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# Dryland river restoration via carnivore reintroduction: Nonnative fauna dominate diets of river otters reintroduced to the Upper Rio Grande

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## ABSTRACT

Dryland rivers often harbor abundant populations of nonnative species that threaten native fauna and negatively alter ecosystem structure and function. Native semiaquatic carnivores, such as river otters (*Lontra canadensis*), that could predate nonnative fauna have been extirpated from many dryland rivers. During 2008–2010, river otters were reintroduced to the Upper Rio Grande (URG), a principal dryland river in the arid southwestern USA that has been colonized by dozens of nonnative fish and invertebrates. We conducted a scat-based food habits study and investigated whether otter reintroduction could be useful for managing nonnative aquatic fauna via predation. Across seasons, nonnative crayfish and fish were the dominant prey items in otter scats; crayfish frequency of occurrence was highest (61–95%), followed by nonnative suckers (7–26%) and trout (3–28%). After accounting for heterogeneous sampling effort between seasons, multi-level models estimated 0.77–0.93 probabilities that scats contained crayfish, compared to 0.05–0.21 and 0.03–0.14 probabilities for suckers and trout, respectively. Reintroducing river otters, and possibly other semiaquatic carnivores, to degraded dryland rivers might be an effective conservation action for controlling nonnative faunal populations within the biomic approach to river restoration, which could reestablish trophic cascades that improve ecosystem structure and function.

## 1. Introduction

Freshwater ecosystems provide the fundamental resource on which hundreds of thousands of species, including humans, depend for life and well-being (Dudgeon et al., 2006). Dryland rivers are critical freshwater ecosystems in many arid landscapes, draining >50% of Earth's terrestrial environments and supporting >20% of the global human population (Nanson et al., 2002; United Nations, 2011). Dryland rivers are characterized as those flowing through landscapes where annual evaporation exceeds annual precipitation, or the aridity index is < 0.65 (Hoover et al., 2020). Natural regulation of biodiversity in dryland rivers occurs primarily via periodical flooding events that are interspersed with droughts; however, most dryland rivers have suffered intense anthropogenic disturbances for decades, including over-exploitation, pollution, flow modifications, habitat degradation, and nonnative species invasions, which collectively reduced native biodiversity (Dudgeon et al., 2006; Laub et al., 2015). Further, many dryland rivers already have or likely will be subjected to longer droughts and reduced precipitation because of climate change (Cook et al., 2015;

Hoover et al., 2020). Consequently, dryland rivers are among the most imperiled freshwater ecosystems in the world (Wong et al., 2007).

River restoration blends components of water-resources science and restoration ecology, with an overarching objective to improve hydrologic, geomorphic, and/or ecological processes, while replacing lost or damaged natural components in degraded watersheds (Wohl et al., 2015). Most river restoration projects have focused primarily on improving water quality and instream habitat conditions, whereas few projects have been implemented specifically to improve biodiversity, return extirpated flora and fauna, or eradicate nonnative species (Bernhardt et al., 2005; Wohl et al., 2015). River restoration projects that focus on improving hydromorphological characteristics or instream habitat conditions often result in no changes to aquatic faunal biodiversity (Jähnig et al., 2011; Palmer et al., 2010). Furthermore, these projects can unintentionally create additional favorable conditions for nonnative or invasive species to colonize, propagate, and outcompete native species (Coulter et al., 2017; Palmer et al., 2010). Thus, a paradigm shift in the river restoration discipline has been initiated, from the long-standing approach based primarily on physical science to a biomic

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approach that harnesses the unique biological and ecological adaptations of native species and provides the conditions for those species to build, maintain, and adaptively manage rivers and associated habitats (Johnson et al., 2020).

A prevailing problem, however, is that some species of native fauna that may be needed for effective implementation of the biomic approach have been extirpated from many rivers, which is particularly the case in dryland rivers (Miyazono et al., 2015). Reintroduction has become a commonly used tool in restoration ecology for returning native species to habitats from which they were extirpated and likely will have an increasing role in the biomic approach to river restoration (Johnson et al., 2020). Perhaps the most prominent example is the reintroduction of beavers (*Castor canadensis*; *C. fibre*) to restore flow regimes and recreate complex river-floodplain-wetland systems that increase river resilience to climate change and human uses. Although the benefits of beaver reintroduction for improving water quality and habitat conditions are evident, recent research has also shown that in dryland river ecosystems, the habitat changes that follow beaver reintroduction can cause nonnative aquatic fauna to increase in number and distribution (Gibson et al., 2015).

Dryland rivers are well-known to harbor abundant populations of nonnative and/or invasive fish and invertebrates (Hoagstrom et al., 2010; Gibson et al., 2015), but targeted removal methods as part of river restoration efforts are often expensive, labor intensive, and ineffective (Rytwinski et al., 2019). Predation by carnivores can limit colonization and population growth of nonnative species, potentially halting or controlling the negative impacts of these fauna on natural ecosystems (Codron et al., 2018). Mustelids, such as mink (*Neogale vison*; *Mustela lutreola*) and otters (*Lutrinae*), are semiaquatic carnivores that typically function as apex predators at the highest trophic levels in freshwater ecosystems (Holland et al., 2018). They tend to have wide dietary niche breadths that include fish, crustaceans, mollusks, reptiles, and mammals, and they have been documented to disproportionately prey on nonnative fauna in some freshwater ecosystems (Juarez-Sanchez et al., 2019; Silva et al., 2012). However, semiaquatic mustelids have been extirpated from multiple dryland river ecosystems, which likely had cascading negative ecological effects that included facilitating the colonization of those systems by nonnative fauna. A biomic approach to river restoration would include the reintroduction of semiaquatic carnivores to native ranges, with the potential benefit of controlling nonnative fish and invertebrate populations.

