CANADIAN WILDLIFE BIOLOGY & MANAGEMENT

CWBM AN ALPHA WILDLIFE PUBLICATION

CWBM 2024: Volume 13, Number 2 *ISSN: 1929–3100*

Point to Ponder ***Special Issue on Mountain Lion Conservation and Management***

Mountain Lion Predation on Mule and Black-tailed Deer: A Perspective on The Complex Impacts of An Iconic Predator

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Abstract

Predation is a fundamental process that shapes ecological communities. The impact of mountain lion (*Puma concolor*) predation on their prey, however, is a debated topic among wildlife managers and their primary constituents, hunters and conservationists in North America. Here we present a perspective and highlight recent literature on the direct and indirect (i.e., non-consumptive) effects of mountain lion predation on 2 of its primary prey species in western North America, mule and black-tailed deer (*Odocoileus hemionus*). We assert that direct effects of mountain lion predation outweigh indirect effects. The population level impact of mountain lion predation on deer, however, is often context dependent and is influenced by complex species interactions including with other carnivores (e.g., kleptoparasitism) and prey (apparent competition). We also contend that understanding the impacts of additive and compensatory predation on the population dynamics of deer are ultimately required to ascertain population level effects of mountain lion predation. Finally, we highlight several key areas for future research.

Key Words: Black-tailed Deer, Mountain Lion, Mule Deer, *Odocoileus hemionus*, Population, Predation, *Puma concolor*, Regulation.

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Introduction

Predation is one of the fundamental processes that shape ecological communities (Hairston *et al.* 1960; Sinclair and Krebs 2002). Predators primarily impact their respective communities through direct effects of prey limitation and regulation (Sinclair 2003) but exert further influence through indirect, non-consumptive effects (NCEs) (Sinclair and Arcese 1995; Say-Sallaz *et al.* 2019). Proposed NCEs range from trophic cascades following fear-induced changes in habitat use of herbivores and subsequent impacts on plant species (Ripple and Beschta 2012), to positive impacts on scavenger communities (Elbroch *et al.* 2017), and influences on nutrient cycling (Wilson and Wolkovich 2011; Barry *et al.* 2019). The link between indirect effects of predation and population level impacts on prey species, however, is often unclear (Say-Sallaz *et al.* 2019). Nevertheless, the combined direct and indirect impacts of predation result in many predators having large effects on the function and composition of the communities they inhabit.

The mountain lion (*Puma concolor*) is a widely distributed predator occurring in very different ecosystems across much of South and North America. In North America, mountain lions have received comparatively high research interest mainly due to their perceived population level impact on many ungulate (game) species (Ballard *et al.* 2001). Research, however, has been concentrated in temperate forests ecosystems (LaBarge *et al.* 2022; Cristescu *et al.* 2022) and disproportionally focused on the effects of mountain lion predation on deer (*Odocoileus* spp.) and elk (*Cervus canadensis*) (Ballard *et al.* 2001; Forrester and Wittmer 2013). Mountain lions in North America have also been heavily managed although management has changed as attitudes towards predators have shifted. Populations in many States including Oregon, Washington, Idaho, and Montana, were significantly reduced by government bounty programs that began in the 1800s and continued in many areas until the 1960s (Oregon Department of Fish and Wildlife 1993; Peck *et al.* 1998; Montana Fish, Wildlife, and Parks 2019; Idaho Department of Fish and Game 2024), although some areas ended bounty programs earlier (New Mexico Department of Game and Fish 1997). As mountain lion populations began recovering following the cessation of bounty programs, sport hunting has increasingly been used to manage their numbers and the perceived impact on their prey (e.g., Montana Fish, Wildlife, and Parks 2019). Given the continuing interest in the impact of mountain lion predation on deer and varying approaches to setting harvest rates to manage mountain lion populations (Logan 2019), it is timely to examine recent research on mountain lion predation and assess future research topics.

Here we present a perspective on the impacts of mountain lion predation on mule (*O. hemionus*) and black-tailed deer (*O. h. columbianus*) (hereafter referred to as deer). First, we synthesize information from recent literature and review papers highlighting the variability in the direct impacts of mountain lion predation on deer populations. Second, we discuss the task of determining if mountain lion predation on deer is additive or compensatory and whether evidence of additive predation indicates actual regulation of deer populations by mountain lion predation. Third, we highlight research on deer that shows lower impact of NCEs of mountain lion predation than observed in other ungulate species and the larger impacts of complex multi-species interactions, such as apparent competition and kleptoparasitism. Finally, we highlight several directions for future research aimed at understanding the effect of mountain lion predation on deer.

