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A Review of Cougar Biology and Management in British Columbia

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ABSTRACT

Cougars (*Puma concolor*) are the most widespread large carnivore in the Americas, and British Columbia is home to one of the largest and most intact populations of any jurisdiction. Cougars occur throughout most of the southern half of the province and are expanding their range northward. Based on an extrapolation using capable deer habitat and estimated cougar densities, the provincial population is estimated to be 5 000–7 000 animals. As a top carnivore, cougars play an important functional role in many ecosystems. As a big game species, cougars provide an important hunting opportunity for resident and non-resident hunters in British Columbia. Cougar conflicts with people are common in British Columbia and injuries to people, although far less common, have been increasing over the last century. However, this increase may be at least in part due to better recording. Human fatalities are extremely rare; the last human fatality caused by a cougar in British Columbia was in the 1990s. Cougars killed in conflicts with people have occasionally exceeded 160 animals in a year and the average is about 100. Conflict kill rates appear to be related to population size. The Conservation Officer Service receives greater than 3 000 calls per year regarding cougar conflicts when populations are high. Hunting seasons in British Columbia are liberal relative to most other jurisdictions, but kittens and females accompanied by kittens are protected. Hunting is a significant source of mortality for cougars where it has been studied in British Columbia. Hunters kill an average of about 200 animals annually, and the kill occasionally exceeds 300. Hunting is largely focussed on males and often leads to much lower male abundance and average age. Essentially no old males occur in heavily hunted populations. The more subtle effects of this male selection on population demography and the long-term abundance of females and young are not clear. In other jurisdictions, higher levels of infanticide have been documented in areas with high male harvest. Cougar populations appear to be correlated with prey abundance, and in some places, populations may be cyclic. Cougars demonstrated considerable resilience to intense persecution during the first half of the 20th century. In the interior of British Columbia, cougar numbers peaked in the late 1990s and then declined significantly, recovered in the mid-2000s, and peaked again in about 2010 before declining yet again. This cyclic pattern of abundance roughly correlates with deer hunter harvest and was also observed in other neighbouring jurisdictions that had different management strategies and harvest levels. A unique case of cougar population trend occurred on Vancouver Island where the population was thought to be very high in the latter half of the last century as a result of wolf eradication in the 1950s. When wolves recovered in the late 1970s, the cougar population declined and has remained low since then.

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1 SPECIES INFORMATION

This section provides a general overview of cougar (*Puma concolor*) biology and management. See Hatler et al. (2008) and Wainwright et al. (2010) for further details about cougars in British Columbia. There are also several recent management plans that contain reviews of cougar biology and management issues, including recommendations for future actions (Cougar Management Guidelines Working Group 2005; Alberta Environment and Sustainable Resource Development 2012; Montana Fish, Wildlife and Parks 2019). A recent book and monograph both present detailed research about cougar behaviour, population biology, and management, including thorough literature reviews (Ruth et al. 2019; Logan and Runge 2021) and Lindzey (1987) provides a good general overview of cougar biology.

1.1 Description

Adult cougars are typically tan in colour but may have grey to dark brown shades of pelage with whitish underparts (Hornocker and Negri 2009). Their chin and throat are white and outer ears and tail tips are black. Kittens are brown with black spotting until 4–6 months of age (Hornocker and Negri 2009) and then retain spotting and/or a barred pattern on the inside of their legs until up to 2 years old. Males are larger than females; females typically weigh 36–60 kg and males weigh 50–105 kg. Life expectancy in the wild is 10–13 years for females and 8–10 years for males (Hornocker and Negri 2009).

1.2 Population Size and Distribution

1.2.1 Global Cougars are the most widespread large carnivore in the Americas, ranging continuously across western North America from British Columbia and Alberta south through Mexico and Central America to most of the South American continent (Sunquist and Sunquist 2002). Cougar densities observed across western North America range from 1 to 4 cougars/100 km² (Table 1). The western United States population was estimated to be 10 000 animals in the early 1990s (Nowell and Jackson 1996).

Cougars once occurred from coast to coast but have been extirpated from most of eastern North America, and information is currently insufficient to describe the status of the eastern cougar population (Cardoza and Langlois 2002). Low densities of cougars range as far east as Manitoba, South Dakota, and Texas, with a remnant population persisting in Florida (Cardoza and Langlois 2002; Caso et al. 2008) made up of an estimated 100–180 individuals (Sunquist and Sunquist 2002). Small, disjunct populations also occur in the Saskatchewan Cypress Hills (Bacon et al. 2010), North Dakota Badlands (Johnson et al. 2019), South Dakota Black Hills (Lehman et al. 2017), and the Nevada National Forest (Warren and Warheit 2016). Transients and some residents likely range into northwestern Ontario. The "Florida panther" population is considered a subspecies, *P. concolor couguar*, having been geographically isolated from western subpopulations for some time.

1.2.2 Canada Canada supports a relatively small portion of the geographic range of cougars (Spreadbury et al. 1996). Population estimates vary substantially from 3 500–5 000 (Nowell and Jackson 1996) to 7 000–10 000 animals in the 1990s (Wilson and Reeder 2005). Cougar populations occur as far west as Vancouver Island, east to Saskatchewan's Cypress Hills (Morrison et al. 2014), and in gradually decreasing density in northern regions of British Columbia and Alberta

TABLE 1 *Mean estimated home range size and density for cougars from studies that reported these metrics in a comparable manner. Data were modified from Hemker et al. (1984) and expanded to incorporate more recent studies.*

Location	Male home range (km^2)		Female home range (km^2)		Density (cougars/100 km^2)	Reference
	Size	SE[a]	Size	SE[a]		
Idaho	453		268	45	2.1–7.4	Seidensticker et al. (1973)
					0.8–1.0	Laundré and Clark (2003)
California	78		39–45		3.5–4.4	Sitton (1977)
Colorado					1.7–3.3	Currier et al. (1977)
Arizona	123–162		25–176		3.2–3.5	Shaw (1977, 1979) in Hemker et al. (1984)
California	152	29	66	9	1.5–3.3	Kutilek et al. (1980)
Nevada	616		161		1.4–1.6	Ashman (1981)
Utah	826		685	257	0.3–0.5	Hemker et al. (1984); Lindzey et al. (1994)
Wyoming	269–370		54–91		3.4–4.5	Logan et al. (1986)
Oregon	741		509		5.14	Clark et al. (2014)
Washington					2.3–5.0	Robinson et al. (2008); Cooley et al. (2009)
Southwest Saskatchewan	172		73			Morrison et al. (2014)
Western Alberta	334	37.1	140	13.7	2.7–3.3	Ross and Jalkotzy (1992)
West-central Alberta	769	406	208	85	2.7–2.9	Knopff (2010)
Southeast B.C.	130–172		55	25	3.5–3.7	Spreadbury et al. (1996)
South Columbia Mountains, B.C.					0.85–1.47	Lambert et al. (2006)
North Columbia Mountains, B.C.	1 200		398			Bird et al. (2010)
Northwest Bay, Vancouver Island	128–233		117	22	2.6–7.3	Wilson et al. (2004)
Adam and Eve Rivers, Vancouver Island			258	36	1.4–2.0	Wilson et al. (2004)

a SE: Standard error.

(Caso et al. 2008; Alberta Resource and Sustainable Development 2012). Sightings of cougars have been reported in the southern Northwest Territories since the 1980s (Gau et al. 2001) and in southeast Yukon since 2001 (Jung and Merchant 2005; Boonstra et al. 2018). Sightings of dispersing cougars have also been documented eastward, in Manitoba, northern Ontario, and Quebec (Bacon 2010).

In Alberta, cougars occur primarily on the eastern slopes and foothills of the Rocky Mountains and in the southern boreal forest (Knopff 2010; Alberta Resource and Sustainable Development 2012). Bounty payments for cougars were in place between the 1930s and mid-1960s and were thought to have contributed to population declines and a range restricted to the mountains (Knopff 2010). Cougars were given protection in 1971 by being declared a big-game species with hunting seasons; this change from uncontrolled harvest to regulated harvest resulted in local range expansion and an increase in cougar populations. Additional protection in the form of a quota was established in 1990. Provincial estimates were 685 individuals in the early 1990s (Jalkotzy et al. 1992), increasing to an estimated 2 050 individuals by 2012 (Alberta Resource and Sustainable Development 2012).

Cougars are protected in Saskatchewan under the *Species at Risk Act* with an S2 designation (imperilled, very rare) due to the small and disjunct populations reported in the province. Cypress Hills contains the easternmost breeding population of cougars in Canada (Morrison et al. 2014). Saskatchewan's cougar population is conservatively estimated to be around 300 individuals (Bacon 2010), although reports of cougar–human conflict have increased since 2016.

Cougars are listed as endangered under Ontario's *Endangered Species Act* and are thought to occur in small numbers in the northern boreal forest, although there is no current population estimate (https://www.ontario.ca/page/mountain-lion-cougar).

1.2.3 British Columbia Cougars occur across the southern half of British Columbia from Vancouver Island east to the Alberta border and north to Fort St. John, although the greatest numbers occur on the south coast and in the Thompson-Okanagan, Kootenay, and Cariboo areas (Wildlife Management Regions 1, 2, 3, 4, 5, and 8; Figure 1; Caso et al. 2008). There are sparse museum and occasional kill records from areas north of their secondary range (Hatler et al. 2008; Figure 2) all the way to the Yukon where cougars likely persist in low densities (Jung and Merchant 2005; Boonstra et al. 2018). There are insufficient records to determine how continuous the cougar population is in the northern part of British Columbia.

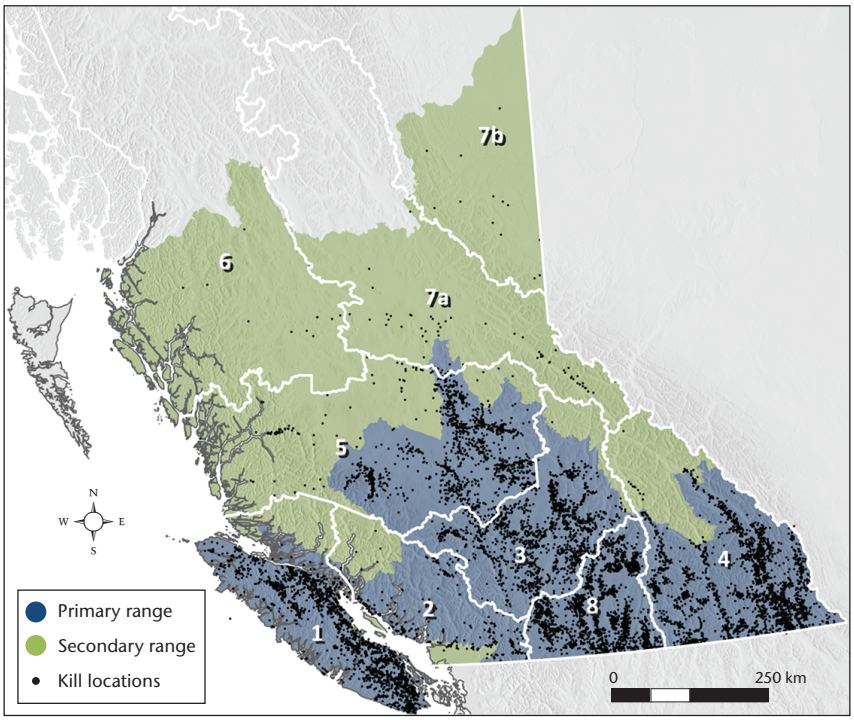

FIGURE 1 *The estimated distribution of cougars in British Columbia. Primary and secondary ranges are areas of relatively high and low densities, respectively, based on reported kill locations from compulsory inspection reports (shown as black dots) and the capability of habitats to support deer, which follows ecosection boundaries (Demarchi 1996). Also shown are the nine Wildlife Management Regions in British Columbia. There are occasional records of cougars north of the secondary range, extending into the Yukon and Northwest Territories.*

