


REVIEW

Pumas *Puma concolor* as ecological brokers: a review of their biotic relationships


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ABSTRACT

1. The puma *Puma concolor* is the fourth largest wild felid and the most widespread native terrestrial mammal of the Americas. We synthesised published literature documenting the biotic interactions of pumas, in order to: 1) advance our understanding of the ecological roles pumas play in natural systems, and 2) support strategic decision-making about conservation investments, public education, and whole-ecosystem conservation management.
2. We divided puma biotic interactions into five categories: 1) diet and prey regulation, 2) fear effects on prey (including trophic cascades), 3) effects via carrion production, 4) effects on other carnivores, and 5) ecosystem services. We reviewed 162 studies that met our search criteria, which described 543 ecological interactions between pumas and 485 other species.
3. Puma diet and prey regulation was the most common research topic. The geographic distribution of research was highly skewed towards the USA and Canada, and research in Tropical moist forests was underrepresented. We found a steep increase in the number of scientific publications exploring the biotic interactions associated with pumas over time, but publications that reported effect sizes or measured the strength of interactions did not increase as quickly. We noted numerous gaps in our knowledge of puma biotic interactions and found few well-controlled studies of prey fear effects, trophic cascades, or ecosystem services.
4. We conclude that pumas are influential ecological actors in natural systems and important brokers of energy and nutrients throughout ecosystems in the

Western Hemisphere, linking disparate species from many trophic levels. Ultimately, we found evidence for investing in and prioritising the protection and restoration of puma populations to conserve biodiversity in the Americas.

Palabras clave

biodiversidad, especies clave, especies que interactúan fuertemente, hemisferio occidental, león de montaña *Puma concolor*, limitación de presas, red trófica

RESUMEN EN ESPAÑOL

1. El puma *Puma concolor* es el cuarto felino salvaje más grande y el mamífero terrestre nativo con mayor rango de distribución en las Américas. Sintetizamos la literatura publicada que documenta las interacciones bióticas de los pumas, con el fin de: 1) avanzar en nuestra comprensión de los roles ecológicos que juegan los pumas en los sistemas naturales, y 2) apoyar la toma de decisiones estratégicas sobre inversiones en conservación, educación pública y gestión de la conservación de todo el ecosistema.
2. Dividimos las interacciones bióticas del puma en cinco categorías: 1) regulación de la dieta y las presas, 2) efectos del miedo en las presas (incluidas las cascadas tróficas), 3) efectos a través de la producción de carroña, 4) efectos en otros carnívoros y 5) servicios ecosistémicos. Revisamos 162 estudios que cumplieron con nuestros criterios de búsqueda, que describieron 543 interacciones ecológicas entre pumas y otras 485 especies.
3. La dieta de los pumas y la regulación de las presas fue el tema de investigación más común. La distribución geográfica de la investigación estuvo más inclinada hacia los EE. UU y Canadá, además la investigación en los bosques tropicales húmedos estuvo subrepresentada. Encontramos un fuerte aumento en el número de publicaciones científicas que exploraban las interacciones bióticas asociadas a los pumas a lo largo del tiempo, pero las publicaciones que informaron tamaños de efectos o midieron la fuerza de las interacciones no aumentaron tan rápidamente. Observamos numerosas lagunas en el conocimiento de las interacciones bióticas del puma, y encontramos pocos estudios bien controlados sobre los efectos del miedo de las presas, las cascadas tróficas o los servicios ecosistémicos.
4. Concluimos que los pumas son actores ecológicos influyentes en los sistemas naturales e importantes intermediarios de energía y nutrientes en los ecosistemas del hemisferio occidental, vinculando especies disparejas de muchos niveles tróficos. En última instancia, encontramos evidencia para invertir y priorizar la protección y restauración de las poblaciones de pumas para conservar la biodiversidad en las Américas.

INTRODUCTION

Large, terrestrial carnivores are key regulators exerting strong and irreplaceable effects on biological community assemblages, and their absence can lead to fundamentally downgraded ecosystems (Estes et al. 2011, Enquist et al. 2020). Due to their relatively low reproductive rates and high energetic requirements, large predators are also among the most imperilled species on Earth and are highly sensitive to human-induced environmental change (Ripple et al. 2014). In fact, in human-dominated systems, low tolerance for large carnivores imposes social carrying capacities

generally lower than biological carrying capacities (Bruskotter & Wilson 2014, Knopff et al. 2016).

Predators play outsized roles in the ecosystems they inhabit, primarily via prey regulation and limitation (Sinclair 2003). Predators also structure biological communities through a variety of indirect effects. For example, fear of predators can alter prey behaviour and induce physiological costs that affect the fecundity and fitness of prey (Sheriff et al. 2009). Predator-induced changes in smaller carnivore and prey abundance and behaviour can also precipitate ‘trophic cascades’ affecting faunal community structure, floral communities, and other trophic

levels (Preisser et al. 2007, Prugh & Sivy 2020). Additionally, predators affect energy flow in communities by leaving carcasses for scavengers (Allen et al. 2015, Elbroch et al. 2017c, Sebastián-González et al. 2020), which affects community structure, soil chemistry, and nutrient cycling (Bump et al. 2009, Wilson & Wolkovich 2011, Barry et al. 2019, Sebastián-González et al. 2020).

Pumas *Puma concolor*, also known as mountain lions, cougars, and Florida panthers, are among the largest and most iconic carnivores in the Americas. They exhibit the widest geographical range of any native terrestrial mammal in the Western Hemisphere, inhabiting land between the Canadian Yukon and the southern Andes (Iriarte et al. 1990). The International Union for Conservation of Nature (IUCN) classifies pumas as 'Least Concern', but also indicates that the species is declining in Latin America (Nielsen et al. 2017). Nevertheless, Dickman et al. (2015) ranked pumas among felids of highest conservation priority based upon their intrinsic characteristics, extrinsic ecological variables, IUCN category, and the potential for pumas to act as a conservation umbrella for other species.