The Rio Grande is a principal North American dryland river that flows for >3000 km, from the San Juan Mountains in Colorado, USA, through New Mexico, along the Texas-Mexico border, and discharges into the Gulf of Mexico. Draining approximately 472,000 km<sup>2</sup> of land area, much of which is desert, the Rio Grande functions as the primary lifeline for endemic desert flora and fauna as well as >6-million humans that inhabit the watershed. The Upper Rio Grande (URG), north of Albuquerque, New Mexico, contains the greatest volume of water and among the most productive ecosystems along the entire river (Blythe and Schmidt, 2018). Approximately 115 km of the Upper Rio Grande was designated a National Wild and Scenic River by U.S. Congress and also classified as a Category V waterway by the IUCN, thereby denoting its significant ecological and cultural value as well as criticalness to sustaining life and ecological function in this arid region (Wong et al., 2007). Despite its importance, portions of the URG have been impacted by pollution from mining, agriculture, and urbanization, and multiple river restoration projects have been implemented, with most focused on river channel re-shaping, water quality improvement, and increasing instream habitat heterogeneity (Follstad Shah et al., 2007). Furthermore, dozens of nonnative flora and fauna have been intentionally and unintentionally introduced, including multiple fish and crayfish species that threaten native aquatic fauna and have negatively altered ecosystem structure (Hoagstrom et al., 2010; Lodge et al., 2000). For example, the presence of large populations of some nonnative fish is the primary impediment to recovery of imperiled Rio Grande cutthroat trout

(*Oncorhynchus clarkii virginalis*) within the URG (Bakevich et al., 2019).

Problematically, North American river otters (*Lontra canadensis*), which could potentially prey on many of those nonnative species, were extirpated from the Rio Grande by the mid-twentieth century. To attempt to restore riverine ecosystem structure and function, while returning a lost species to its historical range, 33 river otters from Washington, USA, were reintroduced to the URG in northern New Mexico during 2008–2010 (Savage and Klingel, 2015). The post-release population growth rate averaged 1.12–1.15/year and by 2018 the otter population was comprised of 83–104 individuals in 359-km of perennial waterways in the URG (Murphy et al., 2021). Despite the return of otters to this important dryland river, little is known about their potential or realized ecological influence, though anecdotal evidence based on reports from anglers has suggested that otters may be preying disproportionately on trout (Salmonidae; Reed, 2018).

Food habits studies are a critical first step towards identifying and understanding the ecological relationships and effects of apex predators, particularly where carnivores were extirpated, remained absent for decades, and then were reintroduced (Barding and Lacki, 2012). Furthermore, such investigations can be vital for informing ecosystem restoration efforts in dryland rivers, especially if the biomic approach to restoration is employed (Johnson et al., 2020; Laub et al., 2015). Herein, we present results of a river otter food habits study in which we investigated the seasonal dietary composition and presence of native and nonnative fauna in otter scats collected in the URG. The findings of this study should be useful for informing continued restoration efforts in the Rio Grande and other dryland rivers in the arid southwestern USA, as well as conservation and management of aquatic fauna within the URG.

## 2. Materials and methods

### 2.1. Study area

The Taos Plateau Ecoregion is considered a high elevation desert that is bounded to the west and east by the San Juan and Sangre de Cristo mountains, respectively (Walston et al., 2016). The entirety of this ecoregion is within the URG, which contains the north-south trending Rio Grande Rift, through which the Rio Grande River flows. The Taos Plateau receives an average of just 15–25 cm of precipitation annually, though the neighboring San Juan and Sangre de Cristo mountains receive an average of 75–100 cm of winter snowfall, the runoff of which drains into the Rio Grande (Walston et al., 2016). Winter temperatures range from an average low of −19 °C to an average high of 1 °C, whereas summer temperatures range from an average low of 4 °C to an average high of 28 °C. Elevations in the portion of the Taos Plateau within which our study occurred range from 1831 m to 2261 m a.s.l. Predominant woody vegetation along the Rio Grande and its tributaries includes cottonwood (*Populus deltoides*), desert willow (*Chilopsis linearis*), and salt cedar (*Tamarix* spp.). Hiking, boating, and angling are popular recreation activities, and the largest and most productive rainbow trout (*Oncorhynchus mykiss*) hatchery in New Mexico is located on the Red River, which is a perennial tributary of the Rio Grande.

