

Indirect effects of bear hunting: a review from Scandinavia

Author(s): Shane C. Frank, Andrés Ordiz, Jacinthe Gosselin, Anne Hertel, Jonas Kindberg, Martin Leclerc, Fanie Pelletier, Sam M. J. G. Steyaert, Ole-Gunnar Støen, Joanie Van de Walle, Andreas Zedrosser, and Jon E. Swenson

Source: *Ursus*, 28(2):150-164.

Published By: International Association for Bear Research and Management

<https://doi.org/10.2192/URSU-D-16-00028.1>

URL: <http://www.bioone.org/doi/full/10.2192/URSU-D-16-00028.1>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Indirect effects of bear hunting: a review from Scandinavia

Shane C. Frank^{1,7}, Andrés Ordiz², Jacinthe Gosselin³, Anne Hertel², Jonas Kindberg^{4,5}, Martin Leclerc³, Fanie Pelletier³, Sam M. J. G. Steyaert^{1,2}, Ole-Gunnar Støen^{2,4}, Joanie Van de Walle³, Andreas Zedrosser^{1,6}, and Jon E. Swenson^{2,4}

¹Faculty of Arts and Sciences, Department of Environmental and Health Studies, University College of Southeast Norway, NO-3800 Bø i Telemark, Norway

²Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, NO-1432 Ås, Norway

³Département de Biologie, Canada Research Chair in Evolutionary Demography, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada

⁴Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

⁵Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-90183 Umeå, Sweden

⁶Institute for Wildlife Biology and Game Management, University for Natural Resources and Life Sciences, Vienna, Gregor Mendel Str. 33, A-1180 Vienna, Austria

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*

DOI: 10.2192/URSUS-D-16-00028.1

Ursus 28(2):150–164 (2017)

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

⁷email: shane.frank@usn.no

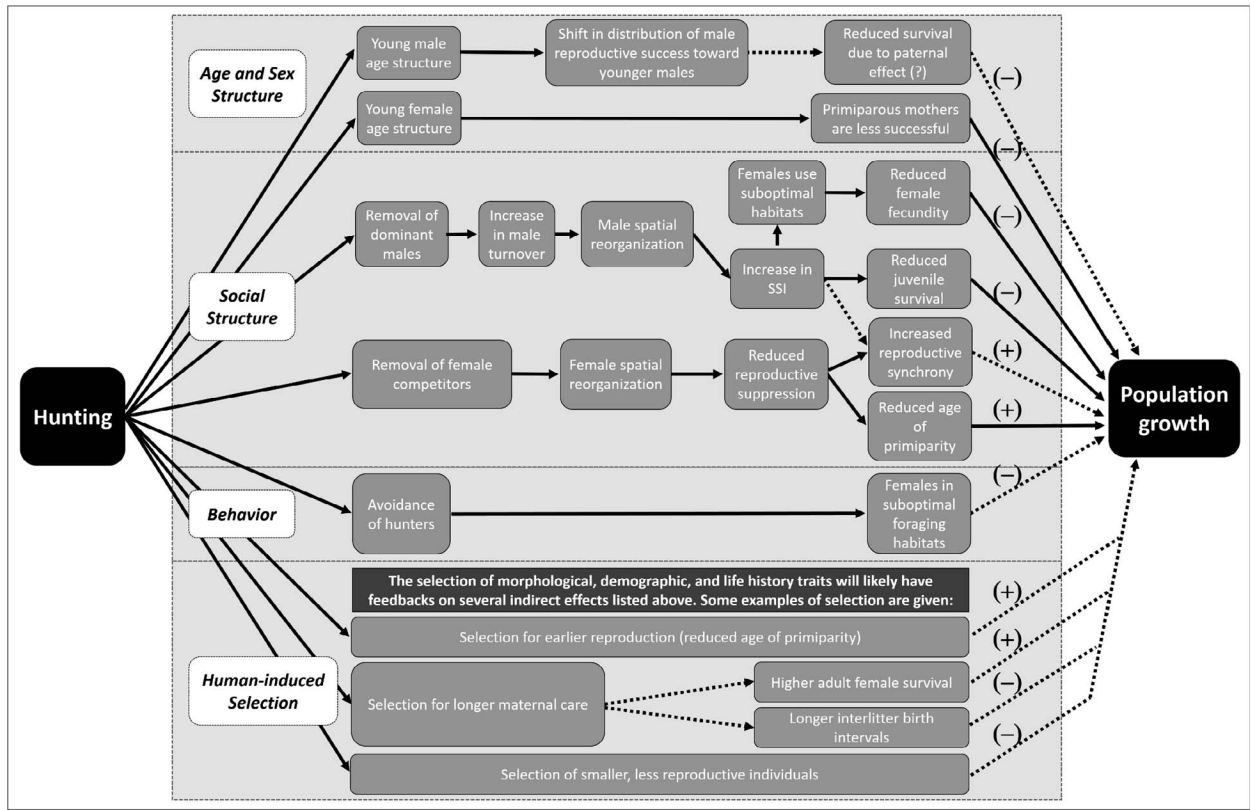


Fig. 1. A summary of the indirect effects on population growth of bear hunting discussed in this paper. The solid arrows show relationships that have been documented statistically and the dotted arrows show potential relationships. Effects on population growth are noted in parentheses along the lines 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 km²; termed “north”), and one in central Sweden–southeastern Norway from 1985 to the present (13,000 km²; 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 km² in the north and reaches approximately 30 bears/1,000 km² 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-

