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Puma Population Limitation and Regulation: What Matters in Puma Management?

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ABSTRACT Wildlife managers require reliable information on factors that influence animal populations to develop successful management programs, including the puma (*Puma concolor*), in western North America. As puma populations have recovered in recent decades because of restrictions on human-caused mortality, managers need a clear understanding of the factors that limit or regulate puma populations and how those factors might be manipulated to achieve management objectives, including sustaining puma and other wildlife populations, providing hunting opportunity, and reducing puma interactions with people. I synthesized technical literature on puma populations, behavior, and relationships with prey that have contributed to hypotheses on puma population limitation and regulation. Current hypotheses on puma population limitation include the social limitation hypothesis and the food limitation hypothesis. Associated with each of those are 2 hypotheses on puma population regulation: the social regulation hypothesis and the competition regulation hypothesis. I organize the biological and ecological attributes of pumas reported in the literature under these hypotheses. I discuss the validity of these hypotheses based on the limits of the research associated with the hypotheses and the evolutionary processes theoretically underlying them. I review the management predictions as framed by these hypotheses as they pertain to puma hunting, puma-prey relationships, and human-puma interactions. The food limitation and competition regulation hypotheses explain more phenomena associated with puma and likely would guide more successful management outcomes. © 2019 The Wildlife Society.

KEY WORDS limitation, management, natural selection, North America, population, puma, *Puma concolor*, regulation.

Fundamental to the process of wildlife management is the identification of factors that constrain animal population growth. Factors can be biotic or abiotic and affect populations by limiting growth, independent of animal density, or by regulating growth through density-dependent means (Fryxell and Sinclair 2000). Wildlife managers want to understand the factors constraining populations and identify those that can be manipulated to achieve objectives. Objectives could be for larger, more productive populations, such as needed for recovering endangered and threatened species (Hervieux et al. 2014), and providing sustainable hunting of preferred game species (Cooley et al. 2011). Conversely, the objectives could be to stabilize or reduce populations of animals deemed to be overabundant (Russell et al. 2001, Kamler et al. 2002, VerCauteren et al. 2011). Another objective might be custodial, explicitly to minimize human effects on a population and its habitat to allow natural processes to operate (Fryxell et al. 2014). The puma (*Puma concolor*) in North America is managed for any one of these objectives, depending on location.

In North America, the status and management of the puma varies from east to west. The only known breeding puma population in the eastern United States occurs in Florida, is federally listed as endangered, and is managed for recovery and restoration (United States Fish and Wildlife Service 2008). Florida panther managers identified inbreeding depression, human-caused mortality, and habitat fragmentation as factors constraining growth of that population (Onorato et al. 2010), which numbers <200 in the wild (United States Fish and Wildlife Service 2008). In contrast, puma populations thrive in most of the western United States and Canada where they are managed with restricted hunting in all western states and provinces, except California, USA, where hunting is banned. In the Midwest, pumas are managed with restricted hunting in North Dakota and South Dakota, and protected in Nebraska, USA (Anderson and Lindzey 2010, Knopff et al. 2010). Texas, USA, has 2 geographically distinct puma populations (in south and west Texas) that are not protected, where pumas can be hunted at any time (Texas Parks and Wildlife 2019), and exhibit low productivity and high mortality primarily from hunting and trapping (Harveson 1997, Young et al. 2010, Harveson et al. 2012).

Wildlife managers responsible for implementing puma management programs need to identify factors that limit or regulate puma populations to reliably sustain those

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populations, provide hunting opportunity, mitigate puma predation on wild ungulates and livestock, and address public safety (Cougar Management Guidelines Working Group 2005, Jenks 2011). Research results revealing potential limiting and regulating factors have been interpreted in different theoretical frameworks leading to different puma management approaches. These dissimilar interpretations have also been used by special interest groups to support their own positions on puma management (Boone and Crocket Club 2016, The Humane Society of the United States 2017), and authors of popular literature in their explanations of puma ecology (Patten 2018, Williams 2018).

I reviewed current hypotheses on puma population limitation and regulation. Two proposed hypotheses on puma population limitation are the social limitation hypothesis and the food limitation hypothesis. Associated with each of those hypotheses, respectively, are 2 proposed hypotheses on biological regulation of puma populations: the social regulation hypothesis and the competition regulation hypothesis. I organize the biological and ecological attributes of pumas reported in the literature under the hypotheses derived from them, or which the attributes best fit. I discuss limits of this body of research associated with these hypotheses and propose ways to gain better knowledge. I also contrast the underlying evolutionary processes theoretically involved with each hypothesis. Moreover, I discuss how some aspects of the competing hypotheses are not mutually exclusive. I review puma management predictions as framed by these hypotheses pertaining to major issues in puma management, namely puma hunting, puma-prey relationships, and human-puma interactions. My discussion on human-puma interactions pertains primarily to mitigating puma predation on domestic animals or livestock. Puma attacks on people are rare (Mattson et al. 2011), and not all puma encounters with humans are dangerous (Apker et al. 2011). State or province management agencies develop policies and protocols to handle reported interactions between humans and pumas based on the relative risk of harm to humans (Apker et al. 2011). Finally, I use this synthesis of the material to arrive at the best-supported hypotheses on puma population limitation and regulation to guide puma management.

METHODS

I first defined terminology used in the foundational concepts of population limitation and regulation, particularly for terrestrial mammals. Next, I synthesized a thorough compilation of original studies containing information germane to puma population limitation and regulation published in peer-reviewed journals and books in the western United States and Canada from 1969–2019. I present information that established the hypotheses or provided information to support or refute them. I use quoted passages from the literature to provide conceptual clarity from the original authors. I briefly provide durations, methods, and sample sizes for key studies on puma behavior and social organization to provide context to the resulting assumptions and inferences. As part of the review process, I extracted the biological and ecological attributes of pumas,

considered them as evidence supporting any hypothesis, and organized this information (Table 1). I weighed the validity of any hypothesis based on how much they explain about puma biology and ecology. Likewise, I weighed the hypotheses based on the theoretical evolutionary processes underlying the hypotheses as provided by original authors of the hypotheses and additional literature. I structured expected puma management outcomes on puma hunting, puma-prey relationships, and human-puma interactions based on, for the most part, how authors affiliated their work with these hypotheses. In addition, I included other literature on expected puma management outcomes that was consistent with any hypothesis.

CONCEPTUAL FRAMEWORK

Limitation

Limitation is any natural or anthropogenic process that determines the growth rate of a population within an environment (Fryxell and Sinclair 2000). Factors that demonstrably affect the rate of population change are limiting factors (Leopold 1933). Limiting factors can be any agents that influence reproduction or mortality, and may be density independent or dependent (Fryxell et al. 2014). For example, an abiotic density-independent limiting factor could be weather, such as a severe winter with higher than average snowfall resulting in increased animal mortality. Biotic factors might include food, predation, disease, and hunting. Abiotic and biotic factors may interact with each other, and the combined, complex effect could increase or decrease the degree of limitation on a population.

Regulation

Biological regulation is the density-dependent process that reduces the *per capita* rate of population growth as the population increases so that population density is bounded over time (Fryxell et al. 2014). Regulating factors that govern this dynamic are a subset of limiting factors that act as the negative feedback mechanisms to depress population growth rate as the population increases (Messier 1991). For example, a regulating factor could be increasing competition for food as consumer density increases, resulting in an increasing *per capita* risk of death from starvation or competitive killing. Predation or disease can operate as regulating factors. Territorialism regulates when the rate of population growth declines as individuals occupy the limited amount of space.

Some regulating factors might not cause immediate population responses. An example of this could be competition for food whereby a predator population decline lags behind a prey population decline. In this case the density-dependent effect on the predator from competition is related to previous, instead of current, prey abundance. There may also be an inverse density-dependent, or compensatory, response where the strength of a regulating factor is inversely related to population trend. Imagine a prey population declining primarily from a non-predation cause (e.g., disease) with predators having a lagged numerical response to prey abundance, thus taking an

Table 1. Proposed hypotheses on natural puma population limitation and regulation in the United States and Canada, 1969–2019. Biological and ecological attributes of pumas reported in peer-reviewed literature are placed under hypotheses derived from them, or which the attributes best fit. The food limitation and competition regulation hypotheses explain more of the observed phenomena of puma behavior, and effects of prey density on pumas and puma predation on prey, including in multi-prey and multi-predator systems.