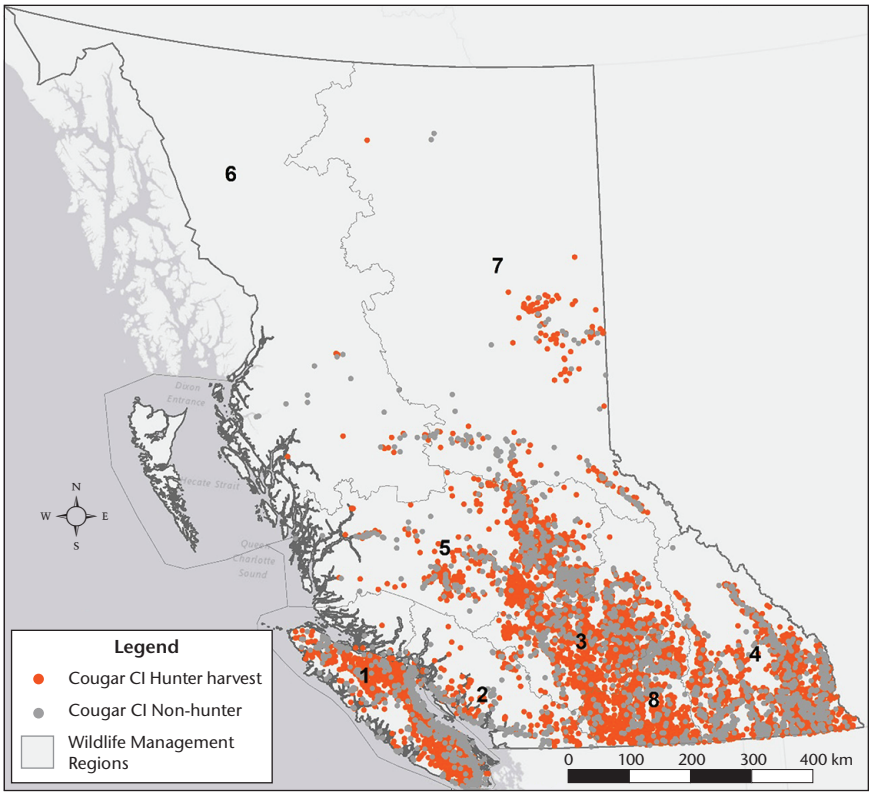

FIGURE 2 *Distribution of cougar mortalities by Wildlife Management Region (1–8) in British Columbia, collected from compulsory inspection (CI) reports from 1982 to 2018 showing hunter harvest and other mortality sources such as conflict kills. Non-hunter kills are often near human settlements.*

Population indices suggest that, like other neighbouring jurisdictions, cougar populations respond to changes in deer density, lagging peaks and troughs of deer abundance by 6–8 years (Laundré et al. 2006; Pierce et al. 2012). The challenge for cougar management is to anticipate these apparently natural shifts in deer and cougar abundance and to respond accordingly to avoid overexploiting local cougar populations. This task is challenging because cougar populations are difficult to inventory, and population indices such as hunter success often lag behind actual population changes.

In the interior of British Columbia, cougar numbers peaked in the late 1990s and then declined significantly, recovered in the mid-2000s, and peaked again in about 2010 before declining yet again (Hatter 2019). Cougar abundance has been surveyed most often in caribou (*Rangifer tarandus caribou*) recovery areas in British Columbia. Aerial or ground-based track counts have been used most often during late winter when deep snow confines cougars to low elevations. In most cases, these surveys have been done in conjunction with wolf surveys (van Oort and Bird 2010; van Oort et al. 2010). Observed densities are typically low, because the remaining caribou populations are found in deep-snow ecosystems where deer and elk prey are not particularly abundant.

Reliable density estimates for cougars in British Columbia are limited to local areas where intensive sampling has occurred, with estimates of 1–5 cougars/100 km² (Table 1). Live-trapping and radiotelemetry-based density estimates

of 3.5–3.7 cougars/100 km² were reported in the Elk and Fording Valleys of southeastern British Columbia from 1985 to 1987 (Spreadbury et al. 1996). Preliminary results from a more recent (2014–2015) DNA-based inventory in similar habitat, also in southeastern British Columbia, estimated a lower density of about 2 cougars/100 km². A study from 1998 to 2003 in the wet belt of southeastern British Columbia and northeastern Washington suggested that cougars had declined during this period, with reported minimum densities of 0.85–1.47 cougars/100 km² (Lambert et al. 2006). In the wet Columbia Mountains of southeastern British Columbia, the cougar density was estimated to be < 1 cougar/100 km² in the late 2000s (Wilson 2009). It has been suggested that cougar densities on Vancouver Island are very high, but two studies in the late 1990s and a DNA-based inventory from 2015 to 2017 did not find exceptionally high densities (Wilson et al. 2004; Table 1). In summary, cougar densities vary from 1–5 cougars/100 km² in western North America (Table 1), and densities in British Columbia fit into that range.

A provincial cougar distribution map (Figure 1) was developed based on Broad Ecosystem Inventory mapping (Resources Inventory Committee 1998) and associated habitat capability ratings for white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*), documented cougar kill locations from compulsory inspection reports, and expert review by regional Ministry of Environment and Ministry of Forests biologists. Although other ungulates are also prey for cougars, deer are their most important food source. Capability for deer habitat used the following classes: nil, very low, low, moderate, high, and very high. Cells rated low to very high for any deer species in either summer or winter were assumed to be capable of supporting cougars, and the resulting range was divided into primary and secondary. Hunting kills in the secondary range are relatively rare because those regions of the province do not have cougar hunting seasons or they have seasons that were only recently established. To provide an ecological basis for the estimated cougar distribution, linework followed the boundaries of ecosections (Demarchi 1996).

The following density estimates were applied to deer capability classes, based on interpretation of published density estimates (Table 1) and the density of cougar kills:

- Very low and nil classes were considered to have a density of zero, because there are very few cougar kill records from these areas.
- A density estimate of 3–4 cougars/100 km² was applied to the very high class, 2–3 cougars/100 km² to high, 1.5–2 cougars/100 km² to moderate, and 1–1.5 cougars/100 km² to low.
- Cougar densities in the secondary range were assumed to be half those in the primary range. While this assumption is unsubstantiated, the provincial estimate has low sensitivity to this assumption.

This method generated a province-wide population estimate of 5 150–7 000 cougars (Table 2). This estimate is very coarse and should be treated with caution because of the many assumptions inherent to this extrapolation (Smallwood 1997; Cougar Management Guidelines Working Group 2005). Wildlife managers may need to develop more recent, local population estimates for harvest management based on local research and more informed relationships between cougar and deer densities.

TABLE 2 *Regional cougar population estimates derived by extrapolating observed cougar densities in Table 1 using deer habitat capability for each Broad Ecosystem Inventory habitat unit (Resources Inventory Committee 1998).*

Wildlife Management Region	Population estimate
1 – Vancouver Island	800–1 100
2 – Lower Mainland	450–650
3 – Thompson	850–1 150
4 – Kootenay	950–1 300
5 – Cariboo	900–1 200
6 – Skeena	250–300
7a – Omineca	150–200
7b – Peace	200–300
8 – Okanagan	600–800
Total	**5 150–7 000**

1.3 Natural History

1.3.1 Habitat and biological requirements

Natural habitat

Cougars are able to persist in nearly any habitat that offers adequate prey and cover (Cougar Management Guidelines Working Group 2005). Habitat quality is affected primarily by the abundance and vulnerability of ungulate prey, which in most cases in western North America is deer (Ackerman et al. 1984; Pierce et al. 2004). Cover is provided by vegetation or rugged terrain, which facilitates the stalking of prey and contributes to their vulnerability (Seidensticker et al. 1973). Previous research has shown that cougars prefer hunting their prey along forest edges (Laundré and Hernandez 2003) and they avoid open grassland habitat (Jennings et al. 2016). Thus, even though they are considered habitat generalists, they do select among habitat features at the site level.

Disturbed habitat

Cougars generally avoid areas of human development. Cougars avoid sounds associated with humans and human activities, such as mining (Beier 1995), and minimize travel near or through human developments during the day (Wilmers et al. 2013; Jennings et al. 2016). Vehicle strikes are a significant source of cougar mortalities across their range (Dickson and Beier 2002), accounting for up to 50% of adult mortalities in unhunted populations (Beier and Barrett 1993). Increased traffic volume and visibility of roads in flatter terrain deter cougars to some extent (Banfield et al. 2020). Recent studies have shown that cougars habituate to increasing levels of human disturbance; they show less avoidance of roads where roads are more prevalent in their territory (Knopff et al. 2014). Cougars respond to some features such as recently burned areas as a function of prey density; they reduce avoidance of open areas with reduced ambush cover when prey density is greater (Jennings et al. 2016). However, the effects of natural and human disturbance on cougars at the population level are largely unknown.

Diet and prey specialization in cougars

Cougars are considered both opportunistic and specialized ambush hunters (Knopff 2010). Deer dominates cougar diet across their North American range,

often making up 60–80% of their diet (Spalding and Lesowski 1971), but they also prey on larger species such as moose (*Alces alces*) and elk (*Cervus canadensis*). The mean weight of cougar prey is 39–48 kg (Sunquist and Sunquist 2002). Mule deer and white-tailed deer are both considered important food sources, although many factors contribute to prey selection, such as seasonal and geographic variation in prey availability and habitat use (Ackerman et al. 1984; Iriarte et al. 1990).

Cougar diet varies across seasons with respect to prey age class and sex. Female ungulates are killed by cougars at a higher rate during the birthing period, and males are killed most often during and after the rut when they are less vigilant and in poorer body condition (Kortello et al. 2007; Knopff et al. 2010). Cougar kill rates have been observed to increase by 1.5 times during the summer when juveniles make up the majority of their diet (Knopff et al. 2010). Other studies have shown an increase in large prey consumption during the winter months (Hornocker 1970; Murphy 1998; Laundré 2008), and an increase in small- to medium-sized prey consumption in the summer (Seidensticker et al. 1973; Ackerman et al. 1984; Williams et al. 1995). On average, cougars kill one deer-sized prey every 6–10 days (Murphy and Ruth 2010). Cougar diets are supplemented by smaller animals such as snowshoe hares (*Lepus americanus*), beavers (*Castor canadensis*), porcupines (*Erethizon dorsatum*), grouse, raccoons (*Procyon lotor*), mustelids (Gladders 2003; Thompson 2010), and seals along the coast.

Prey specialization by cougars can have negative implications for vulnerable prey populations. Cougar predation has been attributed to declines in bighorn sheep (*Ovis canadensis*) in Alberta, Montana (Ross et al. 1997; Festa-Bianchet et al. 2006), California, Nevada (Wehausen 1996), and less directly so in British Columbia (Harrison 1990). Cougars were implicated in the decline of southern mountain caribou in the Purcell and Selkirk Mountains in British Columbia during the early 2000s (Wittmer et al. 2005; Leech et al. 2017). Cougar predation has also been tied to declines in mule deer populations in British Columbia (Lambert et al. 2006). Increasing white-tailed deer populations might indirectly contribute to increasing predation pressure on mule deer through apparent competition; Robinson et al. (2002) reported a near doubling of cougar predation on declining mule deer relative to abundant white-tailed deer in the Kootenay Region of southwestern British Columbia.

Prey-caching behaviour

Cougars exhibit caching behaviour to conceal prey from competitors and scavengers, and possibly to keep their food from spoiling. Prey is often dragged to cache it under cover, usually at the base of a tree. The kill is then buried using sheared prey hair, dirt, leaf litter, sticks, and snow (Lehaman et al. 2017). Characteristics of cougar kills include bald patches of hair, cleanly cut ribs and dissection into the thoracic cavity, incisor puncture wounds on the face and neck, and ground scraping. Latrines containing urine and feces are also common near cougar kills. Cougars will spend up to 10 days consuming a kill (Murphy 1998) and often bed within a kilometre of the kill site in between feeding bouts (Kusler et al. 2017).

Social organization

Cougars are solitary and avoid contact with one another through vocalizations and olfactory and visual cues except while mating and travelling with dependents (Logan and Sweanor 2010). Cougars disperse from their natal range as subadults at 1–1.5 years of age, with females exhibiting a degree of philopatry and males

dispersing sometimes hundreds of kilometres (Fecske et al. 2009). In the Cypress Hills of Saskatchewan, females dispersed an average of 150 km, whereas males dispersed an average of 350 km (Morrison et al. 2015). Resident cougars maintain home ranges that overlap extensively, but individuals avoid each other temporally (Fescke et al. 2009). Territory size when prey is abundant is 65–130 km² for females and 190–390 km² for males (Lindzey et al. 1988; Table 1), although males can occupy 1800 km² or more when prey are scarce, or they are searching for a permanent range (Alberta Environment and Sustainable Resource Development 2012). Mating pairs interact most often at kill sites, and cougars will occasionally scavenge the kills of other cougars and other predator species (Knopff et al. 2010).

