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Abstract: Harvest by means of hunting is a commonly used tool in large carnivore management. To evaluate the effects of harvest on populations, managers usually focus on numerical or immediate direct demographic effects of harvest mortality on a population's size and growth. However, we suggest that managers should also give consideration to indirect and potential evolutionary effects of hunting (e.g., the consequences of a change in the age, sex, and social structure), and their effects on population growth rate. We define "indirect effects" as hunting-induced changes in a population, including human-induced selection, that result in an additive change to the population growth rate "lambda" beyond that due to the initial offtake from direct mortality. We considered 4 major sources of possible indirect effects from hunting of bears: (1) changes to a population's age and sex structure, (2) changes to a population's social structure, (3) changes in individual behavior, and (4) human-induced selection. We identified empirically supported, as well as expected, indirect effects of hunting based primarily on >30 years of research on the Scandinavian brown bear (*Ursus arctos*) population. We stress that some indirect effects have been documented (e.g., habitat use and daily activity patterns of bears change when hunting seasons start, and changes in male social structure induce sexually selected infanticide and reduce population growth). Other effects may be more difficult to document and quantify in wild bear populations (e.g., how a younger age structure in males may lead to decreased offspring survival). We suggest that managers of bear and other large carnivore populations adopt a precautionary approach and assume that indirect effects do exist, have a potential impact on population structure, and, ultimately, may have an effect on population growth that differs from that predicted by harvest models based on direct effects alone.

Key words: brown bear, harvest, hunting, indirect effects, population growth, population structure, Sweden, *Ursus arctos*

The manipulation of populations is the core around which wildlife management activities are organized (Fryxell et al. 2014). Caughley's (1977) original list of 4 general objectives in wildlife management are still relevant (Fryxell et al. 2014): (1) make a population increase, (2) make it decrease, (3) hunt it for a continuing yield, or (4) do nothing except monitor the population. Harvest is a common management practice to reach population goals (i.e., objectives 2 and 3) in mammal populations, including carnivores (Lindsey et al. 2007, Linnell et al. 2008, Packer et al. 2009, Swenson et al. 2017). However, it is essential to understand the population dynamics of exploited species in order to determine the appropriate
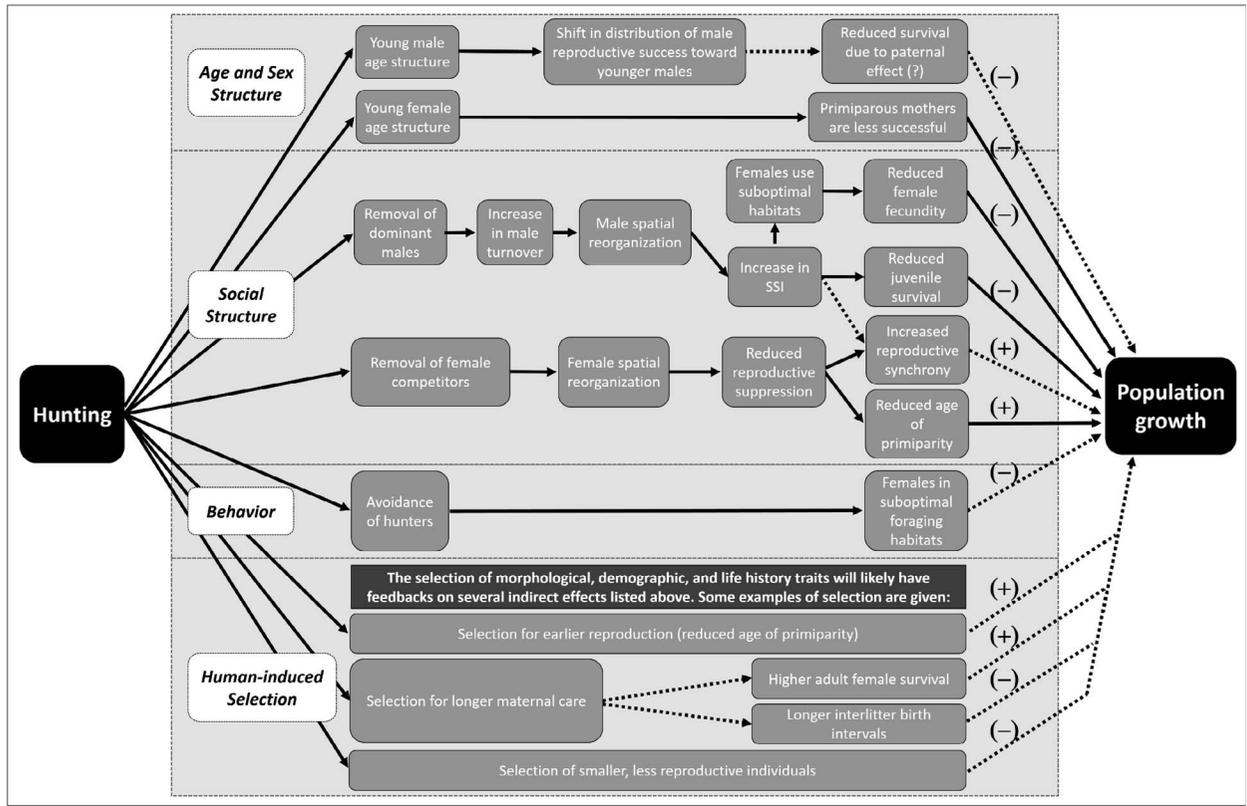
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Fig. 1.   A summary of the indirect effects on population growth of bear hunting discussed in this paper. The solid arrows show relationships that have been documented statistically and the dotted arrows show potential relationships. Effects on population growth are noted in parentheses along the lines directly connecting with the "Population growth" box. This figure was inspired by Milner et al. (2007). SSI, sexually selected infanticide.