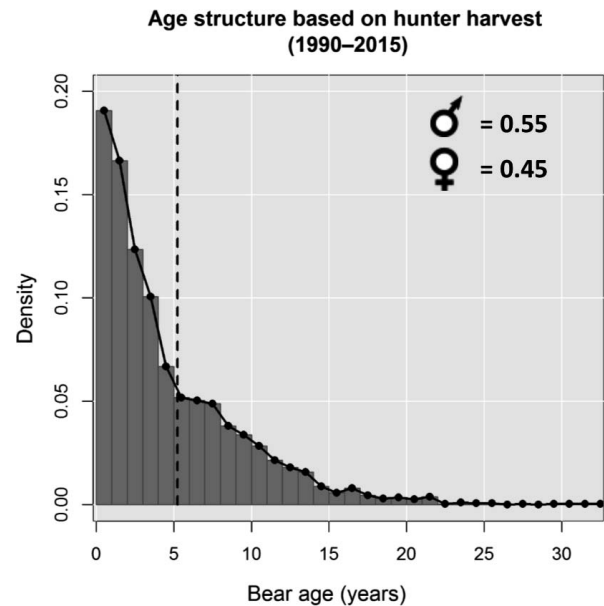


Fig. 2. The age structure of hunter-killed brown bears (*Ursus arctos*) in Sweden during 1990–2015. The vertical dotted line shows the mean age of bears (approx. 5 yr) killed. The frequencies of males and females harvested are shown.

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 (Sweaner 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 (Myserud 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 (Myserud 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, Rugghetti 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 λ ; 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.

Acknowledgments

This is scientific publication No. 237 from the Scandinavian Brown Bear Research Project, which was funded by the Swedish Environmental Protection Agency, the Norwegian Environmental Agency, the Austrian Science Fund, the Research Council of Norway, and the Swedish Association for Hunting and Wildlife Management. We acknowledge the support of the Center for Advanced Study in Oslo, Norway, which funded and hosted our research project “Climate effects on harvested large mammal populations” during the academic year of 2015–2016, and funding from the Polish–Norwegian Research Program operated by the National Center for Research and Development under the Norwegian Financial Mechanism 2009–2014 in the frame of Project Contract No. POL354 NOR/198352/85/2013. We thank G. Kvelprud Moen and R. Bischof for comments on previous versions of the manuscript; and the Associate Editor and reviewers for their suggestions.

Literature cited

- AARNES, S.G., C. TOBIASSEN, H. BRØSETH, B.B. BAKKE, H.G. EIKEN, AND S.B. HAGEN. 2016. Population surveying of brown bear: DNA analysis of sampled collected in Norway in 2015. Norwegian Institute for Bioeconomy Research Technical Report Volume 2: Nr. 56:1–73. [In Norwegian.]
- AGRELL, J., J.O. WOLFF, AND H. YLÖNEN. 1998. Counterstrategies to infanticide in mammals: Costs and consequences. *Oikos* 83:507–517.
- ALLENDDORF, F.W., AND J.J. HARD. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences* 106:9987–9994.
- ANDERSSON, M. 1994. Sexual selection. Princeton University Press, Princeton, New Jersey, USA.
- ARNEMO, J.M., A. EVANS, AND Å. FAHLMAN. 2011. Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. Norwegian Directorate for Nature Management, Trondheim, Norway.
- AUSBAND, D.E., C.R. STANSBURY, J.L. STENGLIN, J.L. STRUTHERS, AND L.P. WAITS. 2015. Recruitment in a social carnivore before and after harvest. *Animal Conservation* 18:415–423.
- AYRES, L.A., L.S. CHOW, AND D.M. GRABER. 1986. Black bear activity patterns and human induced modifications in Sequoia National Park. *Ursus* 6:151–154.
- BATCHELLER, G.R., M.C. BAMBERY, L. BIES, T. DECKER, S. DYKE, D. GUYNN, M. MCENROE, M. O'BRIEN, J.F. ORGAN, S.J. RILEY, AND G. ROEHM. 2010. The public trust doctrine: Implications for wildlife management and conservation in