Among fish in the family Salmonidae, New Mexico Department of Game and Fish (NMDGF) releases hatchery-raised nonnative rainbow trout in the Rio Grande and Red rivers multiple times per year, and nonnative brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and cutbow trout (*O. clarkia mykiss*) also have been released. Native, wild populations of imperiled Rio Grande cutthroat trout exist in the URG Basin, mostly in high elevation streams (Bakevich et al., 2019). Among Catostomidae, nonnative white sucker (*Catostomus commersonii*) have been introduced but native populations of Rio Grande sucker (*C. plebeius*) and river carpsucker (*C. carpio*) also exist in the URG. Multiple nonnative species of the family Centrarchidae exist, including smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*M. salmoides*), but native populations of bluegill (*Lepomis macrochirus*) also exist. Similarly, multiple nonnative species of the family Cyprinidae exist in

the URG, including grass carp (*Ctenopharyngodon idella*) and common carp (*Cyprinus carpio*), but native populations of Rio Grande chub (*Gila pandora*), flathead chub (*Platygobio gracilis*), and fathead minnow (*Pimephales promelas*) also exist. The lone species of Esocidae in the URG is the nonnative northern pike (*Esox lucius*). In total, at least 29 nonnative fish species reside in the URG and its tributaries (Hoagstrom et al., 2010). Additionally, three crayfish species (*Orconectes virilis*, *Procambarus clarkii*, and *Orconectes deanae*), all of which are nonnative, have been documented in the Upper and Middle Rio Grande (Nolen et al., 2016). Native molluscan fauna likely have always been sparse in the URG and its tributaries, and no native species are known to exist (Howells, 2003); however, nonnative Asian clam (*Corbicula fluminea*) have been documented in the Middle Rio Grande and could have colonized the URG (Foster et al., 2021).

## 2.2. Sample collection

Scat sampling occurred along 259-km of perennial waterways in two phases during February–December of 2018 to capture seasonal diet variation throughout a year (Fig. 1). First, a noninvasive scat-based capture-recapture survey of 20 latrine sites was conducted during February–April to estimate spatially explicit population density, size, growth rate, and genetic characteristics of the URG river otter population that resulted from reintroduction (Murphy et al., 2021). Information on latrine site selection and sampling methods are described in

detail by Murphy et al. (2021). Second, the same 20 latrines were surveyed less intensively during June–December specifically to obtain additional seasonal data about river otter diet.

In both phases, we attempted to collect all river otter scats that were present within the general vicinity of a latrine, defined as a ~30-m sinuous transect along riverbanks. Each scat was considered an individual sample if there was no physical contact with another scat. Desiccated, powdery scats that were not fresh and were likely missed during previous sampling events were not collected. Entire scats were collected and placed in individual plastic bags labeled with the latrine identification number, an individually unique sample identifier, and collection date, and all scats were subsequently frozen until processing occurred (Murphy et al., 2017). Because this study did not involve the capture or handling of animals and sampling was entirely passive, an Institutional Animal Care and Use Committee protocol was not required.

## 2.3. Laboratory analysis

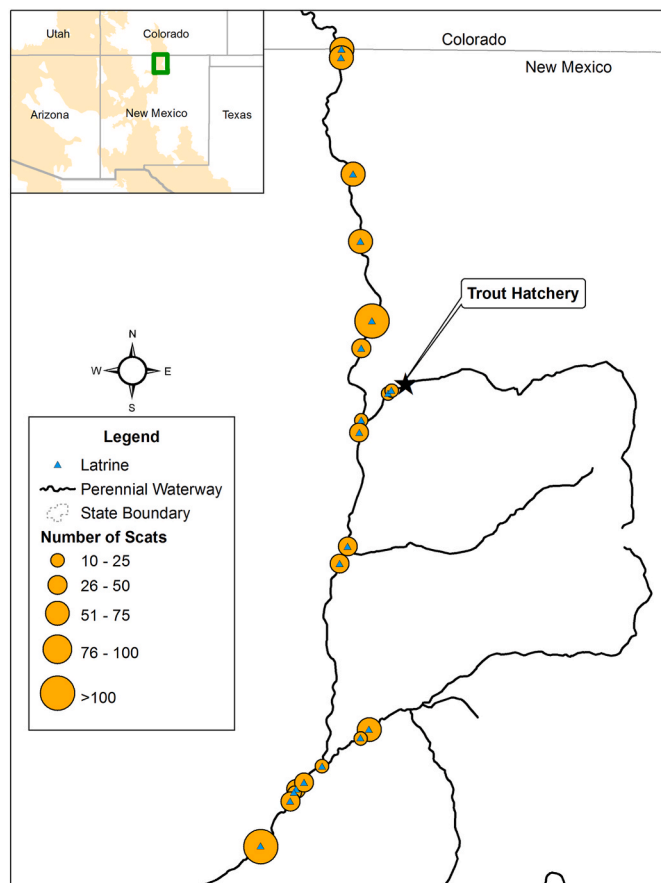
Multiple terrestrial mesocarnivores that also inhabited our study area, such as raccoons (*Procyon lotor*), can produce scats that are often difficult to visually distinguish from river otter scats (Jeffress et al., 2011). Unknowingly including scat samples from non-target species in dietary studies can severely bias results from compositional analyses and lead to erroneous conclusions about diet diversity and prey selection (Morin et al., 2016). To prevent the inclusion of non-otter scats in our data, and therefore mitigate bias, we extracted a ~0.5-cm<sup>3</sup> portion of fecal material from a subset of collected scats and sent those samples to the University of Idaho's Laboratory for Ecological, Evolutionary and Conservation Genetics (Moscow, USA) for molecular species identification using a mitochondrial DNA (mtDNA) control-region species-identification multiplex (Morin et al., 2016). We could not species-type all collected scats using mtDNA because of financial constraints and therefore selected 65% of scats for molecular species identification (Murphy et al., 2021). Scats that were not genetically identified as originating from river otters were discarded from our dataset.