harvest rates to reach a population objective (Sinclair 1991).

Although the harvest of populations is supported by solid scientific underpinnings, there are still knowledge gaps about the consequences of hunting in wild populations, particularly for the harvest of large carnivores (Treves 2009). For example, managers usually focus on the effects of direct hunting mortality on a population's growth rate (e.g., Knight and Eberhardt 1985, Miller 1990, Linnell et al. 2010). Nevertheless, there is an increasing number of studies showing that indirect effects, which managers often do not consider, also may affect population growth (e.g., Milner et al. 2007, Pauli and Buskirk 2007, Treves 2009). For the purpose of this review, we define "indirect effects" as hunting-induced changes in a population, including human-induced selection, that result in an additive change to the population growth rate "lambda" beyond that due to the initial offtake

from direct mortality. Understanding the causal relationships between harvest and indirect effects on population growth is thus crucial for the management and conservation of wild mammal populations.

Here, we focus on hunting-induced changes to population age, sex, and social structures in the behavior of remaining individuals, and we address hunting-induced selection in bear (Ursidae) populations (termed demographic side effects in Milner et al. (2007). We primarily review the literature from the Scandinavian Brown Bear Research Project (SBBRP) because it is illustrative to discuss the subject in one system where brown bears (*Ursus arctos*) have been managed as a game species for >70 years. We distinguish between pathways that have been documented statistically and those that are expected to occur (see Fig. 1). In addition, we also include literature about indirect effects of harvest on growth rates in other bear populations.

Study areas and hunting regime in Sweden

The SBBRP has had 2 study areas; one in northern Sweden from 1984 to 2013, where 254 individual brown bears have been radiomarked and followed, mostly with very high frequency (VHF) telemetry (8,000 km^2; termed "north"), and one in central Sweden–southeastern Norway from 1985 to the present (13,000 km^2; termed "south"). There, 449 individuals were radiomarked and followed with VHF telemetry and, from 2003, with Global Positioning System technology. The north consists of alpine mountain and coniferous forest vegetation communities and includes parts of some national parks. The south is exclusively managed coniferous forests. See Zedrosser et al. (2006) for more detailed descriptions of the study areas, and see Arnemo et al. (2011) for capture methods. Our behavioral studies were conducted in the south.

Hunting brown bears has been legal in Sweden since 1943 outside the national parks, and generally lasts from 21 August until the area-specific, annually established quota has been filled (Swenson et al. 2017). Quotas have been set at variable spatial scales in Sweden, but today are set typically at county or sub-county levels (Swenson et al. 1994, 1998b, 2017). Furthermore, recent population objectives have varied by county and most objectives have not been met, with local numbers of bears either remaining stable or declining (Swenson et al. 2017). The Scandinavian bear population has increased from approximately 300 individuals in the 1940s to approximately 3,000 bears today, with approximately 95% of those found in Sweden (Swenson et al. 1994, 2017; Kindberg et al. 2011). Not until recently (2008–2013) have bears exhibited a decrease in population size across Scandinavia, which is most likely due to an increase in harvest rate in Sweden (Swenson et al. 2017). Population density varies and is approximately 11 bears/1,000 km^2 in the north and reaches approximately 30 bears/1,000 km^2 in the south (Solberg et al. 2006, Zedrosser et al. 2006).