Variability of direct predation impacts

We define mortality rate as the frequency of death in a prey population during a specific time interval; predation rate as the proportion of prey mortality rate attributable to predation; and kill rate as the number of prey killed by a predator per unit time.

Predation and mortality rates

Mountain lions are obligate carnivores that specialize on medium-sized ungulate prey (Logan and Sweanor 2001; LaBarge *et al.* 2022; Allen *et al.* 2023) although they can kill much larger species such as elk, feral horses (*Equus caballus*) and moose (*Alces americanus*) (Knopff *et al.* 2010; Elbroch and Quigley 2019; Andreasen *et al.* 2021), and they sometimes depredate livestock (Guerisoli *et al.* 2021). Depending on availability, they also consume smaller prey and this varies according to reproductive status and age (e.g., non-reproductively active females and subadult individuals; Knopff *et al.* 2010).

As stated above, most research on mountain lion predation appears focused on the impacts on deer or elk populations, although most of this research has measured prey mortality rates attributed to predation rather than impacts of predation on population growth (Forrester and Wittmer 2013; Hurley *et al.* 2023). Research based on mortality rates has shown that predation rates attributable to mountain lion vary widely among deer populations. Some studies have shown predation rates as low as 1% (Hurley *et al.* 2023) while the highest reported predation rate from mountain lions was 24% from a study on mule deer in the southwest deserts of the US during a period of drought and deer population decline (Logan and Sweanor 2001). The mean predation rate of deer by mountain lions for mule deer, across all age categories and sexes, ranges from 6.8% to 15% (Table 1). Yearling

mule deer experience the highest average predation rate from mountain lions while adult males have the lowest, although there were far fewer studies for adult male mule deer (Table 1). Black-tailed deer typically experienced higher mountain lion predation rates and the average predation rate of all age classes and sexes was higher than the comparable category for mule deer (Table 1).

The level of adult female deer mortality caused by mountain lions compared to all other sources of mortality also varied widely. In some areas, most of the mortality of adult females was attributed to mountain lion predation (including one outlier where 94% of all mortality was from mountain lion predation, although a subsequent mountain lion control effort did not increase the growth of the deer population; Logan and Sweanor 2001) while in other areas mountain lion predation comprised less than 5% of total deer mortality (Table 2). On average, black-tailed deer experience a slightly higher proportion of total mortality from mountain lion predation, and the lowest proportion of mountain lion predation vs. total mortality for black-tailed deer was nearly equivalent to the mean proportion of mountain lion predation for mule deer (Table 2).

Kill rates

Kill rates have been a particular focus of research attempting to quantify the impact of mountain lion predation on deer populations. A recent worldwide review of studies on kill rates of large terrestrial carnivores demonstrated that mountain lions accounted for 19.8% of 192 studies conducted for 17 species of large carnivores included in the review and only kill rates of grey wolves (*Canis lupus*) were studied more frequently (Emerson *et al.* 2024). While kill rates are well suited to understanding carnivore ecology and conservation, they are only meaningful to determine the impact of predators on prey if the density of both predator and prey are also known (i.e., the total response or the product of the functional and numerical response; Holling (1959). The prevalence of kill rate studies, particularly in North America, is thus likely due to the reliance of population models used by state agencies charged with setting annual hunting quotas for ungulates. Here we present summaries of kill rates from the area of North America where mountain lions overlap mule and black-tailed deer.

Studies on the kill rates of mountain lions have been predominantly conducted in the temperate forest biome where females with kittens had the highest kill rates of ungulates per time period, followed by adult males and solitary females (Cristescu *et al.* 2022). Studies outside of forested areas have shown that mountain lions in areas with higher productivity (i.e., temperate forests) generally had higher kill rates than mountain lions in xeric areas with lower productivity (e.g., kill rates for adult males > 1 ungulate per week in northern California vs. kill rates of 0.56 ungulates

Table 1 – Puma (*Puma concolor*) predation rates for both mule and black-tailed deer (*Odocoileus hemionus*) summarized from Hurley *et al.* (2023), and for male survival in Marescot *et al.* (2014; page 129). The symbol "-" indicates that there were no studies that reported mortality from mountain lions for that age class while the symbol ǂ indicates values that were averaged from only 2 studies. The lowest value for mule deer adult females is the lowest value reported from populations that did not have nutritional supplementation as part of the study.