Like grey wolves *Canis lupus*, African lions *Panthera leo*, and other apex carnivores, puma populations may be limited by human tolerance (Treves & Bruskotter 2014). They are legally and illegally hunted because they compete with humans for ungulate prey and other resources (Elbroch et al. 2017a), and because they pose both real and perceived risks to people, pets, and livestock (Herrmann et al. 2013, Wolfe et al. 2015, Guerisoli et al. 2021). Eradication campaigns in the 19th and 20th Centuries in North America reduced puma range to west of the central plains, except for a small, isolated population in southern Florida (*Puma concolor coryi*; Iriarte et al. 1990; Fig. 1). Throughout the puma's range, the main threats to population persistence are unregulated hunting and poisoning, retaliatory killing, habitat loss, habitat fragmentation, vehicular collisions, and disease (Miotto et al. 2011, Schwab & Zandbergen 2011, Vickers et al. 2015, Pauli et al. 2018, Kechejian et al. 2019, van de Kerk et al. 2019). While pumas are recolonising parts of their historical range in midwestern North America (LaRue et al. 2012), in others, they are facing increasing pressure from human population growth (Benson et al. 2019). Several isolated populations suffer from low genetic diversity (Castilho et al. 2012, van de Kerk et al. 2019), with severe health consequences long observed in the Endangered Florida panther *Puma concolor coryi* and more recently in southern California populations (Beier et al. 2003, Onorato et al. 2010, Sahagun 2020).

We aimed to synthesise the published literature on ecological interactions associated with pumas to advance our understanding of their biotic roles in ecosystems and identify gaps that need to be addressed to enable evidence-based, strategic conservation management. More

specifically, we hypothesised that pumas are a strongly interactive species (as defined by Brodie et al. 2018), because of their potential ecological effects via: 1) prey limitation or regulation, which may create direct and cascading effects on other trophic levels (Schmitz et al. 2000, Preisser et al. 2007); 2) fear effects on prey behaviours or fitness, which can also impact other trophic levels (Laundré et al. 2010); 3) carrion production that impacts community food webs and interactions (Wilson & Wolkovich 2011); 4) effects on the abundance or fitness of other carnivores; and 5) ecosystem services, defined as benefits and essential services to humans (Millennium Ecosystem Assessment 2005). Ultimately, this information can support managers and conservation practitioners in understanding and communicating the overall benefits of puma conservation to a sometimes sceptical public, as well as aid in designing wildlife management that promotes healthy, integrated human-wildlife ecosystems (Brodie et al. 2018).

METHODS

We conducted literature searches using the Web of Science Core Collection database and Google Scholar for empirical papers presenting new data and published from 1950 to 2020. We largely based our methodology on the Guidelines and Standards for Evidence Synthesis in Environmental Management (Pullin et al. 2018). Our search excluded book chapters, conference proceedings, reviews, and meta-analyses. Specifically, we aimed to exclude papers that used data that had already been published, thus creating duplicates. Criteria for inclusion required a focus on pumas and their direct or indirect species' interactions, broad effects on biological communities, or ecosystem functioning (including nutrient cycling). Research solely focused on puma population size and demographics, habitat selection, or conservation was considered outside the scope of the review. Initial searches were conducted in English, but these identified few Spanish language papers. Since a significant portion of the puma's range is in Latin America, we adapted our search to retrieve papers in Spanish as well.

Our searches used keywords adapted to each database and utilised combinations of species names (English: puma, cougar, mountain lion, or Florida panther; Spanish: puma, cougar, león de montaña, or pantera de Florida) and either potential interactions (English: prey, predator, mesopredator, and scavenger; Spanish: presa, depredador, mesodepredador, and carroñero) or ecosystem roles (English: ecosystem, biodiversity, regulation, food web, keystone, apex predator, landscape of fear, risk effect, trophic cascade, nutrient cycling, and disease; Spanish: ecosistema, biodiversidad, regulación, red alimentaria, especies clave,