Reproduction

Females mature at 16–21 months and males at 24–30 months, but subadults generally do not begin breeding until they establish independent home ranges (Fecske et al. 2009). Cougars have a polygynous and promiscuous mating system (Seidensticker et al. 1973). Breeding can occur at any time of year; however, the peak breeding period in North America is from March to May (Kortello et al. 2007). Cougars have a 3-month gestation period, and peak birthing occurs from June to September in the Pacific Northwest (Elbroch et al. 2015). Litter size is generally 2–4 kittens (Hornocker and Negri 2009; Quigley and Hornocker 2010) and survival rates for kittens to 12 months of age are 42–84% (Clark et al. 2015). Kittens nurse until 8–16 weeks of age (Logan and Sweanor 2001; Ruth et al. 2019) and remain at the nursery site for about the first 8 weeks of life while the female forages.

Population demography

Reported survival and recruitment rates vary widely across their distribution (Quigley and Hornocker 2010; Logan and Runge 2021). Human-related mortalities are the leading cause of mortality in most hunted populations and many unhunted populations (e.g., Spreadbury et al. 1996). In neighbouring Alberta, hunter harvest (77%) was the leading cause of mortality, followed by accidental snaring by trappers (9%), human conflict kills (5%), vehicle strikes (5%), and human self-defence kills (2%) (Anderson et al. 2010; Knopff et al. 2010). Intraspecific strife occurs regularly among cougars; adult males dominate and may kill subadult or dispersing males (Quigley and Hornocker 2010), and infanticide of kittens is common (Cooley et al. 2008; Logan and Runge 2021). Disease, poisoning, and starvation represent a small portion of total mortalities in cougars; however, these rates vary with cougar density, prey availability, competition with other predators, and exposure risk to rodenticides and other contaminants (Ruth 2004; Anderson et al. 2010).

Cougar populations are commonly structured as source–sink metapopulations (Beier 1993; Sweanor et al. 2000; Ruth et al. 2011). Source patches in which cougar mortality rates are low are separated by sinks, where mortality rates are unsustainably high. There is evidence that hunting mortality in cougars can be additive rather than compensatory (Cooley et al. 2009; Logan and Runge 2021), suggesting that where mortality exceeds reproduction, hunted populations are sustained by immigration rather than recruitment (Logan et al. 1986; Cougar Management Guidelines Working Group 2005).

The extent to which a true metapopulation structure exists in British Columbia is not known. In most other jurisdictions in western North America, cougar

habitat is made up of patches of forest in mountain ranges surrounded by large areas of agricultural land and scrub deserts generally unsuitable for cougars. In contrast, British Columbia is largely dominated by continuous forested habitat. Genetic differentiation can occur where populations are separated from each other by unsuitable habitat at scales of hundreds of kilometres (McRae et al. 2005). This spatial arrangement occurs rarely in British Columbia. Rather, demographics might conform to a "compensatory immigration sink" population structure, where cougar mortalities in relatively small sink areas are replaced through immigration from adjacent source areas, resulting in little reduction in apparent densities but instead a shift to a younger age structure (Anderson and Lindzey 2005; Robinson et al. 2008; Logan and Runge 2021). The result of this dynamic is a relatively contiguous cougar population that is resilient to high rates of exploitation in localized areas and is fundamentally limited by prey availability.

Competition with other predators

Cougars compete with other predators such as gray wolves (*Canis lupus*), coyotes (*Canis latrans*), black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*) for resources. Cougars often lose kills to other predators (Kunkel et al. 1999; Kortello et al. 2007) and alter their habitat use or prey choice to avoid conflict (Quigley and Hornocker 2010). Cougars are generally solitary hunters and can incur injuries or be killed by other large predators that outweigh or outnumber them (Donadio and Buskirk 2006; Ruth et al. 2019). In ecosystems where wolves are abundant, approximately 18–22% of cougar kills are scavenged by wolves (Bartnick et al. 2013). Cougars avoid wolves by adjusting their habitat use to higher elevations or steeper terrain and reducing their hunting of larger prey such as elk and moose (Murphy 1998; Ruth et al. 2019). Cougars may be displaced from kills by coyote packs; however, they are more likely to stand their ground against smaller solitary predators. Cougars have been reported to defensively kill coyotes, bobcats (*Lynx rufus*), and foxes (*Vulpes vulpes*) at their kill sites (Beier and Barrett 1993; Murphy 1998; Sweanor et al. 2000).

In some places, bears rely heavily on cougar-killed carrion before and after hibernation (Green et al. 1997) and can detect carrion over 1 km away, often displacing cougars within a few hours of making a kill (Allen et al. 2015). The loss of prey to other predators results in energetic losses for cougars and can promote increased predation rates to compensate (Murphy 1998). Starvation is a significant source of cougar mortality in some areas where cougars coexist with multiple predators (Ruth et al. 2011).

1.3.2 A summary of research in British Columbia Research on cougars in British Columbia has been limited to relatively small study areas and short durations and has been focussed mostly on diet and density. Spalding and Lesowski (1971) conducted an early study of food habits based on stomach contents recovered from harvested cougars in the Okanagan and Cariboo Regions and found that mule deer were their main prey item. Spreadbury et al. (1996) conducted a comprehensive study of cougar spatial ecology in an unhunted area of the Elk Valley in the East Kootenays in the mid-1980s and found that vehicle strikes were the largest cause of death. Kitten production was high, as was juvenile dispersal. On Vancouver Island, researchers documented high natural survival in the 1990s (Wilson et al. 2004) and a preference for young and old forests (Goh 2000). Movement was limited to the male cohort; mortality was mostly due to conflict with

people and secondarily due to intra-population strife (Hahn 2001). Kortello et al. (2007) examined cougar diet response to wolf recovery in Banff National Park during 1993–2004 and found that cougars switched from killing mostly elk to killing mostly deer after the presence of wolves increased. Robinson et al. (2002) examined cougar diet in the West Kootenays and found that cougar predation of mule deer doubled where white-tailed deer were abundant. A number of studies using GPS collars are underway in the Kootenay, Okanagan, and Cariboo Regions to examine survival and recruitment, diet, and habitat use in more detail.

Several more studies were conducted during the early to mid-2000s to examine the role of cougar predation on central mountain caribou:

- Kinley and Apps (2001) conducted mortality monitoring for mountain caribou in the South Purcell Mountains during 1994–2000 and found that half of 16 adult caribou mortalities were attributed to cougar predation, predominantly during the summer and fall.
- Katnik (2002) linked cougar predation of caribou to seasonal shifts in elevation of primary prey.
- Wittmer et al. (2005) conducted a meta-analysis on the decline of 15 subpopulations of threatened caribou in British Columbia and found that predation was the primary source of mortality in 11 subpopulations and concluded that cougars were the primary threat in southern herds.
- Bird et al. (2010) examined cougar diet in the Columbia Mountains of southeast British Columbia and found that caribou mortalities were caused by primary prey expanding into caribou range. They found that one adult female cougar killed mostly deer, although she also killed young moose. Males had much more diverse diets, and for the one radio-collared adult male, moose of all ages were the bulk of the diet. The radio-collared juvenile male had the most diverse diet, which included beavers, coyotes, a black bear, and ungulates.
- Apps et al. (2013) completed a review of caribou mortalities in British Columbia and Alberta over 20 years and found that cougar predation was greatest at lower elevations.
- Leech et al. (2017) documented high rates of cougar predation (up to 75%) of translocated caribou in the South Purcell Mountains.

Based on this body of research, we conclude that cougars prey on caribou where their ranges overlap and that cougars also regularly kill other large ungulates such as moose and elk in wetter areas of British Columbia.

Most recently, cougars were sampled for 3 years on northern Vancouver Island in Management Units (MU) 1-9 to 1-11 and for a single year each in MU 4-2, 4-22, and 4-3 in the East Kootenays. These were DNA-based population inventories, and most samples were collected by treeing individual cougars with hounds and then collecting a hide sample with a remote biopsy dart. Preliminary population densities were 0.66 cougars/100 km^2 on northern Vancouver Island and 1.8 cougars/100 km^2 in the southern East Kootenays. Both inventories were done during periods of relatively low cougar abundance (Hatter 2019). Observed harvest rates were about 30% in both areas, which is likely unsustainable without immigration. A third DNA-based inventory was conducted in the western Okanagan (MU 8-1, 8-2, and 8-8) during the winter of 2021–2022 but no results are available at this time. An inventory is planned for the Boundary area during winter 2023–2024 and for the Chilcotin plateau in the near future.

1.3.3 Ecological role Cougars provide a selective force on their ungulate prey, and consequently play an important role in structuring prey populations (Cougar Management Guidelines Working Group 2005). Cougars further provide carrion to a large diversity of scavenging species throughout the year (Allen et al. 2015) in many different ecosystems. They are a source of interference competition with meso-predators such as bobcats and coyotes and may limit their densities and create a cascade of effects to meso-predator prey and competitors (Terborgh and Estes 2013).

2 THREATS

Threats to cougar distribution and density in British Columbia are mostly of human origin. Hunting can be a threat if harvest levels, especially that of females, are unsustainable. While harvest levels are suspected to be too high in some local areas of the province where there are high densities of hunters, hunting is likely not a major threat provincially due to the large and contiguous distribution of cougars, their ability to disperse long distances, and the mostly low densities of hunters across their range. Non-hunter mortality is related mostly to human conflicts and hence is highest near populated areas (Figure 2). Conflict-related mortalities occur on a small portion of the land base and may threaten the persistence of populations adjacent to human settlements. Smaller numbers of cougars are killed illegally (about 3 per year) and in road and rail accidents (about 8 per year), although many of these events are likely not recorded.

The underlying threat to cougars is the distribution and abundance of prey, which is greatly influenced by human use of the landscape. Land transformation for human use often greatly reduces prey densities. Other threats are related to habitat loss or degradation, some of which, such as urban expansion, are permanent. Climate change is often considered a threat to wildlife, but warming trends have allowed both deer species and elk to expand their range north over the past 40 years, and cougar populations have expanded following these species (Figure 3). Thus, some aspects of climate change appear to benefit cougar populations in British Columbia, while other aspects, such as ecosystem transformation, are likely to have more varied impacts.

Significance of threats

The significance of the threats identified must be considered in light of a number of mitigating characteristics of cougar populations such as:

- Cougars are expanding their range. Kill and sighting data suggest that cougars are expanding their range northward, likely following northward expansions of white-tailed deer. Cougars now extend as far north as the Yukon. Northward expansion of cougars in British Columbia is likely to continue, particularly in response to reduced snow levels from climate change that will generally favour higher ungulate prey abundance.
- Cougar populations are resilient to mortality. Despite decades of historic persecution and unregulated harvest, local extirpations of cougars in British Columbia were rare. Vacant territories are filled by immigrant cougars relatively quickly, and cougars have relatively high fecundity.
- Cougars can disperse large distances. The dispersal ability of cougars makes it unlikely that populations will become fragmented or isolated in British Columbia.

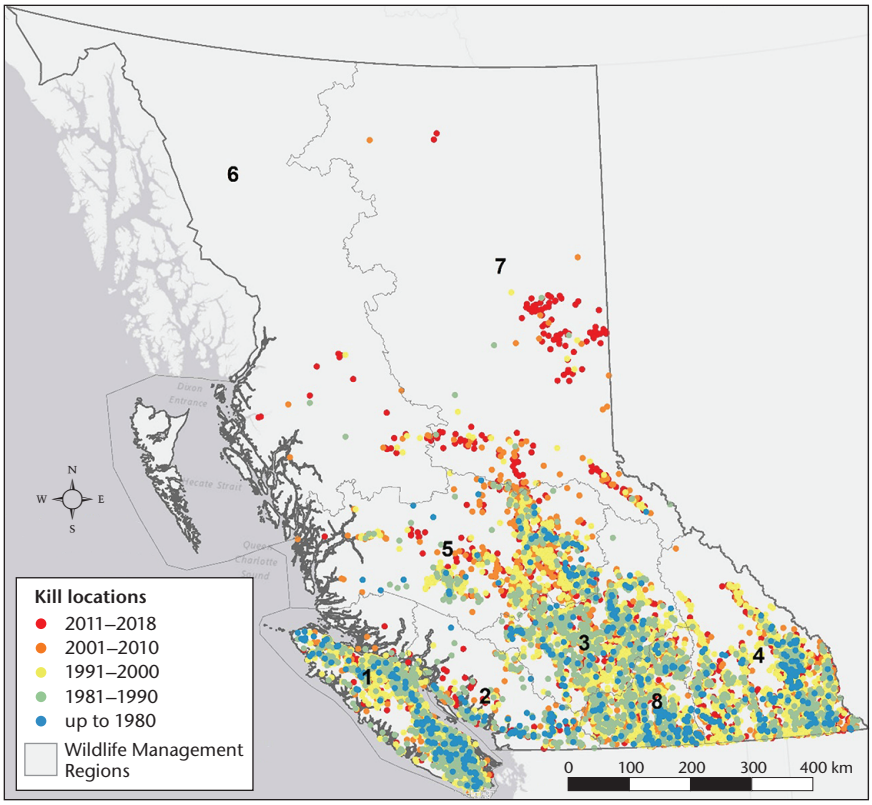

FIGURE 3 *Distribution of human-caused cougar kills from 1976 to 2018 from all sources reported in the compulsory inspection database. Wildlife Management Regions are numbered 1–8 and the kill locations are colour-coded by decade. These data suggest a range expansion or an increase in density in the northern half of the province in the last 20 years.*

3 MANAGEMENT HISTORY

3.1 Problem Wildlife Management (Bounty Period)

Cougars were considered problem wildlife through most of the first half of the 20th century in British Columbia. Bounties were in place from sometime before 1907 until 1957, and incentives varied according to the perceived population of cougars (Province of British Columbia 1980). Wildlife control kills by government officers began in 1930 and increased substantially with the formation of the Predator Control Branch in 1947.