		Age Class			
	Value	Neonates	6–12 month-old	Adult female	Adult Male
Black-tailed Deer	Mean	0.094	-	0.152ǂ	0.090ǂ
	Lowest	0.011	-	0.120ǂ	0.090ǂ
	Highest	0.210	-	0.183ǂ	0.090ǂ
Mule Deer	Mean	0.077	0.090	0.078	0.068ǂ
	Lowest	0.010	0.016	0.013	0.053ǂ
	Highest	0.111	0.250	0.240	0.090ǂ

Table 2 – Predation rates from mountain lions (*Puma concolor*) for adult female mule and black-tailed deer (*Odocoileus hemionus*) compared to total mortality rates for adult females. Values are summarized from the values reported in Table 7.3 from Hurley *et al.* (2023) as well as Marescot *et al.* (2014). The proportion of mountain lion predation was calculated for each study individually for each value (mean, minimum, and maximum) and then these proportions were averaged across all studies for each species. The symbol ǂ indicates values that were averaged from only 2 studies.

	Value	Adult female Mountain lion Predation	All Mortality	Proportion Mountain lion Predation
Black-tailed Deer	Mean	0.152ǂ	0.246	42.9%ǂ
	Lowest	0.120ǂ	0.180	33.3%ǂ
	Highest	0.183ǂ	0.360	52.4ǂ%
Mule Deer	Mean	0.078	0.175	35.4%
	Lowest	0.013	0.043	4.17%
	Highest	0.240	0.300	94.1%

per week for adult males in Utah) (Cristescu *et al.* 2022). Measuring kill rates in biomass resulted in different rankings of age class and reproductive status compared to measuring kill rate as the number of deer killed. When biomass was measured adult males killed slightly more ungulate biomass (12.04 +/- 5.17 kg SD) than adult females with kittens (10.38 +/- 3.84 kg) (Cristescu *et al.* 2022). As mountain lions tend to kill prey according to their availability (Bates-Mundell *et al.* 2024), this may reflect the varying availability of larger ungulates, such as elk, across study areas. Differences in kill rates measured in biomass may also be indicative of the tendency of adult males to concentrate on killing adult deer whereas more spatially constrained adult females with kittens will likely kill more neonates and juveniles (Cristescu *et al.* 2022).

Where mountain lions co-occur with dominant competitors such as black bears (*Ursus americanus*), kill rates appear higher due to observed kleptoparasitism by bears (see Species Interactions below) (Allen *et al.* 2021). Kleptoparasitism has increasingly been recognized as an important determinant of higher kill rates of subordinate predators (Emerson *et al.* 2024).

Population limitation vs regulation – Does additive predation matter?

One approach of determining whether mountain lion predation is impacting a deer population is determining whether predation is additive or compensatory (sensu Sinclair 2003). However, even if predation is additive, it may limit population growth to some degree, but evidence for mountain lion predation that "regulates" (i.e., is density-dependent) deer populations far below what a nutritional carrying capacity would support is limited (Forrester and Wittmer 2013; Hurley *et al.* 2023). Messier (1994) provides a heuristic framework that is useful for understanding why this may be the case. This framework has 4 scenarios of population regulation: regulation by food availability, limited by predation and regulated by food with 1 possible steady state, limited by predation and food with a high (food regulated) and low (predation regulated) steady state, and regulated well below forage carrying capacity by heavy predation (scenarios where prey populations are limited far below carrying capacity are often termed "predator pits") (Messier 1994). Since mountain lions specialize on ungulates, and are thus likely to follow the population fluctuations of their primary prey, it is unlikely that they would be able to hold prey at either the low end of a two-state predation equilibrium or regulate deer well below food based carrying capacity indefinitely, given that their populations would eventually decline with lower prey numbers and eventually allow deer to escape predation regulation (O'Donoghue *et al.* 1997; Sinclair 2003). Given the specialist nature of mountain lions, we contend that mountain lions contribute to a food-regulated population that predation limits somewhere near the food-based carrying

Table 3 – Metrics used to measure the impact of mountain lion (*Puma concolor*) predation on deer (*Odocoileus* spp.) and the value and weaknesses of each metric.