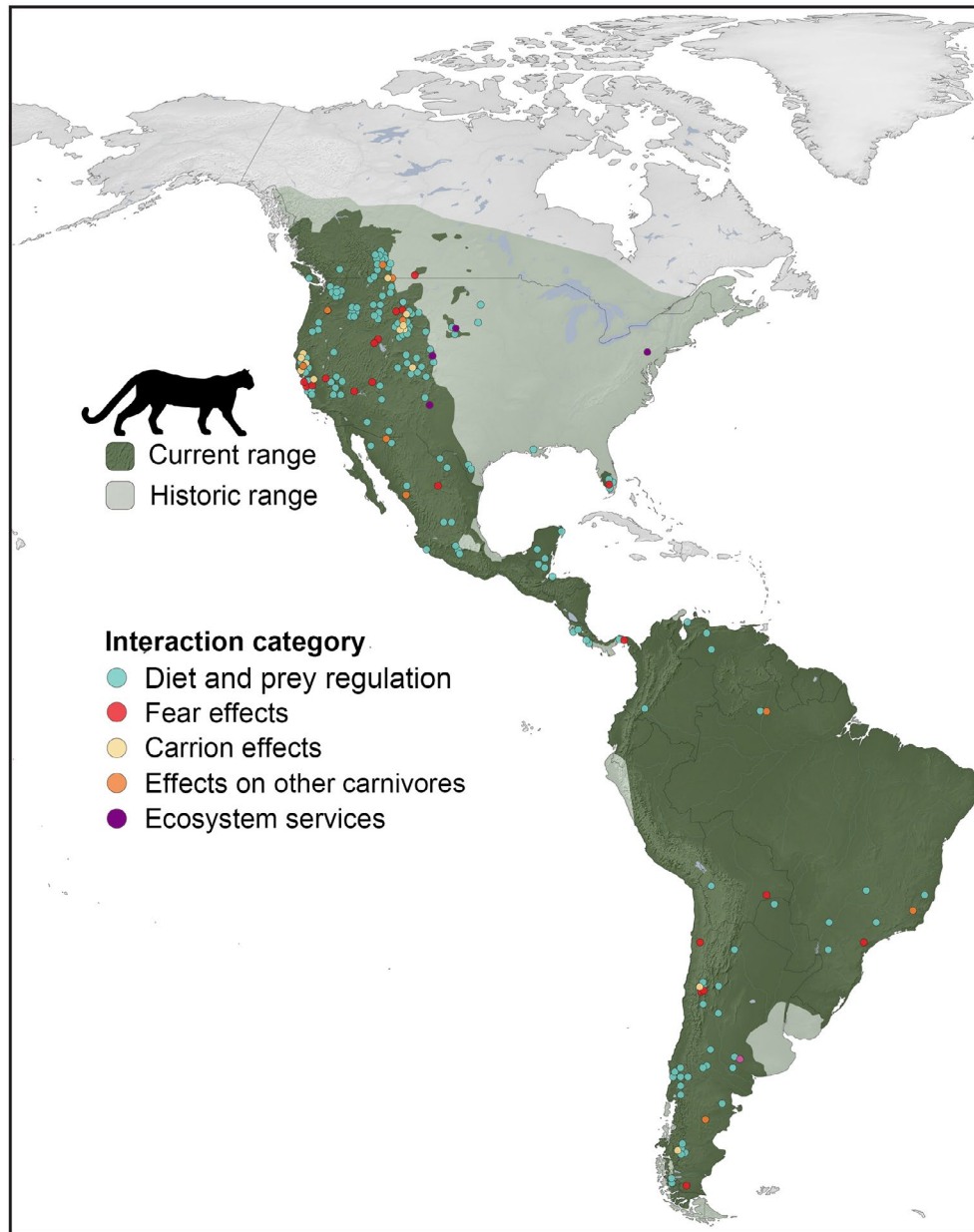


Fig. 1. Locations of research on the puma *Puma concolor* included in our review, and the current and historical (pre-European settlement) geographic range of the species in North and South America. Each of the 162 studies is assigned to one of the five interaction categories we defined (11 studies were assigned to two categories).

depredador mayor, paisaje del miedo, riesgo de depredación, cascada trófica, ciclaje de nutrientes, and enfermedad). Prior to initiating our searches, we used these keywords to conduct a brief scoping exercise to validate that they could retrieve known English-language studies (100% retrieval for 11 previously identified papers). Upon finishing our initial search, we conducted ‘snowball sampling’ by drawing on the knowledge of authors and examining the references of relevant reviews (Livoreil et al. 2017). On several occasions, we identified and included

reports or theses in press that were subsequently published in journals after our search timeframe (published in 2021).

For each study, we recorded the country, state/province, and geographic coordinates of the study site. When the location was not explicit, we searched for the name of the study area and used coordinates found on Google Earth Pro (Version 7.3, 2020). We also recorded the major focus or question of the research, main methods, sample size, findings as interpreted by the authors, and whether the study included some measure of effect size or the

strength of ecological effects. Additionally, we recorded species listed within each study that explicitly interacted with or were affected by puma (directly or indirectly). We placed each paper into one or more of the following interaction categories: 1) diet and prey regulation, 2) fear effects (including cascading effects on plants and invertebrates), 3) carrion effects, 4) effects on other carnivores, and 5) ecosystem services.

We used the following criteria to assess whether a paper measured the strength or magnitude of ecological effects: 1) for diet and prey regulation, we recorded whether a study reported evidence of prey limitation or regulation; 2) for effects on other carnivores, we assessed whether the study reported pumas impacting competitor fitness or abundance; and 3) for all other categories, we assessed whether studies used controls, comparisons among treatment types, or before–after designs (Appendix S1).

Research trends and spatial distributions of studies

All statistical analyses were performed using R v4.0.3 software (R Core Team 2018). We evaluated whether the geographic distribution of studies was representative of the different terrestrial biomes within the puma's range. We rasterised the *Terrestrial Ecoregions of the World* polygons provided by the World Wildlife Fund (Olson et al. 2001) via the 'sp' (Pebesma & Bivand 2005) and 'raster' (Hijmans & van Etten 2015) packages and extracted the biome type for each study location. We then compared the distribution of study site biomes with the distribution

of biomes within the puma's range using an exact multinomial goodness-of-fit test (Table 1).

We also binned our search results into five-year periods from 1970 to 2019 (excluding papers after 2019 to match the five-year design for this specific analysis) to assess potential publication trends reflecting research interest. We plotted the number of papers published over time in two categories: 1) those that reported any measure of effect or strength of interaction, and 2) those that did not. We tested whether there was evidence supporting a positive linear or exponential slope over time by fitting linear models of counts as a function of time using a Poisson error distribution with either an identity or exponential link function, respectively. We used the strength of correlation (R^2) to indicate fit.

Finally, we used a mixed effects logistic model to estimate the probability that effect sizes or control groups were reported in a study. We fit a model that estimated the probability that ecological effects were reported in a study using a fixed effect on research category, and a random effect on the intercept per study as independent variables. The response variable consisted of binary data indicating whether study results reported ecological effects. Some studies reported results from multiple interaction categories and this model structure accounted for interdependence. We estimated model parameters in a Bayesian framework using the 'rstanarm' package (Goodrich et al. 2018), using default priors and sampling 1000 iterations of four Markov chains following a 1000 iteration burn-in period. We identified differences in the probability that effect sizes or control groups were used between research

Table 1. Representation of biomes in puma *Puma concolor* geographic range by interaction category. For each interaction category, the column shows which biomes studies are concentrated in by their total percentage. The biomes represented in interaction categories differed from the expected distribution based on the percentages found within puma range, indicating bias towards research in North America

Biome	Percentage of total puma range	Diet and prey regulation	Fear effects	Carrion effects	Effects on other carnivores	Ecosystem services
Deserts and Xeric Shrublands	<1%	21%	22%	0%	8%	0%
Flooded Grasslands and Savannas	1%	2%	4%	0%	0%	0%
Mediterranean Forests, Woodlands, and Scrub	14%	6%	22%	36%	0%	0%
Montane Grasslands and Shrublands	3%	5%	4%	21%	0%	0%
Temperate Broadleaf and Mixed Forests	2%	3%	0%	0%	0%	0%
Temperate Conifer Forests	10%	30%	17%	43%	39%	25%
Temperate Grasslands, Savannas, and Shrublands	8%	15%	13%	0%	23%	75%
Tropical and Subtropical Coniferous Forests	2%	3%	0%	0%	8%	0%
Tropical and Subtropical Dry Broadleaf Forests	8%	1%	4%	0%	0%	0%
Tropical and Subtropical Grasslands, Savannas, and Shrublands	13%	1%	0%	0%	0%	0%
Tropical and Subtropical Moist Broadleaf Forests	36%	12%	13%	0%	23%	0%
Tundra	2%	0%	0%	0%	0%	0%
Boreal Forests/Taiga	<1%	0%	0%	0%	0%	0%
Mangroves	<1%	0%	0%	0%	0%	0%

categories via 95% credible intervals (CI) around pairwise contrasts.