Hypotheses	References
Social limitation and social regulation: Puma population growth is limited and regulated by a social system of territoriality or land tenure.	Hornocker (1969, 1970), Seidensticker et al. (1973)
Attributes:	
1) Adult male and female pumas exhibit territorial behavior or establish tenure to areas that deters other pumas from settling there.	Hornocker (1969, 1970), Seidensticker et al. (1973), Elbroch et al. (2015c)
2) Puma density does not correlate with fluctuations in primary prey abundance, and instead is relatively stable.	Hornocker (1969, 1970), Seidensticker et al. (1973)
3) Puma predation does not limit growth of the primary prey populations.	Hornocker (1970), Seidensticker et al. (1973)
4) Subadult pumas emigrate as a mechanism of population limitation.	Hornocker (1969)
Evolutionary adaptation: The puma social system evolved to maintain the density of breeding adults below the level set by the food supply for efficient food resource utilization.	Seidensticker et al. (1973)
Food limitation and competition regulation: Puma population growth is ultimately limited by food (i.e., prey) availability. Male population growth is regulated by competition for mates, and female population growth is regulated by competition for food.	Logan and Sweanor (2001, 2010)
Attributes:	
1) Adult male pumas exhibit territorial behavior. Males compete for access to mates, including through fighting, and infanticide. Overlap between male territories fluctuates with status of competing males and breeding females.	Logan and Sweanor (2001)
2) Male territories are larger than female home ranges to contact more prospective mates.	Logan and Sweanor (2001), Lendrum et al. (2014), Maletzke et al. (2014), Elbroch et al. (2015c)
3) Adult female pumas are not territorial. Adult female home ranges overlap extensively to gain access to available prey.	Seidensticker et al. (1973), Logan and Sweanor (2001), Lendrum et al. (2014), Maletzke et al. (2014)
4) Female home ranges are positioned on the landscape to provide high access to prey and to avoid competition with other predators.	Seidensticker et al. (1973), Pierce et al. (2000), Lendrum et al. (2014), Elbroch et al. (2015c)
5) Associations between pumas are most prevalent during breeding activity and when food resources are aggregated.	Seidensticker et al. (1973), Logan and Sweanor (2001), Elbroch et al. (2015d), Elbroch and Quigley (2017)
6) Fluctuations in primary prey abundance affect puma physical condition, survival, and density.	Seidensticker et al. (1973), Laundré et al. (2007), Pierce et al. (2012), Elbroch et al. (2018)
7) Competition with other carnivores affects puma survival, density, and predation rates on prey.	Elbroch et al. (2015a, b), Elbroch et al. (2018)
8) Puma predation affects prey population growth in certain circumstances.	Logan and Sweanor (2001), Robinson et al. (2002), McKinney et al. (2006), Pierce et al. (2012), Johnson et al. (2012), Johnson et al. (2019)
9) Pumas switch to using other prey following declines in primary prey or as competing predators and their effect on prey density increase.	Atwood et al. (2007), Kortello et al. (2007), Elbroch et al. (2015b)
10) Subadult pumas emigrate to avoid competition.	Hornocker (1969), Logan and Sweanor (2001), Laundré and Hernandez (2003), Stoner et al. (2013)
Evolutionary adaptation: The social behavior of pumas evolved to maximize individual lifetime reproductive success, with each sex having different strategies.	Logan and Sweanor (2001, 2010)

increasing proportion of the prey and increasing the prey's rate of decline (Fryxell et al. 2014).

HYPOTHESES ON PUMA POPULATION LIMITATION AND REGULATION

Social Limitation and Social Regulation Hypotheses

The social limitation and social regulation hypotheses propose that puma population growth is limited and regulated by a social system based on territoriality or land tenure. This system

acts to limit puma numbers and maintain population stability below a level set by the food supply (Table 1).

Puma population limitation theory was established by Hornocker (1969, 1970), who studied puma ecology in the central Idaho, USA, wilderness for 5 years. His pioneering research relied on captures and recaptures of pumas marked with numbered color-coded collars and eartags, and ground-tracking of pumas to infer puma behavior. The puma population was hunted at the time, with 7 of 14 recorded deaths during the study attributed to hunting. Hornocker

(1969) concluded that adult pumas exhibited territoriality, loosely defined as an attraction to a particular area, with males using relatively exclusive areas and females using overlapping areas. Hornocker (1969:16) also identified a class of pumas he called transients, young pumas born on the study area that, after independence from their mothers, dispersed from the natal area. He considered this behavior to be an “important limiting mechanism” (Hornocker 1969:37). Mutual avoidance behavior, aided by visual and olfactory cues, appeared to distribute pumas in both space and time, and in a socially peaceful manner (i.e., no evidence of fighting was observed). Hornocker (1969:464) concluded, “The primary function of territoriality in the [puma] population appears to be a spatial distribution of individuals. This spacing, brought about without apparent conflict, acts to limit population size.”

Hornocker (1970) also examined effects of puma predation on mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*). Some pumas stayed at lower elevations all year, whereas other pumas migrated between high-elevation summer and low-elevation winter ranges. Finding that the density of pumas remained the same while deer and elk numbers increased, Hornocker (1970:37) concluded that “Intraspecific relationships, manifested through territoriality, acted to limit numbers of [pumas] and maintain population stability,” and the “elk and deer populations were limited by the winter food supply, and that predation by [pumas] was inconsequential in determining ultimate numbers of elk and deer.” Hornocker (1970) proposed, however, that puma predation dampened oscillations in ungulate prey populations, and influenced ungulate distributions, both of which could be beneficial to ungulate habitat.

That research continued another 3 years, with an emphasis on puma social organization (Seidensticker et al. 1973). The researchers used newly developed very high frequency (VHF) radio-collars and attached them to 15 pumas. The pumas were radio-located from an airplane and the ground at intervals of 1–21 days for 1,386 locations. This work, which occurred primarily in winter, revealed that adult pumas were “essentially solitary in their activities” (Seidensticker et al. 1973:36–37) and their most frequent social behavior was avoiding other pumas. Pumas interacted infrequently; 6 adult pumas (2 males, 4 females) monitored during 2 years interacted with other adult pumas 5–13% of the days they were radio-located. Adult males and adult females interacted the most (71% of associations), with half of those associations involving adult males with adult females and their large cubs (i.e., >1 yr old). These associations were thought to be related to the female’s reproductive status. The mating system was polygynous; “The resident male breeds with a number of different females whose home areas overlap his own” (Seidensticker et al. 1973:53). In addition, a majority (59%) of the associations occurred at carcasses of ungulates killed by pumas.

In this work the researchers favored the term “home area” instead of territory to describe the area used by individual resident pumas, because the latter term traditionally referred

to a defended area (Seidensticker et al. 1973:53–54). Adult pumas exhibited fidelity to large home areas that were “in a constant state of flux in terms of location of mule deer and elk” and “Resident male home areas overlapped but little. Those of resident females often overlapped completely and were overlapped by resident male areas” (Seidensticker et al. 1973:58). In addition, the authors recognized that young born on the study area that survived to self-sufficiency emigrated independent of the local adult density, and it was important that other young independent pumas that emigrated from other populations immigrate into the local population to sustain it. The researchers surmised that tenure of a home area was established by prior rights, whereby a puma claimed a home area only when it was vacated, and once it established a home area its occupancy would deter other pumas from settling there. Thus, the presence of adult males limited adult male density, and presence of breeding females limited the female breeding population. Moreover, because puma numbers declined slightly while mule deer and elk, the primary puma prey, increased in numbers, Seidensticker et al. (1973:59) inferred that “the land tenure system maintains the density of breeding adults below the level set by food supply in terms of absolute numbers of mule deer and elk.”

Thus, the Idaho researchers hypothesized that pumas limited their own breeding population density via the social spacing mechanism, land tenure. Yet, they also acknowledged that the amount of terrain needed by an adult puma and the degree of home area overlap between adult females was set by a “vegetation-topography/prey numbers-vulnerability complex with limits set by proximate and ultimate energy considerations” (Seidensticker et al. 1973:57). Although the Idaho researchers clearly identified habitat structure and prey availability as important elements in puma spatial distribution, prey availability was not considered to be what determined the upper limits of the breeding puma population; land tenure based on prior rights did as “an adaptation for efficient food resource utilization” (Seidensticker et al. 1973:52). The authors acknowledged that these conclusions might be dependent on the conditions under which they studied the puma, and that the system might differ given a different environment with a different prey base and other competing carnivores.

Puma studies during the 1980s and 1990s using VHF radio-telemetry reported similar behavior patterns to those described by Hornocker (1969, 1970) and Seidensticker et al. (1973) and could not refute their thesis. After a 3-year study in Utah, USA, Hemker et al. (1984:1275) added food as a potential limiting factor, concluding, “Density of adult [pumas] was apparently regulated by a social pattern based on land tenure, but limited by the abundance of mule deer, ... their principal prey.” But later, Lindzey et al. (1994) examined an 8-year data set on that same Utah study area and, finding a poor relationship between puma and deer numbers, concluded that the increase in deer numbers was insufficient to test the social limitation hypothesis. This Utah study was also the first to experimentally show that hunting mortality was largely additive and could limit a

puma population (Lindzey et al. 1992). In Alberta, Canada, Ross and Jalkotzy (1992:424) were ambiguous about puma population limitation or regulation, stating, “Due to the territorial component of the land tenure system (Seidensticker et al. 1973), it is probable that population growth in our study area will be curtailed at a level regulated by social interactions and/or prey densities.”

Puma studies in Utah (Hemker et al. 1984, Lindzey et al. 1994), Alberta (Ross and Jalkotzy 1992), Colorado, USA (Anderson et al. 1992), and California (Beier 1995) reported dispersal of young pumas (generally 1–2 yr old) occurred independent of adult density and immigrant recruitment was important to population maintenance, consistent with the Idaho study. Males generally dispersed more frequently and farther than females. Female young, in particular, were recruited into the local populations (Anderson et al. 1992, Lindzey et al. 1992, Ross and Jalkotzy 1992), some establishing home ranges (i.e., the area where a puma restricts its movements during a specified time; Burt 1943) overlapping their mothers’ (Ross and Jalkotzy 1992). Evidence of fighting among pumas (i.e., scarring in males, puma deaths) emerged in each of these studies, indicating that pumas were not always peaceful as suggested by the Idaho study.

In the early 2000s, researchers in Washington, USA, studied effects of low and high hunting mortality on 2 puma populations. They used VHF radio-telemetry and new global positioning system (GPS) technology. Hunting mortality was additive, and there was no evidence that increased reproduction compensated for increased mortality. Increased hunting mortality resulted in reduced adult and cub survival, reduced female population growth, and a younger population age structure. Puma abundances, however, were relatively unchanged, with losses compensated by immigration, particularly of young males (Robinson et al. 2008, Cooley et al. 2009). Authors emphasized the importance of metapopulation source-sink population dynamics in regional puma demographics and population stability (Robinson et al. 2008, Cooley et al. 2009). Their results suggested that hunting did not limit or regulate puma abundance, particularly in management units <math><1,000 \text{ km}^2</math> in size. Beausoleil et al. (2013) interpreted that these studies supported the concepts of Hornocker (1969, 1970), whereby the social organization of adult pumas tends to maintain population stability over time.