Predation metric	Effect type	Measurement	Value	Weaknesses
Predation rate	Direct	Number of deer predated per time interval	Quantifying impact of predation compared to other sources of mortality	Must determine whether predation is additive or compensatory to truly determine predation impacts
Kill rate	Direct	Number or biomass of prey killed per predator per unit time	Understanding per capita predator consumption as well as importance of sex, reproductive status, etc. on predation patterns.	Must know predator and prey density to determine population-level impact on prey
Predation sensitive foraging	Indirect	Location and duration of foraging	Linking forage quality/availability and predation risk	Determining duration of foraging can be difficult. Requires information on body condition of prey.
Changes in space use	Indirect	Location of foraging and resting locations of prey species	Documenting impacts on plant communities because of changing foraging patterns (i.e., trophic cascades). Documenting increased overlap between prey species and increased competition	Directly linking shifts in space use to predators rather than prey life history (e.g., seasonal shifts). Accounting for circadian or seasonal changes in predator activity
Prey stress	Indirect	Stress hormone levels	Direct measure of indirect effects of predation	Partitioning stress from competition or lack of forage from predation risk. Stress must be linked to fitness measures.

capacity or a system where mountain lion predation is almost entirely compensatory and deer populations are regulated by food alone (sensu Messier 1994). Mountain lions should only be capable of regulating mule and black-tailed deer well below their carrying capacity if their population was sustained by high populations of alternate prey such as white-tailed deer (*O. virginianus*) or elk (see apparent competition section below). Evidence for these hypotheses would require long-term monitoring of deer populations over periods of growth and decline that included estimates of predation, large scale predator removals to evaluate the effects of predation on deer, or large-scale nutritional supplementation of deer populations to determine if these populations are nutritionally limited. Such studies are understandably rare given the large cost and effort required, but a few exist, and evidence from these studies support the

single state model of deer populations that are primarily regulated by food with limiting effects of predation. A predator removal study in New Mexico monitored predation and population growth of both mountain lions and prey species for several years in a treatment and control area after predator removal (Logan and Sweanor 2001). After predator reduction, both mountain lion and deer populations increased, and mountain lion predation slowed the population growth of deer but did not prevent it (Logan and Sweanor 2001). During a drought in the latter half of the study, deer populations declined while mountain lion predation was the highest reported for any mule deer population (Logan and Sweanor 2001). Despite the high rate of predation, deer population growth appeared driven by forage availability rather than predation (Logan and Sweanor 2001). A long-term observational study in California that included effects of predation found that mountain lion predation did not explain the periods of population growth or decline in mule deer as well as changing forage availability (Pierce *et al.* 2012). Mountain lion predation was partially additive at certain time periods and affected the slope of the population growth curve but did not determine whether it was positive or negative (Pierce *et al.* 2012). A 9-year large-scale predator removal study by Hurley *et al.* (2011) also found evidence that mule deer populations were mostly regulated by nutrition. Large reductions in mountain lion populations did lead to increased deer survival and population growth, but during the first harsh winter of the study, high mortality reduced the deer population to pre-mountain lion removal levels (Hurley *et al.* 2011). Finally, an experiment in the Rocky Mountains of Colorado found that after providing winter nutrition supplements to mule deer to simulate optimum habitat quality, mountain lion predation on adult females that received nutrition supplements in the winter was 86% lower than on the groups that did not have nutritional supplementation (Bishop *et al.* 2009). It is unclear if this reduction in predation was a direct result of the improved body condition of mule deer or if mule deer were able to avoid areas with higher predation risk that were also associated with foraging. In all of these studies, mountain lion predation was partially additive or additive at certain times but the population growth rate of the deer population was more affected by nutrition than predation.

While some studies have found that the body condition of deer has little effect on the risk of mountain lion predation (Pierce *et al.* 2000), nutrition can still affect mountain lion predation. Logan and Sweanor (2001) found that predation rates increased during a drought, Bishop *et al.* (2009) showed that nutrition influenced the vulnerability of deer to mountain lion predation, and a study on black-tailed deer in California by Forrester *et al.* (2015) showed how lack of forage can increase predation risk. Specifically, Forrester *et al.* (2015) found that adult females were more likely to be killed by mountain lions when they ventured outside their home range boundaries. Female deer that had less forage available within their home range were more likely to engage in extended forays outside of their home range boundaries and were thus more likely to be predated (Forrester *et al.* 2015). These examples show that increased mountain predation on mule deer was linked to nutrition even in deer that did not have poor body condition.