All bear hunters are required to possess an annual hunting license and pass an annual shooting test; it is common to take a hunting test specific for bears, but is not required by law. There is no bag limit on bears, and any bear can be killed except females and their cubs, which are protected regardless of the cubs' age. Bears are hunted using stalking, sitting at posts, with dogs, or at bait sites; dog hunting is increasing in importance (Bischof et al. 2008, Swenson et al. 2017). It is legally required that all harvested bears and dead bears found be reported to local authori-
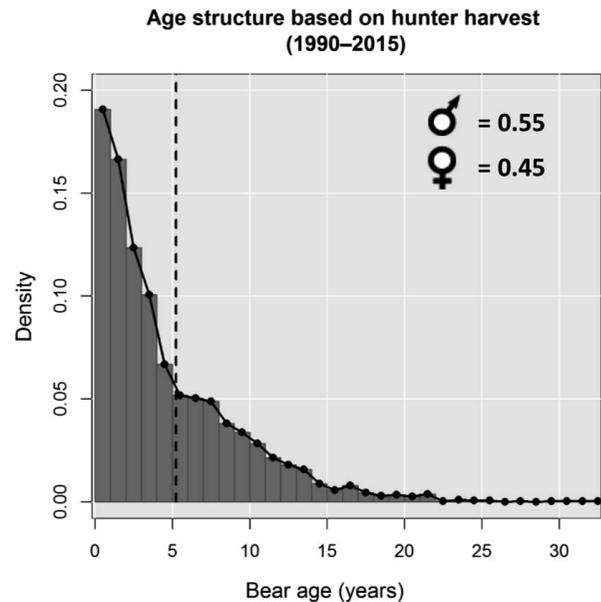

Age structure based on hunter harvest (1990–2015)

♂ = 0.55
♀ = 0.45

Fig. 2. The age structure of hunter-killed brown bears (*Ursus arctos*) in Sweden during 1990–2015. The vertical dotted line shows the mean age of bears (approx. 5 yr) killed. The frequencies of males and females harvested are shown.

ties, at which point samples (e.g., tissue, hair, a premolar tooth for aging) and measurements (e.g., weight, sex) are taken.

Hunting is the most important cause of bear mortality in Sweden. Sixty percent of all marked bears ≥1 year of age that are recovered dead have been killed legally by hunters, with an additional 13% dying naturally (Bischof et al. 2009). In Sweden, data from 1984 to 2006 suggest that hunters exhibit low selectivity for age, size, and sex, except for a slight bias toward males in the north (Bischof et al. 2009). This is probably because of limited encounter rates, traditions, and difficulties in distinguishing males from females in the wild (Bischof et al. 2008). Also, because there are no individual bag limits and harvest quotas, Swedish hunters may have a small incentive to pass up an opportunity to kill a bear that they encounter (Bischof et al. 2009). However, more recent analyses, based on an expanded data set collected during a time of increased harvest pressure, shows greater selectivity toward older bears, larger yearlings, and larger adult females over time (Leclerc et al. 2016a). The mean age of a harvested bear was approximately 5 years and males made up a slightly greater share of the harvest than females (55:45) in 1981–2015 (Fig. 2).

We used annual harvest rates of the Swedish population in conjunction with periodic population estimates (Swenson et al. 2017) to define a threshold for "high harvest" in relation to the indirect effects of hunting. A temporal threshold between low and high hunting pressure was set by Gosselin et al. (2015), who found that up to 14% of the variation in population growth rate could be explained by an indirect effect of harvest during high hunting pressure (i.e., after 2005; hereafter, "high harvest"). Therefore, we use here the same temporal threshold (2005–2006) as the boundary between low and high harvest rates. We conservatively defined the minimum harvest rate observed in the high harvest period as high harvest, which was 7% of the population estimate in Sweden. Although we do this for convenience in having a quantifiable measure to discuss indirect effects, we recognize that indirect effects can come from lower harvest rates than those set here, there can be compensatory effects, and this will vary across populations and hunting regimes.

Changes in a population's age and sex structure

Harvest can affect a population's age and sex structure, influenced by the degree of hunters' selectivity, hunting method, habitat, food availability, and other factors, as shown for different bear species (e.g., McLellan and Shackleton 1988, Derocher et al. 1997, Noyce and Garshelis 1997, Bischof et al. 2008). Although harvesting can change a population's sex structure, this will not necessarily affect reproductive rates in species with polygamous mating systems (e.g., Ginsberg and Milner-Gulland 1994, Milner et al. 2007), such as bears (Steyaert et al. 2012). The harvest of the most productive segment of the population—adult females—has the greatest effect on bear population growth rate (Knight and Eberhardt 1985, Miller 1990, Zedrosser et al. 2013, Gosselin et al. 2015). Harvest can result in a smaller proportion of older animals in the population, even if harvest is not selective to age (Bischof et al. 2008). A reduction in the population-wide age of females should reduce population growth, because primiparous females have a smaller litter size and greater cub mortality than multi-parous females (Zedrosser et al. 2009, Gosselin et al. 2017; Fig 1.).