Researchers in the Southern Yellowstone Ecosystem (SYE) studied puma social organization in a hunted population using GPS technology. Their 8-year study (2005–2012) involved 18 pumas with GPS-collars programmed to fix locations 3–6 times/day (Elbroch et al. 2015*d*). They documented 92 puma associations from 28,874 GPS locations, 64% of which were between male and female pumas, and with 86% of those occurring during the puma breeding season (Feb–Jul). Overall, pumas associated 6.7 times more during the breeding season and when pumas and ungulates were congregated on low-elevation winter habitat, compared to the non-breeding season. Lendrum et al. (2014) reported that male puma

home ranges were 2–3 times larger than female home ranges, and that pumas, especially females, selected home ranges with high hunting opportunity and farther from wolves (*Canis lupus*) to mitigate conflict. Furthermore, Elbroch et al. (2015*c*) reported that puma sex was the primary factor explaining variation in home range overlap, with males overlapping significantly with females as males moved across large territories searching for and defending mates. Females overlapped less with each other and were said to defend territories with sufficient food resources needed to maintain themselves and their offspring. Overlap of female home ranges and male and female home ranges was higher in winter when greater hunting opportunity was provided by aggregated ungulates, particularly elk, supported at an exaggerated density by supplemental winter feeding (Elbroch et al. 2013, 2018).

Later, Elbroch and Quigley (2017) examined social behavior of 12 GPS-collared adult pumas (4 males, 8 females) monitored over 3 years (2012–2015). The GPS-collars were programmed to locate pumas 12 times/day. The GPS-collared pumas had 89 independent interactions with other collared pumas, 60% of which occurred at puma kills. An additional 24 interactions of non-collared pumas were recorded by automated cameras, another new technology applied to animal behavior, placed at ungulate carcasses by the researchers. A majority (58%) of interactions occurred between males and females, followed by associations between females (43%). At these interactions, 2 deaths of females occurred: 1 subadult female was killed by a subadult male for food and 1 adult female with 2 cubs was killed by an adult male. Mean minimum weekly contact rates were 5.5 times higher in winter, compared to summer, when elk (the primary prey) aggregated at lower elevations and pumas were breeding. Individual adult pumas interacted with other adults an average of 26 times/year minimum (i.e., not all adult pumas wore GPS-collars).

The SYE researchers used network analysis of associations between 11 (4 males, 7 females) of the GPS-collared pumas and 2 non-collared female pumas (Elbroch and Quigley 2017). They concluded that conspecific tolerance was best explained by direct reciprocity in which food (primarily elk carcasses) could be shared, establishing a benefit to participating individuals, and potentially increasing individual fitness. In such cases, the cost of tolerating a conspecific and sharing a large prey item where large prey also are aggregated would be less costly than defending the food and potentially being injured (Elbroch and Quigley 2017, Elbroch et al. 2017). In addition, territorial males appeared to structure social interactions among all pumas. “Pumas exhibited more frequent interactions within network clusters delineated by male territories, indicating that our population of solitary pumas was in fact a collection of smaller social communities defined by male territories” (Elbroch et al. 2017:4–5).

Elbroch and Kusler (2018:12) surmised, “In the absence of human hunting, pumas self-regulate” and cited Seidensticker et al. (1973) and Wallach et al. (2015). Although, Elbroch and Kusler (2018) had just provided

evidence that pumas are subordinate competitors to sympatric wolves, grizzly bears (*Ursus arctos horribilis*), black bears (*U. americanus*), jaguars (*Panthera onca*), and humans. For clarification, Wallach et al. (2015) proposed that socially stable large carnivore populations exhibit self-regulation through socially mediated internal mechanisms, including extended parental care, female reproductive suppression, infanticide by dominant females killing young of subordinate females, and female territoriality. Wallach et al. (2015:1453) concluded, "Self-regulation in large carnivores may ensure that the largest and the fiercest do not overexploit their resources." After synthesizing 14 years of data on the SYE puma population, Elbroch et al. (2018) concluded that 3 factors most influenced puma survival: hunting mortality, reduction of primary prey (i.e., elk), and competition with wolves. Estimated adult puma densities in winter ranged from 0.29–1.0 adults/100 km², one of the lowest recorded densities in North America.

Food Limitation and Competition Regulation Hypotheses

The food limitation and competition regulation hypotheses propose that puma population growth is ultimately limited by food (i.e., prey) availability. Male population growth is regulated by competition for mates, and female population growth is regulated by competition for food. Puma social behavior evolved to maximize individual lifetime reproductive success, with each sex having different strategies (Table 1).

Puma studies from the 1980s to early 2000s revealed data supporting the food limitation and competition regulation hypotheses. In California's Sierra Nevada, Pierce et al. (1999, 2000) used VHF radio-telemetry to study pumas and mule deer (i.e., major prey), most of which migrated between winter and summer ranges. They proposed that, for a land tenure or territorial system to limit a puma population below the level set by the prey, territorial pumas would have to sequester more prey than was necessary for reproduction and limit the availability of prey to other pumas. They reported that individual pumas exhibited distinct distributions, but the distribution of deer killed by individual pumas was identical in both areas of exclusive puma use and areas of overlap with other pumas. The distribution of deer killed was best explained by the distribution of deer alone. Thus, the pumas did not sequester the available prey by excluding other pumas. The researchers "observed no indication of a land-tenure system that would lead to regulation of the population" (Pierce et al. 2000:1542). In that environment, Pierce et al. (1999) reported a more flexible puma social system than expected in a land tenure system, where individual pumas exhibited different strategies for coping with changing prey abundance. Some had 1 annual home range spanning winter and summer ranges, whereas others had exclusive winter and summer ranges connected by long-range movements. Pierce et al. (2000:1542) concluded, pumas "most likely were limited by prey availability and not territoriality."

Later, Pierce et al. (2012) documented periods of a rapid mule deer population decline (1984–1990) followed by an increase at a lower rate (1991–1998) during which puma numbers declined with an 8-year time lag. The researchers inferred that the deer population was limited by forage availability and that puma predation was additive mortality during the deer increase phase, slowing but not preventing growth. These results suggested that the puma population was not limited by territoriality but by the food supply and that puma predation could affect their major prey.

In Chihuahua Desert of New Mexico, USA, researchers studied puma demographics, social behavior, and puma-prey relationships for 10 years and tested the social limitation hypothesis (Logan and Sweanor 2001). The puma, mule deer (primary prey), and desert bighorn (*Ovis canadensis mexicana*; secondary prey) populations were not hunted, and not migratory. That work was based on 112 VHF radio-collared independent pumas (86 adults, 26 subadults). Each was located 1 time/8 days on average and as frequently as 1 time/day, with a combination of aerial and ground locations. Logan and Sweanor (2001) observed 269 separate puma associations in 12,490 total locations. A majority (57%) of the associations were between adult males and females. Interactions between adult males and females with dependent cubs were the second most frequent type (15%). Three-quarters of all male interactions with females were thought to be related to breeding. Furthermore, Logan and Sweanor (2001) examined direct associations between neighboring pumas during 4 years when a majority of independent pumas wore VHF radio-collars. They monitored 14–18 males and 17–23 females/year. The most frequent interactions occurred between adult males and females, averaging 2.6–6.2% of simultaneous locations each year, and were primarily associated with mating. Adult female-female and male-male associations averaged 0.5–1.2% and 0–1.4%, respectively, of simultaneous locations each year.

The New Mexico researchers experimentally reduced puma abundance in a treatment portion of the study area after 5 years of population growth to study responses of the puma and ungulate populations to changes in puma abundance (Logan and Sweanor 2001). The puma population segment on a reference portion of the study area was left alone to examine its natural response to the environment. In the treatment area, pumas were removed in a 6-month period, including 53% of adults and 58% of independent pumas (i.e., adults and subadults). It took 31 months of protection for the adult portion of the population to recover to the pre-removal level. Recruitment of adult females depended on a combination of females born on the treatment area and immigrants; adult male recruits were all immigrants. Territorial male pumas responded to losses of neighboring adult males, newly recruited males, and losses of adult females by shifting their territories. Adult females exhibited greater home range fidelity (than males) in response to losses of neighboring adult females and males. Immigration and emigration were important components of puma population dynamics, which the researchers expanded

to the range and basin structure of the Southwest desert biome, and recognized this as source-sink metapopulation dynamics (Sweaner et al. 2000, Logan and Sweaner 2001).

Mule deer and desert bighorn populations, survival, and agent-specific mortality also were monitored in the treatment area (Logan and Sweaner 2001). The puma population increased as did the mule deer population early in the study. Puma predation was the main proximate cause of mortality for deer and slowed the deer population growth rate. Puma predation did not stop the deer population from increasing; hence, puma predation alone did not limit the deer population. Afterwards, during a drought-induced deer population decline, puma abundance remained high and predation rates increased (i.e., depensatory), hastening the decline in deer abundance. Cub survival and puma abundance were not sensitive to the deer decline, leading the researchers to predict a time lag before the puma population would respond to a reduced prey base. In the reference area, the adult puma population continued to grow during the deer decline, but at a slower rate than when deer increased, with adult female growth stymied more than adult male growth. Also during the deer decline, puma predation on rare desert bighorns increased and was the main proximate mortality factor causing the biological extirpation of that bighorn population. Thus, pumas did not naturally limit their own numbers below the level set by the prey, as would be expected in the social limitation and social regulation hypotheses.

