

1           **Indirect effects of bear hunting: a review from Scandinavia**

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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 four 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 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 induces sexually-selected infanticide and reduces 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 apply the cautionary principle 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.

41           The manipulation of populations is the core around which wildlife management activities  
42 are organized (Fryxell et al. 2014). Caughley's (1977) original list of four general objectives in  
43 wildlife management are still relevant (Fryxell et al. 2014): 1) make a population increase, 2)  
44 make it decrease, 3) hunt it for a continuing yield, or 4) do nothing except monitor the  
45 population. Harvest is a common management practice to reach population goals (i.e., objectives  
46 2 and 3) in mammal populations, including carnivores (Lindsey et al. 2007, Linnell et al. 2008,  
47 Packer et al. 2009, Swenson et al. 2017). However, it is essential to understand the population  
48 dynamics of exploited species in order to determine the appropriate harvest rates to reach a  
49 population objective (Sinclair 1991).

50           Although the harvest of populations is supported by solid scientific underpinnings, there  
51 are still knowledge gaps about the consequences of hunting in wild populations, particularly for  
52 the harvest of large carnivores (Treves 2009). For example, managers usually focus on the  
53 effects of direct hunting mortality on a population's growth rate (e.g., Knight and Eberhardt  
54 1985, Miller 1990, Linnell et al. 2010). Nevertheless, there is an increasing number of studies  
55 showing that indirect effects, which managers often do not consider, also may affect population  
56 growth (e.g., Milner et al. 2007, Pauli and Buskirk 2007, Treves 2009). For the purpose of this  
57 review, we define "indirect effects" as hunting-induced changes in a population, including  
58 human-induced selection, that result in an additive change to the population growth rate  
59 "lambda" beyond that due to the initial offtake from direct mortality. Understanding the causal  
60 relationships between harvest and indirect effects on population growth is thus crucial for the  
61 management and conservation of wild mammal populations.

62           Here, we focus on hunting-induced changes to population age, sex and social structures,  
63 in the behavior of remaining individuals, and we address hunting-induced selection in bear

64 populations (termed demographic side effects in Milner et al. (2007)). We primarily review the  
65 literature from the Scandinavian Brown Bear Research Project (SBBRP), because it is illustrative  
66 to discuss the subject in one system where brown bears (*Ursus arctos*) have been managed as a  
67 game species for >70 years. We distinguish between pathways that have been documented  
68 statistically and those that are expected to occur (see Fig. 1). In addition, we also include  
69 literature about indirect effects of harvest on growth rates in other bear populations.

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### 71 **Study areas and hunting regime in Sweden**

72         The SBBRP has had two study areas; one in northern Sweden from 1984-2013, where  
73 254 individual brown bears have been radiomarked and followed, mostly with VHF telemetry  
74 (8,000 km<sup>2</sup>; termed “north”), and one in central Sweden-southeastern Norway from 1985 to the  
75 present (13,000 km<sup>2</sup>; termed “south”). There, 449 individuals were radiomarked and followed  
76 with VHF telemetry and, from 2003, with GPS technology. The north consists of alpine  
77 mountain and coniferous forest habitats and included parts of some national parks. The south  
78 was exclusively managed coniferous forests. See Zedrosser et al. (2006) for more detailed  
79 descriptions of the study areas, and see Arnemo et al. (2011) for capture methods. Our behavioral  
80 studies were conducted in the south.

81         Hunting brown bears has been legal in Sweden since 1943, outside the national parks,  
82 and generally lasts from 21 August until the area-specific, annually established quota has been  
83 filled (Swenson et al. 2017). Quotas have been set at variable spatial scales in Sweden, but today  
84 are set typically at county or subcounty levels (Swenson et al. 1994, Swenson et al. 1998b,  
85 Swenson et al. 2017). Furthermore, recent population objectives have varied by county and most  
86 objectives have not been met, with local numbers of bears either remaining stable or declining

87 (Swenson et al. 2017). The Scandinavian bear population has increased from around 300  
88 individuals in the 1940s to around 3,000 bears today, with approximately 95% of those found in  
89 Sweden (Swenson et al. 1994, Kindberg et al. 2011, Swenson et al. 2017). Not until recently  
90 (2008-2013) have bears exhibited a decrease in population size across Scandinavia, which is  
91 most likely due to an increase in harvest rate in Sweden (Swenson et al. 2017). Population  
92 density varies and is approximately ~11 bears/1,000 km<sup>2</sup> in the north and ~30 bears/1,000 km<sup>2</sup> in  
93 the south (Solberg et al. 2006, Zedrosser et al. 2006).

94 All bear hunters are required to possess an annual hunting license, pass an annual  
95 shooting test, and it is common to take a hunting test specific for bears, but is not required by  
96 law. There is no bag limit on bears, and any bear can be killed, except females and their cubs,  
97 which are all protected regardless of the cubs' age. Bears are hunted using stalking, sitting at  
98 posts, with dogs, or at bait sites; dog hunting is gaining in importance (Bischof et al. 2008,  
99 Swenson et al. 2017). It is legally required for all harvested bears and dead bears found to be  
100 reported to local authorities, at which point samples (e.g., tissue, hair, a premolar tooth for aging)  
101 and measurements (e.g., weight, sex) are taken.