RESULTS

We reviewed 162 papers that fit our criteria, conducted across 15 countries, and concentrated in the western USA ($n = 84$), Canada ($n = 16$), Argentina ($n = 16$), and Mexico ($n = 14$; Fig. 1, Appendix S1). The majority of studies ($n = 120$) were focused on puma 'diet and prey regulation', while 23 studies were focussed on 'fear effects' or fear-based trophic cascades, 14 on 'carrion effects', 12 on 'effects on other carnivores', and five on 'ecosystem services'. Only 11 studies fit into more than one interaction category. Together, the 162 papers identified 485 taxa that interacted with pumas (Fig. 2). This count included species connected via an intermediate species (e.g. where studies found evidence that puma effects on herbivore browsing affected plants or invertebrates). Two hundred and three species were puma prey, of which 148 were mammals, 36 were birds, 14 were amphibians or reptiles, and five were fish. Two hundred and eighty-one species were connected via carrion effects, including 215 invertebrates, 33 mammals, and 33 birds. Twelve species were competitors,

11 of which were mammals in the order Carnivora, and one was a bird. Forty species interacted with pumas via fear effects, 17 of which were mammals, with cascading effects studied on eight plants, six invertebrates, four fish, and five amphibians or reptiles. Studies of ecosystem services involved four mammals and three plant species.

Studies were not distributed across biomes in accordance with expectations based on the puma's geographic range (exact multinomial test, all $P < 0.001$; Table 1). We could not formally test this for 'ecosystem services' because we only located five studies that fit our review criteria and one of these did not use a specific study site; however, ecosystem services research occurred in either temperate grasslands (75%, $n = 3$) or temperate conifer forests (25%, $n = 1$). Notably, 36% of the puma's geographic range is classified as 'Tropical and Subtropical moist broadleaf forest' (Olson et al. 2001), but only 12% of studies on 'diets and prey regulation', 13% of studies on 'fear effects', and zero studies on 'carrion effects' were conducted in this biome (Table 1).

Fewer studies reported a measure of the strength of interspecific interactions ($n = 35$) than did not report this information ($n = 126$). We found a steep increase

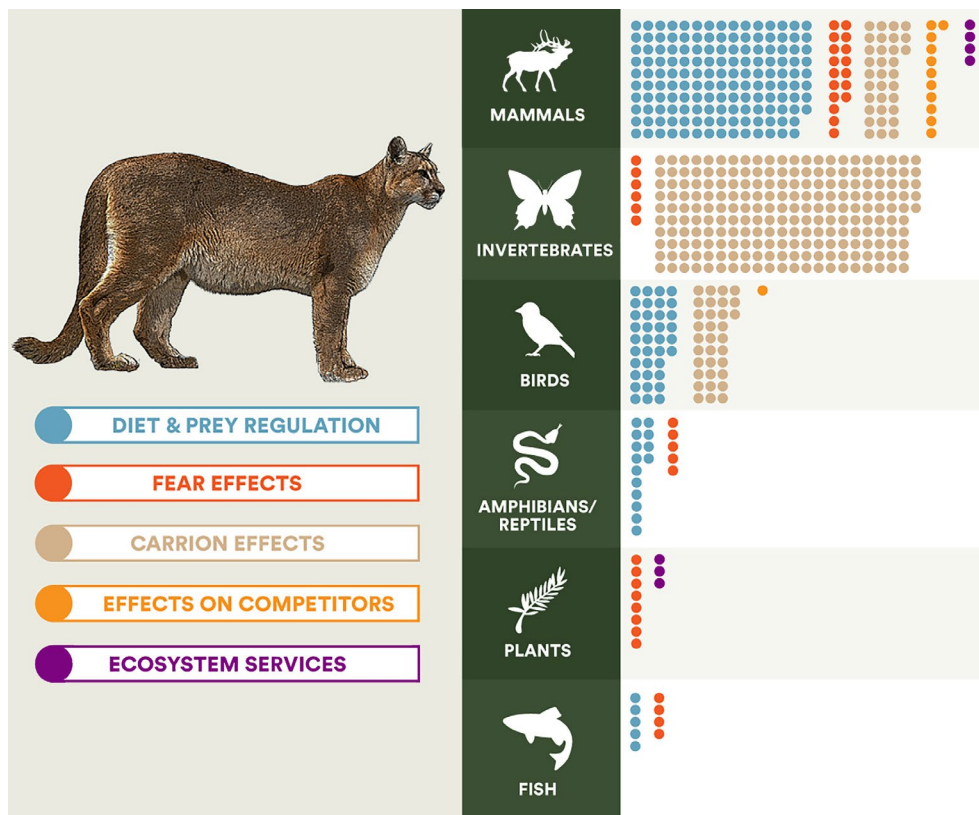


Fig. 2. Puma *Puma concolor* biotic interactions by taxon and interaction category. Our review compiled evidence of 543 different ecological interactions between pumas and other biota, involving 485 distinct taxa. Each interaction is represented with a dot.

in the number of publications about pumas that did not report effect sizes or measure the strength of species' interactions over time. This trend reflected increasing scientific interest in the puma and was better explained by an exponential curve ($R^2 = 0.92$) than by a line ($R^2 = 0.78$). The number of publications about pumas that reported effect sizes or the strength of species' interactions also increased, in a linear fashion ($R^2 = 0.83$) and at a more moderate slope than research that did not report the strength of effects (Fig. 3).

We found no evidence of differences in the probability of ecological effects reported among the five research categories. Our model had an explanatory power (R^2) of 85% (95% CI = [0.75, 0.94]), and the 95% CI around all pairwise contrasts included zero.