Instead, Logan and Sweaner (2001) inferred that the social behavior of pumas functioned to maximize individual lifetime reproductive success, with each sex having evolved different strategies. Adult males exhibited territorial behavior by defending area and mates, sometimes through overt fighting. Intraspecific strife was the main proximate cause of death for adult and subadult pumas of both sexes. Adult males were the dominant characters in those events, which apparently were associated with defending mating opportunities, competition for food, and male-induced infanticide. Apparently, all the male pumas involved in infanticide were not sires of the cubs. Adult male territories averaged 3 times larger than adult female home ranges. Male and female home ranges overlapped other puma home ranges of the same sexes but had core use areas with less overlap. Male territories overlapped on average 3–6 adult female home ranges each year. The most reproductively successful adult males in this polygynous mating system were those that lived the longest and had the most adult females in their territories. Adult females did not exhibit territorial behavior, meaning they did not aggressively defend a resource, such as space or mates. Adult females sometimes formed matrilineal groups (i.e., groups of maternally related females with extensively overlapping home ranges) in which individuals did not exhibit reproductive suppression. Instead, they exhibited higher reproductive success than non-matrilineal females. Adult females generally avoided contact with other pumas, presumably to lessen competition for food and threats to their young. The adult female reproductive biology appeared to be timed so that

females could maximize lifetime reproduction. The most stable social unit consisted of an adult female with her dependent young, lasting 14 months on average. Adult females that lived the longest had the highest reproductive success.

Logan and Sweaner (2001, 2010) hypothesized that the puma population was ultimately limited by food (i.e., prey). In addition, they hypothesized that natural population regulation would be due to competition (i.e., the density-dependent factor) for resources that would most likely limit individual reproductive success. Thus, adult male population growth would be regulated by competition for mates and adult female population growth would be regulated by competition for food. Various types of competition, including competitive killing, interference competition, and exploitation competition (Logan and Sweaner 2001, Ruth and Murphy 2010) could operate as male pumas competed for mates. For females, those 3 types of competition for food could operate between pumas and between pumas and other sympatric carnivores and humans (Murphy et al. 1998, Kunkel et al. 1999, Kortello et al. 2007, Ruth and Murphy 2010).

Research has revealed some of the consequences of competition between pumas and other predators. In Alberta (Kortello et al. 2007) and Montana, USA (Atwood et al. 2007) pumas switched from elk to mule deer and other prey following declines in primary prey abundance and changes in prey distribution associated with predation by competing wolves. Similarly, pumas switched from elk to mule deer to mitigate competition with recolonizing wolves in the SYE where elk and mule deer availability were declining (Elbroch et al. 2015b). In some cases, wolves usurp prey carcasses from pumas and kill pumas (Kunkel et al. 1999, Kortello et al. 2007, Ruth et al. 2011, Elbroch et al. 2015b). Also, when in competition with wolves, pumas may shift their habitat use (Kortello et al. 2007, Ruth and Buotte 2007) or die of starvation (Kunkel et al. 1999, Elbroch et al. 2015b). Grizzly and black bears usurp ungulate carcasses from pumas (Murphy et al. 1998), and pumas may compensate for losses of food to black bears by increasing kill rates of ungulates (Elbroch et al. 2015a).

Another test of the food limitation hypothesis was conducted by Laundré et al. (2007), who used a 15-year data set on a hunted puma population in southern Idaho and northwestern Utah. The authors reported that puma abundance increased exponentially with an increase in mule deer abundance, and there was a 4-year time lag before puma abundance declined after a deer population decline. Furthermore, adult female and cub survival was higher before a decline in deer abundance compared to after deer decline and female body mass declined after the puma population declined. Laundré et al. (2007) concluded that their results supported the hypothesis that the abundance of mule deer limited the puma population.

Studies in the Pacific Northwest also supported the food limitation hypothesis. Robinson et al. (2002) studied effects of puma predation on mule deer and white-tailed deer (*O. virginianus*) in south-central British Columbia, Canada,

and reported that puma predation was the proximate cause for decline in a seasonally migratory mule deer population. In that circumstance, more abundant white-tailed deer were the primary puma prey and less abundant mule deer were secondary prey. Mule deer exhibited significantly lower survival rates and higher predation rates than did white-tailed deer. Robinson et al. (2002:566) surmised “that the number of [pumas] in the system is set by the number of primary prey (white-tailed deer).” Later, Maletzke et al. (2014) used GPS technology to study puma spatial organization in relation to hunting in the same 2 study areas as Cooley et al. (2009). They collared 22 adult pumas in the lightly hunted population, and 20 in the heavily hunted population. Adult male pumas in the heavily hunted population exhibited greater spatial overlap with other males compared to the lightly hunted population where high use areas were mutually exclusive. But adult females in both populations showed no differences in home range overlap with other females or males and there was no difference in overlap between males and females. Maletzke et al. (2014) presumed adult male puma territorial behavior increased access to mates and adult female puma behavior secured access to adequate prey to successfully raise young, as individual adults in both sexes strived for reproductive success.

Relationships between resources and puma density also have been revealed in a broad geographic analysis. Stoner et al. (2018) reported that mule deer and adult female puma density increased linearly with primary production over 3 major ecoregions in western North America: Great Basin, Colorado Plateau, and Mojave Desert. They concluded that the response of puma density to primary production could be explained by the related change in mule deer abundance. Because there was no saturation of puma abundance with increasing productivity, they deduced that “food availability, and not social dominance, was the ultimate factor” determining adult female puma spatial requirements and density (Stoner et al. 2018:4461).

DISCUSSION

The plausibility of these hypotheses on natural puma population limitation and regulation depends on the validity and generalizability of inferences from each study in this synthesis that produced, supported, or refuted the hypotheses. Natural processes were potentially altered by management affecting all of the puma populations either during, or in years prior to, the studies. Puma populations were affected by hunting mortality and culling to mitigate predation on wild ungulates and human-puma interactions. Also, these studies were conducted with varying durations, designs, environments, study area sizes, puma abundances, numbers of marked pumas, data types, and technologies used in the field work and analyses. Most studies were observational rather than experimental. The former could reveal biological peculiarities to a single population or place. The latter could test for general mechanisms that underlie biological processes (Mitchell et al. 2018). Some studies addressed puma population limitation and regulation

directly; others speculated on those themes incidental to observations in a study or in references to literature. A rigorous approach to testing these hypotheses and revealing effects of human interventions on natural processes involves long-term (e.g., ≥ 10 yr) experimental research designed to include non-hunted puma populations experiencing fluctuations in prey, sympatric competing carnivores, and the environment (Boyce 2018).

The plausibility of each hypothesis on natural puma population limitation and regulation can also be weighed in relation to the theoretical underlying evolutionary processes. Only Seidensticker et al. (1973) has suggested a process for the social limitation and social regulation hypotheses. He submitted the Wynne-Edwards (1962) proposition that “the social system has evolved because of its limiting effect on population size which prevents overpopulation and the resulting destruction of prey populations” (Seidensticker et al. 1973:57). Wynne-Edwards (1962, 1963, 1965) identified territorial behavior as a mechanism for population control, consistent with the social limitation and social regulation hypotheses for pumas (Hornocker 1969, 1970; Elbroch et al. 2015c). Competition for and tenure of territory would regulate population size and ensure an adequate supply of resources, particularly food, for members of a group (Wynne-Edwards 1963, 1965). Following this premise, if pumas evolved a social system to limit and regulate their own densities “as an adaptation for efficient food resource utilization” (Seidensticker et al. 1973:52), that system would likely have arisen and need to be maintained by group selection. In this way natural selection would not operate at the individual level but at the higher level of a group of pumas cooperating in a social system to favor the survival of the group by limiting their population density. Group selection is expected to “override the concurrent process of selection for individual advantage” and include sacrifices of individuals in the group by impairment of fertility and survival (Wynne-Edwards 1963:626) to altruistically help members of the group (Leigh 2010). Otherwise, individuals maximizing reproductive success would potentially procreate to the point of swamping the population genetically. Additional conditions for natural selection to operate in pumas at the group level would require immigrants to be very rare (Wiens 1966, Wilson 1983, Leigh 2010), especially of individuals expressing traits that cheat the system (e.g., reproductive competition; Leigh 2010), and a social mechanism such as territorial behavior that would limit the density of group members (Wynne-Edwards 1963). The required conditions for group-level selection in pumas are improbable, however, considering their wide-spread distribution (Young and Goldman 1946, Fecske et al. 2011), the general propensity for puma population segments to interact at the landscape scale through long-distance dispersal and immigration (Sweaner et al. 2000, Newby et al. 2013, Stoner et al. 2013), and that female pumas are not territorial (Seidensticker et al. 1973, Logan and Sweaner 2001). Lacking is any explanation of how

natural selection at the individual level can result in pumas limiting or regulating their population density so the population does not over-exploit the food supply.

Furthermore, pumas evolved with other predators that could out compete them, including wolves, jaguars, black and grizzly bears, and humans (Kunkel et al. 1999, Kortello et al. 2007, Elbroch and Kusler 2018). The social limitation and social regulation hypotheses do not explain how pumas as a group, or as individuals for that matter, intrinsically limit or regulate their population density to efficiently use food resources while in competition with those predators.

Alternatively, the food limitation and competition regulation hypotheses require the simpler process of natural selection at the individual level (Mayr 1996) applied to puma (Logan and Sweanor 2001, 2010). Thus, better adapted individuals have higher reproductive success within variable environments, compete with other pumas and sympatric predators, or disperse to other environments with the potential to procreate. There is no pretense that pumas limit their density so as not to reduce the abundance of their food supply. To the contrary, under certain circumstances pumas do so (Logan and Sweanor 2001, Robinson et al. 2002, Johnson et al. 2012, Johnson et al. 2019).