- the United States and Canada. *The Wildlife Society Technical Review* 10-01:1–29.
- BECKMANN, J.P., AND J. BERGER. 2003. Rapid ecological and behavioural changes in carnivores: The responses of black bears (*Ursus americanus*) to altered food. *Journal of Zoology* 261:207–212.
- BELLEMANN, E., J.E. SWENSON, AND P. TABERLET. 2006a. Mating strategies in relation to sexually selected infanticide in a non-social carnivore: The brown bear. *Ethology* 112:238–246.
- , A. ZEDROSSER, S. MANEL, L.P. WAITS, P. TABERLET, AND J.E. SWENSON. 2006b. The dilemma of female mate selection in the brown bear, a species with sexually selected infanticide. *Proceedings of the Royal Society B* 273:283–291.
- BIRO, P.A., AND J.R. POST. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences* 105:2919–2922.
- BISCHOF, R., R. FUJITA, A. ZEDROSSER, A. SODERBERG, AND J.E. SWENSON. 2008. Hunting patterns, ban on baiting, and harvest demographics of brown bears in Sweden. *Journal of Wildlife Management* 72:79–88.
- , AND J.E. SWENSON. 2012. Linking noninvasive genetic sampling and traditional monitoring to aid management of a trans-border carnivore population. *Ecological Applications* 22:361–373.
- , ———, N.G. YOCOZO, A. MYSTERUD, AND O. GIMENEZ. 2009. The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology* 78:656–665.
- BUNNEFELD, N., D. BAINES, D. NEWBORN, AND E.J. MILNER-GULLAND. 2009. Factors affecting unintentional harvesting selectivity in a monomorphic species. *Journal of Animal Ecology* 78:485–492.
- CAUGHLEY, G. 1977. *Analysis of vertebrate populations*. John Wiley and Sons, New York, New York, USA.
- CIUTI, S., T.B. MUHLY, D.G. PATON, A.D. MCDEVITT, M. MUSIANI, AND M.S. BOYCE. 2012. Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B* 279:4407–4416.
- CLUTTON-BROCK, T., AND E. HUCHARD. 2013. Social competition and its consequences in female mammals. *Journal of Zoology* 289:151–171.
- COLTMAN, D., P. O'DONOGHUE, J. JORGENSEN, J.T. HOGG, C. STROBECK, AND M. FESTA-BIANCHET. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426:655–658.
- 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. *Animal Conservation* 12:321–328.
- CZETWERTYNSKI, S.M., M.S. BOYCE, AND F.K. SCHMIEGELOW. 2007. Effects of hunting on demographic parameters of American black bears. *Ursus* 18:1–18.
- DAHLE, B., AND J.E. SWENSON. 2003. Factors influencing length of maternal care in brown bears (*Ursus arctos*) and its effect on offspring. *Behavioral Ecology and Sociobiology* 54:352–358.
- DARIMONT, C.T., S.M. CARLSON, M.T. KINNISON, P.C. PAQUET, T.E. REIMCHEN, AND C.C. WILMERS. 2009. Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences* 106:952–954.
- DEROCHER, A.E., I. STIRLING, AND W. CALVERT. 1997. Male-biased harvesting of polar bears in western Hudson Bay. *Journal of Wildlife Management* 61:1075–1082.
- DOCHTERMANN, N.A., T. SCHWAB, AND A. SIH. 2015. The contribution of additive genetic variation to personality variation: Heritability of personality. *Proceedings of the Royal Society B* 282:20142201.
- DOUHARD, M., M. FESTA-BIANCHET, D.W. COLTMAN, AND F. PELLETIER. 2016. Paternal reproductive success drives sex allocation in a wild mammal. *Evolution* 70:358–368.
- EBENSPERGER, L.A. 1998. Strategies and counterstrategies to infanticide in mammals. *Biological Reviews* 73: 321–346.
- FARLEY, S.D., AND C.T. ROBBINS. 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Canadian Journal of Zoology* 73:2216–2222.
- FATTEBERT, J., G.A. BALME, H.S. ROBINSON, T. DICKERSON, R. SLOTOW, AND L.T.B. HUNTER. 2016. Population recovery highlights spatial organization dynamics in adult leopards. *Journal of Zoology* 299:153–162.
- FENBERG, P.B., AND K. ROY. 2008. Ecological and evolutionary consequences of size-selective harvesting: How much do we know? *Molecular Ecology* 17:209–220.
- FESTA-BIANCHET, M. 2003. Exploitative wildlife management as a selective pressure for the life-history evolution of large mammals. Pages 191–207 in M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, DC, USA.
- FORTIN, J.K., K.D. RODE, G.V. HILDERBRAND, J. WILDER, S. FARLEY, C. JORGENSEN, AND B.G. MARCOT. 2016. Impacts of human recreation on brown bears (*Ursus arctos*): A review and new management tool. *PLoS ONE* 11:e0141983.
- FRANK, S.C., M. LECLERC, F. PELLETIER, F. ROSELL, J.E. SWENSON, R. BISCHOF, J. KINDBERG, H. EIKEN, S.B. HAGEN, AND A. ZEDROSSER. 2017. Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting. *Journal of Animal Ecology* 00: 1–12.
- FRYXELL, J.M., A.R.E. SINCLAIR, AND G. CAUGHLEY. 2014. *Wildlife ecology, conservation, and management*. Third edition. John Wiley & Sons Limited, West Sussex, UK.
- GAREL, M., J.-M. CUGNASSE, D. MAILLARD, J.-M. GAILLARD, A.J.M. HEWISON, AND D. DUBRAY. 2007. Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecological Applications* 17:1607–1618.