## 2.4. Scat processing and food item identification

Scats were thawed and then cleaned by soaking in warm water, rinsing off fecal material, and then filtering with a ~15-cm Oneida sieve with 1-mm mesh (Oneida, USA). An initial screening of each scat was subsequently conducted in which food items were separated into major prey groups (e.g., fish, crayfish, etc.) and vegetation and other non-food items (e.g., microplastics, angling equipment, etc.) were removed. A fish scale identification key did not exist for the URG, so we created a key using reference specimens housed at the University of New Mexico's Museum of Southwestern Biology (Albuquerque, USA), supplemented with fish samples collected by NMDGF. Radii, circuli, and the presence or absence of ctenoids were used to develop the fish scale identification key. Scales were hydrated in water prior to using a small paintbrush to remove organic material and then scales were photographed using a Nikon dissecting scope (Nikon Corporation, Tokyo, Japan) attached to a Canon T3i Rebel mounted camera (Canon, Inc., Tokyo, Japan). In addition to scales, jaws and pharyngeal teeth were used to confirm or differentiate among fish families; species-specific fish identification was often not possible, so all fish were grouped by family. Scale-less fish and soft-bodied prey items could not be accounted for because of their high digestibility. Crayfish were identified based on exoskeleton characteristics, birds by the presence of feathers and hollow bones, mammals by dense bones, and herpetofauna by bones and skin.

## 2.5. Statistical analysis

Food items were subdivided by the season during which the corresponding scat was collected to enable seasonal comparisons. Based on



**Fig. 1.** Locations of sampled latrines and spatial variation in the number of scats collected at each latrine, relative to the New Mexico Department of Game and Fish's Red River Trout Hatchery, in the Upper Rio Grande River Basin of New Mexico, USA (2018). Inset map depicts the study area (green box) relative to the extent of deserts (tan shaded areas) in the southwestern USA. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

precipitation trends in the study area (Western Regional Climate Center, <https://wrcc.dri.edu>), all scats collected during May–October represented the wet season, whereas all scats collected during February–April and November–December represented the dry season. We used Bayesian bootstrapping of 5000 iterations implemented via the bayesboot package in the R statistical computing environment (R Core Team, 2021; Rubin, 1981) to estimate 95% credible intervals for the mean number of scats collected at each latrine and the mean number of scats collected per month. For each prey item, we calculated seasonal frequency of occurrence (FO) and relative frequency of occurrence (RFO), where FO represents the frequency of a given item across all scats and RFO represents the frequency of a given item relative to all other items. Although these metrics do not account for the imperfect detection of food items in scats and also represent pseudoreplication, they have been shown to be robust and provide similar inference as multinomial modeling approaches (Morin et al., 2019), are well-suited for investigating diet diversity, and provide useful comparisons with other studies (Murphy et al., 2017).

In addition to calculating FO and RFO, we recorded binary presence/absence of prey items in each scat and used Bayesian multi-level models to estimate the seasonal probabilities that otter scat contained a given prey item (Murphy et al., 2017). We did not use FO or RFO for this analysis because multiple items were present in most scats and therefore those metrics lacked independence (Murphy et al., 2017; Morin et al., 2019). In each model, we specified the prey item group as the response variable that followed a Bernoulli distribution, season and sampling effort as the binary population-level explanatory variables, and latrine site as the group-level effect (*sensu* random intercepts in the frequentist mixed effects approach). The sampling effort variable denoted whether or not a given scat was collected during the capture-recapture study when sampling intensity was high (Murphy et al., 2021), which we included in all models to account for variation that may have been induced by heterogeneous sampling effort between seasons.

For the Salmonidae model only, we also included a distance-from-hatchery continuous variable that represented the sinuous river distance (km) of each latrine from the NMDGF trout hatchery located on Red River, near the confluence with the Rio Grande. We calculated river distances using the riverdist package in R (Tyers, 2021) and standardized the variable to have a mean of zero and unit variance prior to model fitting. Inclusion of this variable allowed us to investigate spatial variation in river otter predation of trout relative to the location of the hatchery. Trout are important recreational and ecological species in the URG, and the potential for high consumption of trout by otters has been a primary justification for not restoring otters to other river systems in New Mexico (Reed, 2018).

We specified weakly informative priors for all model parameters; population-level parameters had Normal (0, 1) priors, the intercepts had Student-*t* (3, 0, 2.5) priors, and the latrine site group-level variance parameters had half-Cauchy (0, 2) priors, the latter of which appropriately restricted the parameter space to positive values (Gelman, 2006). We fit models using the Stan computational platform (Carpenter et al., 2017) implemented via the R packages rstan and brms (Bürkner, 2017; Stan Development Team, 2020). For each model, four chains of 5000 iterations each were run with a burn-in of 2000 iterations for each chain, resulting in 12,000 total posterior samples. Model convergence was assessed using trace plots, potential scale reduction factors ( $\hat{R}$ ) of 1.00–1.01, and effective sample sizes >1000 (Gelman and Shirlet, 2011). We assessed model fit with posterior predictive check plots and used posterior probabilities (*P*) and Bayes factors (*K*) that were estimated via nonlinear Bayesian hypothesis tests to quantify the strength of support for population-level effects (Bürkner, 2017).

