016). This availability is hard to quantify and likely contributes to an increase in livestock consumption, making it tough to discern depredation events from carrion consumption in the diet. For example, in 2021, drought caused the loss of numerous heads of livestock in the area (Gobierno del Estado de Chihuahua 2022); which allowed wolves and other carnivores to take advantage of the carcasses and may have led to an increase in their consumption in their diet (López-González et al. 2021).

Table 2. Selection of models with lower AIC value to explain the relationships between cattle presence (binomial model) and richness of ingested items (Poisson model). K – parameters.

Cattle ~	K	AIC	Δ AIC	Weight AIC	Accumulated weight	Log likelihood
Diversionary feeding + white-tailed deer	3	795.08	0	1	1	−394.53
White-tailed deer + prey	3	814.56	19.48	0	1	−404.27
Diversionary feeding + prey	3	893.96	98.87	0	1	−443.97
White-tailed deer + individual	3	926.27	131.18	0	1	−460.12
White-tailed deer + season	4	941.82	146.73	0	1	−466.89
Prey ~						
Diversionary feeding + cattle + white-tailed deer + season	5	1232.43	0	0.22	0.22	−611.19
Diversionary feeding + cattle + white-tailed deer	4	1232.46	0.03	0.22	0.44	−612.21
Diversionary feeding + cattle + white-tailed deer + individual	5	1233	0.57	0.17	0.6	−611.47
Diversionary feeding + cattle + white-tailed deer + season + individual	6	1233.48	1.06	0.13	0.73	−610.7
Diversionary feeding + cattle + white-tailed deer + season + sex	6	1234.45	2.02	0.08	0.81	−611.19
Diversionary feeding + cattle + white-tailed deer + sex	5	1234.47	2.05	0.08	0.89	−612.21
Diversionary feeding + cattle + white-tailed deer + sex + individual	6	1235.02	2.59	0.06	0.95	−611.47
Diversionary feeding + cattle + white-tailed deer + season + sex + individual	7	1235.51	3.08	0.06	1	−610.7

Our models estimated that the consumption of livestock, diversionary feeding, and white-tailed deer decreased the diversity of wild prey consumed, which implies that the consumption of small- and medium-sized prey will be replaced by the availability and consumption of large-sized species, despite an increased risk when taking larger prey (Metz et al. 2020). This is expected from a reintroduced population, such as the Mexican wolf. The initial numbers that comprised the Mexican wolf population come from a source under human care. Therefore, the proportion of small prey items is expected on naive individuals to a wild landscape. Smaller-sized species, such as squirrels, rabbits, and striped skunks, were frequent in the diet of the Mexican wolf; but their biomass contribution was low, so they can be considered similarly to the USA. This group of items can be classified as accompanying prey because of the high consumption of ungulates (Reed et al. 2006, Carrera et al. 2008, Merkle et al. 2009).

Although the collared peccary is a mid-sized ungulate present and available in the area, it is possible that it is rarely consumed (0.3–0.5%) because of its aggressive and gregarious behavior (Carrera et al. 2008). It is an incidental prey, despite having been widely mentioned as a potential resource that wolves could take advantage of after their reintroduction (Parson and Nicholopoulos 1995, USFWS 1996).

The diet of the Mexican wolf was composed mostly of wild animals and diversionary feeding, but the perception of high and continuous consumption of livestock increases the amount of conflicts with livestock producers and considerably limits efforts to reintroduce, monitor, and conserve the Mexican wolf in the country (López-González et al. 2021, Lara-Díaz et al. 2022). For Mexican wolf release events to move forward and be successful, the implementation and rotation of coexistence techniques such as deterrent tools, efficient compensation tools, surveillance and protection of livestock, and changes in traditional extensive livestock management plans, among other strategies, are required (Bailey and Brown 2011, Eklund et al. 2017, LeFlore et al. 2019, Thompson et al. 2023). Those strategies will only succeed with the continuous participation of local residents, academia, government, and civil society.

Meanwhile, the indiscriminate presence of cattle in the landscape causes changes and losses in animals, plants, and

Table 3. Estimates β of the coefficients of the best model that explained cattle and richness of ingested items (Poisson model) in Mexican wolves. (Y) indicates consumption.

Coefficients	Estimate	SE	z-value	Pr(>|z|)
Cattle ~				
Intercept	−0.31	0.09	−3.22	−0.001
Diversionary feeding (Y)	−2.92	0.34	−8.68	$< 2 \times 10^{-16}$
White-tailed deer (Y)	−3.35	0.35	−9.56	$< 2 \times 10^{-16}$
Prey ~				
Intercept	−0.0865	0.00021181	–	0.4596
Diversionary feeding (Y)	−1.8820	0.01017174	–	$< 2 \times 10^{-16}$
Cattle (Y)	−1.8388	0.30845615	–	$< 2 \times 10^{-16}$
White-tailed deer (Y)	−1.8031	0.00942759	–	$< 2 \times 10^{-16}$
Season (dispersal)	0.0727	0.00009956	–	0.1857
Individual	−0.0012	0.00000002	–	0.2745
Sex (male)	0.0002	0.00000001	–	0.9875

functional diversity in the ecosystem (Castellano and Valone 2007, Chillo et al. 2017, Filazzola et al. 2020, Jordon 2021). Unless husbandry practices change, cattle will continue to be a contributor of biomass for wolves and other large predators in the region. In addition, the implementation of rules and regulations for the harvest and an increment in the availability of large wild prey can help reduce the likelihood of wolves and other predators preying on livestock (Newsome et al. 2016). This, in turn, can lead to a decrease in both actual and perceived conflicts between humans and predators. Such actions provide an opportunity for reintroduced Mexican wolves and other large carnivores to increase their populations in northwestern Mexico in an environment of coexistence, and avoid a return to the conditions that led to the extirpation of Mexican wolves from the landscape in the first place.

We can conclude that Mexican wolf reintroduction efforts in Mexico for the past 11 years have shown that the majority of their diet is represented by large-sized items represented by white-tailed deer, cattle, and diversionary feeding. Our findings show that Mexican wolf diets slightly differed by sex and season. We found that cattle consumption was negatively correlated with an increase of white-tailed deer and diversionary feeding in the diet. Diversionary feeding appeared to be a successful coexistence technique to improve the current conflicts with producers in the region, and to help increase the size of this recolonizing population of Mexican wolves within its historic range.

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Author contributions

Jorge L. Reyes-Díaz: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Nalleli E. Lara-Díaz**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **María Gabriela Camargo-Aguilera**: Data curation (equal); Methodology (equal); Validation (equal); Writing – review and editing (equal). **Laura L. Saldívar-Burrola**: Data curation (equal); Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Carlos A. López González**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.f1vhhmh57 (Reyes-Díaz et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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