Human-induced mortality can also change the male age structure and influence age-specific reproductive rates (Bellemain et al. 2006b, Zedrosser et al. 2007). Possibly as a result of greater illegal or unrecorded harvest of bears in the north, only one reproductively dominant adult male brown bear was present in this area for

several years, leading to a more skewed operational sex ratio (OSR), with more reproductive females per adult male compared with the south, which had a less human-influenced age structure resulting in a less skewed OSR (Zedrosser et al. 2007). This resulted in a significantly greater mean male reproductive success in the north than in the south. Although older and larger males had a greater reproductive success in both areas, age was relatively more important in the north because the single old male dominated the reproduction (approx. 33% of known offspring in 1990–1997; A. Zedrosser, unpublished data). This uneven age distribution enabled a relatively larger proportion of young males to gain reproductive success in the north than in the south (Zedrosser et al. 2007). In the south, age was more similar among males, potentially favoring larger individuals during intrasexual competition (Zedrosser et al. 2007). Female brown bears exhibit mate choice (Bellemain et al. 2006a, b), so the removal of older and larger males could result in less desired, younger, and smaller males siring offspring, which could result in lower quality cubs (i.e., with fitness-decreasing traits or those reducing survival), and therefore potentially lower recruitment. This has not been shown in large carnivores to our knowledge, but it has been shown in large ungulates (Milner et al. 2007, Martin et al. 2014, Douhard et al. 2016, Kvalnes et al. 2016).

Changes in a population's social structure

There is growing evidence that the harvest of large carnivores can cause changes to their social structure, the space use of survivors, and population growth rate (Rutledge et al. 2010, Newby et al. 2013, Maletzke et al. 2014, Ausband et al. 2015, Fattebert et al. 2016). For bears, the removal of conspecifics through hunting creates vacancies on the landscape and induces surviving animals to shift their home ranges toward these vacancies (Leclerc et al. 2017a, Frank et al. 2017). Home range shifts are strongest when the surviving animal is the same sex as the killed animal, which can increase sexually selected infanticide (SSI) by males and reflect a release from female–female competition (Leclerc et al. 2017a, Frank et al. 2017). Although little is known about how this spatial reorganization affects individual fitness, links have been made between hunting, male home-range shifts, SSI, and variation in population growth (Swenson et al. 1997, 2001; Swenson 2003; Gosselin et al. 2015, 2017; Leclerc et al. 2017a).

Sexually selected infanticide is a male reproductive strategy whereby males gain mating opportunities by killing dependent young (Hrdy 1979). Males should only kill offspring that they have not fathered (SSI Requirement 1), litter loss should trigger estrus in a victimized mother and shorten her inter-litter interval (Requirement 2), and the perpetrator should sire the victimized mothers' subsequent offspring (Requirement 3; Trivers 1972, Hrdy 1979). Sexually selected infanticide can be increased through male turnover in both solitary and social species (Soltis et al. 2000, Loveridge et al. 2007) and is the most plausible explanation for infanticide among Scandinavian brown bears (Swenson 2003, Steyaert et al. 2012). Brown bears have extended maternal care (typically 1.5–2.5 yr in Scandinavia; Dahle and Swenson 2003), and mothers generally do not mate during this period (but see Swenson and Haroldson 2008). After losing a litter during the mating season, however, females are able to enter estrus within a few days (Steyaert et al. 2014). The majority (>90%) of females that lose their litter during a mating season mate successfully and give birth during the subsequent winter (Requirement 2 of the SSI hypothesis; Steyaert et al. 2014). Males can thus generate an almost immediate mating opportunity by killing a litter of cubs-of-the-year instead of waiting until the female becomes receptive again after weaning her young 1.5–2.5 years later. In Scandinavia, approximately 80% of all cub mortality, which is approximately 42% annually, occurs during the mating season (Gosselin et al. 2015, 2017) and is due to infanticide by males (Bellemain et al. 2006a, b; Steyaert et al. 2014). No male has been recorded killing his own offspring, likely because males recognize females from their mating history (Wolff and Macdonald 2004), and perpetrators typically sire the offspring of victimized mothers (Requirements 1 and 3 of the SSI hypothesis; Bellemain et al. 2006a, b; Steyaert et al. 2014). Residents are defined as males whose home ranges overlap with a victimized mother's home range during the mating season before and during the year of infanticide (Bellemain et al. 2006a), and both resident and immigrant males can commit SSI (McLellan 2005, Bellemain et al. 2006a).