DISCUSSION OF ECOLOGICAL INTERACTIONS

Diet and prey regulation

The debate over whether pumas and other predators regulate or limit their prey has produced a rich literature

centred on density dependence (Sinclair 2003). Core to the regulation framework is the assumption that animal populations tend towards some equilibrium and that density-dependent mechanisms generally govern these natural processes; predation is then one mechanism by which populations are guided back towards equilibrium (called regulation; Sinclair 2003). As a tangible example of regulation, carnivore predation might reduce an overabundant prey population in order to restore equilibrium, and the strength of the impact of predation on that prey population would be governed by the distance that prey population was from its equilibrium. Proponents of limitation, in contrast, make no assumption about the influence of density on population growth and tend to view predation as a mechanistic constraint on prey vital rates, and ultimately a bookend on abundance (Krebs et al. 1995). We hypothesised that pumas would exhibit strong interactions with prey species by limiting vital rates. Our search identified 24 papers addressing puma prey regulation and limitation or reporting that puma predation was an additive cause of mortality. We did not find any explicit evidence of regulation, but 17 papers provided evidence of limitation (Appendix S2). Of these, 12 (71%) were

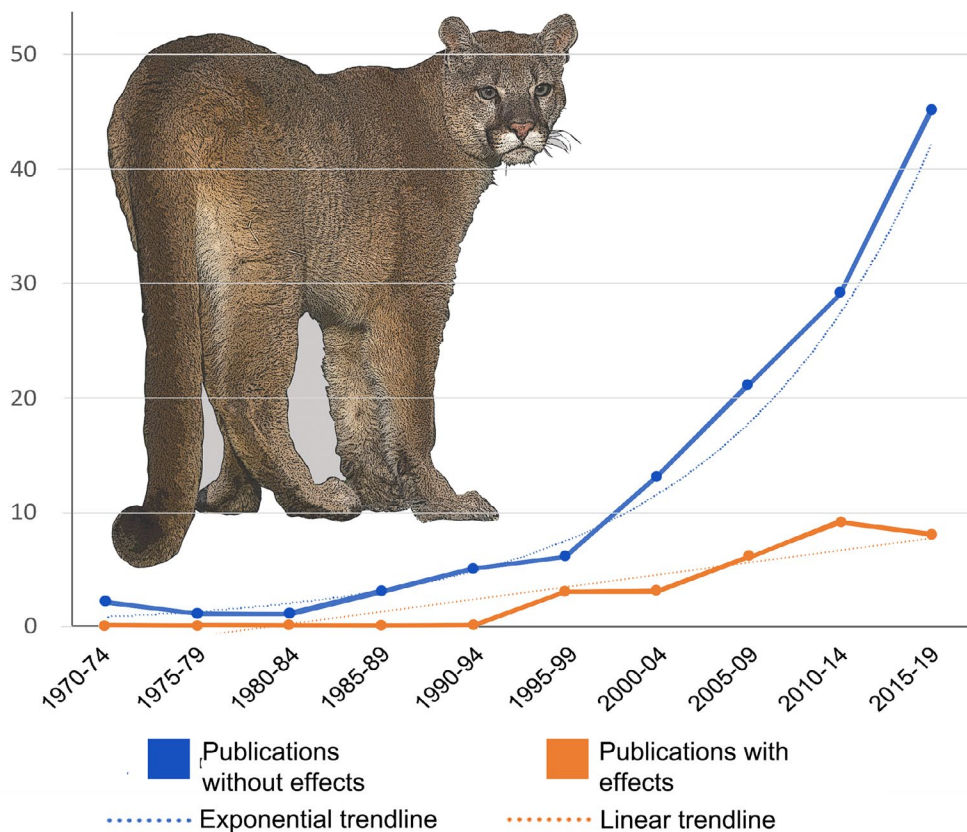


Fig. 3. Peer-reviewed publication trends for research on the ecological interactions between pumas *Puma concolor* and other biota, reflecting both total research and research which assessed the strength of interactions or used experimental designs.

studies on rare prey impacted by apparent competition (Holt & Bonsall 2017). An important caveat is that we did not use prey species names in our searches, which may have limited our findings.

Prior reviews corroborate our finding that pumas constrain prey numbers. In a review of 32 studies, Ruth and Murphy (2010) concluded that puma predation resulted in prey limitation in 17 cases, some of which were captured in our own review, and none of which were from study areas where prey populations were above carrying capacity. In a meta-analysis of mule deer *Odocoileus hemionus* survival, puma predation was found to be largely compensatory (Forrester & Wittmer 2013). Puma predation had only a minor effect on female elk *Cervus canadensis* survival throughout the western USA (Brodie et al. 2013) and was not a major driver of calf recruitment in western North America (Griffin et al. 2011). Nevertheless, in some localities, puma predation does influence ungulate growth rates (e.g. Proffitt et al. 2020), which could have cascading effects on community structure, including the abundance of other biota (Bressette et al. 2012).

The primary mechanism influencing ungulate population dynamics is almost always weather (White 2008), or, more specifically, temperature and rainfall that translate into primary productivity and food availability. Anthropogenic influences, including ungulate hunting (Brodie et al. 2013) and artificial resource subsidies (Muhly et al. 2013), can also overshadow the effects of large carnivores on prey vital rates. Therefore, the evidence for prey limitation exhibited by pumas should be interpreted with caution. For example, a meta-analysis by Clark and Hebblewhite (2020) found that controlling carnivores generally led to increased survival and recruitment of the youngest ungulate age-class, but that controlling carnivore numbers appeared equivocal in improving adult ungulate survival or overall ungulate abundance. Thus, the effects of puma predation are likely to be small, except on less abundant, alternative prey populations via apparent competition. In apparent competition, an abundant primary prey sustains the puma population, which in turn can have disproportionate impacts on rare prey sympatric in the system (e.g. predation on bighorn sheep *Ovis canadensis*, in a bighorn-mule deer system; Kamler et al. 2002).

Puma predation on alternative prey is also often driven by intraspecific variation in prey selection and is therefore stochastic rather than constant (Festa-Bianchet et al. 2006). When predation on rare prey (those occurring at low densities) is stochastic, prey limitation is mitigated, and prey populations persist much longer than they would under constant predation rates (e.g. puma predation on huemul *Hippocamelus bisulcus*; Wittmer et al. 2014). Nevertheless, when alternative prey are ecosystem engineers or other keystone species, even a small impact on their

abundance could result in strong trophic cascades (e.g. predation of American beavers *Castor canadensis*, North American porcupines *Erethizon dorsatum*, and nine-banded armadillos *Dasypus novemcinctus*; Monroy-Vilchis et al. 2009, Elbroch et al. 2017b). For example, Sweitzer et al. (1997) reported puma prey limitation on porcupines in Nevada's Great Basin, which could lead to cascading impacts on plant communities.