### 3. Results

#### 3.1. Sample collections

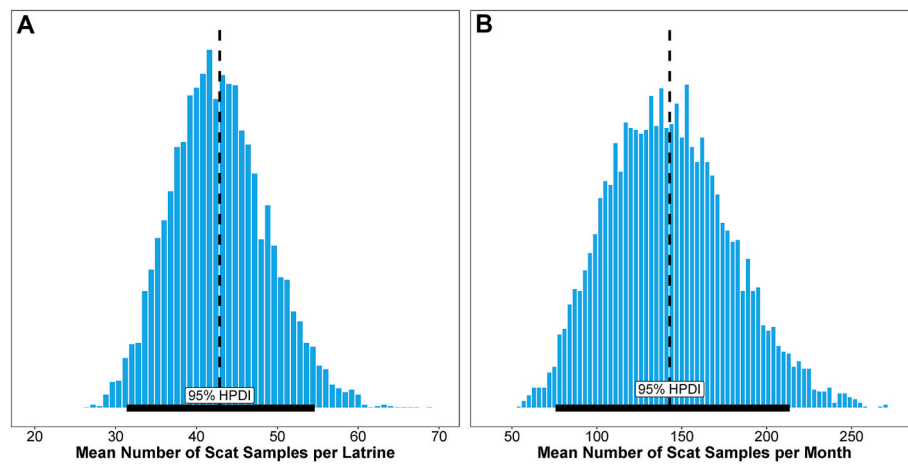
We collected a total of 958 scat samples from the 20 latrine sites during 2018. Among the 622 scats that were species-typed using genetic methods (65%), 543 were confirmed as river otter, representing a 13% visual misidentification rate in the field. An additional 20 scats were either improperly labeled during collection or were contaminated. After discarding those 99 scats, a total of 859 scats were available for analysis. The corresponding mean number of river otter scats that were collected per latrine was 43 (bootstrapped 95% CI: 32–55) and the mean number of river otter scats collected per month was 142 (bootstrapped 95% CI: 77–214; Fig. 2). More scats were collected as part of the three-month capture-recapture study (63%) conducted by Murphy et al. (2021) than were collected across the subsequent eight months (37%); consequently, most scats were representative of the dry season (85%).

#### 3.2. Frequency of occurrence

Crayfish (66.2%) and all fish combined (61.8%) had the highest overall annual FO (Table 1). Comparing among fish based on annual FO, the primary consumed fish families were Salmonidae (24.5%) and Catostomidae (22.9%). Other fish prey included the families Esocidae (8.6%), Cyprinidae (7.7%), and Centrarchidae (3.2%); although, we were unable to identify fish parts in 102 scats (FO = 11.9%) to the family level. Minor prey items (3.4%) in scats included freshwater mollusks (2.7%), birds (0.5%), reptiles (0.1%), and mammals (0.1%); mollusks were identified as Asiatic clams, birds as unknown species or family, reptiles as unknown species or family, and mammals as Cricetidae. Considerable seasonal variation in FO existed for fish, particularly Salmonidae and Catostomidae, as well as crayfish. Crayfish had the highest FO during the wet season (Dry = 61.3%; Wet = 94.5%) and similar FO as all fish during the dry season (Dry = 68.54%; Wet = 23.44%), which was primarily comprised of the families Salmonidae (Dry = 28.2%; Wet = 3.1%) and Catostomidae (Dry = 25.7%; Wet = 7.0%). Similar trends existed for RFO, such that crayfish had the highest during the wet season (Dry = 29.5%; Wet = 68.4%) and similar RFO as all fish during the dry season (Dry = 33.0%; Wet = 16.9%), which was primarily comprised of the families Salmonidae (Dry = 13.6%; Wet = 2.3%) and Catostomidae (Dry = 12.4%; Wet = 5.1%).

#### 3.3. Probability of prey items in scat

Samples sizes for birds, reptiles, and mammals were too small to permit model fitting ( $n < 5$ ). Most prey item models indicated support for a sampling effort effect (Fig. 3), thereby demonstrating that variation in the probability of a scat containing a given prey item was influenced by heterogeneous sampling effort. Accounting for the sampling variation, strong support existed for seasonal differences in the probability of scats containing crayfish and fish, specifically Catostomidae, Cyprinidae, Esocidae, and Salmonidae ( $P \geq 0.99$ ;  $K > 200$ ; Fig. 4). Seasonal differences in probabilities were not supported for Centrarchidae or mollusks ( $P < 0.90$ ;  $K < 3$ ). For both seasons, crayfish had the highest probabilities of being in river otter scat (Dry = 0.77 [95% CI: 0.57–0.89]; Wet = 0.93 [95% CI: 0.85–0.97]), followed by Catostomidae (Dry = 0.21 [95% CI: 0.10–0.36]; Wet = 0.05 [95% CI: 0.02–0.10]) and Salmonidae (Dry = 0.14 [95% CI: 0.05–0.33]; Wet = 0.03 [95% CI: 0.01–0.10]). Some support ( $P = 0.90$ ;  $K = 7.60$ ) existed for a negative distance-from-hatchery effect on the probability of a scat containing Salmonidae ( $\beta = -0.39$  [95% CI: -1.05–0.26]; Fig. 5). The probability of Salmonidae being in otter scats was highest ( $P = 0.27$ ) at distances <2 km from the Red River trout hatchery and declined precipitously as distance from the hatchery increased.