In the Scandinavian brown bear, hunting promotes SSI and can indirectly contribute to negative population growth through increased juvenile mortality (Swenson et al. 1997, 2001; Swenson 2003; Gosselin et al. 2015, 2017). Between 1984 and 1995, Swenson et al. (1997, 2001) contrasted cub survival between the north and south. In the north, with few old males and no legal hunting, cub survival was very high (98%) and relatively stable over time. In the south, even under a low harvest rate, cub survival was negatively correlated with the removal of males from the population (24% and 42% lower 0.5 and 1.5 yr after harvest, respectively; Swenson et al. 1997). Furthermore, Swenson et al. (1997, 2001) calculated that removing 1 male from the population was equivalent to a recruitment loss of 0.5–1.0 adult female and decreased population growth rate by 3.4%. Gosselin et al. (2015) found similar patterns: cub survival was lower under high harvest (2006–2011) as compared with low hunting pressure (1990–2005) and, assuming that all cub mortality during the mating season is due to SSI, it could explain approximately 14% of the variation in population growth rate. Furthermore, Gosselin et al. (2017) showed that male removal decreased cub survival only during the mating season, consistent with the SSI hypothesis that cub survival increased with distance to the nearest male killed during the previous 1.5 years, and that the spatiotemporal distribution of male harvest is more important than the absolute number of males killed. After the death of a resident male, its male neighbors shift their home ranges toward the "vacant" area (Leclerc et al. 2017a). This shift is most apparent during the second year after the resident's death, and provides a mechanistic explanation for the 1.5-year time lag in decreased cub survival after male removal (Leclerc et al. 2017a).

Hunting can promote SSI in Scandinavia; therefore, it may also stimulate infanticide counterstrategies and associated costs for females (Agrell et al. 1998, Ebensperger 1998, Palombit 2015). Female brown bears apply several strategies to reduce SSI risk, including aggression to deter infanticidal males (Swenson 2003), multi-male mating, and multiple paternity litters to confuse paternity (Bellemain et al. 2006a, b). Mothers also adjust their movements and modify their habitat selection to avoid infanticidal males (Steyaert et al. 2013a, 2014, 2016a). Furthermore, avoiding infanticidal males restricts foraging behavior and carries a nutritive cost (Steyaert et al. 2013b). The reproductive costs imposed by constraints on habitat and diet selection to counter SSI risk have not been estimated in the Scandinavian brown bear, but it has been estimated to decrease female reproductive success by 6% in a hunted brown bear population in Alberta, Canada (Wielgus and Bunnell 1994, 2000; Wielgus et al. 2001a).

Sexually selected infanticide might also have a compensatory effect on population growth by synchronizing reproduction. Ordiz et al. (2008) discussed that SSI may be a mechanism involved in the observed reproductive synchrony among female bears whose home ranges centroids were 10–20 km apart. This implies that an increase in reproductive synchrony, due indirectly to

harvest, conceivably could have a positive effect on population growth (Fig. 1), thus somewhat compensating for the negative effect of harvesting. However, this implication is theoretical and there is no empirical support for it.

Whereas hunting promotes SSI in Scandinavia, hunting can have the opposite effect in other populations and enhance cub survival (McLellan 2005). Male-biased hunting can reduce the OSR and may relax male–male competition and eventually reduce SSI risk (Miller et al. 2003, McLellan 2005). Such a mechanism has been suggested in several populations of North American brown bears (Miller et al. 2003; McLellan 2005, 2015) and American black bears (*Ursus americanus;* Czetwertynski et al. 2007, Obbard and Howe 2008). The role of OSRs in explaining variation in SSI and the potential effects on population growth rate may thus vary among bear populations according to local ecological and evolutionary constraints. It should be noted, however, that the occurrence of SSI in North America is a controversial subject. Little evidence of SSI has been found in several North American black and brown bear populations (Miller et al. 2003, McLellan 2005, Czetwertynski et al. 2007, Obbard and Howe 2008), although it has been reported in one study of American black bears (LeCount 1987).

The disruption of female social structure in bear populations has been studied less than for males. However, female social structure likely influences how females compete for the resources necessary for reproduction (Clutton-Brock and Huchard 2013). Indeed, female spatial distribution is one of the most important drivers of mating systems (Andersson 1994, Shuster and Wade 2003) and, for most mammals, including brown bears, the female is the more philopatric sex (Greenwood 1980). Harvest has altered dispersal rates in other large carnivores (Sweanor et al. 2000, Newby et al. 2013), which could have large impacts on female distribution and, consequently, population growth (Robinson et al. 2008, Cooley et al. 2009). Harvest effects on animal movement can also be more localized (e.g., inducing home range shifts [Lovallo and Anderson 1995]). Female–female competition for reproduction has been reported in our study area (Støen et al. 2006, Ordiz et al. 2008, Zedrosser et al. 2009), and female Scandinavian brown bears appear to exhibit a competitive release following the removal of nearby females through harvest (Frank et al. 2017). Reduced female–female competition through harvest may improve female condition and reproductive performance with a positive effect on population growth rate, although this remains to be documented.