Cougar removals, through bounties and wildlife control kills, represent the only source of population trend data in British Columbia for most of the 20th century (Figure 4). These data are likely a poor index of population trend, but if accurate, the magnitude of removals indicates that the cougar population in British Columbia was substantial throughout the bounty period and was resilient to intense reduction efforts. There is no evidence that the geographical range of cougars changed as a result of removals during the bounty period, but local abundance certainly declined in many areas.

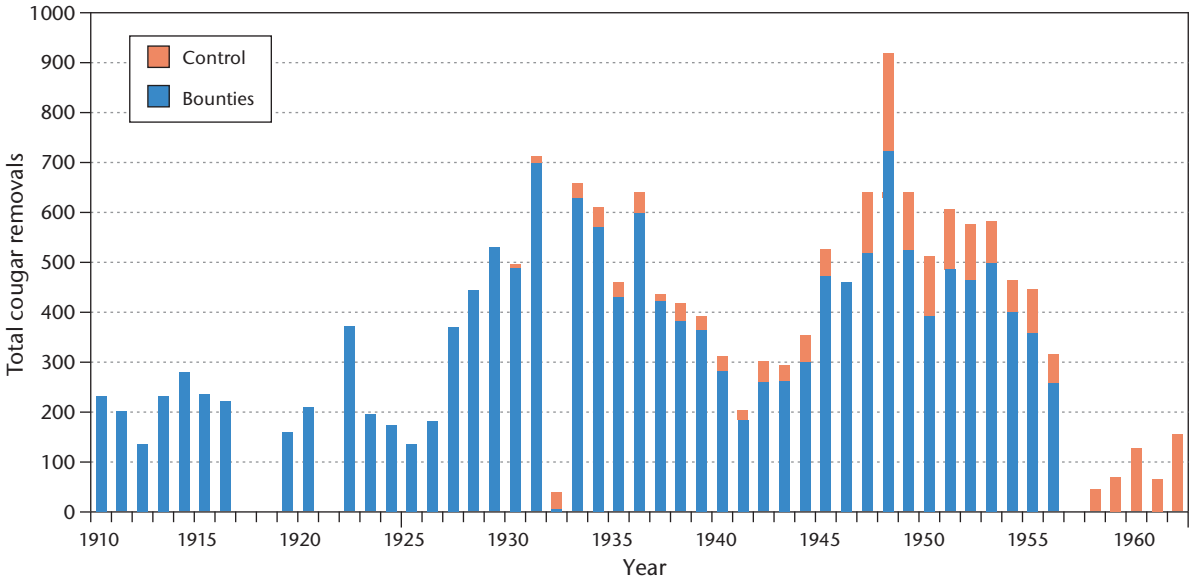

FIGURE 4 *Recorded cougar removals in British Columbia from 1910 to 1962 (Province of British Columbia 1980). Wildlife control by government officers began in 1930 and increased with the formation of the Predator Control Branch in 1947. Bounties were removed in 1957.*

3.2 Game Management

Management of cougars as a game species began in 1966. Bag limits were gradually reduced during the late 1960s and early 1970s and reached their current limits of either 1 or 2 animals, depending on the Wildlife Management Region, by 1973. Since then, there have been a series of minor, region-specific changes to hunting season dates and bag limits, including the use of female or combined-sex quotas for both resident and non-resident hunters. Because of the elusive nature of the species, most cougars are harvested by people using hounds during the winter months; however, hunting using predator calls has recently become more popular.

3.2.1 Harvest data

Like most wildlife, cougar populations are managed spatially by the nine Wildlife Management Regions in British Columbia (Figure 1). Most regulations are specific to management units, and all harvest data are collected at this scale or smaller. Hunting seasons and bag limits can vary by management unit.

All cougars killed by people in British Columbia, including human conflict kills and government control kills, are subject to compulsory inspection where information related to the cause of death, date, kill location, and the cougar's sex, age, and size are recorded. Cougars are aged by counting cementum annuli on a premolar tooth collected during the inspection. Data on hunter effort and success are collected via the British Columbia Hunter Sample Survey, which is mailed to a portion of licensed hunters each year. These data are available at www2.gov.bc.ca/gov/content/sports-culture/recreation/fishing-hunting/hunting/hunting-data. Hunter kill data can be viewed directly at https://kootenaywildlife.shinyapps.io/BCHarvestData/. The locations of cougar kills recorded from 1976 to 2018 from all sources (hunting, human conflict kills, illegal kills, and animals collected for other reasons) suggest that the species has expanded northward in the last 10–20 years (Figure 3).

Trends in cougar population abundance are calculated from a combination of age of hunter-killed cougars, hunter success, and local estimates of vital rates and densities (Hatter 2019). Estimates of population size require considerable extrapolation across time and space, thus province-wide estimates of abundance will always be coarse.

During the mid- to late 1990s, cougar harvest approached levels (approximately 400 per year) not observed since the bounty period (1930s to early 1950s; Figure 5). Between 2000 and 2005, harvest declined by nearly two-thirds, but has increased again since. The general decline in hunter success would suggest a decline in abundance; however, this trend may simply be a result of the increase in hunter numbers over the period.

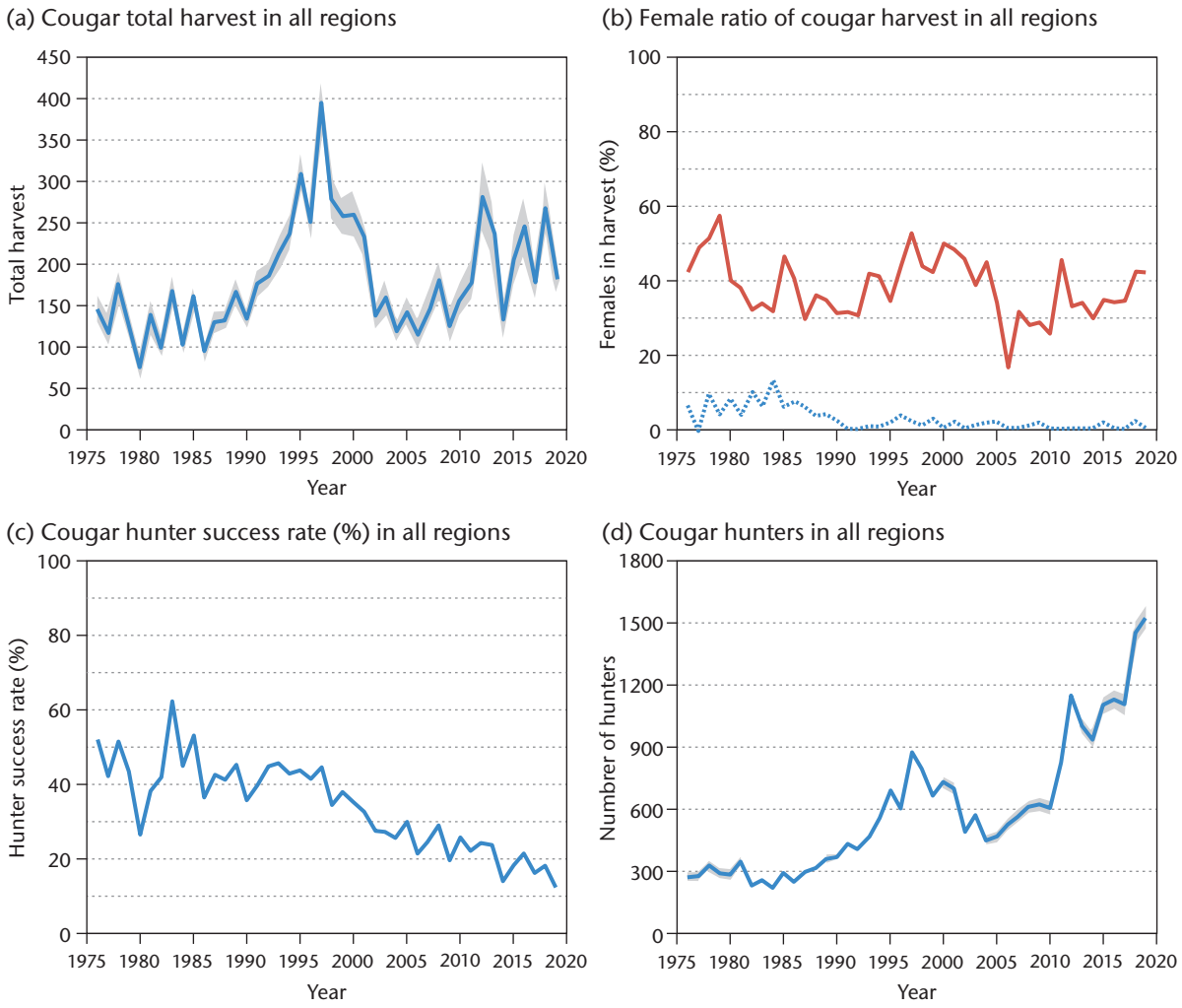

FIGURE 5 *(a) Total cougar harvest, (b) proportion of females in the harvest, (c) hunter success rate, and (d) total cougar hunters in British Columbia from 1976 to 2018. Figures a and b are derived from compulsory inspection data, while c and d are from the Hunter Sample Survey. Grey shading indicates 95% confidence intervals. The red line in b is the female proportion of harvest, and the dotted blue line is the proportion of killed animals that were not sexed. Hunter success is calculated based on the number of animals reported killed and the number of hunters that purchased a cougar tag. This figure can be reproduced at https://kootenaywildlife.shinyapps.io/BCHarvestData/.*

4.1 Hunting

Hunting cougars with hounds is permitted throughout most of the provincial distribution of cougars, and season dates, bag limits, and quotas vary by region (Figure 6). The edible portions of a harvested cougar must be removed and packed out. The Okanagan and Kootenay hunting seasons used to have pursuit-only openings, where cougars were allowed to be pursued with hounds but not harvested. The intent was to allow hunters to train their dogs and to continue pursuing cougars for recreation after their personal bag limit, or the regional bag limit was reached. The hunting practices committee of the Provincial Hunting and Trapping Advisory Team reviewed the pursuit season and determined it was contrary to the committee's values regarding the ethical and legitimate use of wildlife resources. For this reason, these seasons were closed in the Okanagan and Kootenay Regions in 2016 and 2020, respectively.