- GEORGE, S.L., AND K.R. CROOKS. 2006. Recreation and large mammal activity in an urban nature reserve. *Biological Conservation* 133:107–117.
- GILROY, J.J., A. ORDIZ, AND R. BISCHOF. 2015. Carnivore coexistence: Value the wilderness. *Science* 347:382.
- GINSBERG, J.R., AND E.J. MILNER-GULLAND. 1994. Sex-biased harvesting and population dynamics in ungulates: Implications for conservation and sustainable use. *Conservation Biology* 8:157–166.
- GOODRICH, J.M., AND J. BERGER. 1994. Winter recreation and hibernating black bears *Ursus americanus*. *Biological Conservation* 67:105–110.
- GOSSELIN, J., M. LECLERC, A. ZEDROSSER, S.M.J.G. STEYAERT, J.E. SWENSON, AND F. PELLETIER. 2017. Hunting promotes sexual conflict in brown bears. *Journal of Animal Ecology* 86:35–42.
- , A. ZEDROSSER, J.E. SWENSON, AND F. PELLETIER. 2015. The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. *Proceedings of the Royal Society B: Biological Sciences* 282:20141840.
- GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- HERTEL, A.G., S.M. STEYAERT, A. ZEDROSSER, A. MYSTERUD, H.K. LODBERG-HOLM, H.W. GELINK, J. KINDBERG, AND J.E. SWENSON. 2016a. Bears and berries: Species-specific selective foraging on a patchily distributed food resource in a human-altered landscape. *Behavioral Ecology and Sociobiology* 70:831–842.
- , A. ZEDROSSER, A. MYSTERUD, O.G. STOEN, S.M. STEYAERT, AND J.E. SWENSON. 2016b. Temporal effects of hunting on foraging behavior of an apex predator: Do bears forego foraging when risk is high? *Oecologia* 182:1019–1029.
- HRDY, S.B. 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* 1:13–40.
- JOHNSON, H.E., S.W. BRECK, S. BARUCH-MORDO, D.L. LEWIS, C.W. LACKEYE, K.R. WILSON, J. BRODERICK, J.S. MAO, AND J.P. BECKMANN. 2015. Shifting perceptions of risk and reward: Dynamic selection for human development by black bears in the western United States. *Biological Conservation* 187:164–172.
- JONZÉN, N., H. SAND, P. WABAKKEN, J.E. SWENSON, J. KINDBERG, O. LIBERG, AND G. CHAPRON. 2013. Sharing the bounty—Adjusting harvest to predator return in the Scandinavian human–wolf–bear–moose system. *Ecological Modelling* 265:140–148.
- JØRGENSEN, C., K. ENBERG, E.S. DUNLOP, R. ARLINGHAUS, D.S. BOUKAL, K. BRANDER, B. ERNANDE, A. GÅRDMARK, F. JOHNSTON, S. MATSUMURA, H. PARDOE, K. RAAB, A. SILVA, A. VAINIKKA, U. DIECKMANN, M. HEINO, AND A.D. RIJNSDROP. 2007. Managing evolving fish stocks. *Science* 318:1247–1248.
- KINDBERG, J., J.E. SWENSON, G. ERICSSON, E. BELLEMMAIN, C. MIQUEL, AND P. TABERLET. 2011. Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biology* 17:114–123.
- KLINKA, D.R., AND T.E. REIMCHEN. 2002. Nocturnal and diurnal foraging behaviour of brown bears (*Ursus arctos*) on a salmon stream in coastal British Columbia. *Canadian Journal of Zoology* 80:1317–1322.
- , AND ———. 2009. Darkness, twilight, and daylight foraging success of bears (*Ursus americanus*) on salmon in coastal British Columbia. *Journal of Mammalogy* 90:144–149.
- KNIGHT, R.R., AND L.L. EBERHARDT. 1985. Population dynamics of Yellowstone grizzly bears. *Ecology* 66:323–334.
- KOHLMANN, S.G., R.L. GREEN, AND C.E. TRAINER. 1999. Effects of collection method on sex and age composition of black bear (*Ursus americanus*) harvest in Oregon. *Northwest Science* 73:34–38.
- KROFEL, M., M. JONOZOVIĆ, AND K. JERINA. 2012. Demography and mortality patterns of removed brown bears in a heavily exploited population. *Ursus* 23:91–103.
- KVALNES, T., B.-E. SÆTHER, H. HAANES, K.H. RØED, S. ENGEN, AND E.J. SOLBERG. 2016. Harvest-induced phenotypic selection in an island population of moose, *Alces alces*. *Evolution* 70:1486–1500.
- LASKE, T.G., D.L. GARSHELIS, AND P.A. IAIZZO. 2011. Monitoring the wild black bear's reaction to human and environmental stressors. *BMC Physiology* 11:13.
- LAW, R. 2007. Fisheries-induced evolution: Present status and future directions. *Marine Ecology Progress Series* 335:271–277.
- LECLERC, M., S.C. FRANK, A. ZEDROSSER, J.E. SWENSON, AND F. PELLETIER. 2017a. Hunting promotes spatial reorganization and sexually selected infanticide. *Scientific Reports* 7:45222.
- , J. VAN DE WALLE, A. ZEDROSSER, J.E. SWENSON, AND F. PELLETIER. 2016a. Can hunting data be used to estimate unbiased population parameters? A case study on brown bears. *Biology Letters* 12:20160197.
- , E. VANDER WAL, A. ZEDROSSER, J.E. SWENSON, J. KINDBERG, AND F. PELLETIER. 2016b. Quantifying consistent individual differences in habitat selection. *Oecologia* 180:697–705.
- , A. ZEDROSSER, F. PELLETIER, AND M.-A. VILLARD. 2017b. Harvesting as a potential selective pressure on behavioural traits. *Journal of Applied Ecology*. doi: 10.1111/1365-2664.12893.
- LECOUNT, A.L. 1987. Causes of black bear cub mortality. *International Conference on Bear Research and Management* 7:75–82.
- LIMA, S.L., AND L.M. DILL. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619–640.