Reproduction is suppressed in young philopatric female brown bears, with age of primiparity being higher for philopatric females compared with dispersers (Støen et al. 2006, Ordiz et al. 2008). Harvesting females could relax reproductive suppression and competition for food, favoring earlier reproduction and early cub survival (Zedrosser et al. 2009), which is expected to have a positive effect on population growth rate (Fig. 1). Competition among females for reproduction also occurs after primiparity; the probability of a female brown bear having cubs in a given year varies in relation with distance to the closest neighboring female and whether or not the latter has cubs (Ordiz et al. 2008). Thus, dominant pregnant adult female brown bears appear to inhibit reproduction in their female neighbors, imposing reproductive asynchrony (Ordiz et al. 2008). This reproductive asynchrony may be a factor limiting population growth, suggesting the existence of a population-regulatory nature that is typically found in social species, rather than solitary animals (Ordiz et al. 2008).

Dispersal in large carnivores has been shown to change as a result of harvest (e.g., Cooley et al. 2009), which could affect the distribution of females across the landscape (e.g., Robinson et al. 2008); there is some evidence of this in brown bears near the Swedish–Norwegian border (Bischof and Swenson 2012, Gilroy et al. 2015). The number of bears in Sweden has decreased in the past few years, as a result of higher hunting quotas (Swenson et al. 2017), and simultaneously the number of bears detected in Norway has decreased from 2009 to 2015 (Aarnes et al. 2016). The increased harvest in Sweden has probably reduced the dispersal of bears from the high-density areas and provided more vacancies in the nearby peripheral areas in Sweden, such as along the Norwegian border (Swenson et al. 1998a), which could result in reduced movement of bears into Norway. However, the effect of altered dispersal and female distribution on lambda is still unknown.

Indirect behavioral effects from hunting

Wildlife are generally sensitive to human-induced disturbances (e.g., see George and Crooks 2006 and references therein). Bears are no exception and generally avoid people and their activities (e.g., Peyton et al. [1998] for Andean bears [*Tremarctos ornatus*]; Goodrich and Berger [1994] and Stillfried et al. [2015] for American black bears; Fortin et al. [2016] for North American brown bears; Nellemann et al. [2007] and Ordiz et al. [2013b] for Scandinavian brown bears). Here we review

the effects caused by the disturbance of hunting on bears' behavior and their potential effects on population growth.

After encountering a human (e.g., a hunter), a Scandinavian brown bear's daily activity patterns are altered immediately and for several days (Moen et al. 2012, Ordiz et al. 2013b, Sahlén et al. 2015). At the onset of the hunting season, bears immediately alter their habitat use and movement pattern (Ordiz et al. 2011, 2012). Solitary bears increase their movement during the dark hours, losing their normal nocturnal rest, presumably to compensate for reduced diurnal activity (Ordiz et al. 2012, Hertel et al. 2016b). However, the change in movement patterns of females with cubs, which are legally protected from hunting, was much smaller in magnitude (17%) than that observed for solitary bears at the onset of the hunting season, perhaps because they still have to meet the elevated energy requirements of maternal care (Ordiz et al. 2012).

An important question is whether the consequences of hunter-caused disturbances are great enough to influence population growth. To maximize food intake, foraging bears select locations providing the biggest energetic gain (Hertel et al. 2016a) or forage at times when prey detection is easiest (MacHutchon et al. 1998) and prey are most vulnerable (Klinka and Reimchen 2002, 2009). For instance, brown bears are very efficient in preying on Pacific salmon (*Oncorhynchus* spp.) and reindeer calves (*Rangifer tarandus*) at night (Klinka and Reimchen 2002, Ordiz et al. 2017), whereas bears forage in the best berry habitat patches during the crepuscular and light hours (McLellan and McLellan 2015, Hertel et al. 2016b). Bears have a limited period to acquire resources prior to hibernation, so any alteration to their foraging behavior may have negative effects on their body condition and fitness (Hertel et al. 2016b).