Hunting regulations are developed in the context of several policy principles, including:

- hunting regulations should maximize hunting opportunity within the constraints of conservation;
- regulations should be easy to interpret, stable, effective, and enforceable;
- ethics such as fair chase and humane treatment of animals are recognized;

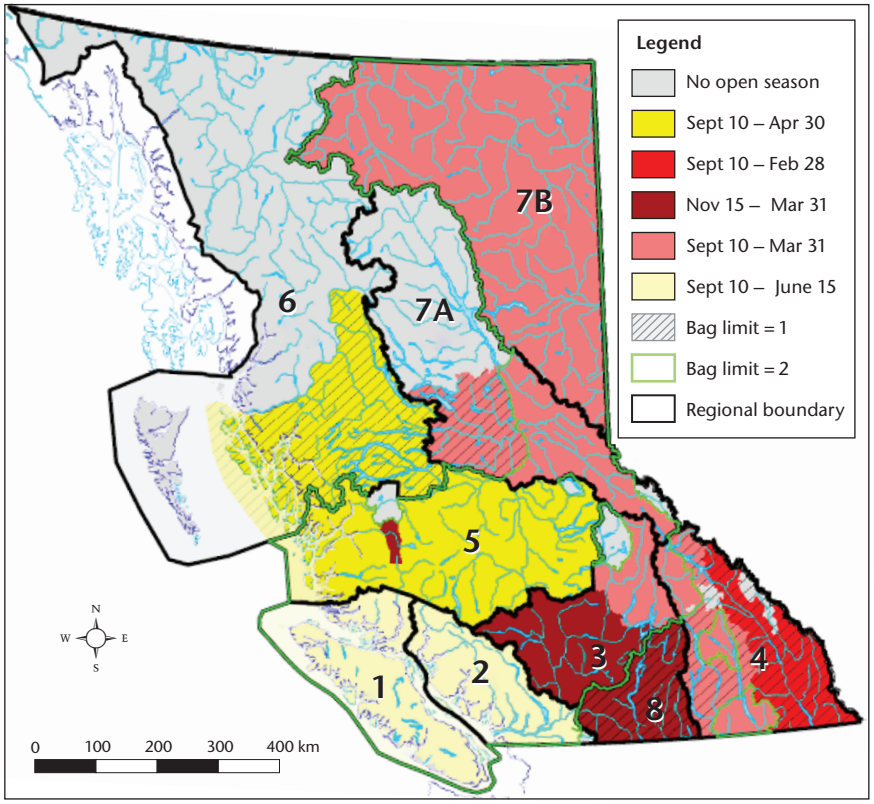

FIGURE 6 *General open-season lengths and regional bag limits for cougars in British Columbia. Some exceptions to season dates and bag limits apply (see the 2022–2024 Hunting and Trapping Regulations Synopsis for detailed harvest regimes). Wildlife Management Regions are numbered 1–8 and the provincial bag limit for cougar is 2.*

- population viability or genetic variability should not be compromised by harvest activities; and
- interests of First Nations and stakeholders are recognized and considered in management decisions.

Cougars are not managed as a furbearing species in British Columbia and it is unlawful to trap them; cougars that are caught as bycatch in normal trapping operations must be surrendered to the B.C. Wildlife Branch. The number of cougars killed in traps or snares each year has varied from two to 47 since 1986 and has averaged 16 per year.

4.1.1 Assessing sustainability of human-caused mortality Like other large mammals, cougar population growth is most sensitive to the removal of adult females (Lindzey et al. 1992). However, male-targeted removals have been shown to lower kitten survival due to infanticide caused by immigrating males (Cooley et al. 2009; Wielgus et al. 2013; Keehner et al. 2015). Many jurisdictions protect females with dependent kittens from hunter harvest, including British Columbia, where it is an offence to hunt a kitten, defined as a cougar with spots or under 1 year of age, or any cougar in its company. However, at any time of the year, up to 86% of adult females are accompanied by dependent young (Logan 1983; Ross and Jalkotzy 1992; Logan and Sweanor 2001), but kittens are not always with their mothers. Barnhurst and Lindzey (1989) found that females that were rearing kittens were observed with their kittens only 19% of the time. Thus, hunters may unintentionally orphan kittens, which reduces their chances of survival (Jalkotzy et al. 1992; Logan and Runge 2021). The orphaning of kittens can be reduced by starting the hunting season as late as possible in the fall when kittens are older and have a higher chance of survival if they are orphaned.

Some researchers have proposed that cougar populations can sustain an annual 15% mortality rate (Logan et al. 1986; Jalkotzy et al. 1992; Anderson and Lindzey 2005), thus if the natural mortality rate is 5%, as these studies suggest, the human-caused mortality rate should not exceed 10%. Other researchers have suggested that cougar harvest rates should not exceed 40% of the total population of adults greater than 4 years of age (Stoner et al. 2006) and should not exceed 25% of the adult female population (Anderson and Lindzey 2005). Adult harvest exceeding these rates can lead to a younger age demographic, lower reproductive rates, lower kitten survival, and social instability (Stoner et al. 2006; Robinson et al. 2008). More recent research suggests that even lower harvest rates are needed to ensure sustainability (Ruth et al. 2019, Logan and Runge 2021). Sustainable harvest rates are location- and time-specific and are best assessed by analyzing harvest and population data in an integrated fashion across time using tools such as a statistical population reconstruction (Clawson and Skalski 2016) or an integrated population model (Fieberg et al. 2010).

4.1.2 Harvest management tools in British Columbia Across British Columbia, cougar hunting is managed through general open seasons for resident and non-resident hunters, with tags available over the counter rather than via a draw system. Every hunter must buy a cougar tag before hunting cougar and must possess a general B.C. hunting licence. Season lengths vary but generally begin on September 10 and end in late winter (Figure 6). Most cougars are killed by hunters during December through February, with many fewer killed in November and March (Figure 7). Where the hunting season runs into late winter, more

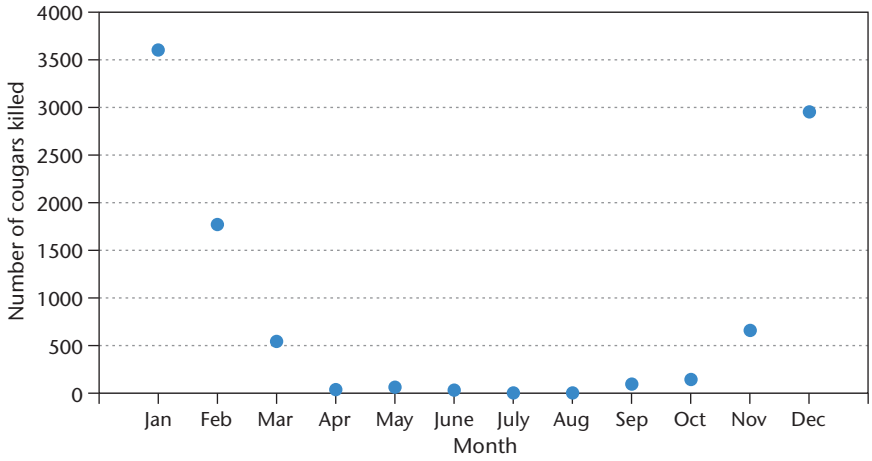

FIGURE 7 *Number of cougars killed by hunters in British Columbia, plotted by month of kill, from 1992 to 2021.*

cougars are killed by hunters in late winter in Regions 1 and 2 than in other regions. Quotas are currently used only in the Skeena Region but were previously used in many other regions. The cougar hunting season in the Skeena Region closes 72 hours after a total of 5 females are harvested in a licence year; however, that quota has never been reached. Other regions dropped this system because to initiate a closure, it required constant overview and rapid communication with hunters, which were not always achievable.

Methods available to manage cougar harvest include:

- limiting total or female harvest through regional or management unit quotas;
- limiting the length of general open seasons;
- limiting bag limits, both regionally and provincially;
- restricting the harvest of certain age classes; and
- regulating hunting methods such as the use of hounds, calls, and attractants.

4.1.3 Statistical population reconstruction modelling Statistical population reconstruction (SPR) is a modelling method that uses age-at-harvest and hunter effort data to estimate population size and trend (Clawson and Skalski 2016). SPR assumes that animals have similar natural survival and harvest vulnerability in each age and sex class (Clawson 2015), although the models can be structured to model the sexes independently. The method also assumes equal rates of immigration and emigration within the analysis area (Clawson 2015). The larger the area, the more likely this assumption is valid.

Age-at-harvest data are measured from teeth collected during the inspection of harvested animals. Age is measured by a laboratory specializing in counting cementum ages for mammals. Hunter effort data are collected from the annual Hunter Sample Survey. Auxiliary data such as local cougar density and survival estimates can be integrated and often improve the accuracy of models at regional scales, especially population estimates.

SPR models were built to estimate cougar population trends over the past 25 years across British Columbia's nine Wildlife Management Regions (Hatter 2019). Models were developed separately for males and females due to differences in their survival rates and structured by age classes. The results suggested that this tool can provide a cost-effective method of measuring population trends if more than 80% of all cougars killed by hunters are aged, but the models do not provide

reliable estimates of abundance. Reliable population trends were generated only for the two regions that had the largest aged samples: Vancouver Island (Region 1; Figure 8) and the Kootenays (Region 4: Figure 9). Trends for other interior regions were derived by combining data with the Kootenays.

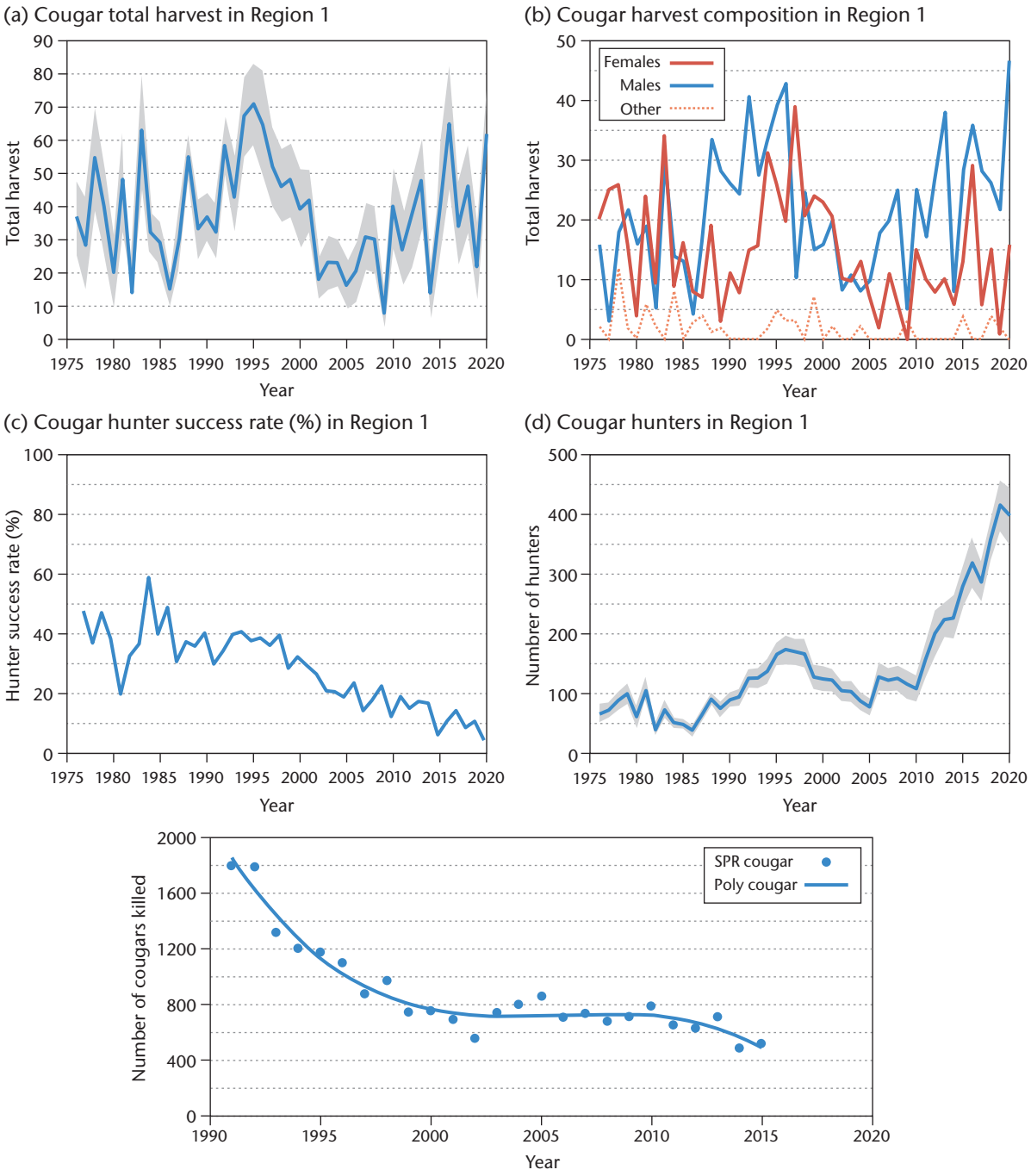

FIGURE 8 *The top panel of four graphs is the cougar hunter harvest data for Region 1 (Vancouver Island) from 1976 to 2020. The lower image is the trend estimate generated by the SPR model for cougar abundance in Region 1 from 1990 to 2015. The SPR model generates annual population estimates, and the trend line labelled "Poly cougar" was fitted to these data afterward. While the abundance estimates themselves are likely inaccurate, the trend is likely more reliable.*