- LINDSEY, P., P. ROULET, AND S. ROMANACH. 2007. Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation* 134:455–469.
- LINNELL, J., V. SALVATORI, AND L. BOITANI. 2008. Guidelines for population level management plans for large carnivores in Europe. A Large Carnivore Initiative for Europe report prepared for the European Commission (contract 070501/2005/424162/MAR/B2). http://ec.europa.eu/environment/nature/conservation/species/carnivores/pdf/guidelines_for_population_level_management.pdf. Accessed 15 Sep 2017.
- LINNELL, J.D., H. BROSETH, J. ODDEN, AND E.B. NILSEN. 2010. Sustainably harvesting a large carnivore? Development of Eurasian lynx populations in Norway during 160 years of shifting policy. *Environmental Management* 45: 1142–1154.
- LONE, K., L.E. LOE, T. GOBAKKEN, J.D.C. LINNELL, J. ODDEN, J. REMMEN, AND A. MYSTERUD. 2014. Living and dying in a multi-predator landscape of fear: Roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos* 123:641–651.
- LÓPEZ-ALFARO, C., C.T. ROBBINS, A. ZEDROSSER, AND S.E. NIELSEN. 2013. Energetics of hibernation and reproductive trade-offs in brown bears. *Ecological Modelling* 270:1–10.
- LOVALLO, M.J., AND E.M. ANDERSON. 1995. Range shift by a female bobcat (*Lynx rufus*) after removal of neighboring female. *American Midland Naturalist* 134:409.
- LOVERIDGE, A., A. SEARLE, F. MURINDAGOMO, AND D. MACDONALD. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation* 134:548–558.
- MACHUTCHON, A.G., S. HIMMER, H. DAVIS, AND M. GALLAGHER. 1998. Temporal and spatial activity patterns among coastal bear populations. *Ursus* 10:539–546.
- MALETZKE, B.T., R. WIELGUS, G.M. KOEHLER, M. SWANSON, H. COOLEY, AND J.R. ALLDREDGE. 2014. Effects of hunting on cougar spatial organization. *Ecology and Evolution* 4:2178–2185.
- MARTIN, A.M., M. FESTA-BIANCHET, D.W. COLTMAN, AND F. PELLETIER. 2014. Sexually antagonistic association between paternal phenotype and offspring viability reinforces total selection on a sexually selected trait. *Biology Letters* 10:20140043.
- MCLELLAN, B.N. 2005. Sexually selected infanticide in grizzly bears: The effects of hunting on cub survival. *Ursus* 16:141–156.
- . 2015. Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *Journal of Wildlife Management* 79:749–765.
- , AND D.M. SHACKLETON. 1988. A comparison of grizzly bear harvest data from Montana and southeastern British Columbia. *Wildlife Society Bulletin* 16:371–375.
- MCLELLAN, M.L., AND B.N. MCLELLAN. 2015. Effect of season and high ambient temperature on activity levels and patterns of grizzly bears (*Ursus arctos*). *PLoS ONE* 10:e0117734.
- MILLER, S.D. 1990. Population management of bears in North America. *International Conference on Bear Research and Management* 8:357–373.
- , R.A. SELLERS, AND J.A. KEAY. 2003. Effects of hunting on brown bear cub survival and litter size in Alaska. *Ursus* 14:130–152.
- MILNER, J.M., E.B. NILSEN, AND H. ANDREASSEN. 2007. Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology* 21:36–47.
- MOEN, G.K., O.G. STOEN, V. SAHLEN, AND J.E. SWENSON. 2012. Behaviour of solitary adult Scandinavian brown bears (*Ursus arctos*) when approached by humans on foot. *PLoS ONE* 7:e31699.
- MYSTERUD, A. 2011. Selective harvesting of large mammals: How often does it result in directional selection? *Journal of Applied Ecology* 48:827–834.
- NAWAZ, M.A., J.E. SWENSON, AND V. ZAKARIA. 2008. Pragmatic management increases a flagship species, the Himalayan brown bears, in Pakistan's Deosai National Park. *Biological Conservation* 141:2230–2241.
- NELLEMAN, C., O.-G. STØEN, J. KINDBERG, J.E. SWENSON, I. VISTNES, G. ERICSSON, J. KATAJISTO, B.P. KALTENBORN, J. MARTIN, AND A. ORDIZ. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation* 138:157–165.
- NEWBY, J.R., L. SCOTT MILLS, T.K. RUTH, D.H. PLETSCHER, M.S. MITCHELL, H.B. QUIGLEY, K.M. MURPHY, AND R. DESIMONE. 2013. Human-caused mortality influences spatial population dynamics: Pumas in landscapes with varying mortality risks. *Biological Conservation* 159:230–239.
- NOYCE, K.V., AND D.L. GARSHELIS. 1997. Influence of natural food abundance on black bear harvests in Minnesota. *Journal of Wildlife Management* 61:1067–1074.
- OBBARD, M.E., AND E.J. HOWE. 2008. Demography of black bears in hunted and unhunted areas of the boreal forest of Ontario. *Journal of Wildlife Management* 72:869–880.
- OLSEN, E.M., M. HEINO, G.R. LILLY, M.J.J. MORGAN, J. BRATTEY, B. ERNANDE, AND U. DIECKMANN. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932–935.
- ORDIZ, A., R. BISCHOF, AND J.E. SWENSON. 2013a. Saving large carnivores, but losing the apex predator? *Biological Conservation* 168:128–133.
- , C. MILLERET, J. KINDBERG, J. MÅNSSON, P. WABAKKEN, J.E. SWENSON, AND H. SAND. 2015. Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. *Ecosphere* 6:1–14.
- , S. SAEBØ, J. KINDBERG, J.E. SWENSON, AND O.G. STØEN. 2017. Seasonality and human disturbance alter brown bear activity patterns: Implications for circumpolar carnivore conservation? *Animal Conservation* 20: 51–60.