Fear effects on ungulates

Risk perception is a major driver of animal behaviour that can result in cascading effects on lower trophic levels. We hypothesised that pumas would affect prey risk perception and, in our review, we found evidence that cervids inhabiting North American temperate forests (e.g. Bacon & Boyce 2016, Kohl et al. 2019) and desert sky islands (Lowrey et al. 2019), and camelids inhabiting temperate South America exhibit spatial avoidance of pumas (Donadio & Buskirk 2016, Smith et al. 2019a). Predation risk varies across space and time. Therefore, some prey alter their daily activity patterns to access high-quality habitat during specific time periods when predators are less active (Smith et al. 2019b). In their analysis of elk movement, Kohl et al. (2019) found that individuals tended to avoid risky areas mainly when pumas and grey wolves were most likely to be hunting. Smith et al. (2019b) similarly found that vicuña *Vicugna vicugna* avoided risky habitats at night when puma were more likely to hunt, but would use these areas to forage during safer daylight hours. In Florida, white-tailed deer *Odocoileus virginianus* responded more to risk from Florida panthers during breeding and birthing than at other times of the year (Crawford et al. 2019).

Predator-induced changes to prey density or prey behaviour can result in community-wide effects by affecting the biomass, diversity, and distribution of primary producers (Schmitz et al. 2000). By avoiding dangerous places, animals concentrate their browsing pressure (Laundré et al. 2010, Atkins et al. 2019), and this spatial heterogeneity in foraging patterns may ultimately affect plant diversity or architecture, and also the species dependent on the plants (Yovovich et al. 2021). In total, we found 22 species that indirectly benefited from fear effects induced by pumas. The research documenting this included correlative studies, indicating that pumas benefit plants, small vertebrates, and insect communities where they suppress ungulate foraging (Ripple & Beschta 2006, 2008). Exclosure experiments focused on vicuña also indicated weak positive effects from fear-induced browsing suppression on grassland communities (Donadio & Buskirk 2016). Similarly, deer heavily browse plants and influence plant architecture and fitness in communities in central California, where they are at less risk of puma predation (Yovovich et al. 2021).

Overall, relatively few studies have investigated these topics for puma, and none employed strong inference via replication or controls for confounding abiotic factors (e.g. weather, nutrient cycles). Yet, findings from these few studies indicate a strong potential for pumas to affect plant communities. While outside the scope of this review, Suraci et al. (2019) simulated human presence in a natural area via experiments and found that reductions in the presence of large and medium-sized carnivores (including pumas) led to a ‘human-induced cascade’, where small rodents benefitted from reduced risk and increased foraging around treatment sites. This suggests that prey behavioural effects linked to pumas are likely to be modified. Beyond these fear effects in prey, several studies documented avoidance of pumas by smaller predators, which we address in the section ‘Effects on other carnivores’.

Carrion effects

Carrion is an energy-rich, ephemeral resource that drives the population dynamics of scavengers and decomposers and supports local biodiversity via nutrient deposition (Wilson & Wolkovich 2011, Moleón et al. 2015, Sebastián-González et al. 2020). Carrion also increases linkages in food webs, defined as pathways for energy flow, and contributes to community stability and resilience (DeVault et al. 2003, Wilson & Wolkovich 2011, Peers et al. 2020). We hypothesised that pumas would exhibit strong interactions by providing access to carrion for other species, and found 14 studies documenting pumas provisioning carrion, all but three of which occurred in the western USA (Fig. 1). Evidence suggests that pumas and other large, solitary felids that kill prey larger than themselves and are subordinate to other apex predators may provide a disproportionate amount of carrion to ecological communities (Selva & Fortuna 2007, Elbroch et al. 2017c). For example, Elbroch and Wittmer (2012) estimated that pumas in Patagonia contributed more than three times as much carrion to ecosystems as grey wolves did in Yellowstone National Park, USA, even though pumas occurred at lower densities. One study conservatively estimated that pumas contribute 1507348 kg of meat per day to their communities throughout their range in North and South America (Elbroch et al. 2017c).

Collectively, studies of puma-provided carrion identified 65 vertebrate and 215 invertebrate scavengers, contributing to evidence that puma-provided carrion supports additional food-web linkages that are likely to bolster ecosystem health. Notably, puma kills support a high percentage of species in the Greater Yellowstone Ecosystem, USA, where 28% of local mammal species and 11% of local bird species scavenged from puma kills (Elbroch et al. 2017c). Nevertheless, we did not find any studies that utilised

control areas to test directly whether the presence of pumas increased food-web linkages.

Puma kills are likely to be essential for numerous carrion-dependent species, such as Andean condors *Vultur gryphus* (Elbroch & Wittmer 2012, Perrig et al. 2017). Pumas have also been identified as ecosystem engineers because their kills provide invertebrate habitat (Barry et al. 2019). By killing prey repeatedly in the same areas, pumas create ephemeral, nutrient-rich hotspots via nitrogen and carbon deposition that increases $\delta^{15}\text{N}$ in soils and nearby plants (Peziol 2020). Peziol (2020) speculated that over time, the nutrient heterogeneity resulting from puma foraging may be akin to gardening, in that it is likely to increase the future use of these sites by ungulate prey seeking nitrogen-rich forage, and therefore increase the probability that pumas will hunt in these areas again.

When they are present at carcasses, pumas structure scavenger communities by suppressing mesocarnivore access (e.g. bobcats *Lynx rufus*, coyotes *Canis latrans*; Allen et al. 2014), and increasing foraging opportunities for small carnivores (e.g. western spotted skunks *Spilogale gracilis*; Allen et al. 2015). However, human presence can change these relationships. Wang et al. (2015) placed experimental carcasses across a gradient of human development in California and treated some of these carcasses with puma sign. The authors found that bobcats avoided carcasses with puma sign, but that scavenging coyotes did not. Yet, where human housing and activities were higher, carcasses were avoided by most mesocarnivores, except raccoons *Procyon lotor*.