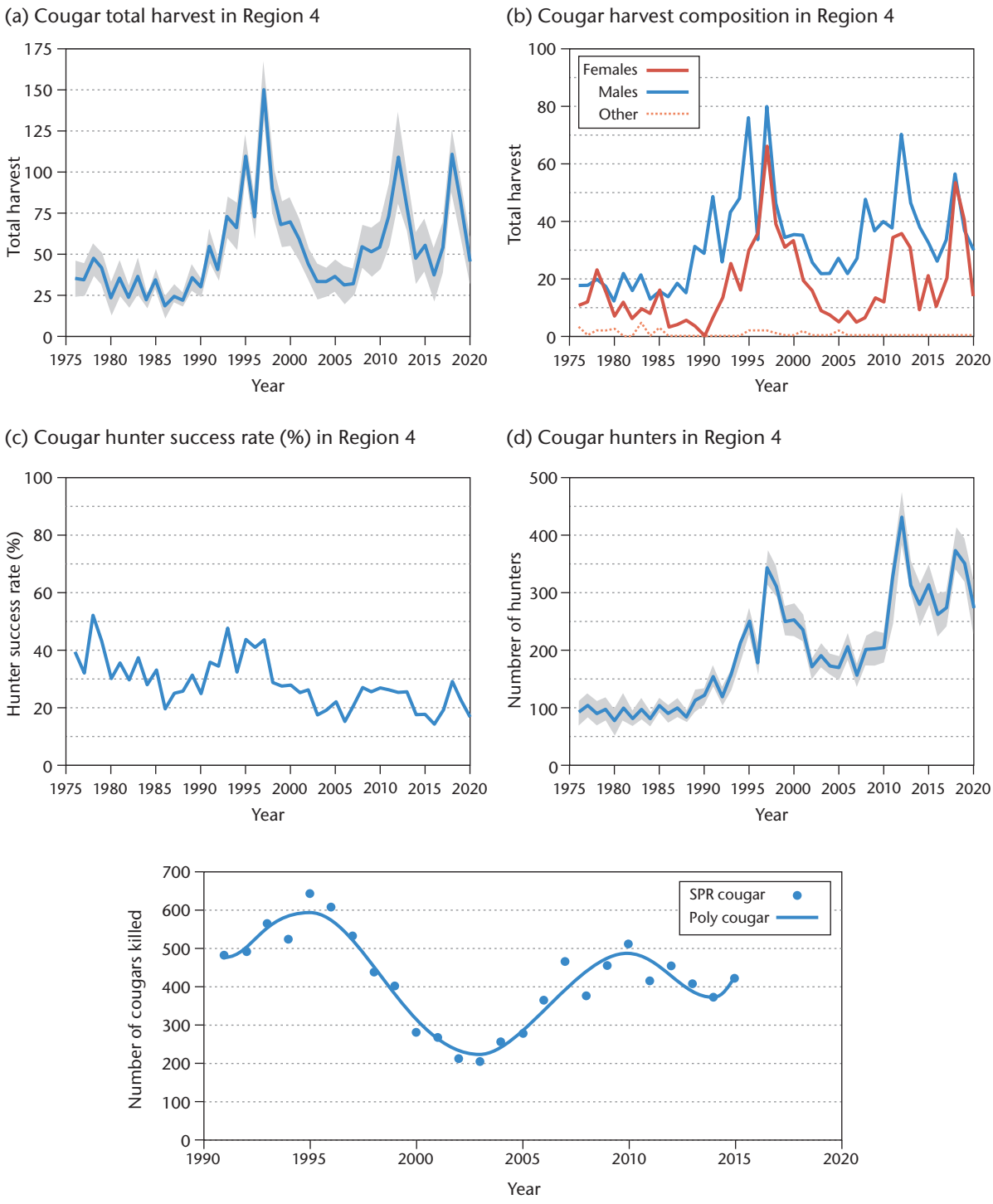

FIGURE 9 *The top panel of four graphs is the cougar hunter harvest data for Region 4 (Kootenay) from 1976 to 2020. The lower image is the trend estimate generated by the SPR model for cougar abundance in Region 4 from 1990 to 2015. The SPR model generates annual population estimates, and the trend line labelled "Poly cougar" was fitted to these data afterward. The absolute abundance estimates are likely inaccurate, while the population trend is likely more accurate.*

Results from the SPR analysis suggest that cougar trends are more closely related to the total number of cougars killed than to hunter success (see data for all regions at https://kootenaywildlife.shinyapps.io/BCHarvestData/). Hunter success can be measured by the proportion of hunters that killed a cougar (hunter success) or the number of days it took to kill an animal (days/kill). These two metrics often showed quite different trends with harvest, and days/kill was often very imprecise. This result may be inherent to the current harvest regime and data collection methods, or it may be due to the large increase in hunters during the analysis period, which was not related to cougar abundance. Hunter numbers did vary with the cougar trend in the Kootenays, but on Vancouver Island, hunter numbers increased as the cougar population declined. We conclude that neither hunter success nor hunter effort were good indices of cougar population trend for the interior, but hunter success may be a better general index on Vancouver Island. We are not sure why this is the case.

4.2 Human and Livestock Conflict Management

Cougars that pose a significant risk to human safety or property may be removed by the Conservation Officer Service. Although cougar attacks on humans in North America have been increasing as human settlement and cougar populations expand (Beier 1991; Torres et al. 1996), such occurrences are still extremely rare. In British Columbia, the number of people recorded as injured by cougars increased over the last century (Figure 10), although this is likely at least partly due to better reporting in later periods. The number of people killed by cougars in British Columbia has been few; eight human mortalities have been recorded since 1900, and there has not been a fatal cougar attack recorded in British Columbia since 1996 (Figure 10).

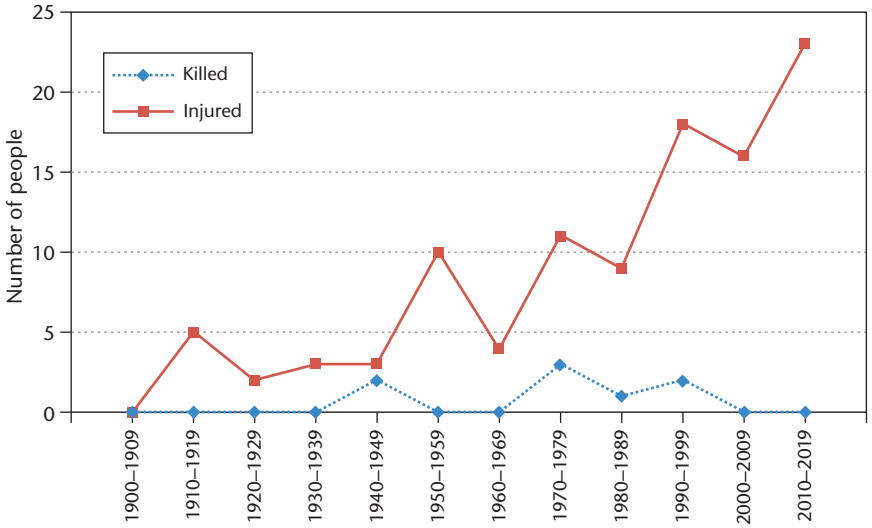

FIGURE 10 *The recorded number of people injured or killed by cougars since 1900 in British Columbia, by decade.*

The Conservation Officer Service has established a human attack protocol that is implemented in the rare instances when cougars attack people. The removal of specific individuals is the most common approach to deal with threats to human safety. Control actions are not intended to threaten the long-term viability of cougar populations nor reduce the local population size. In British Columbia, individual cougars are killed as a result of threats to public safety or conflicts with

people following loss of pets or livestock. Population reduction, via hunting or predator control, has not been a strategy used to reduce conflicts during the past four decades, despite suggestions to the contrary (Teichman et al. 2016). Cougar conflicts, mostly the result of livestock depredation, are common in British Columbia. Both the frequency of conflicts and the frequency of conflict kills roughly track changes in estimated cougar abundance in interior British Columbia (compare Figures 5 and 11). Alberta has nearly as many cougar conflicts as British Columbia, but many fewer cougars are killed during conflict response in Alberta, presumably due to different response guidelines between the jurisdictions (Alberta Environment and Sustainable Resource Development 2012).

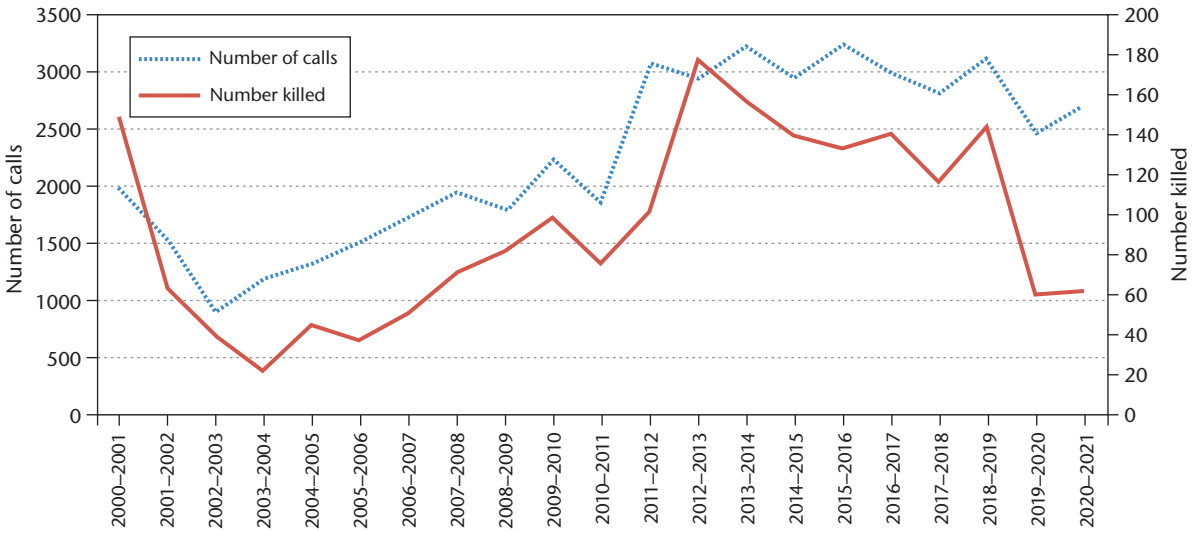

FIGURE 11 *The number of calls to the Conservation Officer Service regarding cougars, and the number of cougars killed for human and livestock conflict reasons in British Columbia from 2000 to 2020.*

Cougars prey on livestock, although only a small proportion of all reported livestock losses have been attributed to cougars (Hebert 1989). Cougars kill cattle, sheep, goats, llamas, and poultry, as well as dogs and cats (Murphy and Ruth 2010). The provincial government promotes actions that can reduce conflicts, such as good animal husbandry, community planning, and public education, and encourages non-lethal control measures. More information about predator management actions can be found at https://www2.gov.bc.ca/gov/content/environment/plants-animals-ecosystems/wildlife/wildlife-conservation/predator-management and specific responses related to cougar conflict can be found at www2.gov.bc.ca/gov/content/environment/plants-animals-ecosystems/wildlife/human-wildlife-conflict/staying-safe-around-wildlife/cougars.

4.3 Management of Species at Risk

In the 1980s, British Columbia discontinued predator control programs aimed at increasing populations of game species. Current policy does not support predator control for the purpose of enhancing ungulate populations for hunting. However, as a top predator, cougars have the potential to be a significant conservation threat to some species at risk. The Government of British Columbia supports the control of cougars where there is reason to believe that they threaten the viability or recovery of species at risk, as defined by provincial blue and red lists or by federal designation under the *Species at Risk Act*. This policy has been

invoked for the removal of individual cougars threatening endangered mountain caribou and bighorn sheep herds in the province.

4.4 Knowledge Gaps

The principal knowledge gap for cougar management in British Columbia continues to be assessing population size and trend in relation to different ecological circumstances and management regimes. It is unclear whether an open season or a quota system on either all cougars or just females will better ensure harvest sustainability, hunter opportunity and satisfaction, and the integrity of the social structure of cougar populations. Obtaining local measures of density, survival, and reproduction can help to improve local estimates of population size and trend.