- , O.G. STØEN, M. DELIBES, AND J.E. SWENSON. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* 166:59–67.
- , ———, S. SÆBØ, J. KINDBERG, M. DELIBES, AND J.E. SWENSON. 2012. Do bears know they are being hunted? *Biological Conservation* 152:21–28.
- , ———, ———, V. SAHLÉN, B.E. PEDERSEN, J. KINDBERG, AND J.E. SWENSON. 2013b. Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology* 50:306–314.
- , ———, J.E. SWENSON, I. KOJOLA, AND R. BISCHOF. 2008. Distance-dependent effect of the nearest neighbor: Spatiotemporal patterns in brown bear reproduction. *Ecology* 89:3327–3335.
- ORIOLO-COTTERILL, A., D.W. MACDONALD, M. VALEIX, S. EK-WANGA, AND L.G. FRANK. 2015. Spatiotemporal patterns of lion space use in a human-dominated landscape. *Animal Behaviour* 101:27–39.
- PACKER, C., M. KOSMALA, H.S. COOLEY, H. BRINK, L. PINTEA, D. GARSHELIS, G. PURCHASE, M. STRAUSS, A. SWANSON, G. BALME, L. HUNTER, AND K. NOWELL. 2009. Sport hunting, predator control and conservation of large carnivores. *PLoS ONE* 4:e5941.
- PALOMBIT, R.A. 2015. Infanticide as sexual conflict: Coevolution of male strategies and female counterstrategies. *Cold Spring Harbor Perspectives in Biology*. doi: 10.1101/cshperspect.a017640.
- PALUMBI, S.R. 2001. Humans as the world's greatest evolutionary force. *Science* 293:1786–1790.
- PAULI, J.N., AND S.W. BUSKIRK. 2007. Risk-disturbance overrides density dependence in a hunted colonial rodent, the black-tailed prairie dog *Cynomys ludovicianus*. *Journal of Applied Ecology* 44:1219–1230.
- PELLETIER, F., D. GARANT, AND A.P. HENDRY. 2009. Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society B* 364:1483–1489.
- PEYTON, B., E. YERENA, D.I. RUMIZ, J. JORGENSEN, AND J. OREJUELA. 1998. Status of wild Andean bears and policies for their management. *Ursus* 10:87–100.
- PIGEON, G., M. FESTA-BIANCHET, D.W. COLTMAN, AND F. PELLETIER. 2016. Intense selective hunting leads to artificial evolution in horn size. *Evolutionary Applications* 9:521–530.
- POSTMA, E. 2014. Four decades of estimating heritabilities in wild vertebrate populations: Improved methods, more data, better estimates? Pages 16–33 in A. Charmantier, D. Garant, AND L.E.B. Kruuk, editors. *Quantitative genetics in the wild*. Oxford University Press, Oxford, England, UK.
- REGEHR, E.V., R.R. WILSON, K.D. RODE, M.C. RUNGE, H.L. STERN, AND B. COLLEN. 2017. Harvesting wildlife affected by climate change: A modelling and management approach for polar bears. *Journal of Applied Ecology*. DOI: 10.1111/1365-2664.12864.
- ROBINSON, H.S., R.B. WIELGUS, H.S. COOLEY, AND S.W. COOLEY. 2008. Sink populations in carnivore management: Cougar demography and immigration in a hunted population. *Ecological Applications* 18:1028–1037.
- RODE, K.D., S.D. FARLEY, J. FORTIN, AND C.T. ROBBINS. 2007. Nutritional consequences of experimentally introduced tourism in brown bears. *Journal of Wildlife Management* 71:929–939.
- RUGHETTI, M., AND M. FESTA-BIANCHET. 2014. Effects of selective harvest of non-lactating females on chamois population dynamics. *Journal of Applied Ecology* 51: 1075–1084.
- RUTLEDGE, L.Y., B.R. PATTERSON, K.J. MILLS, K.M. LOVELESS, D.L. MURRAY, AND B.N. WHITE. 2010. Protection from harvesting restores the natural social structure of eastern wolf packs. *Biological Conservation* 143: 332–339.
- SAHLÉN, E., S. NOELL, C.S. DEPERNO, J. KINDBERG, G. SPONG, AND J.P.G.M. CROMSIGT. 2016. Phantoms of the forest: Legacy risk effects of a regionally extinct large carnivore. *Ecology and Evolution* 6:791–799.
- SAHLÉN, V., A. ORDIZ, J.E. SWENSON, AND O.-G. STØEN. 2015. Behavioural differences between single Scandinavian brown bears (*Ursus arctos*) and females with dependent young when experimentally approached by humans. *PLoS ONE* 10:e0121576.
- SERVANTY, S., J.-M. GAILLARD, F. RONCHI, S. FOCARDI, É. BAUDET, AND O. GIMENEZ. 2011. Influence of harvesting pressure on demographic tactics: Implications for wildlife management. *Journal of Applied Ecology* 48: 835–843.
- SHUSTER, S.M., AND M.J. WADE. 2003. *Mating systems and strategies*. Princeton University Press, Princeton, New Jersey, USA.
- SINCLAIR, A.R.E. 1991. Science and the practice of wildlife management. *Journal of Wildlife Management* 55: 767.
- SOLBERG, E.J., A. LOISON, B.-E. SAETHER, AND O. STRAND. 2000. Age-specific harvest mortality in a Norwegian moose *Alces alces* population. *Wildlife Biology* 6:41–52.
- SOLBERG, K.H., E. BELLEMMAIN, O.-M. DRAGESET, P. TABERLET, AND J.E. SWENSON. 2006. An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. *Biological Conservation* 128:158–168.
- SOLTIS, J., R. THOMSEN, K. MATSUBAYASHI, AND O. TAKENAKA. 2000. Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behavioral Ecology and Sociobiology* 48:195–202.
- STEARNS, S.C. 1992. *The evolution of life histories*. Oxford University Press, London, England, UK.
- STEYAERT, S.M.J.G., A. ENDRESTØL, K. HACKLÄNDER, J.E. SWENSON, AND A. ZEDROSSER. 2012. The mating system of the brown bear *Ursus arctos*. *Mammal Review* 42: 12–34.
- , J. KINDBERG, J.E. SWENSON, AND A. ZEDROSSER. 2013a. Male reproductive strategy explains spatiotemporal