102 Hunting is the most important cause of bear mortality in Sweden, as 60% of all marked  
103 bears  $\geq 1$  year of age that are recovered dead have been killed legally by hunters, with an  
104 additional 13% dying naturally (Bischof et al. 2009). In Sweden, data from 1984-2006 suggest  
105 that hunters exhibit low selectivity for age, size, and sex, except for a slight bias towards males  
106 in the north (Bischof et al. 2009). This is probably because of limited encounter rates, traditions,  
107 and difficulties to distinguish males from females in the wild (Bischof et al. 2008). Also, because  
108 there are no individual bag limits and harvest quotas, Swedish hunters may have a low incentive  
109 to pass up an opportunity to kill a bear that they encounter (Bischof 2009). However, more recent

110 analyses, based on an expanded data set collected during a time of increased harvest pressure,  
111 shows greater selectivity towards older bears (SBBRP, unpublished data), larger yearlings, and  
112 larger adult females over time (Leclerc et al. 2016a). The mean age of a harvested bear was ~5  
113 years and males made up a slightly greater share of the harvest than females (55:45) in 1981-  
114 2015 (Fig. 2).

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

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## 128 **Changes in a population's age and sex structure**

129 Harvest can affect a population's age and sex structure, influenced by the degree of  
130 hunters' selectivity, hunting method, habitat, food availability, and other factors, as shown for  
131 different bear species (e.g., McLellan and Shackleton 1988, Derocher et al. 1997, Noyce and  
132 Garshelis 1997, Bischof et al. 2008). Although harvesting can change a population's sex

133 structure, this will not necessarily affect reproductive rates in species with polygamous mating  
134 systems (e.g., Ginsberg and Milner-Gulland 1994, Milner et al. 2007), such as bears (Steyaert et  
135 al. 2012). The harvest of the most productive segment of the population, adult females, has the  
136 greatest effect on a bear population growth rate (Knight and Eberhardt 1985, Miller 1990,  
137 Zedrosser et al. 2013, Gosselin et al. 2015). Harvest can result in a lower proportion of older  
138 animals in the population, even if harvest is not selective to age (Bischof et al. 2008). A  
139 reduction in the population-wide age of females should reduce population growth, because  
140 primiparous females have a lower litter size and higher cub mortality than multiparous females  
141 (Zedrosser et al. 2009, Gosselin et al. 2017) (Fig 1.).

142         Human-induced mortality can also change the male age structure and influence their age-  
143 specific reproductive rates (Bellemain et al. 2006b, Zedrosser et al. 2007). Suggested as a result  
144 from greater illegal or unrecorded harvest of bears in the north, only one reproductively  
145 dominant adult male brown bear was present in this area for several years, leading to a more  
146 skewed operational sex ratio (OSR), with more reproductive females per adult male, compared  
147 with the south, which had a less human-influenced age structure, resulting in a less skewed OSR  
148 (Zedrosser et al. 2007). This resulted in a significantly higher mean male reproductive success in  
149 the north than in the south. Although older and larger males had a higher reproductive success in  
150 both areas, age was relatively more important in the north, because the one old male dominated  
151 the reproduction (~33% of known offspring in 1990-1997; A. Zedrosser, unpublished data). This  
152 uneven age distribution enabled a relatively higher proportion of young males to gain  
153 reproductive success in the north than in the south (Zedrosser et al. 2007). In the south, age was  
154 more similar among males, potentially favoring larger individuals during intrasexual competition  
155 (Zedrosser et al. 2007). As female brown bears exhibit mate choice (Bellemain et al. 2006a,

156 Bellemain et al. 2006b), the removal of older and larger males could result in less desired,  
157 younger, and smaller males siring offspring, which could result in lower-quality cubs, i.e. with  
158 fitness-decreasing traits or those reducing survival, and therefore potentially lower recruitment.  
159 This has not been shown in large carnivores, to our knowledge, but it has been shown in large  
160 ungulates (Milner et al. 2007, Martin et al. 2014, Douhard et al. 2016, Kvalnes et al. 2016).

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### 162 **Changes in a population's social structure**

163         There is growing evidence that the harvest of large carnivores can cause changes to their  
164 social structure, the space use of survivors, and population growth rate (Rutledge et al. 2010,  
165 Newby et al. 2013, Maletzke et al. 2014, Ausband et al. 2015, Fattebert et al. 2016). For bears,  
166 the removal of conspecifics through hunting creates vacancies on the landscape and induces  
167 surviving animals to shift their home ranges toward these vacancies (Frank et al, in review;  
168 Leclerc et al. 2017a). Home range shifts are strongest when the surviving animal is the same sex  
169 as the killed animal, which can increase sexually selected infanticide (SSI) by males and enhance  
170 female-female competition (Frank et al, in review; Leclerc et al. 2017a). Although little is known  
171 about how this spatial reorganization affects individual fitness, links have been made between  
172 hunting, male home range shifts, SSI, and variation in population growth (Swenson et al. 1997,  
173 Swenson et al. 2001, Swenson 2003, Gosselin et al. 2015, Gosselin et al. 2017, Leclerc et al.  
174 2017a).