Species interactions and indirect effects

A special case of species interactions affecting mountain lion predation on deer populations is through apparent competition, the indirect interaction between 2 species of prey sharing the same predator (Holt 1977). If 1 prey species is abundant or increases in population size (i.e., the primary prey species), it can support a high abundance of predators ultimately leading to increased predation on the less abundant, secondary prey species (Holt 1977). There are several well documented cases of mountain lions being involved in apparent competition for rare or declining species, including Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) in California (Holl *et al.* 2004), woodland caribou (*Rangifer tarandus caribou*) in some areas of British Columbia (Wittmer *et al.* 2005), and huemul deer (*Hippocamelus bisulcus*) in Chile (Elbroch and Wittmer 2013). However, apparent competition between deer species involving mountain lions is poorly investigated and is limited to a handful of studies in the Pacific Northwest region of the US and Canada. In south-central British Columbia, Robinson *et al.* (2002) found that mule deer survival was lower than that for white-tailed deer. White-tailed deer were approximately 3 times more abundant than mule deer, and mortality rates from causes other than mountain lion predation were similar. The higher white-tailed deer population appeared to support a large mountain lion population that was causing a lower survival for less abundant mule deer through predation (Robinson *et al.* 2002). After a period of heavy mountain lion hunting in this same area, an increase in both mule and white-tailed deer populations was observed, providing further evidence for apparent competition mediated by mountain lions rather than direct competition between the deer species (Wielgus and Shipley 2002). In northeastern Washington State, mountain lions were found to preferentially select for mule deer over more abundant white-tailed deer in the summer months (Cooley *et al.* 2008). Mule deer made up 60% of prey killed in the summer but only constituted 28% of available prey, and Cooley *et al.* (2008) hypothesized that abundant white-tailed deer populations on the winter range were sustaining

high mountain lion populations that followed mule deer to their summer range. Given the expansion of white-tailed deer throughout western North America (e.g., Dickie *et al.* 2024), apparent competition between mule and white-tailed deer mediated by mountain lions may have greater impact on mule deer populations in the future.

Grey wolves and bear (*Ursus* spp.) species can also change how mountain lion predation impacts deer populations. While grizzly (*U. arctos*) and black bears mainly prey on neonate deer (Bastille-Rousseau *et al.* 2011; Forrester and Wittmer 2019), both bear species frequently usurp mountain lion kills, which can lead to mountain lions losing large amounts of biomass that they would have otherwise consumed (Elbroch *et al.* 2015; Allen *et al.* 2021). For example, in northern California, mountain lions killed adult deer more frequently, as measured by inter-kill interval, when displaced by bears, although they also shifted to killing more juvenile deer and other smaller prey items and total prey biomass may not have been affected (Allen *et al.* 2021). Grizzly bears in Yellowstone also displace mountain lions from kills, and 1 study found that mountain lions displaced from kills by grizzly bears lost roughly 17 – 26% of their daily energy requirements (Murphy *et al.* 1998). The effects on subsequent kill rates of mountain lions, however, was not measured in this study. More recent research in Yellowstone also found high kleptoparasitism rates of mountain lion kills by both bear species (Feltner 2020). The impact on mountain lion kill rates was also not measured in this study, but the densities of adult mountain lions and dependent offspring were lower in years with high rates of kleptoparasitism, suggesting that mountain lions were not able to increase kill rates enough to offset losses by bears (Feltner 2020). The current evidence in interactions among both bear species and mountain lions shows that losses of prey biomass from kleptoparasitism from bears can be significant in areas with high bear populations, which has a potential to increase kill rates of deer (Allen *et al.* 2021) or negatively impact mountain lion populations (Feltner 2020). These results will have opposite impacts, either increasing or decreasing mountain lion predation on deer respectively.