Further knowledge gaps exist regarding the role of cougar predation in declines of prey populations, including mule deer and caribou, and cougar response to landscape disturbances such as wildfire, roads, and forestry activity. Studies in the Okanagan, Kootenay, and Cariboo Regions are currently helping to address these knowledge gaps.

An integrated population model has been built that incorporates all available data and knowledge about cougars into a single platform that can be queried by any user. See chapter 6 in the Montana Mountain Lion Strategy (Montana Fish, Wildlife and Parks 2019) for a description of the model. The model uses the age-at-harvest data and hunter success to estimate trend and can integrate other data such as hunter and non-hunter kill numbers and local estimates of survival and reproduction rates. Future versions may include indices of prey abundance, such as annual deer population estimates, which would give the model a community ecology context. Population size and density are generated by including measures of abundance from around the province. The model estimates reproduction, survival, and abundance through time. The user can derive estimates of population size, hunter harvest rate, non-hunting human-caused mortality rate, and trend through time for each management unit in the province. This integrated tool will make the best use of all relevant data, provide easy access to population metrics such as hunter harvest or non-hunter mortality, and point to local or regional data weaknesses and thus facilitate resource allocation. Model results will be available to users via a web-based dashboard.

5 RECOMMENDATIONS

Based on this review, we present some ideas to consider in future data collection and management in British Columbia.

1. Use the cougar integrated population model to predict and evaluate management changes, derive population information for annual decision-making needs, and consider future investments in inventory and research.
2. Age all human-killed cougars, including hunter harvests and conflict kills, because the age data are key to estimating trend analysis in the integrated population model.
3. Add deer population abundance to the cougar integrated population model to address both top-down pressures, such as harvest, and bottom-up drivers, such as prey abundance. The model may then better balance the indirect effects of environmental change and direct human impacts, such as hunting.

4. Assess the merits of the various harvest management options including quota-based strategies to consider how best to balance conservation, economic, and social priorities.
5. Discuss cougar hunting season adjustments to reduce the risk of orphaning kittens.
6. Consider developing and administering an educational course for cougar hunters.
7. Evaluate the current conflict response rules for cougars to see if they align with conservation, economic, and social priorities.
8. Evaluate and implement more preventative measures to help livestock and pet owners protect their animals to reduce conflict with cougars.

REFERENCES

Ackerman, B.B., F.G. Lindzey, and T.P. Hemker. 1984. Cougar food habits in Southern Utah. Wildl. Soc. Bull. 48:147–155.

Alberta Environment and Sustainable Resource Development. 2012. Management plan for cougars in Alberta. Wildl. Manag. Plan. Ser. Number 8. Edmonton, Alta.

Allen, M.L., L.M. Elbroch, C.C. Wilmers, and H.U. Wittmer. 2015. The comparative effects of large carnivores on the acquisition of carrion by scavengers. Am. Naturalist 185:822–833. DOI:10.1086/681004.

Anderson, C.R. and F.G. Lindzey. 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. Wildl. Soc. Bull. 33:179–188.

Anderson, C.R., F. Lindzey, K.H. Knopff, M.G. Jalkotzy, and M.S. Boyce. 2010. Cougar management in North America. In: Cougar ecology and conservation. M. Hornocker and S. Negri (editors). Univ. Chicago Press, Chicago, Ill., pp. 41–54.

Apps, C.D., B.N. McLellan, T.A. Kinley, R. Serrouya, D.R. Seip, and H.U. Wittmer. 2013. Spatial factors related to mortality and population decline of endangered mountain caribou. J. Wildl. Manag. 77:1409–1419.

Ashman, D. 1981. Mountain lion investigations. Fed. Aid Prog. Rep. W-17-9 and W-17-10, Job 5. Nevada Dep. Fish and Game, Carson City, Nev.

Bacon, M.M. 2010. The ecology of a re-established cougar (*Puma concolor*) population in southeastern Alberta and southwestern Saskatchewan. Thesis. Univ. Alberta, Edmonton, Alta.

Banfield, J.E., S. Ciuti, C.C. Nielsen, and M.S. Boyce. 2020. Cougar roadside habitat selection: incorporating topography and traffic. Glob. Ecol. Cons. 23:1–11. DOI:10.1016/j.gecco.2020.e01186.

Barnhurst, D. and F.G. Lindzey. 1989. Detecting female mountain lions with kittens. N.W. Sci. 63:35–37.

Bartnick, T.D., T.R. van Deelen, H.B. Quigley, and D. Craighead. 2013. Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern greater Yellowstone ecosystem. Can. J. Zool. 91(2):82–93. DOI:10.1139/cjz-2012-0147.

Beier, P. 1991. Cougar attacks on humans in the United States and Canada. Wildl. Soc. Bull. 19:403–412.

_____. 1993. Determining minimum habitat areas and habitat corridor for cougars. Conserv. Biol. 7:94–108.

_____. 1995. Dispersal of juvenile cougars in fragmented habitat. J. Wildl. Manag. 59(2):228–237.

Beier, P. and R.H. Barrett. 1993. The cougar in the Santa Ana Mountain Range, California. In: Final report, Orange County cooperative mountain lion study. Dep. For. Res. Manag., Univ. California Berkeley.

Bird, C., R. Clarke, D. Lewis, and R. Serrouya. 2010. Cougar ecology, predation, and caribou in the Columbia Mountains of British Columbia. Report for the Fish and Wildlife Compensation Program–Columbia Basin, B.C.

Boonstra, R., S. Boutin, T.S. Jung, C.J. Krebs, and S. Taylor. 2018. Impact of rewilding, species introductions and climate change on the structure and function of the Yukon boreal forest ecosystem. Integrative Zool. 13:123–138.

Cardoza, J.E. and S.A. Langlois. 2002. The eastern cougar: a management failure? Wildl. Soc. Bull. 30:265–273.

Caso, A., C. Lopez-Gonzalez, E. Payan, E. Eizirik, T. de Oliveira, R. Leite-Pitman, M. Kelly, C. Valderrama, and M. Lucherini. 2008. *Puma concolor*. In: IUCN 2010. IUCN red list of threatened species. Version 2010.1. www.iucnredlist.org (Accessed: March 24, 2010).

Clark, D.A., G.A. Davidson, and B.K. Johnson. 2014. Cougar kill rates and prey selection in a multiple-prey system in northeast Oregon. J. Wildl. Manag. 78(7):1161–1176. DOI:10.1002/jwmg.760.

Clark, D.A., B.K. Johnson, D.H. Jackson, A. Clark, A. Darren, and K. Bruce. 2015. Monthly and annual survival rates of cougar kittens in Oregon. N.W. Sci. 89:393–400.

Clawson, M.V. 2015. Management application of statistical population reconstruction to wild game populations. PhD thesis. Univ. Washington, Seattle, Wash.

Clawson, M.V. and J. Skalski. 2016. Statistical population reconstruction: a tool to improve how states monitor wildlife trends. Wildl. Prof. Mar./Apr.:34–37.

Cooley, H.S., H.S. Robinson, R.B. Wielgus, and C.S. Lambert. 2008. Cougar prey selection in a white-tailed deer and mule deer community. J. Wildl. Manag. 72(1):99–106. DOI:10.2193/2007-060.

Cooley, H.S., R.B. Wielgus, G. Koehler, and B. Maletzke. 2009. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. Anim. Conserv. 12:321–328.

Cougar Management Guidelines Working Group. 2005. Cougar management guidelines. 1st edition. WildFutures, Bainbridge Isl., Wash.

Currier, M.J.P., S.L. Sheriff, and K.P. Russell. 1977. Mountain lion population and harvest near Canon City, Colorado, 1974–1977. Colo. Div. Wildl., Spec. Rep. 42.

Demarchi, D.A. 1996. An introduction to the ecoregions of British Columbia. Wildl. Br., Min. Env., Lands Parks, Victoria, B.C.

Dickson, B.G. and P. Beier. 2002. Home-Range and Habitat Selection by Adult Cougars in Southern California. The Journal of Wildlife Management 66:1235–1245.

Donadio, E. and S.W. Buskirk. 2006. Diet, morphology, and interspecific killing in carnivora. Am. Nat. 167:524–36.

Elbroch, L.M., P.E. Lendrum, P. Alexander, and H. Quigley. 2015. Cougar den site selection in the southern Yellowstone ecosystem. Mammal Res. 60(2):89–96. DOI:10.1007/s13364-015-0212-6.

Fecske, D.M., D.J. Thompson, and J.A. Jenks. 2009. Cougar ecology and natural history. In: Managing cougars in North America, pp. 6–35. West. Assoc. Fish Wildl. Agencies.

Festa-Bianchet, M., T. Coulson, J.M. Gaillard, J.T. Hogg, and F. Pelletier. 2006. Stochastic predation events and population persistence in bighorn sheep. Proc. Royal Soc. B: Biol. Sci. 273(1593):1537–1543. DOI:10.1098/rspb.2006.3467.

Fieberg, J.R., K.W. Shertzer, P.B. Conn, K.V. Noyce, and D.L. Garshelis. 2010. Integrated population modeling of black bears in Minnesota: implications for monitoring and management. PLOS ONE 5:e12114.

Gau, R.J., R. Mulders, T. Lamb, and L. Gunn. 2001. Cougars (*Puma concolor*) in the Northwest Territories and Wood Buffalo National Park. Arctic 54(2):185–187.

Gladders, A.D. 2003. Predation behaviour of Vancouver Island cougar (*Puma concolor vancouverensis*) and its relation to micro- and macroscale habitat. MSc thesis. Univ. British Columbia, Vancouver, B.C.

Goh, K.M. 2000. Macrohabitat selection by Vancouver Island cougar (*Puma concolor vancouverensis*). PhD Thesis, University of British Columbia.

Green, G.I., D.J. Mattson, and J.M. Peek. 1997. Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. J. Wildl. Mgmt. 61:1040–1055.

Hahn, A.M. 2001. Social and spatial organization of Vancouver Island cougar (*Puma concolor vancouverensis*, Nelson and Goldman, 1943). PhD Thesis, University of British Columbia.

Harrison, S. 1990. Cougar Predation on Bighorn Sheep in the Junction Wildlife Management Area, British Columbia. MSc Thesis, University of British Columbia.

Hatler, D.F., D.W. Nagorsen, and A.M. Beal. 2008. Carnivores of British Columbia. Volume 5: The mammals of British Columbia. Royal B.C. Museum, Victoria, B.C.

Hatter, I.W. 2019. Statistical population reconstruction of cougars in British Columbia. Report for Resource Management Division, Kootenay-Boundary Region, B.C. Min. For., Lands, Nat. Resource Op. Rural Dev., Nelson, B.C.

Hebert, D. 1989. The status and management of cougar in British Columbia. Proc. 3rd Mountain Lion Workshop 3:1–14.

Hemker, T.P., F.G. Lindzey, and B.B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. J. Wildl. Manage. 48:1275–1284.

Hornocker, M.G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife monographs No. 21.

Hornocker, M. and S. Negri (editors). 2009. Cougar: ecology and conservation. Univ. Chicago Press, Chicago, Ill.

Iriarte, J.A., W.L. Franklin, W.E. Johnson, and K.H. Redford. 1990. Biogeographic variation of food habits and body size of the America puma. Oecologia 85:185–190.

Jalkotzy, M.G., P.I. Ross, and J.R. Gunson. 1992. Management plan for cougars in Alberta. Wildl. Manag. Plan. Ser. No. 5. Alta. For., Lands Wildl., Fish Wildl. Div.

Jennings, M.K., R.L. Lewison, T.W. Vickers, and W.M. Boyce. 2016. Puma response to the effects of fire and urbanization. J. Wildl. Manag. 80:221–234.

Johnson, R.D., J.A. Jenks, S.A. Tucker, and D.T. Wilckens. 2019. Mountain lion (*Puma concolor*) population characteristics in the Little Missouri Badlands of North Dakota. Am. Midland Nat. 181(2):207. DOI:10.1674/0003-0031-181.2.207.

Jung, T.S. and P.J. Merchant. 2005. First confirmation of cougar, *Puma concolor*, in the Yukon. Can. Field Nat. 119:580–581.

Katnik, D.D. 2002. Predation and habitat ecology of mountain lions (*Puma concolor*) in the southern Selkirk mountains. PhD thesis. Washington State Univ., Pullman, Wash.