**Fig. 2.** Results from Bayesian bootstrapping of A) the mean number of scat samples collected per latrine, and B) the mean number of scat samples collected per month. Vertical dashed black lines denote the estimated mean and horizontal solid black lines denote the 95% highest posterior density intervals (i.e., credible intervals).

**Table 1**

Seasonal and annual frequency of occurrence (FO) and relative frequency of occurrence (RFO) for prey items detected in river otter scats from the Upper Rio Grande River Basin of New Mexico, USA (2018).

Prey Item	Wet Season			Dry Season			Annual		
	May–Oct.			Feb.–Apr., Dec.			Feb.–Dec.		
	$n_1 = 128$ , $n_2 = 177$			$n_1 = 731$ , $n_2 = 1518$			$n_1 = 859$ , $n_2 = 1695$		
	$n$	FO (%)	RFO (%)	$n$	FO (%)	RFO (%)	$n$	FO (%)	RFO (%)
Avian	1	0.78	0.56	3	0.41	0.20	4	0.47	0.24
Crayfish	121	94.53	68.36	448	61.29	29.51	569	66.24	33.57
Fish	30	23.44	16.95	501	68.54	33.00	531	61.82	31.33
Catostomidae	9	7.03	5.08	188	25.72	12.38	197	22.93	11.62
Centrarchidae	0	0.00	0.00	17	2.33	1.12	17	1.98	1.00
Cyprinidae	7	5.47	3.95	59	8.07	3.89	66	7.68	3.89
Esocidae	2	1.56	1.13	74	10.12	4.87	76	8.85	4.48
Salmonidae	4	3.13	2.26	206	28.18	13.57	210	24.45	12.39
Unknown fish	22	17.19	12.43	80	10.94	5.27	102	11.87	6.02
Mammal	1	0.78	0.56	0	0.00	0.00	1	0.12	0.06
Mollusks	1	0.78	0.56	22	3.01	1.45	23	2.68	1.36
Reptile	1	0.78	0.56	0	0.00	0.00	1	0.12	0.06

Notes:  $n$  = number of scats containing a food item;  $n_1$  = total number of scats collected;  $n_2$  = total number of prey item identifications.

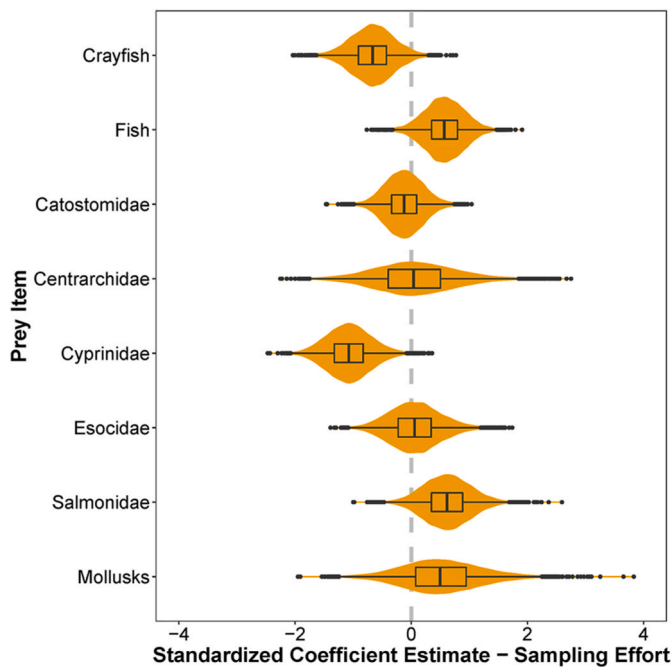
#### 4. Discussion

Our analysis of river otter scats from the URG, an important dryland river in the southwestern USA, indicated that nonnative aquatic fauna dominated river otter diets across both the dry and wet seasons. Crayfish were the most consumed prey item and had the highest probabilities of being in otter scats, notably exceeding 0.90 for the wet season. The river otter FO and RFO values for crayfish in the URG are among the highest reported for any river otter population in North America and the highest reported for any dryland river; to our knowledge, only one other North American study has reported crayfish as the most frequently consumed prey by river otters, which was for two rivers in hydric landscapes of Missouri, USA (Roberts et al., 2008). Native crayfish do not inhabit the URG but at least two, possibly three, species of nonnative crayfish exist in the URG and its tributaries, which were likely introduced as fishing bait by anglers (Nolen et al., 2016). Nonnative crayfish are well-known to exert negative cascading effects on the structure and function of riverine ecosystems and have both indirect and direct consequences on native fish, invertebrate, and macrophyte populations (Gherardi et al., 2011; Lodge et al., 2000). Eradication of nonnative crayfish from riverine ecosystems has been a fisheries management objective for decades, but human intervention methods for doing so are often expensive and have varying effectiveness (Gherardi et al., 2011). Although the population sizes of crayfish in the URG are unknown, and therefore the

impact that river otter predation has had remains unclear, our findings suggest that otters likely could help control or reduce crayfish populations in the URG via predation.