- segregation in brown bears. *Journal of Animal Ecology* 82:836–845.
- , M. LECLERC, F. PELLETIER, J. KINDBERG, S. BRUNBERG, J.E. SWENSON, AND A. ZEDROSSER. 2016a. Human shields mediate sexual conflict in a top predator. *Proceedings of the Royal Society B: Biological Sciences* 283.
- , C. REUSCH, S. BRUNBERG, J.E. SWENSON, K. HACKLÄNDER, AND A. ZEDROSSER. 2013b. Infanticide as a male reproductive strategy has a nutritive risk effect in brown bears. *Biology Letters*. DOI:10.1098/rsbl.2013.0624.
- , J.E. SWENSON, AND A. ZEDROSSER. 2014. Litter loss triggers estrus in a nonsocial seasonal breeder. *Ecology and Evolution* 4:300–310.
- , A. ZEDROSSER, M. ELFSTRÖM, A. ORDIZ, M. LECLERC, S. FRANK, J. KINDBERG, O.-G. STØEN, S. BRUNBERG, AND J. SWENSON. 2016b. Ecological implications from spatial patterns in human-caused brown bear mortality. *Wildlife Biology* 22:144–152.
- STILLFRIED, M., J.L. BELANT, N.J. SVOBODA, D.E. BEYER, AND S. KRAMER-SCHADT. 2015. When top predators become prey: Black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes* 120: 30–39.
- STØEN, O.G., A. ORDIZ, A.L. EVANS, T.G. LASKE, J. KINDBERG, O. FROBERT, J.E. SWENSON, AND J.M. ARNEMO. 2015. Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). *Physiology and Behavior* 152:244–248.
- , A. ZEDROSSER, P. WEGGE, AND J.E. SWENSON. 2006. Socially induced delayed primiparity in brown bears *Ursus arctos*. *Behavioral Ecology and Sociobiology* 61: 1–8.
- SWEANOR, L.L., K.A. LOGAN, AND M.G. HORNOCKER. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology* 14:798–808.
- SWENSON, J.E. 1999. Does hunting affect the behavior of brown bears in Eurasia? *Ursus* 11:157–162.
- . 2003. Implications of sexually selected infanticide for the hunting of large carnivores. Pages 171–189 in M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, DC, USA.
- , AND M.A. HAROLDSON. 2008. Observations of mixed-aged litters in brown bears. *Ursus* 19:73–79.
- , F. SANDEGREN, A. BJÄRVALL, A. SODERBERG, P. WABAKKEN, AND R. FRANZEN. 1994. Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. *Biological Conservation* 70: 9–17.
- , ———, ———, AND P. WABAKKEN. 1998a. Living with success: Research needs for an expanding brown bear population. *Ursus* 10:17–23.
- , ———, S. BRUNBERG, AND P. SEGERSTRØM. 2001. Factors associated with loss of brown bear cubs in Sweden. *Ursus* 12:69–80.
- , ———, AND A. SODERBERG. 1998b. Geographic expansion of an increasing brown bear population: Evidence for presaturation dispersal. *Journal of Animal Ecology* 67:819–826.
- , ———, ———, A. BJÄRVALL, R. FRANZÉN, AND P. WABAKKEN. 1997. Infanticide caused by hunting of male bears. *Nature* 386:450–451.