Effects on other carnivores

Due to risks of intraguild predation, smaller competitors are expected to avoid encounters with apex predators (Prugh & Sivy 2020). Thus, we hypothesised that pumas could affect the abundance or fitness of other carnivores. Theory suggests that the presence of apex carnivores such as pumas can lead to ‘intraguild cascades’, in which the suppression of medium-sized carnivores releases smaller species occupying more distant niches (Berger et al. 2008, Roemer et al. 2009, Wang et al. 2015). Mesocarnivores are in fact commonly recorded as part of the diet of pumas (e.g. Monroy-Vilchis et al. 2009), although they are killed less frequently than herbivores. Nevertheless, most research to date suggests that medium-sized carnivores mitigate competition with pumas via avoidance (e.g. coyotes, bobcats, ocelots *Leopardus pardalis*; Koehler et al. 1991, Hass 2009, Massara et al. 2016, Santos et al. 2019, Ruprecht et al. 2021). We found only one study that suggested that predation by pumas was a significant cause of mortality of a medium-sized carnivore (the coyote; Ruprecht et al. 2021). Ruprecht et al. (2021) reported

that pumas killed 23% of a local coyote population in eastern Oregon, USA, each year. One additional study provided evidence via camera sampling over 14 years that pumas may limit the abundance of culpeo foxes *Lycalopex culpaeus*, but not South American grey foxes *Lycalopex griseus*, in Argentina (Díaz-Ruiz et al. 2020).

The defining question is whether food provided by pumas has an overall positive effect and facilitates small and medium-sized carnivore populations, or a negative effect as an ecological trap for subordinate species that may be killed by pumas while visiting their kills (Prugh & Sivy 2020). Based on the literature to date, puma food provisioning is likely to provide greater benefits than negative consequences to smaller carnivores, with some caveats. In temperate climates, where all research on this subject has been conducted (Fig. 1), smaller carnivores, including red foxes *Vulpes vulpes*, bobcats, and coyotes, increase their scavenging at puma kills in winter (Koehler et al. 1991, O'Malley et al. 2018). Thus, subsidies provided by pumas are likely to be important during times of food scarcity and higher energetic demand (i.e. according to the Stress Gradient Hypothesis; Barrio et al. 2013). Ruprecht et al. (2021), however, found that coyotes were often killed by pumas at puma kill sites in northeast Oregon, highlighting the potential negative effects of provisioning. In systems with red foxes or grey foxes *Urocyon cinereoargenteus*, coyotes are infrequent scavengers of puma kills, suggesting that, for reasons yet unknown, coyotes may expand their activities to exploit this niche in the absence of foxes (Allen et al. 2015, O'Malley et al. 2018). Allen et al. (2015) found that when pumas are present at their kills, they generally suppress medium-sized carnivores, which, in turn, increases access to carrion resources for small species such as ringtails *Bassariscus astutus* and western spotted skunks *Spilogale gracilis*. This study was the only evidence we found supporting the intraguild cascade hypothesis (Berger et al. 2008); however, research such as that by Ruprecht et al. (2021) could be extended to determine whether pumas reducing coyote abundance also releases smaller carnivore populations.

Pumas overlap with more dominant competitors in 48% of their range (Elbroch & Kusler 2018). Although pumas have occasionally been documented killing grey wolves and American black bears *Ursus americanus* (e.g. Cunningham et al. 1999, Elbroch et al. 2015), we did not find evidence that they negatively influence the fitness or abundance of other large carnivores (bears *Ursus* spp., wolves, or jaguars *Panthera onca*). Pumas kleptoparasitise jaguar kills (Escobar-Lasso et al. 2016, Fonseca et al. 2018), but the frequency or impacts of this behaviour are unknown. There is, however, significant evidence suggesting that pumas are subordinate to bears, wolves, and perhaps jaguars, and that pumas are likely to suffer fitness

consequences where they are sympatric with these species (Elbroch & Kusler 2018). Wolves, in particular, affect puma space use, diet, and abundance (Kortello et al. 2007, Elbroch et al. 2020). Comparatively, the potential influences of bears and jaguars on pumas are not well understood (see review in Elbroch & Kusler 2018). Pumas may, in fact, have positive effects on brown bear *Ursus arctos* and black bear populations, as both species are frequent scavengers of puma kills (Murphy et al. 1998, Elbroch et al. 2015). Elbroch et al. (2015) speculated that if pumas subsidise bear populations, bears could lower ungulate recruitment by increasing predation of neonates. Yet, we did not find any research directly testing whether resources provided by pumas increase bear fitness or abundance.

Ecosystem services

We found few studies that explicitly examined whether biotic interactions associated with pumas provided ecosystem services, defined broadly as benefits and essential services that support human economies, health, and well-being (Millennium Ecosystem Assessment 2005). Of the five relevant studies we reviewed, three considered the effects of pumas in mitigating chronic wasting disease (CWD) in cervids. CWD is a prion disease that causes spongiform encephalopathy and can be passed across species barriers, resulting in significant economic damage to hunting industries (Rivera et al. 2019). Some evidence suggests that pumas may selectively prey on infected mule deer (Krumm et al. 2010), potentially because diseased animals have a lower ability to escape before other symptoms become apparent (Miller et al. 2008). In a study of predation and CWD on elk, both were found to be additive sources of mortality (Sargeant et al. 2011). It remains unclear whether pumas that eat CWD-infected prey pass infective prions through their guts back into the environment (as documented in coyotes; Nichols et al. 2015), which would negate the idea that pumas provide the ecosystem service of reducing the spread of this disease.

Across large scales, pumas may also provide ecosystem services via prey limitation that mitigates vehicle collisions with cervids and therefore reduces human injuries, fatalities, and economic costs incurred by victims and society. For example, the recolonisation of North Dakota, USA, by pumas is estimated to have reduced costs associated with deer-vehicle collisions by US\$ 1.1 billion (Gilbert et al. 2017). Extending these findings, Gilbert et al. (2017) estimated that recolonisation of the eastern USA by pumas could reduce deer-vehicle collisions by 22% over 30 years, averting 21400 human injuries, 155 human fatalities, and US\$ 2.13 billion in costs.

It is also possible that pumas control invasive species. Seward et al. (2004) suggested that Florida panthers in

the USA may play a role in regulating invasive feral pig *Sus scrofa* populations, but we did not find any evidence in the published literature. Feral pigs cause significant damage to agricultural landscapes and fragile wetland habitats (Shwiff et al. 2020), and limitation by pumas would comprise a substantial economic benefit.

Finally, researchers working in Argentina concluded that pumas provided an ecosystem service through their role in dispersing seeds from plant species consumed by eared doves *Zenaidura macroura* (Sarasola et al. 2016). Seed dispersal is a key process that is important for sustaining plant communities. Nevertheless, we encourage caution when interpreting these results for two reasons. First, the authors did not employ genetic tools when identifying the scats they analysed to study carnivore diet (see Morin et al. 2016). Second, the diet they reported for pumas in their study system – which was overwhelmingly made up of doves – is an outlier when considering puma diet. It seems plausible that the authors may have included the scats of smaller carnivores in the analysis.