Pumas would not be the only large carnivores naturally limited by prey availability and regulated by competition. Evidence of these limiting and regulating factors have also been reported in wolves (Peterson et al. 1998, McRoberts and Mech 2014, Zimmerman et al. 2015), polar bears (*U. maritimus*; Rode et al. 2010), and African wild dogs (*Lycan pictus*; Creel and Creel 1996). Similarly, population density for a number of other large carnivore species has been reported to be positively correlated with prey density, including snow leopard (*Panther uncia*), leopard (*P. pardus*), African lion (*P. leo*), tiger (*P. tigris*), cheetah (*Acinonyx jubatus*), and spotted hyena (*Crocuta crocuta*; Fuller and Sievert 2001, Carbone et al. 2011).

Notably some features of these hypotheses on puma population limitation and regulation are not mutually exclusive. Regulation of adult male puma abundance through territoriality or land tenure (i.e., social regulation hypothesis) could also result from density-dependent competition among territorial males for access to mates (i.e., competition regulation hypothesis). Similarly, subadult pumas may emigrate to avoid competition regardless of the hypotheses (Hornocker 1969, Logan and Sweanor 2001, Laundré and Hernandez 2003). The “vegetation-topography/prey numbers-vulnerability complex” (Seidensticker et al. 1973:57) that defined the amount of terrain needed by an adult puma and the degree of home area overlap between adult females in the social limitation and social regulation hypotheses are important components in the food limitation and competition regulation hypotheses. In addition, the larger male territories that overlap multiple females (i.e., prospective mates) with smaller, non-territorial home ranges, along with a polygynous breeding system, results in lower male than female densities (food limitation and competition regulation hypotheses). Thus, territorial

males are expected to be foci for interaction networks of pumas in their territories (social limitation and social regulation hypotheses). On the whole, however, the food limitation and competition regulation hypotheses explain more of the observed phenomena related to puma behavior, puma-prey relationships, and effects of prey abundance on pumas, including in multi-prey and multi-predator systems (Table 1).

Depending on the ultimate motivations or goals, managers or stakeholders could use information from any of the studies in this synthesis to establish different positions on puma management. Thus, it is useful to discuss how these hypotheses guide expected management outcomes on major issues in western North America, namely puma hunting, puma-prey relationships, and human-puma interactions.

Social Limitation and Social Regulation Hypotheses

Hunting.—Under the social limitation and social regulation hypotheses, puma density is expected to remain stable with hunting mortality rates ranging from 11–24%, particularly in management units <1,000 km² (Robinson et al. 2008, Cooley et al. 2009). In such areas, emigration and immigration are expected to compensate for population gains and losses, especially of males (Robinson et al. 2008, Cooley et al. 2009). Thus, hunting at small spatial extents may not limit or regulate puma abundance. Hunting, however, is expected to reduce survival of adult and cub pumas, density of females, and the age structure of independent pumas (Robinson et al. 2008, Cooley et al. 2009). Hunting of adult territorial males is expected to increase immigration and abundance of young males, disrupt the puma social organization, cause spatial resorting of males, and increase infanticide and adult female mortality (Wielgus et al. 2013, Elbroch et al. 2017). Thus, restricting puma hunting and maintaining connected expanses of puma habitat are essential to puma population management and conservation.

With the expectation that puma behavior and social organization would naturally maintain population stability, the state of Washington adopted a uniform harvest-stable population management approach (Beausoleil et al. 2013), also called equilibrium hunting management (Wielgus et al. 2013). This approach proposed adult hunting mortality limits (i.e., not to be exceeded) based on the intrinsic rate of population growth of 14% (i.e., the average for 3 puma populations in Washington), and assumed a uniform density of 1.7 adult pumas/100 km² in each management unit. Actual hunting mortality composition was anticipated to be comprised of a combination of adults and subadults. This approach was expected “to balance immigration and emigration among [management] units and result in greater stability of [puma] densities and age structure” (Beausoleil et al. 2013:684). For this to work, puma harvest would need to be distributed evenly among management units in the state to prevent local overharvest of adult pumas (Beausoleil et al. 2013). Alternatively, under-harvest might permit overall abundance of pumas to increase via dispersing young

pumas settling into marginal habitats (Seidensticker et al. 1973:51).

Puma-prey relationships.—In the social limitation and social regulation hypotheses, puma density is not expected to correlate with prey density. Likewise, puma predation is not expected to limit or regulate ungulate population growth (Hornocker 1970, Seidensticker et al. 1973). Therefore, pumas and human hunters are not expected to be in competition for a surplus of ungulate prey. Reduction of pumas would not be expected to increase the amount of surplus ungulate prey unless human hunters were in competition with pumas for prey animals that would be killed by pumas. Puma predation is expected to dampen the severity of fluctuations in ungulate prey populations and influence the distribution of ungulates in their habitat (Hornocker 1970).

Human-puma interactions.—In the social limitation and social regulation hypotheses, puma density is expected to be constant under remedial hunting meant to mitigate human-puma interactions (Peebles et al. 2013). Losses of adults are expected to be compensated by immigration. Young independent male pumas are expected to increase and use human-developed areas more than adult and young female pumas because of their larger movement patterns (Maletzke et al. 2014), and this behavior is expected to increase puma interactions with people (Lambert et al. 2006, Peebles et al. 2013). Thus, hunting pumas to mitigate interactions is expected to have the opposite effect by increasing interactions (Peebles et al. 2013, Teichman et al. 2016). Conversely, maintaining an older age structure in local populations may reduce puma presence in residential areas and reduce interactions because adult pumas tend to use residential areas less than subadults (Kertson et al. 2013). Because pumas will still use human-developed habitat to some extent to exploit available resources, and interactions can be a function of individual behavior (Kertson et al. 2013), some interactions with humans are inevitable. In such cases, targeted removal of individual pumas involved in interactions, public education about living with large carnivores, and improved animal husbandry may be more effective in reducing interactions between pumas and people (Cougar Management Guidelines Working Group 2005, Apker et al. 2011, Kertson et al. 2013, Teichman et al. 2016).

Food Limitation and Competition Regulation Hypotheses

Hunting.—Under the food limitation and competition regulation hypotheses, hunting mortality ranging from 10–44% of independent pumas is expected to be additive, and reduce puma populations within a few months or years (Logan and Sweanor 2001; Anderson and Lindzey 2005; Robinson et al. 2014; Wolfe et al. 2015, 2016). When this happens, hunting mortality limits puma populations, overriding natural limitation and regulation. Hunting mortality that reduces adult puma survival is also expected to result in a younger population age structure (Anderson and Lindzey 2005, Stoner et al. 2006). High hunting mortality in adult

females is expected to have the greatest limiting effect on puma populations (Anderson et al. 1992, Logan and Sweanor 2001, Anderson and Lindzey 2005, Robinson et al. 2014). High hunting mortality in adult territorial males is expected to increase infanticide and mortality in mothers (Logan and Sweanor 2001, Ruth et al. 2011). Additionally, it is expected to reduce abundance of older males and the propensity for pumas to mate with pumas with which they previously mated. Thereby, this increases mating opportunities for available young males, each with low life-time reproductive success (because their survival also is low). Consequently, the sexual selection process is altered (Murphy 1998; Logan and Sweanor 2001, 2010; Mysterud 2011). Conversely, hunting mortality averaging 5–18% of independent pumas (Anderson and Lindzey 2005, Wolfe et al. 2016) or its elimination, could result in higher puma survival and population growth, if not already limited by food, maintain an older age structure, and allow for natural sexual selection processes (Logan and Sweanor 2001, 2010). Recruitment of male pumas into local populations will depend primarily upon immigration, and of females, a combination of *in situ* reproduction and immigration (Seidensticker et al. 1973, Anderson et al. 1992, Logan and Sweanor 2001). Consequently, restrictions on puma hunting, especially of adult females, and maintaining connected expanses of puma habitat are essential to puma management and conservation.

That human-caused mortality can limit puma populations also is supported by history. Unrestrained hunting and predator control, including government-sanctioned culling and bounties, caused the extirpation of pumas from eastern North America by the late 1800s except for a remnant population in south Florida, and dwindling numbers of pumas in western North America by the early 1900s (Ligon 1927, Young and Goldman 1946, Cahalane 1964, Nowak 1976, Anderson and Lindzey 2010). In 1964, wildlife agency authorities in each of 7 states (CA, CO, ID, NM, OR, UT, WA) reported puma abundances ranging in the hundreds of pumas, with population trends in each state static or decreasing (Cahalane 1964). Pumas were “nearly extirpated in Wyoming,” USA (Long 1965:705). Western states and provinces started restricting puma hunting with laws and regulations from 1965 to 1973 (Nowak 1976, Anderson et al. 2010, Knopff et al. 2010). By 2003, wildlife managers in those same 7 states reported puma abundances ranging from 2,000–6,000 (Becker et al. 2003a, Whittaker 2005). Wyoming managers reported pumas “are distributed throughout nearly all habitats in Wyoming although densities are not uniform” (Becker et al. 2003b:64).