- , M. SCHNEIDER, A. ZEDROSSER, A. SÖDERBERG, R. FRANZÉN, AND J. KINDBERG. 2017. Challenges of managing a European brown bear population; lessons from Sweden, 1943–2013. *Wildlife Biology*. Doi:10.2981/wlb.00251.
- , P. WABAKKEN, F. SANDEGREN, A. BJÄRVALL, R. FRANZEN, AND A. SÖDERBERG. 1995. The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildlife Biology* 1:11–25.
- TALLIAN, A., A. ORDIZ, M.C. METZ, C. MILLERET, C. WIKENROS, D.W. SMITH, D.R. STAHLER, J. KINDBERG, D.R. MACNULTY, P. WABAKKEN, J.E. SWENSON, AND H. SAND. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proceedings of the Royal Society B* 284: 20162368. Doi: <http://dx.doi.org/10.1098/rspb.2016.2368>.
- TREVES, A. 2009. Hunting for large carnivore conservation. *Journal of Applied Ecology* 46:1350–1356.
- , G. CHAPRON, J.V. LOPEZ-BAO, C. SHOEMAKER, A.R. GOECKNER, AND J.T. BRUSKOTTER. 2017. Predators and the public trust. *Biological Reviews* 92:248–270.
- TRIVERS, R.L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, editor. *Sexual selection and the descent of man 1872–1971*. University of California, Aldine Publishing Company, Los Angeles, California, USA.
- WIELGUS, R.B., AND F.L. BUNNELL. 1994. Sexual segregation and female grizzly bear avoidance of males. *Journal of Wildlife Management* 58:405–405.
- , AND ———. 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. *Biological Conservation* 93:145–154.
- , F. SARRAZIN, R. FERRIERE, AND J. CLOBERT. 2001a. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biological Conservation* 98:293–303.
- , ———, ———, AND ———. 2001b. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biological Conservation* 98:293–303.
- WOLFF, J.O., AND D.W. MACDONALD. 2004. Promiscuous females protect their offspring. *Trends in Ecology & Evolution* 19:127–134.
- ZEDROSSER, A., E. BELLEMAIN, P. TABERLET, AND J.E. SWENSON. 2007. Genetic estimates of annual reproductive success in male brown bears: The effects of body size, age, internal relatedness and population density. *Journal of Animal Ecology* 76:368–375.

———, B. DAHLE, O.G. STOEN, AND J.E. SWENSON. 2009. The effects of primiparity on reproductive performance in the brown bear. *Oecologia* 160:847–854.

———, ———, AND J.E. SWENSON. 2006. Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy* 87:510–518.

———, F. PELLETIER, R. BISCHOF, M. FESTA-BIANCHET, AND J.E. SWENSON. 2013. Determinants of lifetime reproduction in female brown bears: Early body mass, longevity, and hunting regulations. *Ecology* 94:231–240.

———, S.M.J.G. STEYAERT, H. GOSSOW, AND J.E. SWENSON. 2011. Brown bear conservation and the ghost of persecution past. *Biological Conservation* 144:2163–2170.

Received: October 10, 2016

Accepted: May 16, 2017

Associate Editor: Svoboda