Grey wolves affect mountain lion predation through direct wolf impacts on mountain lion populations (Elbroch *et al.* 2020), direct impacts of wolf predation on shared prey species with mountain lions (Elbroch *et al.* 2015), and indirect impacts of wolves on shared prey species with mountain lions. However, these effects seem to be context specific. Research in Grand Teton National Park showed that wolves lowered mountain lion survival most likely through decreasing availability of elk (Elbroch *et al.* 2015), while research elsewhere in the Greater Yellowstone Ecosystem (GYE) found that increasing wolf population size was not strongly related to mountain lion survival (Ruth *et al.* 2011). Wolves have also been shown to increase mountain lion predation on deer by reducing alternate prey. When wolf populations recovered in Banff National Park (Alberta, Canada), the elk population in the park declined by 65%, which led to mountain lions shifting their winter diet from mostly elk to mostly deer and other prey, greatly increasing winter mountain lion predation rates on deer (Kortello *et al.* 2007). Research in the GYE, both in Yellowstone National Park (Bartnick *et al.* 2013) and near Grand Teton National Park (Elbroch *et al.* 2015), found that increasing numbers of wolves led to an increase in mule deer predation by mountain lions. However, in southwest Montana, researchers found an opposite effect. Elk shifted to more structurally complex habitats to avoid wolf predation, but this change in habitat use increased the risk of mountain lion predation for elk (Atwood *et al.* 2009). The increase in availability of elk for mountain lions likely reduced the predation risk of mule deer in this system, although this was not directly measured (Atwood *et al.* 2009). These varying results show that species interaction impacts on mountain lion predation are as likely to be context dependent as direct predation impacts.

Finally, we highlight recent research that shows that non-consumptive effects (NCEs) are likely to have less impact on mule and black-tailed deer than other ungulate species. Much has been written about the importance or lack thereof of NCEs in predator-prey interactions (Say-Sallaz *et al.* 2019). Given the amount of research on NCEs, the impacts of indirect effects of mountain lions on deer populations are poorly documented and may be reduced because of the life history strategies of deer. Huggler *et al.* (2022) found that mule deer did not avoid areas of high predation risk from mountain lions (predicted by a model based on kill sites) and in fact were more likely to take steps toward areas of high predation risk. This was likely a result of mountain lions selecting strongly for high quality deer habitat rather than deer selecting for areas of high predation risk (Huggler *et al.* 2022). This selection paradox may be caused by the lack of immediate cues of predation risk from mountain lions (Huggler *et al.* 2022). Deer did exhibit a functional response to predation risk from mountain lions, however, and were less likely to select areas of high predation risk as the overall risk of predation within their home ranges increased (Huggler *et al.* 2022). These results may be a result of high site familiarity by mule deer similar to findings on black-tailed deer. Forrester *et al.* (2015) found that black-tailed deer were much less likely to be predated by mountain lions within their home ranges, and the effect was strongest in the 50% isopleth. Mule and black-tailed deer may be relying on

familiarity of their small home ranges to avoid predation risk instead of changing habitat use or shifting their home range.

The reliance on site fidelity as a core life history strategy has important implications for applying the landscape of fear concept to deer populations compared to other ungulate species. Many NCEs involve changes in space use, and mule and black-tailed deer are less likely to exhibit large changes in space use because they maintain strong fidelity to both seasonal home ranges and migration routes (Bose *et al.* 2017; Sawyer *et al.* 2019), even in the face of human development (Wyckoff *et al.* 2018). High levels of site fidelity will result in NCEs from mountain lions on deer that are expressed in different and more subtle ways than much of the literature on NCEs from other species (Say-Sallaz *et al.* 2019). For example, deer will be more likely to resort to predation-sensitive foraging on a very fine scale within their established home ranges (Huggler *et al.* 2022). NCEs may also be expressed by deer increasing movement rates (Brown *et al.* 2020) or being at higher risk of predation in unfamiliar areas (Forrester *et al.* 2015) instead of making large changes to habitat use (as shown in elk; Fortin *et al.* 2005) or making large shifts in space use to avoid predators altogether (Kohl *et al.* 2019). These subtle responses to predation risk are unlikely to impact population growth. Any demonstrated NCE must be linked to actual fitness measures, such as survival or body condition, to determine if the NCE will have population level effects (Wirsing *et al.* 2021).