Variations in puma management and the environment that influence local puma population growth can be incorporated into regional puma management plans. Managers vary the intensity of hunting to provide hunting opportunity, reduce pumas around residential areas, reduce pumas to mitigate predation on wild ungulates and livestock, and sustain puma populations (Cougar Management Guidelines Working Group 2005, Cooley et al. 2011). Likewise, puma habitat quantity and quality varies in space

and time through changes in prey availability and risks to puma survival. Such a broad landscape where puma population segments are declining, stable, or increasing and interact numerically and genetically via dispersing pumas create source-sink metapopulation conditions (Logan and Sweanor 2001, Laundré and Clark 2003, Stoner et al. 2006, Ruth et al. 2011, Robinson et al. 2014). The Cougar Management Guidelines Working Group (2005) proposed managing pumas as source and sink subpopulations to complement realities in nature. In source-sink puma management, hunting mortality is applied in a spatially variable manner as needed, allowing pumas to emigrate from protected or lightly hunted source population areas (i.e., recruitment exceeds death rates and the area is a net exporter of individuals) and immigrate into more heavily hunted areas that act as sinks (i.e., areas where death rates exceed recruitment) and other source areas (Pulliam 1988, Hanski and Simberloff 1997, Runge et al. 2006, Stoner et al. 2013). The long-term persistence of pumas would depend on the proportion of source to sink subpopulation areas (Novaro et al. 2005) and the conservation of large expanses of connected puma habitat (Sweanor et al. 2000, Andreassen et al. 2012, Gustafson et al. 2019). Wyoming Game and Fish Department (2006) is an example of an agency that adopted a source-sink puma management structure. Moreover, an adaptive source-sink management approach that directly addresses variations in human interests, and puma research, involves specifying puma population management zones for sustainable puma hunting, puma control, and puma protection (Logan and Sweanor 2001:383–388).

Puma-prey relationships.—Puma density is expected to naturally vary with prey density and competition, although a time-lag may occur (Logan and Sweanor 2001, Laundré et al. 2007, Pierce et al. 2012). Therefore, prey-producing wild landscapes are essential to puma conservation. Accordingly, management goals to achieve high wild ungulate densities could stimulate puma population growth.

Puma predation is expected to influence ungulate populations in different ways depending upon environmental conditions and interactions of pumas with different prey and predator populations (Logan and Sweanor 2001; Robinson et al. 2002; Kortello et al. 2007; Elbroch et al. 2015*a, b*; Johnson et al. 2019). Ultimately, the effect of puma predation on prey population growth will depend on the extents that predation is additive or compensatory.

Where puma predation is limiting threatened or endangered ungulate populations that are well below the habitat carrying capacity and the ungulates are healthy, puma control is expected to be effective in ungulate population recovery. Restoration of desert bighorns in parts of the southwestern United States is an example (McKinney et al. 2006, Goldstein and Rominger 2013).

Pumas in multi-prey systems can switch between prey species, and potentially cause decline of a less numerous alternate prey population (Robinson et al. 2002, Johnson et al. 2012). When the status of such an alternate prey species is a management concern and its population is not

limited by habitat or some other factor, maintaining the puma population at a lower density might reduce puma predation on the alternate species and hasten its recovery (Robinson et al. 2002). Furthermore, Robinson et al. (2002) suggested that although puma predation was the proximate cause for decline of an alternate prey population, the ultimate cause may be more abundant primary prey (thus supporting more predators) and that gradual reductions in the primary prey might be a more effective long-term solution. Reductions in the primary prey, however, might exacerbate predation on the alternate prey (Logan and Sweanor 2001, Johnson et al. 2012).

Where additive puma predation is limiting an abundant, healthy ungulate population well below the capacity of the habitat and the management goal is to provide increased ungulate hunting opportunity (e.g., Colorado Parks and Wildlife 2014), puma population control is expected to increase ungulate survival (Hurley et al. 2011, Lehman et al. 2017). Puma removal during a 5-year period was reported to produce an increase in adult female and fawn mule deer survival but not a significant population increase (Hurley et al. 2011). Substantial mule deer population growth may depend on sustaining high puma removal rates over a longer period of time. Elk populations, where puma density is high, may be limited primarily by puma predation and less so by nutrition. In that circumstance puma predation can be partially compensatory and partially additive, and reduction in puma density might not result in increased recruitment (Johnson et al. 2019).

Puma predation could be strongly compensatory when other factors such as disease outbreaks, predation by competing carnivores, or change in habitat quality or climate are more limiting to ungulate populations than puma predation (Logan and Sweanor 2001, Hurley et al. 2011, Pierce et al. 2012, Elbroch et al. 2015*b*). Under such circumstances, puma removal may be ineffective in increasing prey populations (Logan and Sweanor 2001, Bender and Rosas-Rosas 2016). In some cases, puma predation might benefit ungulate populations afflicted with disease, such as in Colorado where pumas selected for mule deer infected with chronic wasting disease (CWD; Krumm et al. 2010). Whether puma predation mitigates CWD prevalence in a deer population, however, is unknown.

Human-puma interactions.—In the food limitation and competition regulation hypotheses, increasing hunting mortality in high puma density areas where interaction frequency is linked to puma abundance, particularly targeting independent juvenile males, is expected to reduce puma interactions with people (Hiller et al. 2015). But, hunting could aggravate interactions if it results in an increasing proportion of young independent male pumas (Hiller et al. 2015, Teichman et al. 2016). Again, maintaining an older age structure in the puma population might mitigate conflicts (Kertson et al. 2013). In some puma populations, however, all demographic classes may be involved in similar numbers of interactions (Kertson et al. 2013). As previously noted, some human-puma interactions are inevitable because some pumas will still use human-developed habitat. Thus, targeted

removal of individual pumas involved in interactions, public education, and better animal husbandry may be more effective in reducing interactions, especially in human-developed areas where puma hunting is problematic (Cougar Management Guidelines Working Group 2005, Apker et al. 2011, Kertson et al. 2013, Teichman et al. 2016).

MANAGEMENT IMPLICATIONS

In view of the evidence in this synthesis, the food limitation and competition regulation hypotheses are the more parsimonious explanations for the biological and ecological phenomena associated with pumas. Thus, management issues bearing on hunting, puma-prey relationships, and human-puma interactions are likely more successfully guided under the food limitation and competition regulation hypotheses for now. Regardless of any hypothesis on natural puma population limitation and regulation, however, a principle for successful puma conservation, also supported by history, is to restrict human-caused mortality, especially hunting mortality, and maintain large connected expanses of puma habitat with thriving prey populations. Accordingly, source-sink management is a biologically valid, adaptable framework for managing puma population segments to address variations in interests of wildlife managers and stakeholders while providing for long-term puma conservation. Advancing science may further assess these hypotheses on puma population limitation and regulation, and new hypotheses may emerge, requiring re-examination of expected management outcomes.

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LITERATURE CITED

- Anderson, A. E., D. C. Bowden, and D. M. Kattner. 1992. The puma on the Uncompahgre Plateau, Colorado. Technical Publication No. 40. Colorado Division of Wildlife, Denver, USA.
- Anderson, C. R., and F. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. *Wildlife Society Bulletin* 33:179–188.
- Anderson, C. R., and F. Lindzey. 2010. Cougar management in North America: United States and Canada. Pages 41–50 in M. Hornocker and S. Negri, editors. *Cougar: ecology & conservation*. Chicago Press, Chicago, Illinois, USA.
- Andreasen, A. M., K. M. Stewart, W. S. Longland, J. P. Beckmann, and M. L. Forister. 2012. Identification of source-sink dynamics in mountain lions of the Great Basin. *Molecular Ecology* 21:5689–5701.
- Apker, J. W., D. Updike, and D. Holdermann. 2011. Strategies to manage cougar-human interactions. Pages 145–163 in J. A. Jenks, editor. *Managing cougars in North America*. Jack H. Berryman Institute, Utah State University, Logan, USA.
- Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2007. Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison Range. *Journal of Wildlife Management* 71:1098–1106.
- Beausoleil, R. A., G. M. Koehler, B. T. Maletzke, B. N. Kertson, and R. B. Wielgus. 2013. Research to regulation: cougar social behavior as a guide for management. *Wildlife Society Bulletin* 37:680–688.
- Becker, S. A., D. D. Bjornlie, F. G. Lindzey, and D. S. Moody, editors. 2003a. *Proceedings of the Seventh Mountain Lion Workshop*. Wyoming Game and Fish Department, Lander, USA.
- Becker, S. A., D. D. Bjornlie, and D. S. Moody. 2003b. Wyoming mountain lion status report. Pages 64–70 in S. A. Becker, D. D. Bjornlie, F. G. Lindzey, and D. S. Moody, editors. *Proceedings of the Seventh Mountain Lion Workshop*. Wyoming Game and Fish Department, Lander, USA.
- Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management* 59:228–237.
- Bender, L. C., and O. C. Rosas-Rosas. 2016. Compensatory puma predation on adult female mule deer in New Mexico. *Journal of Mammalogy* 97:1399–1405.
- Boone and Crockett Club. 2016. Boone and Crockett Club position statement: predator management. Boone and Crockett Club, Missoula, Montana, USA.
- Boyce, M. S. 2018. Wolves for Yellowstone: dynamics in time and space. *Journal of Mammalogy* 99:1021–1031.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346–352.
- Cahalane, V. H. 1964. A preliminary study of distribution and numbers of cougar, grizzly and wolf in North America. New York Zoological Society, Bronx, New York, USA.
- Carbone, C., N. Pettorelli, and P. A. Stephens. 2011. The bigger they are, the harder they fall: body size and prey abundance influence predator-prey ratios. *Biology Letters* 7:312–315.
- Colorado Parks and Wildlife. 2014. Colorado West Slope Mule Deer Strategy. Colorado Parks and Wildlife, Denver, USA. <https://cpw.state.co.us/Documents/MuleDeer/MuleDeerStrategy.pdf>. Accessed 4 Oct 2018.
- Cooley, H. S., K. D. Bunnell, D. C. Stoner, and M. L. Wolfe. 2011. Population management: cougar hunting. Pages 111–133 in J. A. Jenks, editor. *Managing cougars in North America*. Jack H. Berryman Institute, Utah State University, Logan, USA.
- Cooley, H. S., R. B. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. *Ecology* 90:2913–2921.
- Cougar Management Guidelines Working Group. 2005. *Cougar management guidelines, first edition*. WildFutures, Bainbridge Island, Washington, USA.
- Creel, S., and N. M. Creel. 1996. Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology* 10:526–538.
- Elbroch, L. M., and A. Kusler. 2018. Are pumas subordinate carnivores, and does it matter? *PeerJ* 6:e4293.
- Elbroch, L. M., P. E. Lendrum, M. L. Allen, and H. U. Wittmer. 2015a. Nowhere to hide: pumas, black bears, and competition refuges. *Behavioral Ecology* 26:247–254.
- Elbroch, L. M., P. E. Lendrum, J. Newby, H. Quigley, and D. Craighead. 2013. Seasonal foraging ecology of non-migratory cougars in a system with migrating prey. *PLoS One* 8(12):e83375.
- Elbroch, L. M., P. E. Lendrum, J. Newby, H. Quigley, and D. J. Thompson. 2015b. Recolonizing wolves influence the realized niche of resident cougars. *Zoological Studies* 54:41.
- Elbroch, L. M., P. E. Lendrum, H. Quigley, and A. Caragiulo. 2015c. Spatial overlap in a solitary carnivore: support for the land tenure, kinship or resource dispersion hypotheses? *Journal of Animal Ecology* 85: 487–496.
- Elbroch, L. M., M. Levy, M. Lubell, H. Quigley, and A. Caragiulo. 2017. Adaptive social strategies in a solitary carnivore. *Science Advances* 3: e1701218.
- Elbroch, L. M., L. Marescot, H. Quigley, D. Craighead, and H. U. Wittmer. 2018. Multiple anthropogenic interventions drive puma survival following wolf recovery in the Greater Yellowstone Ecosystem. *Ecology and Evolution* 8:7236–7245.
- Elbroch, L. M., and H. Quigley. 2017. Social interactions in a solitary carnivore. *Current Zoology* 63:357–362.
- Elbroch, L. M., H. B. Quigley, and A. Caragiulo. 2015d. Spatial associations in a solitary predator: using genetic tools and GPS technology to assess cougar social organization in the Southern Yellowstone Ecosystem. *Acta Ethologica* 18:127–136.