CONCLUSIONS

Our review provides evidence that pumas engage in >500 distinct biotic interactions throughout the Americas, including prey limitation, fear effects, ecosystem effects via carrion provisioning, impacts on other carnivores, and ecosystem services. This may be the most diverse set of biotic relationships documented for any carnivore in the world, which is perhaps due to the significant research attention granted the puma (Tensen 2018), the expansive geographic range of the species, and the scientific capacity of some of the countries with which the range overlaps, including the USA and Canada (dos Santos et al. 2020). These findings demonstrate that pumas are leading ecological brokers of energy and nutrients in ecosystems in the Western Hemisphere, linking disparate species from many taxa and trophic levels.

Without doubt, this conservative estimate represents only a fraction of the puma's biotic relationships throughout its range, especially given that published research greatly underrepresents some of the most diverse ecosystems on Earth, such as those in the Tropics (Wilson et al. 2016, Clarke et al. 2017). We found geographic bias in published research towards high-latitude, temperate biomes in all five interaction categories (Table 1), which may be explained in part by differences in scientific capacity among nations in the Americas (dos Santos et al. 2020). This geographic bias likely underpins numerous gaps in our understanding about puma biotic relationships, including the potential competitive effects of jaguars on puma fitness (Elbroch & Kusler 2018). Additionally, our taxonomic gaps reveal that we currently know little about the effects

of pumas on microbial or fungal communities, which would seem a logical next step in studies of puma-produced carrion.

Further, our review highlights the disproportionately small number of puma ecology studies that measure effect sizes or use experimental designs. This pattern suggests that general interest in pumas is outpacing the scientific rigour of research. While we found evidence of puma effects on ecological communities in all five of our interaction categories, the lack of strong inference, experiments, or attempts to measure the magnitude of these ecological effects limited our ability to measure the puma's complete ecosystem value, which would benefit the setting of conservation priorities (Brodie et al. 2018) and refining public outreach aimed at improving peoples' sentiment about large carnivores (Bruskotter & Wilson 2014).

Among the largest gaps in our understanding of the ecological roles pumas play are the ecosystem services they provide for humans. We encourage future researchers to determine whether pumas provide services via controlling ungulates and other species that inflict crop and timber damage, limiting or regulating invasive species that damage or degrade natural systems (Seward et al. 2004), or controlling the spread of wildlife diseases (Miller et al. 2008). Leopards *Panthera pardus*, for example, control feral dogs and rabies risk to people where their populations are abundant (Braczkowski et al. 2018), and this may be true of pumas in Latin America as well. Predation of feral dogs by pumas would also be an ecosystem service if it mitigated predation of livestock and endangered ungulates by dogs, which can be significant in Latin America (Corti et al. 2010, Villatoro et al. 2019). Controlling feral cats or hogs could similarly provide important ecosystem and economic benefits (Bonacic et al. 2019, Trouwborst et al. 2020). In addition, our focus on biotic interactions in this review did not capture 'non-material' ecosystem services (Small et al. 2017). Throughout their range, pumas are culturally salient, and a prominent character in diverse spiritual beliefs and historical narratives (Herrmann et al. 2013), suggesting that pumas play a cultural keystone role in addition to an ecological one (Garibaldi & Turner 2004). Neither did we capture the economic, recreational, and cultural benefits of puma tourism, which are only just beginning to be described in the literature (Tortato et al. 2020).

Given that human activity can change puma behaviour (Smith et al. 2017, Suraci et al. 2019), it seems reasonable to assume that any continued expansion of the human footprint will constrain the key ecosystem roles played by pumas in the future. This adds urgency to the need to understand, synthesise, and publicise the effects of pumas on biological community dynamics in a wide range of biomes. Pumas inhabiting human-dominated landscapes

modify their kill rates (Smith et al. 2015), feeding time (Smith et al. 2017), and space use (Ditmer et al. 2021, Nickel et al. 2021), and abandon kills to avoid direct human encounters (Suraci et al. 2019). Puma survival also varies with landscape modification (Burdett et al. 2010, Benson et al. 2019). These effects may be more or less pronounced for different behavioural processes (e.g. reproduction vs. feeding; Wilmers et al. 2013), and interacting species may display individualised responses to human pressure (Wang et al. 2015). Therefore, anthropogenic impacts on puma ecology may be non-linear and synergistic, yet capturing this complexity is critical for maintaining ecosystem resilience. Anticipating these changes may be particularly relevant given two intersecting patterns: the human footprint is expanding (Di Marco et al. 2018), and pumas are recolonising landscapes in western North America (Burdett et al. 2010, Kertson et al. 2011), mid-western North America (LaRue et al. 2012, Morrison et al. 2014), and southern and eastern South America (Walker & Novaro 2010). This pattern is likely to forecast increasing conflict between pumas and people, highlighting the need for education and mitigation strategies (Dickman et al. 2015).

In summary, our review provides strong evidence that pumas are leading ecological actors engaged in diverse biotic relationships that broker energy and resources among a great diversity of other species. Pumas are likely to play an important role in stabilising food webs and ecosystems due to the number and diversity of their trophic interactions across taxonomic groups (Paine 1992, Worm & Duffy 2003). The lack of research quantifying the magnitude of the puma's ecological effects at this time precludes us from definitively determining whether the puma is a 'strongly interactive species', as defined by Brodie et al. (2018), but some research supports characterising the puma as a keystone species (e.g. Barry et al. 2019) worthy of conservation priority. In short, our review highlights the exciting opportunities that lie ahead in addressing knowledge gaps and quantifying the puma's numerous ecosystem effects. We believe this work is essential for strategically guiding whole-ecosystem management, inclusive of potential puma reintroduction efforts (Laundré 2013), and the prioritising of defensible conservation investments (Brodie et al. 2018).

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DATA AVAILABILITY STATEMENT

Data are available at: <https://doi.org/10.6084/m9.figshare.14485419.v1> or on request from the authors.

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SUPPORTING INFORMATION

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

Appendix S1. Information extracted from each reviewed study and explanation of data.

Appendix S2. Reviewed studies of puma effects on prey populations, a subset of the interaction category 'diet and prey regulation'. For each study, analysis examined the prey species in question, whether we determined an effect had been shown, and whether the species was an abundant primary prey or a rare or secondary prey.