Keehner, J.R., R.B. Wielgus, and A.M. Keehner. 2015. Effects of male targeted harvest regimes on prey switching by female mountain lions: implications for apparent competition on declining secondary prey. Biol. Conserv. 192:101–108.

Kinley, T.A. and C.D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. Wildl. Soc. Bull. 29(1):158–164.

Knopff, A.A., K.H. Knopff, M.S. Boyce, and C.C. St. Clair. 2014. Flexible habitat selection by cougars in response to anthropogenic development. Biol. Conserv. 178:136–145. DOI:10.1016/j.biocon.2014.07.017.

Knopff, K.H. 2010. Cougar predation in a multi-prey system in West-Central Alberta. PhD thesis. Univ. Alberta, Edmonton, Alta.

Knopff, K.H., A.A. Knopff, and M.S. Boyce. 2010. Scavenging makes cougars susceptible to snaring at wolf bait stations. J. Wildl. Manag. 74(4):644–653. DOI:10.2193/2009-252.

Knopff, K.H., A.A. Knopff, A. Kortello, and M.S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. J. Wildl. Manag. 74:1435–1447.

Knopff, K.H., A.A Knopff, M.B. Warren, and M.S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. J. Wildl. Manag. 73(4):586–597. DOI:10.2193/2008-294.

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. Ecosci. 14(2):214–222.

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. J. Wildl. Manage. 63:901–910.

Kusler, A., L.M. Elbroch, H. Quigley, and M. Grigione. 2017. Bed site selection by a subordinate predator: an example with the cougar (*Puma concolor*) in the greater Yellowstone ecosystem. PeerJ. 2017(11):1–20. DOI:10.7717/peerj.4010.

Kutlilek, J., T.E. Smith, R.A. Hopkins, and E.W. Clinite. 1980. California mountain lion track transect survey, 1980. PR Project W 51. Calif. Fish Game.

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. J. Wildl. Manag. 70(1):246–254. DOI:10.2193/0022-541x(2006)70[246:cpdavi]2.0.co;2.

Laundré, J.W. 2008. Summer predation rates on ungulate prey by a large keystone predator: how many ungulates does a large predator kill? J. Zool. 275:341–348.

Laundré, J.W., and T.W. Clark. 2003. Managing puma hunting in the western United States: through a metapopulation approach. In: Animal conservation forum. Volume 6, pp. 159–170. Cambridge Univ. Press, Cambridge, U.K.

Laundré, J.W. and L. Hernández. 2003. Winter hunting habitat of pumas *Puma concolor* in northwestern Utah and southern Idaho, USA. Wildl. Biol. 9:123–129.

Laundré, J.W., L. Hernández, and S.G. Clark. 2006. Impact of puma predation on the decline and recovery of a mule deer population in southeastern Idaho. Can. J. Zool. 84(11):1555–1565. DOI:10.1139/z06-150.

Leech, H., D.E. Jelinski, L. DeGroot, and G. Kuzyk. 2017. The temporal niche and seasonal differences in predation risk to translocated and resident woodland caribou (*Rangifer tarandus caribou*). Can. J. Zool. 95:809–820.

Lehman, C.P., C.T. Rota, M.A. Rumble, and J.J. Millspaugh. 2017. Characteristics of successful puma kill sites of elk in the Black Hills, South Dakota. Wildl. Biol. 2017(1):wlb.00248. DOI:10.2981/wlb.00248.

Lindzey, F. G. 1987. Mountain lion. Pages 657–658. In: Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Toronto, Ontario.

Lindzey, F.G., B.B. Ackerman, D. Barnhurst, and T.P. Hemker. 1988. Survival rates of mountain lions in southern Utah. J. Wildl. Manag. 52:664–667.

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. J. Wildl. Manag. 58:619–624.

Lindzey, F.G., W.D. Van Sickle, S.P. Laing, and C.S. Mecham. 1992. Cougar population responses to manipulation in southern Utah. Wildl. Soc. Bull. 20:224–227.

Logan, K.A. 1983. Mountain lion population and habitat characteristics in the Big Horn Mountains of Wyoming. MSc thesis. Univ. Wyoming, Laramie, Wyo.

Logan, K.A., L.L. Irwin, and R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. J. Wildl. Manage. 50:648–654.

Logan, K.A. and J.P. Runge. 2021. Effects of hunting on a puma population in Colorado. Wildl. Monogr. 209:1–35.

Logan, K.A. and L.L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Wash., D.C.

_____. 2010. Behavior and social organization of a solitary carnivore. In: Cougar ecology and conservation. M. Hornocker and S. Negri (editors). Univ. Chicago Press, Chicago, Ill., pp. 105–117.

McRae, B.H., P. Beier, L.E. Dewald, L.Y. Huynh, and P. Keim. 2005. Habitat barriers limit gene flow and illuminate historical events in the American puma. Mol. Ecol. 14:1965–1977.

Montana Fish, Wildlife and Parks. 2019. Montana mountain lion monitoring and management strategy. https://fwp.mt.gov/binaries/content/assets/fwp/conservation/wildlife-reports/mountain-lion/mountain-lion-monitoring-and-management-strategy_final_adopted-1.pdf (Accessed: Dec. 17, 2021).

Morrison, C.D., M.S. Boyce, and S.E. Nielson. 2015. Space-use, movement and dispersal of sub-adult cougars in a geographically isolated population. PeerJ. 8:1–24.

Morrison, C.D., M.S. Boyce, S.E. Nielsen, and M.M. Bacon. 2014. Habitat selection of a re-colonized cougar population in response to seasonal fluctuations of human activity. J. Wildl. Manag. 78(8):1394–1403. DOI:10.1002/jwmg.799.

Murphy, K.M. 1998. The ecology of the cougar (*Puma concolor*) in the Northern Yellowstone ecosystem: interactions with prey, bears, and humans. Thesis. Univ. Idaho, Moscow, Idaho.

Murphy, K. and T.K. Ruth. 2010. Diet and prey selection of a perfect predator. In: Cougar ecology and conservation. M. Hornocker and S. Negri (editors). Univ. Chicago Press, Chicago, Ill., pp. 118–137.

Nowell, K. and P. Jackson. 1996. Wild cats: status survey and conservation action plan. IUCN/SSC Action Plans for the Conservation of Biological Diversity. Gland: IUCN.

Pierce, B.M., R.T. Bowyer, and V.C. Bleich. 2004. Habitat selection by mule deer: forage benefits or risk of predation? J. Wildl. Manag. 68(3):533–541.

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.

Province of British Columbia. 1980. Preliminary cougar management plan for British Columbia. B.C. Min. Environ., Lands and Parks, Victoria, B.C. https://a100.gov.bc.ca/pub/eirs/lookupDocument.do?fromStatic=true&repository=BDP&documentId=5947.

Quigley, H. and M. Hornocker. 2010. Cougar population dynamics. In: Cougar ecology and conservation. M. Hornocker and S. Negri (editors). Univ. Chicago Press, Chicago, Ill., pp. 59–73.

Resources Inventory Committee (RIC). 1998. Standard for terrestrial ecosystem mapping in British Columbia. Version 2.0. B.C. Min. For. and B.C. Min. Environ., Lands and Parks, Victoria, B.C.

Robinson, H.S., R.B. Wielgus, H.S. Cooley, and S.W. Cooley. 2008. Sink population in carnivore management: cougar demography and immigration in a hunted population. Ecol. Appl. 18:1028–1037.

Robinson, H.S., R.B. Wielgus, and J.C. Gwillam. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. Can. J. Zool. 80:556–568.

Ross, P.I. and M.G. Jalkotzy. 1992. Characteristics of a hunted population of cougars in southwestern Alberta. J. Wildl. Manage. 56:417–426.

Ross, P.I., M.G. Jalkotzy, and M. Festa-Blanchet. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. Can. J. Zool. 75(5):771–775. DOI:10.1139/z97-098.

Ruth, T.K. 2004. Patterns of resource use among cougars and wolves in northwestern Montana and southeastern British Columbia. Thesis. Univ. Idaho, Moscow, Idaho.

Ruth, T.K., P.C. Buotte, and M.G. Hornocker. 2019. Yellowstone cougars: ecology before and during wolf restoration. Univ. Colorado Press, Louisville, Colo.

Ruth, T., M. Haroldson, K. Murphy, P.C. Boutte, M.G. Hornocker, and H.B. Quigley. 2011. Cougar survival and source-sink structure on Greater Yellowstone's northern range. J. Wildl. Manag. 75(6):1381–1398.

Seidensticker, J.C., M.G. Hornocker, W.V. Wiles, and J.P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildl. Monogr. 35.

Sitton, L.W. 1977. California mountain lion investigations with recommendations for management. PR Project W-51-R. California Dep. Fish and Game, Sacramento, Calif.

Smallwood, K.S. 1997. Interpreting puma (*Puma concolor*) population estimates for theory and management. Environ. Conserv. 24:283–289.

Spalding, D.J. and J. Lesowski. 1971. Winter food of the cougar in south-central British Columbia. J. Wildl. Manage. 35:378–381.

Spreadbury, B.R., K. Musil, J. Musil, C. Kaisner, and J. Kovak. 1996. Cougar population characteristics in southeastern British Columbia. J. Wildl. Manag. 60:962–969.

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. J. Wildl. Manag. 70:1588–1600.

Sunquist, M.E. and F. Sunquist. 2002. Wild cats of the world. Univ. Chicago Press, Chicago, Ill.

Sweanor, L.L., K.A. Logan, and M.C. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conserv. Biol. 14:798–808.

Teichman, K.J., B. Cristescu, and C.T. Darimont. 2016. Hunting as a management tool? cougar-human conflict is positively related to trophy hunting. BMC Ecol. 16:44. DOI:10.1186/s12898-016-0098-4.

Terborgh, J. and J.A. Estes. 2013. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Wash., D.C.

Thompson, D.M. 2010. Noninvasive approaches to reduce human-cougar conflict in protected areas on the west coast of Vancouver Island. MSc thesis. Univ. Victoria, Victoria, B.C.

Torres, S.G., T.M. Mansfield, J.E. Foley, T. Lupo, and A. Brinkhaus. 1996. Mountain lion and human activity in California: testing speculations. Wildl. Soc. Bull. 24:451–460.

van Oort, H. and C. Bird. 2010. Wolf census results in the Lake Revelstoke area. Prepared for Min. Env. and Columbia Basin Fish. Wildl. Compensation Program, Nelson, B.C.

van Oort, H., C. Bird, G. Mowat, C. Gaynor, and L. De Groot. 2010. Winter predator census results in the Kootenay-Columbia Caribou recovery areas. Survey Report, B.C. Min. Env., Nelson, B.C.

Wainwright, C.J., C.T. Darimont, and P.C. Paquet. 2010. British Columbia's neglected carnivore: a conservation assessment and conservation planning guide for cougars. Raincoast Conservation Foundation, Sidney, B.C. www.raincoast.org/wp-content/uploads/2011/00/BCs-Neglected-Carnivore.pdf (Accessed:August 2023).

Warren, M.J. and K.I. Warheit. 2016. Forest cover mediates genetic connectivity of northwestern cougars. Conserv. Genet. 17(5):1011–1024. DOI:10.1007/s10592-016-0840-7.

Wehausen, J.D. 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildl. Soc. Bull. 24:471–479.

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. Biol. Conserv. 167:69–75. DOI:10.1016/j.biocon.2013.07.008.

Williams, J. S., J. J. McCarthy, and H.D. Picton. 1995. Cougar habitat use and food habits on the Montana Rocky Mountain Front. Intermountain Journal of Sciences 1:16–28.

Wilmers, C.C., Y. Wang, B. Nickel, P. Houghtaling, Y. Shakeri, M.L. Allen, J. Kermish-Wells, V. Yovovich, and T. Williams. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. PLOS ONE 8:e60590.

Wilson, D.E. and D.M. Reeder (editors). 2005. Mammal species of the world. a taxonomic and geographic reference. 3rd ed. John Hopkins Univ. Press, Baltimore, Md.

Wilson, S.F. 2009. Recommendations for predator-prey management to benefit the recovery of mountain caribou in British Columbia. Prepared for Min. Env., Victoria, B.C.

Wilson, S.F., A. Hahn, A. Gladders, K.M.L. Goh, and D.M. Shackleton. 2004. Morphology and population characteristics of cougars on Vancouver Island, Canada. Can. Field Nat. 118:159–163.

Wittmer, H.U., A.R.E. Sinclair, and B.N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144:257–267.