Impacts of human activities on deer predation by mountain lions

Humans have large direct impacts on mountain lion populations, and hence indirectly on mountain lion predation on deer, through hunting, trapping, and other direct killing that can lower mountain lion survival, target adult males, and shift the age structure of the population to younger animals (Logan and Runge 2021). Hunting of mountain lions was historically the largest impact of humans, and several studies have found that managed hunting in many areas is typically one of the largest mortality sources for mountain lions (see Cooley *et al.* 2009 and Logan and Runge 2021 among others). Even in the absence of legal hunting, the killing of "problem" individuals resulted in human-caused mortality being the dominant cause of mortality in an otherwise protected mountain lion population (Benson *et al.* 2023).

Several studies have also found that increasing harvest limits for hunting can lead to a decline in mountain lion populations (e.g., Hurley *et al.* 2011; Proffitt *et al.* 2020). Human hunting often creates source-sink dynamics in mountain lions with populations in areas of high hunting mortality sustained through immigration from areas that are hunting refuges because of lack of access to hunters or protected status (Robinson *et al.* 2008; Newby *et al.* 2013; Logan and Runge 2021). The impacts of human hunting of mountain lions typically only have short-term effects on deer predation, however, as immigration or mountain lion population growth after a period of heavy hunting leads to rapid mountain lion recovery (Robinson *et al.* 2008; Hurley *et al.* 2011; Proffitt *et al.* 2020).

Human modification of the landscape can also have indirect effects on mountain lion predation of deer, mainly through urban development and resource extraction activities (timber harvest and energy development). Female mountain lions in developed areas have been found to have higher kill rates of deer (although male kill rates did not change) (Smith *et al.* 2015). The increase in kill rate was mostly linked to female mountain lions spending less time at kill sites in areas with higher housing densities (Smith *et al.* 2015), due to mountain lions fear of humans and increased disturbance in areas with higher human population (Smith *et al.* 2015, 2017). Note that observed changes in prey composition and age structure of deer killed by mountain lions, as well as higher kill rates by female mountain lions overlapping the highest housing densities in the study area (Smith *et al.* 2015, 2017) were consistent with results found in areas with high kleptoparasitism from black bears (Allen *et al.* 2014, Cristescu *et al.* 2022). Resource extraction activities can also impact mountain lion predation on deer through road building, changing cover through timber harvest, and creating other human infrastructure like well pads for natural gas or oil extraction. Mountain lions were found to be more likely to predate deer near roads but farther away from natural gas well pads in a Colorado study (Lendrum *et al.* 2018). However, the impacts of timber harvest and associated road density on predation of deer by mountain lions in the western US are surprisingly not well investigated and more research should be conducted.

Synthesis and future research

Mountain lions are one of the most important predators of adult deer across most of the range of mule and black-tailed deer. Much research has been done on the direct and indirect predation impacts of mountain lions on deer using several different metrics of the impacts of predation (Table 3) and several interesting patterns have emerged:

1. The rate of mountain lion predation on mule and black-tailed deer is context specific and widely variable across ecosystems and habitat types.
2. Measuring kill rates in the number of ungulates per unit time may lead to different conclusions about the importance of predation by different age and reproductive classes of mountain lions than measuring kill rates in terms of ungulate biomass.

3. There is more evidence that mountain lions are limiting deer populations slightly below nutritional based carrying capacity rather than regulating deer populations far below carrying capacity, although there are certain areas where mountain lion predation may have larger additive effects.
4. Apparent competition may be an important dynamic that can lead to high and additive mountain lion predation on mule deer in areas with abundant white-tailed deer populations, an important consideration as white-tailed deer continue to expand their range in the western USA.
5. Human-caused mortality creates source-sink dynamics in cougar populations. This is true even in areas with no legal harvest. The scale at which this operates is likely influenced by the productivity of the ecosystem and should be better defined for cougar management.