- Fecske, D. M., D. J. Thompson, and J. A. Jenks. 2011. Cougar ecology and natural history. Pages 15–40 in J. A. Jenks, editor. *Managing cougars in North America*. Jack H. Berryman Institute, Utah State University, Logan, USA.
- Fryxell, J. M., and A. R. E. Sinclair. 2000. A dynamic view of population regulation. Pages 156–174 in S. Demarais and P. R. Krausman, editors. *Ecology and management of large mammals in North America*. Prentice-Hall, Inc, Saddle River, New Jersey, USA.
- Fryxell, J. M., A. R. E. Sinclair, and G. Caughley. 2014. *Wildlife ecology, conservation, and management*. third edition. John Wiley and Sons, Ltd., Chichester, United Kingdom.
- Fuller, T. K., and P. R. Sievert. 2001. Carnivore demography and consequences of changes in prey availability. Pages 163–178 in J. L. Gittleman, S. M. Funk, D. MacDonald and R. K. Wayne, editors. *Carnivore conservation*. Cambridge University Press, Cambridge, United Kingdom.
- Goldstein, E. J., and E. M. Rominger. 2013. Status of desert bighorn sheep in New Mexico, 2011–2012. *Desert Bighorn Council Transactions* 52:32–34.
- Gustafson, K. D., R. B. Gagne, T. W. Vickers, S. P. Riley, C. C. Wilmers, V. C. Bleich, B. M. Pierce, M. Kenyon, T. L. Drazenovich, J. A. Sikich, W. M. Boyce, and H. B. Ernest. 2019. Genetic source–sink dynamics among naturally structured and anthropogenically fragmented puma populations. *Conservation Genetics* 20:215–227.
- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 in I. A. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Harveson, L. A. 1997. *Ecology of a mountain lion population in southern Texas*. Dissertation, Texas A&M University, Kingsville, USA.
- Harveson, P. M., L. A. Harveson, L. Hernandez-Santin, M. E. Tewes, N. J. Silvy, and M. T. Pittman. 2012. Characteristics of two mountain lion *Puma concolor* populations in Texas, USA. *Wildlife Biology* 18:58–66.
- Hemker, T. P., F. G. Lindzey, and B. B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. *Journal of Wildlife Management* 48:1275–1284.
- Hervieux, D., M. Hebblewhite, D. Stepnisky, M. Bacon, and S. Boutin. 2014. Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta. *Canadian Journal of Zoology* 92:1029–1037.
- Hiller, T. L., J. E. McFadden-Hiller, S. R. Jenkins, J. L. Belant, and A. J. Tyre. 2015. Demography, prey abundance, and management affect number of cougar mortalities associated with livestock conflicts. *Journal of Wildlife Management* 79:978–988.
- Hornocker, M. G. 1969. Winter territoriality in mountain lions. *Journal of Wildlife Management* 33:457–464.
- Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monographs* 21:1–60.
- Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, J. R. Skalski, and C. L. Maycock. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildlife Monographs* 178:1–33.
- Jenks, J. A., editor. 2011. *Managing cougars in North America*. Jack H. Berryman Institute, Utah State University, Logan, USA.
- Johnson, B. K., D. H. Jackson, R. C. Cook, D. A. Clark, P. K. Coe, J. G. Cook, S. N. Rearden, S. L. Findholt, and J. H. Noyes. 2019. Roles of maternal condition and predation in survival of juvenile elk in Oregon. *Wildlife Monographs* 201:3–60.
- Johnson, H. E., M. Hebblewhite, T. R. Stephenson, D. W. German, B. M. Pierce, and V. C. Bleich. 2012. Evaluating apparent competition in limiting the recovery of an endangered ungulate. *Oecologia* 171:295–307.
- Kamler, J. F., R. M. Lee, J. C. deVos, Jr., W. B. Ballard, and H. A. Whitlaw. 2002. Survival and cougar predation of translocated bighorn sheep in Arizona. *Journal of Wildlife Management* 66:1267–1272.
- Kertson, B. N., R. D. Spencer, and C. E. Grue. 2013. Demographic influences on cougar residential use and interactions with people in western Washington. *Journal of Mammalogy* 94:269–281.
- Knopff, K. H., M. G. Jalkotzy, and M. S. Boyce. 2010. Cougar management in North America: Canada. Pages 50–54 in M. Hornocker and S. Negri, editors. *Cougar: ecology & conservation*. Chicago Press, Chicago, Illinois, USA.
- Kortello, A. D., T. E. Hurd, and D. L. Murray. 2007. Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. *Ecoscience* 14:214–222.
- Krumm, C. E., M. M. Conner, N. T. Hobbs, D. O. Hunter, and M. W. Miller. 2010. Mountain lions prey selectively on prion-infected mule deer. *Biology Letters* 6:209–211.
- Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. *Journal of Wildlife Management* 63:901–910.
- Lambert, C. M. S., R. B. Wielgus, H. S. Robinson, D. D. Katnik, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. *Journal of Wildlife Management* 70:264–254.
- Laundré, J. W., and T. W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. *Animal Conservation* 6:159–170.
- Laundré, J. W., and L. Hernandez. 2003. Factors affecting dispersal in young male pumas. Pages 151–160 in S. A. Becker, D. D. Bjornlie and F. G. Lindzey, editors. *Proceedings of the Seventh Mountain Lion Workshop*. Wyoming Game and Fish Department, Lander, USA.
- Laundré, J. W., L. Hernandez, and S. G. Clark. 2007. Numerical and demographic responses of pumas to changes in prey abundance: testing current predictions. *Journal of Wildlife Management* 71:345–355.
- Lehman, C. P., C. T. Rota, J. D. Raithel, and J. J. Millsbaugh. 2017. Pumas affect elk dynamics in absence of other large carnivores. *Journal of Wildlife Management* 82:344–353.
- Leigh, E. G., Jr. 2010. The group selection controversy. *Journal of Evolutionary Biology* 23:6–19.
- Lendrum, P. E., L. M. Elbroch, H. Quigley, D. J. Thompson, M. Jimenez, and D. Craighead. 2014. Home range characteristics of a subordinate predator: selection for refugia or hunt opportunity? *Journal of Zoology* 294:59–67.
- Leopold, A. 1933. *Game management*. C. Scribner's Sons, New York, New York, USA.
- Ligon, J. S. 1927. *Wild life of New Mexico: Its conservation and management*. State Game Commission, Department of Game and Fish, Santa Fe, New Mexico, USA.
- Lindzey, F. G., W. D. Van Sickle, B. B. Ackerman, D. Barnhurst, T. P. Hemker, and S. P. Laing. 1994. Cougar population dynamics in southern Utah. *Journal of Wildlife Management* 58:619–624.
- Lindzey, F. G., W. D. Van Sickle, S. P. Laing, and C. S. Mecham. 1992. Cougar response to manipulation in southern Utah. *Wildlife Society Bulletin* 20:224–227.
- Logan, K. A., and L. L. Sweanor. 2001. *Desert puma: evolutionary ecology and conservation of an enduring carnivore*. Island Press, Washington, D.C., USA.
- Logan, K. A., and L. L. Sweanor. 2010. Behavior and social organization of a solitary carnivore. Pages 105–117 in M. Hornocker and S. Negri, editors. *Cougar: ecology & conservation*. Chicago Press, Chicago, Illinois, USA.
- Long, C. A. 1965. *The mammals of Wyoming*. University of Kansas, Lawrence, USA.
- Maletzke, B. T., R. Wielgus, G. M. Koehler, M. Swanson, H. Cooley, and J. R. Alldredge. 2014. Effects of hunting on cougar spatial organization. *Ecology and Evolution* 4:2178–2185.
- Mattson, D., K. Logan, and L. Sweanor. 2011. Factors governing risk of cougar attacks on humans. *Human-Wildlife Interactions* 5:135–158.
- Mayr, E. 1996. *The modern evolutionary theory*. *Journal of Mammalogy* 77:1–7.
- McKinney, T., T. W. Smith, and J. C. deVos, Jr. 2006. Evaluation of factors potentially influencing a desert bighorn sheep population. *Wildlife Monographs* 164:1–36.
- McRoberts, R. E., and L. D. Mech. 2014. Wolf population regulation revisited—again. *Journal of Wildlife Management* 78:963–967.
- Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *Journal of Animal Ecology* 60:377–393.
- Mitchell, M. S., S. N. Sells, K. J. Barker, S. B. Bassing, A. C. Keever, S. C. Forshee, and J. W. Goerz. 2018. Testing *a priori* hypotheses improves the reliability of wildlife research. *Journal of Wildlife Management* 82:1568–1571.