Hunting can be perceived by bears as a predation risk (Ordiz et al. 2011, Sahlén et al. 2015, Steyaert et al. 2016a), forcing them to increase vigilance at the expense of foraging activity during the hunting season and therefore suggesting that a human-induced landscape of fear exists in our hunted population of brown bears (Sahlén et al. 2015, Støen et al. 2015, Steyaert et al. 2016b). Similar findings have been reported in ungulates (Lone et al. 2014) and other large carnivores (Oriol-Cotterill et al. 2015), including black bears (Laske et al. 2011, Stillfried et al. 2015). Hunting can thus induce behavioral changes that may carry nutritional costs because of decreased energy intake and/or increased energy expenditure (Lima and Dill 1990). During the hunting season in Sweden, bears reduce their foraging activity and, even while foraging, pay a nutritional cost by using less

productive berry patches when mortality risk is greatest (Hertel et al. 2016b). Foraging activity and efficiency remain unaffected during less risky times, so bears appear to be unable to compensate for lost foraging opportunities (Hertel et al. 2016b). Efficient foraging is particularly important in critical phases of energy expenditure or weight gain (e.g., during lactation or preparation for hibernation; Farley and Robbins 1995, López-Alfaro et al. 2013). In years of food shortage, bears may not be able to trade off forage intake with anti-predation behaviors (Johnson et al. 2015), which might make them more vulnerable to hunting.

No study, however, has yet documented quantitatively that these recreational-caused effects on behavior depress food intake to the point that it decreases bear reproduction or survival (Fortin et al. 2016; Fig. 1). This may be because bears seem to be flexible in exhibiting compensatory foraging in disturbance-free periods (Ayres et al. 1986, Beckmann and Berger 2003) or switching to alternative food resources away from risky areas (Rode et al. 2007). Nevertheless, the topic warrants further research.

Human-induced selection and potential evolutionary effects

Harvest by hunting is usually selective, whether intentionally, through conscious selection by hunters and regulations, or unintentionally, through the interplay between individual variation in spatial and temporal vulnerability (Festa-Bianchet 2003, Fenberg and Roy 2008, Bunnefeld et al. 2009). When there is opportunity for a choice, hunters usually show preferences for particular traits (Mysterud 2011). There are several examples of negative selective and demographic effects of size-selective harvesting and trophy hunting in fishes and ungulates (Coltman et al. 2003, Garel et al. 2007, Jørgensen et al. 2007, Allendorf and Hard 2009). However, there is little evidence from large carnivores (but see Loveridge et al. [2007] for a demographic effect in African lions [*Panthera leo*]). In North America, hunters may show preference toward larger and older bears, mostly males (McLellan and Shackleton 1988, Kohlmann et al. 1999). The disproportionate removal of older and male bears could disrupt population age and sex structure (see above), but it could also artificially select for smaller and less reproductively successful phenotypes.

Hunter selectivity does not depend only on animal morphology, but also on the hunting methods used, harvest intensity, and management regulations (Mysterud 2011). For example, harvest could select for behavioral traits

(Leclerc et al. 2017b), and restrictions limiting hunting to daylight hours could select for more nocturnal bears. In addition, it has been suggested that the long persecution period of brown bears in Europe might explain why bears are generally more nocturnal in Europe than in North America (Swenson 1999, Ordiz et al. 2011).

Legal protection of family groups is a common practice in bear management strategies in North America and Europe, including Sweden, and has often been stressed as a factor explaining bias in hunting data and differential vulnerability of age and sex classes to hunting (McLellan and Shackleton 1988, Kohlmann et al. 1999, Krofel et al. 2012, Leclerc et al. 2016a). The main consequence of legally protecting family groups is the protection of adult females with offspring and the increased selective harvest of males and solitary females (Solberg et al. 2000, Zedrosser et al. 2013, Rughetti and Festa-Bianchet 2014). Females may gain a fitness benefit through increased survival when associating longer with dependent offspring (Zedrosser et al. 2013, Leclerc et al. 2016a); therefore, legal protection of family groups can select for longer periods of maternal care (J. Van de Walle et al., unpublished data). The strength of this selective pressure depends on harvest intensity, but also on the duration of maternal care and the timing of the hunting period (before or after weaning time; McLellan and Shackleton 1988), which varies among bear populations. Nevertheless, in Scandinavia we have witnessed a general increase in the average duration of maternal care in recent years (Leclerc et al. 2016a), which may have adverse consequences on recruitment and population growth rate. On the other hand, protecting adult females (i.e., the demographic parameter depicting the greatest elasticity on population growth) should also result in a greater population growth (Knight and Eberhardt 1985, Gosselin et al. 2015), potentially compensating for reduced reproductive output.

Even in the absence of apparent selectivity by hunters or hunting regulation, there is usually heterogeneity in individual vulnerability to hunting. Bolder and more active individuals are more frequently caught in traps or killed by hunters in several species (Biro and Post 2008, Ciuti et al. 2012, Leclerc et al. 2017b). In Sweden, hunters do not kill bears randomly within the landscape, but generally kill them closer to human infrastructure (Steyaert et al. 2016b). In addition, the individual differences in habitat selection patterns found in Scandinavia (Leclerc et al. 2016b) could lead to different levels of vulnerability to hunting. Behaviors are often heritable; therefore, we could expect evolutionary changes in response to harvest-induced selection (Postma 2014, Dochtermann

et al. 2015). For example, it was suggested that the wariness of brown bears in Scandinavia may be an adaptation resulting from the long-term human persecution that almost eradicated the species by 1930 (Swenson et al. 1995).