Following crayfish, Catostomidae had the next highest probability of being in river otter scats in the URG. Three species of this fish family exist in the URG Basin, the native Rio Grande sucker and river carp-sucker (*C. carpio*), and the nonnative white sucker. However, the imperiled Rio Grande sucker has been extirpated from most of its native range in the URG and relegated to small streams absent of white sucker (Calamusso et al., 2002), which we did not sample because no evidence of otter occupancy existed in those streams (Savage and Klingel, 2015; Murphy et al., 2021). Nonnative white sucker was the dominant sucker in the portion of the URG where our study occurred and therefore likely comprised most of this fish family in river otters' diet. Evidence of competitive exclusion of native Rio Grande sucker by expanding nonnative white sucker in the URG exists (Calamusso et al., 2002), so presumably, predation of white sucker by river otters could potentially assist with recovery of Rio Grande sucker. Although, otters likely would also consume native Rio Grande sucker if their population size and distributional extent increased.

The low to moderate presence of Salmonidae in river otter scats that we documented, which varied substantially by season, presents a management conundrum. Imperiled Rio Grande cutthroat trout are the only native trout species in the URG, but they have been extirpated from the

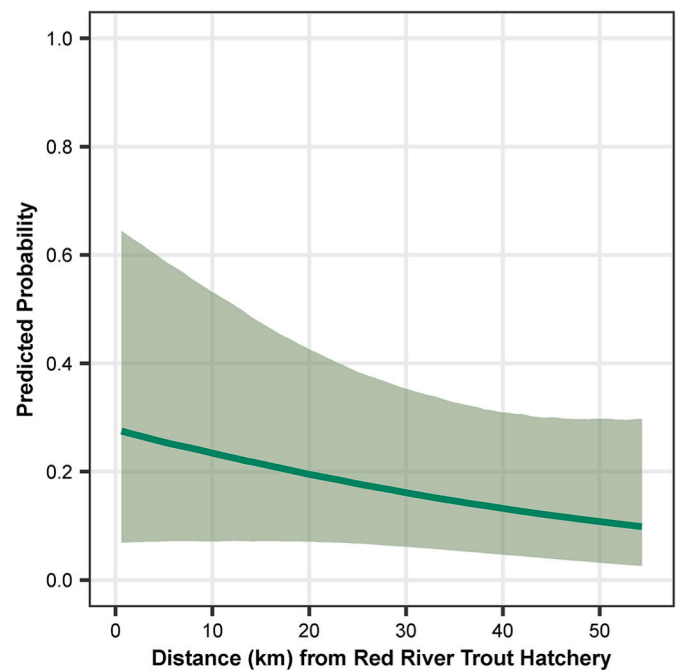


**Fig. 3.** Standardized coefficient estimates (i.e., relative effect sizes) for a population-level sampling effort effect from multi-level models fit to each prey item category. Orange shaded areas denote the posterior distributions for each point estimate; overlaid box plots show the median and quartiles, with black dots representing possible statistical outliers; and the vertical gray dashed line denotes zero. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

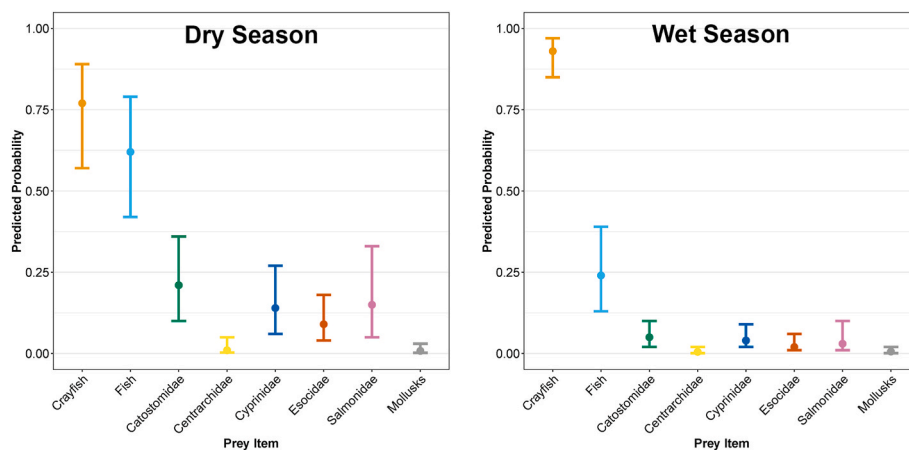
waterways that are occupied by otters and are primarily restricted to high mountain streams (Haak et al., 2010). Therefore, all trout consumed by river otters during our study were likely nonnative species, thereby providing another example of river otters preying on nonnative fauna. This could be at least partially beneficial for recovery of Rio Grande cutthroat trout in parts of the URG, because reintroductions of cutthroat often necessitate pre-release removals of nonnative trout (Bakevich et al., 2019). Yet, those nonnative trout represent important recreational and economic species for anglers and local communities in the URG (Reed, 2018), while also likely filling the ecological roles that Rio Grande cutthroat trout historically occupied. Nonetheless, the probability of trout being in river otter scats throughout the URG was low for both seasons ( $P < 0.15$ ). Although otter predation of trout may indeed be highest in the lower portion of the Red River, downstream of

the hatchery, which is arguably among the best angling waters in the river, the probability of trout being in otter scats was still relatively low in that stretch ( $P = 0.27$ ). Thus, complaints from stakeholders about river otters having disproportionate negative effects on trout populations in the URG are not supported by our results.