- Murphy, K. M. 1998. The ecology of the cougar (*Puma concolor*) in the Northern Yellowstone Ecosystem: interactions with prey, bears, and humans. Dissertation, University of Idaho, Moscow, USA.
- Murphy, K. M., G. S. Felzein, M. G. Hornocker, and T. K. Ruth. 1998. Encounter competition between bears and cougars: some ecological implications. *Ursus* 10:55–60.
- Mysterud, A. 2011. Selective harvesting of large mammals: how often does it result in directional selection? *Journal of Applied Ecology* 48:827–834.
- Newby, J. R., L. S. Mills, T. K. Ruth, D. H. Pletscher, M. S. Mitchell, H. B. Quigley, K. M. Murphy, and R. DeSimone. 2013. Human-caused mortality influences spatial population dynamics: pumas in landscapes with varying mortality risks. *Biological Conservation* 159:230–239.
- Novaro, A. J., M. C. Funes, and R. S. Walker. 2005. An empirical test of source-sink dynamics induced by hunting. *Journal of Applied Ecology* 42:910–920.
- Nowak, R. M. 1976. The cougar in the United States and Canada. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C. and New York Zoological Society, New York, USA.
- Onorato, C. P., R. D. Belden, M. W. Cunningham, E. D. Land, R. T. McBride, and M. E. Roelke. 2010. Long-term research on the Florida panther (*Puma concolor coryi*): historical findings and future obstacles to population persistence. Pages 453–469 in D. W. MacDonald and A. J. Loveridge, editors. *Biology and conservation of wild felids*. Oxford University Press, Oxford, United Kingdom.
- Patten, L. 2018. Ghost walker: tracking a mountain lion's soul through science and story. Far Cry Publishing, thehumanfootprint.wordpress.com.
- Peebles, K. A., R. B. Wielgus, B. T. Maletzke, and M. W. Swanson. 2013. Effects of remedial hunting on cougar complaints and livestock deprecations. *PLoS One* 8(11):e79713.
- Peterson, R. O., N. J. Thomas, J. M. Thurber, J. A. Vucetich, and T. W. White. 1998. Population limitation and the wolves of Isle Royale. *Journal of Mammalogy* 79:828–841.
- Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: Does a land-tenure system regulate population size? *Ecology* 81:1533–1543.
- Pierce, B. M., V. C. Bleich, K. L. Monteith, and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. *Journal of Mammalogy* 93:977–988.
- Pierce, B. M., V. C. Bleich, J. D. Wehausen, and R. T. Bowyer. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. *Journal of Mammalogy* 80:986–992.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Robinson, H. S., R. Desimone, C. Hartway, J. A. Gude, M. J. Thompson, M. S. Mitchell, and M. Hebblewhite. 2014. A test of the compensatory mortality hypothesis in mountain lions: a management experiment in west-central Montana. *Journal of Wildlife Management* 78:791–807.
- Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: Cougar demography and immigration in a hunted population. *Ecological Applications* 18:1028–1037.
- Robinson, H. S., R. B. Wielgus, and J. C. Gwilliam. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. *Canadian Journal of Zoology* 80:556–568.
- Rode, K. D., S. C. Amstrup, and E. V. Regehr. 2010. Reduced body size and cub recruitment in polar bears associated with sea ice decline. *Ecological Applications* 20:768–782.
- Ross, P. I., and M. G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. *Journal of Wildlife Management* 56:417–426.
- Runge, J. P., M. C. Runge, and J. D. Nichols. 2006. The role of local populations within a landscape context: defining and classifying sources and sinks. *American Naturalist* 167:925–938.
- Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *American Midland Naturalist* 146:1–26.
- Ruth, T. K., and P. C. Buotte. 2007. Cougar ecology and cougar-carnivore interactions in Yellowstone National Park. Final Technical Report. Hornocker Wildlife Institute/Wildlife Conservation Society, Bozeman, Montana, USA.
- Ruth, T. K., M. A. Haroldson, K. M. Murphy, P. C. Buotte, M. G. Hornocker, and H. B. Quigley. 2011. Cougar survival and source-sink structure on Greater Yellowstone's Northern Range. *Journal of Wildlife Management* 75:1381–1398.
- Ruth, T. K., and K. Murphy. 2010. Competition with other carnivores for prey. Pages 163–172 in M. Hornocker and S. Negri, editors. *Cougar: ecology & conservation*. Chicago Press, Chicago, Illinois, USA.
- Seidensticker, J. C., M. G. Hornocker, W. V. Wiles, and J. P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monographs* 35:1–60.
- Stoner, D. C., J. O. Sexton, D. M. Choate, J. Nagol, H. H. Bernales, S. A. Sims, K. E. Ironside, K. M. Longshore, and T. C. Edwards, Jr. 2018. Climatically driven changes in primary production propagate through trophic levels. *Global Change Biology* 24:4453–4463.
- Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation levels in Utah: implications for demographic structure, population recovery, and metapopulation dynamics. *Journal of Wildlife Management* 70:1588–1600.
- Stoner, D. C., M. L. Wolfe, C. Mecham, M. Mecham, S. Durham, and D. M. Choate. 2013. Dispersal behavior of a polygynous carnivore: do cougars *Puma concolor* follow source-sink predictions? *Wildlife Biology* 19:289–301.
- Sweaner, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology* 14:798–808.
- Teichman, K., B. Cristescu, and C. T. Darimont. 2016. Hunting as a management tool? Cougar-human conflict is positively related to trophy hunting. *BMC Ecology* 16:44.
- Texas Parks, and Wildlife. 2019. Texas hunting and fishing regulations. <https://tpwd.texas.gov/regulations/outdoor-annual/hunting/nongame-and-other-species>. Accessed 22 Apr 2019.
- The Humane Society of the United States. 2017. State of the mountain lion: a call to end trophy hunting of America's lion. The Humane Society of the United States, Washington, D.C., USA.
- United States Fish, and Wildlife Service. 2008. Florida panther recovery plan, third revision. U.S. Fish and Wildlife Service, Southeast Region, Atlanta, Georgia, USA.
- VerCauteren, K. C., C. W. Anderson, T. R. Van Deelen, D. Drake, W. D. Walter, S. M. Vantassel, and S. E. Hygnstrom. 2011. Regulated commercial harvest to manage overabundance white-tailed deer: an idea to consider? *Wildlife Society Bulletin* 35:185–194.
- Wallach, A. D., I. Izhaki, J. D. Toms, W. J. Ripple, and U. Shanas. 2015. What is an apex predator? *Oikos* 124:1453–1461.
- Whittaker, D. G. 2005. Oregon mountain lion status report. Pages 11–16 in R. A. Beausoleil and D. A. Martorello, editors. *Proceedings of the Eighth Mountain Lion Workshop*. Washington Department of Fish and Wildlife, Olympia, USA.
- Wielgus, R. B., D. E. Morrison, H. S. Cooley, and B. Maletzke. 2013. Effects of male trophy hunting on female carnivore population growth and persistence. *Biological Conservation* 167:69–75.
- Wiens, J. A. 1966. On group selection and Wynne-Edwards' hypothesis. *American Scientist* 54:273–287.
- Williams, J. 2018. *Path of the puma: the remarkable resilience of the mountain lion*. Patagonia Books, Ventura, California, USA.
- Wilson, D. S. 1983. The group selection controversy: history and current status. *Annual Review of Ecology and Systematics* 14:159–187.
- Wolfe, M. L., E. M. Gese, P. Terletzky, D. C. Stoner, and L. M. Aubrey. 2016. Evaluation of harvest indices for monitoring cougar survival and abundance. *Journal of Wildlife Management* 80:27–36.
- Wolfe, M. L., D. N. Koons, D. C. Stoner, P. Terletzky, E. M. Gese, D. M. Choate, and L. M. Aubrey. 2015. Is anthropogenic cougar mortality compensated by changes in natural mortality in Utah? Insight from long-term studies. *Biological Conservation* 182:187–196.
- Wynne-Edwards, V. C. 1962. *Animal dispersion in relation to social behavior*. Hafner, New York, New York, USA.
- Wynne-Edwards, V. C. 1963. Intergroup selection in the evolution of social systems. *Nature* 200:623–626.
- Wynne-Edwards, V. C. 1965. Social organization as a population regulator. Symposium at the Zoological Society of London 14:173–178.
- Wyoming Game, and Fish Department. 2006. Mountain lion management plan. Wyoming Game and Fish Department, Cheyenne, USA.

Young, J. H., M. E. Tewes, A. M. Haines, G. Guzman, and S. J. DeMaso. 2010. Survival and mortality of cougars in the Trans-Pecos Region. *Southwestern Naturalist* 55:411–418.

Young, S. P., and E. A. Goldman. 1946. The puma: mysterious American cat. American Wildlife Institute, Washington, D.C., USA.

Zimmerman, B., H. Sand, P. Wabakken, O. Liberg, and H. P. Andreassen. 2015. Predator-dependent functional response in wolves: from food limitation to surplus killing. *Journal of Animal Ecology* 84:102–112.

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