Several key research questions remain about the impacts of mountain lion predation on deer populations (Figure 1).
1. The role of human impacts on mountain lion predation is important to investigate as human impacts will continue to increase as human populations expand. Research on the effects of hunting on mountain lion populations can be further developed to guide management, particularly the scale at which harvest should be managed to account for source-sink dynamics. The indirect effects of human development on mountain lion predation near urban areas is the most researched, but the impacts of resource extraction and road density remain poorly understood. The impacts of roads associated with energy extraction and logging on canid predation have been investigated (DeMars and Boutin 2018; Dickie *et al.* 2020), but the impacts of these features on mountain lion predation have not seen the same level of research effort.
2. The role of apparent competition in additive predation by mountain lions on mule and black-tailed deer has only been investigated by a few studies. As white-tailed deer populations increase and expand across the western USA, this dynamic will be important to understand, especially since apparent competition is one of the few reported instances of additive predation by mountain lions that caused population impacts on mule deer. The role of mountain lion predation in communities with multiple predators, particularly grey wolves and bears, also requires more investigation. Areas with possible apparent competition and multiple predator species were the most likely to show larger additive effects of predation by mountain lions.
3. The importance of site fidelity as a life history strategy of mule and black-tailed deer seems to impact both the direct impacts of mountain lion predation and the importance of NCEs from predation. This should be considered in future research on subjects and will likely change the view of NCEs for mule and black-tailed deer compared to other ungulate species.
4. Researchers often assess the potential of mountain lion predation to impact deer populations by attempting to determine wither predation mortality is additive or compensatory. This is an important component of understanding the effects of predation, but even some amount of additive predation may not be a regulatory force for deer populations. Current research findings do not support the existence of widespread population regulation of deer populations by mountain lions. Establishing a threshold of additive predation from mountain lions that changes growth rates of deer populations is a needed step for this field. There are areas with multiple ungulate species and multi-predator species that show higher levels of additive predation, and the research questions shown in Figure 1 remain to be investigated and may prove consequential. Given the difficulties of predator control (Hurley *et al.* 2023) and our current understanding of mountain lion predation, managers who are focused on maintaining abundant deer herds would likely do better focusing on habitat and nutrition rather than control of mountain lion populations.

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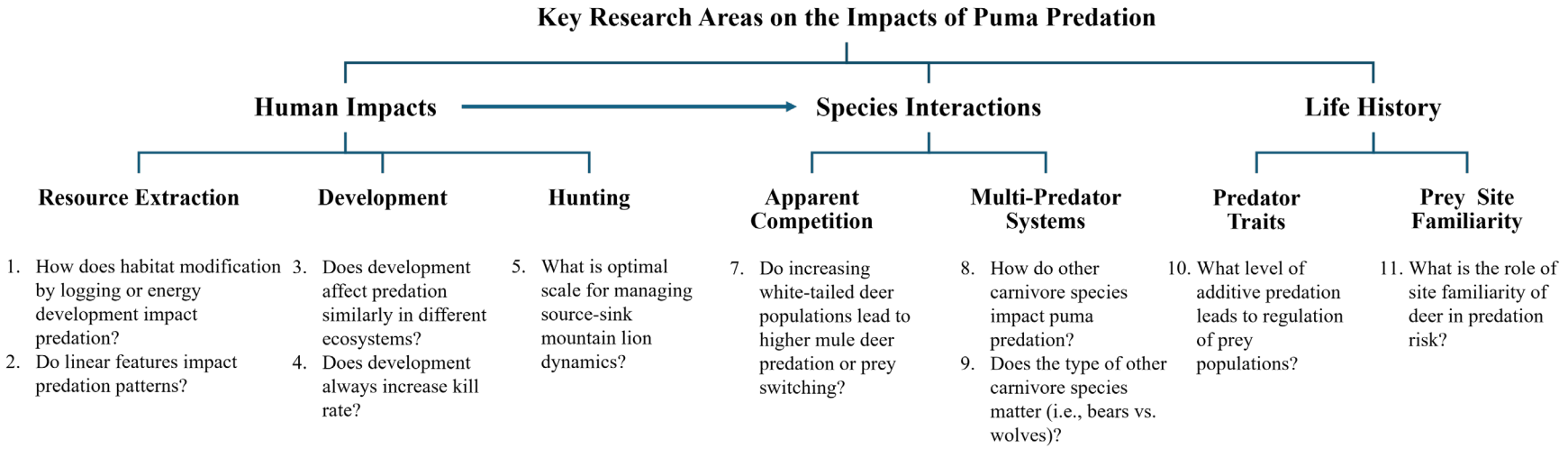

Figure 1 – Eleven key research questions that remain under investigated on the impacts of puma (*Puma concolor*) predation on mule and black-tailed deer (*Odocoileus hemionus*) in 3 areas: human impacts, species interactions, and life history of both predator and prey. Human impacts are also likely to influence species interactions, shown by the arrow connecting these topics.

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Received 12 August 2024 – Accepted 29 November 2024