Even in the absence of age, sexual, morphological, and behavioral selectivity, high mortality rates can exert selective pressure on life-history traits (Festa-Bianchet 2003, Olsen et al. 2004). Higher mortality rates select for reproduction at smaller size and younger age (Stearns 1992); therefore, hunting can select for larger investment in reproduction (Festa-Bianchet 2003, Law 2007, Darimont et al. 2009) and accelerate life histories (Servanty et al. 2011). Centuries of brown bear persecution in Europe may have selected for faster life histories, potentially explaining why females there reproduce earlier and produce more cubs relative to their body mass compared with their North American counterparts (Zedrosser et al. 2011). This "ghost of persecution past" may explain why the historically heavily persecuted Swedish population has one of the fastest life histories documented (reviewed in Nawaz et al. 2008) and can now sustain relatively high levels of harvest.

Although evolution was once thought to be a process occurring over a very long time including many generations, recent studies show that evolution can occur over just a few generations (Olsen et al. 2004, Kvalnes et al. 2016, Pigeon et al. 2016) and influence ecological processes (Pelletier et al. 2009). Human-induced selection has the potential to cause rapid phenotypic changes (Darimont et al. 2009) and hard-to-reverse evolutionary changes in exploited populations (Palumbi 2001, Olsen et al. 2004, Pigeon et al. 2016). Therefore, it represents one of the most pervasive effects of hunting, warranting caution when making management decisions (Festa-Bianchet 2003, Jørgensen et al. 2007).

Concluding remarks

Usually managers focus on the effects of direct harvest mortality on vital rates and population growth rate (e.g., Miller 1990) and rarely consider indirect effects of hunting (Milner et al. 2007, Pauli and Buskirk 2007, Ordiz et al. 2013a). In this review, we show both statistically supported evidence and reason to suspect that indirect effects of hunting can have measurable effects on a population's growth rate (Fig. 1). We have concentrated on the Scandinavian population of brown bears because it is a particularly well-studied system since the 1980s, but we suggest that indirect effects of hunting on population dynamics is likely a general phenomenon. In addition,

hunting can cause human-induced selection, which may further affect vital rates and population growth in the long-term. Our focus on brown bears alone has excluded the indirect and potential evolutionary effect of bear harvest on community and ecosystems processes. Hunting bears and other large carnivores also could affect their ecological role in an ecosystem (Ordiz et al. 2013a), and indirectly affect other species in the trophic network. For example, Scandinavian bears can have a strong, lasting effect on the behavior of their prey species, such as moose (*Alces alces;* Sahlén et al. 2016), and may affect the expansion patterns and predation rates of other large carnivores, such as the gray wolf (*Canis lupus;* Ordiz et al. 2015, Tallian et al. 2017). Such information on interspecific interactions is also useful for management, for instance, to adjust hunting quotas of ungulates that are both hunted and predated upon by bears and sympatric wolves (Jonzén et al. 2013).

The main point of our review is to stress that indirect effects of harvest deserve more attention by managers because they can influence population growth rates. Some of the effects have been documented and most certainly exist (Fig. 1), but indirect and evolutionary effects are generally more difficult to document and quantify than direct effects of harvest. We found 2 quantitative estimates of indirect effects of hunting of bears on lambda; an increased mortality of cubs of the year due to SSI in brown bears in Scandinavia (Swenson et al. 1997, 2001; Gosselin et al. 2015, 2017), and a reduced reproductive rate of female grizzly bears in Alberta due to females selecting less productive sites as a counter strategy to SSI (Wielgus et al. 2001b).

In societies where wildlife management is an important public issue (e.g., where wildlife populations are managed under the public trust doctrine; Batcheller et al. 2010, Treves et al. 2017), the public may increasingly require that managers not only document the direct, numerical effects of management decisions, but also their indirect and potential human-induced selection effects. Although research on indirect effects of hunting on fitness is difficult and requires long-term monitoring of individuals in a population that has experienced different harvest rates, it is an important responsibility for managers to carry out or fund research on this topic. Long-term monitoring of harvest effects on bears also provides opportunities for managers to make informed decisions while considering uncertainty (Regehr et al. 2017). As we await the outcome of such research, managers of bear populations should adopt a precautionary approach and assume that indirect effects do exist and have a potential impact on bear population structure and growth that may differ from that predicted by harvest models based on direct effects alone.

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