We found additional nonnative fauna in otter scats, particularly during the dry season. For example, northern pike comprised all Esocidae occurrences in otter scats and it is likely that bass and carp comprised much of the Centrarchidae and Cyprinidae occurrences; although, native bluegills, Rio Grande and flathead chubs, and fathead minnows were probably also a portion of those occurrences (Rees et al., 2005). The detection of mollusks in otter scats was surprising, partially because they are highly digestible and only recorded when shells are contained in scats, but also because all mollusk species native to the URG were extirpated within the last century (Howells, 2003). Examination of



**Fig. 5.** Estimated probability of Salmonidae (trout) being in river otter scats in the Upper Rio Grande River Basin of New Mexico, USA, as a function of distance from New Mexico Department of Game and Fish's Red River Trout Hatchery. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 4.** Estimated probabilities of major prey groups being in river otter scats during the dry and wet seasons in the Upper Rio Grande River Basin of New Mexico, USA (2018), accounting for heterogeneous sampling effort between seasons.

the mollusk shells that we found in otter scats indicated that they were from Asiatic clams, which represents the first recorded occurrences of this exotic species in the Rio Grande north of Valencia, New Mexico (Foster et al., 2021).

A primary limitation of our study was the scat sample size discrepancy between dry and wet seasons. Most scats that were collected during the dry season were obtained as part of the intensive capture-recapture survey conducted by Murphy et al. (2021), whereas sampling effort and intensity were much lower during the wet season, which resulted in nearly 6 × more dry season than wet season scats. We therefore urge caution in interpreting both the seasonal differences and annual totals for FO and RFO. In particular, pooling scats across seasons to obtain annual FO and RFO values for prey items resulted in skew toward the dry season, which corresponded to more weight being attributed to prey in dry season scats (i.e., pooling fallacy; Murphy et al., 2017). Consequently, FO and RFO may have overestimated the annual importance of Catostomidae and Salmonidae in river otter diet, considering trout and sucker spawning in the URG generally coincides with the dry season, while underestimating the annual importance of crayfish, given they are typically less active during the dry season and may become dormant when water temperatures are low. However, our estimated probabilities from the regression models should be nominally influenced by the seasonal sample size differences, because we included both season and sampling effort as population-level predictors in each model. For most food item models, both season and sampling effort effects were supported, thereby indicating that our models accounted for the confounding that would have been caused by the seasonal sample size discrepancies when estimating seasonal probabilities. Thus, the estimated seasonal probabilities of prey items in scats are probably more reliable proxies of river otter diet than the calculated FO and RFO values.

## 5. Conclusions

Dryland rivers are critically important ecosystems in arid landscapes, but many of those waterways have been degraded by human activities and likely will be subjected to longer and more frequent drought conditions and more variable precipitation patterns because of climate change. Although river restoration is a rapidly advancing discipline, few projects have been implemented with the intent of enhancing biodiversity, returning native flora and fauna, or eradicating nonnative species. Nonnative fish and invertebrates are abundant in many dryland rivers and often have severe negative effects on native fauna, including multiple threatened and endangered species (Hoagstrom et al., 2010; Gibson et al., 2015). Manual or mechanical methods for controlling or eradicating nonnative aquatic fauna are typically expensive, labor intensive, and ineffective (Gherardi et al., 2011; Rytwinski et al., 2019). We found compelling evidence from the upper portion of the Rio Grande River that reintroducing river otters, and possibly other semiaquatic apex carnivores such as mink, to degraded dryland rivers could potentially be an effective component of the biomic approach to river restoration for controlling or reducing populations of nonnative fish and invertebrates (Johnson et al., 2020). Given the direct and indirect negative influences that nonnative species can have, the top-down effects of restoring otters could also reestablish trophic cascades that improve overall ecosystem structure and function. Nevertheless, if imperiled native fauna inhabit the dryland river of interest, we suggest a cautionary approach to such restorations would be prudent, because potential exists for unintentional adverse consequences on those species from predation by otters.

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## CRedit authorship contribution statement

**Gabriela A. Wolf-Gonzalez:** Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft. **Sean M. Murphy:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Matthew T. Springer:** Conceptualization, Formal analysis, Resources, Writing – review & editing, Supervision, Funding acquisition. **John J. Cox:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: John J. Cox reports financial support was provided by New Mexico Department of Game and Fish. Sean M. Murphy reports a relationship with New Mexico Department of Game and Fish that includes: employment. Author S.M. Murphy was an employee of the primary funding entity, New Mexico Department of Game and Fish, during the first two months of data collection. All other authors declare no conflicts

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2022.104793>.

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