175         SSI is a male reproductive strategy where males gain mating opportunities by killing  
176 dependent young (Hrdy 1979). Males should only kill offspring that they have not fathered (SSI  
177 requirement #1), litter loss should trigger estrus in a victimized mother and shorten her interlitter  
178 interval (requirement #2), and the perpetrator should sire the victimized mothers' subsequent



179 offspring (requirement #3) (Trivers 1972, Hrdy 1979). SSI can be increased through male  
180 turnover in both solitary and social species (Soltis et al. 2000, Loveridge et al. 2007) and is the  
181 most plausible explanation for infanticide among Scandinavian brown bears (Swenson 2003,  
182 Steyaert et al. 2012). Brown bears have extended maternal care (typically 1.5 – 2.5 years in  
183 Scandinavia; Dahle and Swenson 2003), and mothers generally do not mate during this period  
184 (but see Swenson and Haroldson 2008). After losing a litter during the mating season, however,  
185 females are able to enter estrus within a few days (Steyaert et al. 2014). The majority (>90%) of  
186 females that lose their litter during a mating season mate successfully and give birth during the  
187 subsequent winter (requirement #2 of the SSI hypothesis) (Steyaert et al. 2014). Males can thus  
188 generate an almost immediate mating opportunity by killing a litter of cubs-of-the-year instead of  
189 waiting until the female becomes receptive again after weaning her young 1.5 to 2.5 years later.  
190 In Scandinavia, ~80% of all cub mortality, which is about 42% annually, occurs during the  
191 mating season (Gosselin et al. 2015, Gosselin et al. 2017) and is due to infanticide by males  
192 (Bellemain et al. 2006a, Bellemain et al. 2006b, Steyaert et al. 2014). No male has been recorded  
193 killing his own offspring, likely because of female recognition through his mating history (Wolff  
194 and Macdonald 2004) and perpetrators typically sire the offspring of victimized mothers  
195 (requirements #1 and #3 of the SSI hypothesis; Bellemain et al. 2006a, Bellemain et al. 2006b,  
196 Steyaert et al. 2014). Residents are defined as males whose home ranges overlap with a  
197 victimized mother's home range during the mating season before and during the year of  
198 infanticide (Bellemain et al. 2006a), and both resident and immigrant males can commit SSI  
199 (McLellan 2005, Bellemain et al. 2006a).

200           In the Scandinavian brown bear, hunting promotes SSI and can indirectly contribute to  
201 negative population growth through increased juvenile mortality (Swenson et al. 1997, Swenson

202 et al. 2001, Swenson 2003, Gosselin et al. 2015, Gosselin et al. 2017). Between 1984 and 1995,  
203 Swenson et al. (1997, 2001) contrasted cub survival between the north and south. In the north,  
204 with few old males and no legal hunting, cub survival was very high (98%) and relatively stable  
205 over time. In the south, even under a low harvest rate, cub survival was negatively correlated  
206 with the removal of males from the population (24% and 42% lower 0.5 and 1.5 years after  
207 harvest, respectively) (Swenson et al. 1997). Furthermore, Swenson et al. (1997, 2001)  
208 calculated that removing one male from the population was equivalent to a recruitment loss of  
209 0.5 to 1.0 adult female and decreased population growth rate by 3.4%. Gosselin et al. (2015)  
210 found similar patterns; cub survival was lower under high harvest (2006-2011) compared to low  
211 hunting pressure (1990-2005) and, assuming that all cub mortality during the mating season is  
212 due to SSI, it could explain ~14% of the variation in population growth rate. Furthermore,  
213 Gosselin et al. (2017) showed that male removal decreased cub survival only during the mating  
214 season, consistent with the SSI hypothesis, that cub survival increased with distance to the  
215 nearest male killed during the previous 1.5 years, and that the spatiotemporal distribution of male  
216 harvest is more important than the absolute number of males killed. After the death of a resident  
217 male, its male neighbors shift their home ranges towards the ‘vacant’ area (Leclerc et al. 2017a).  
218 This shift is most apparent during the second year after the residents’ death, and provides a  
219 mechanistic explanation for the 1.5-year time lag in decreased cub survival after male removal  
220 (Leclerc et al. 2017a).

221       Because hunting can promote SSI in Scandinavia, it may also stimulate infanticide  
222 counterstrategies and associated costs for females (Agrell et al. 1998, Ebensperger 1998,  
223 Palombit 2015). Female brown bears apply several strategies to reduce SSI risk, including  
224 aggression to deter infanticidal males (Swenson 2003), multimale mating, and multiple paternity

225 litters to confuse paternity (Bellemain et al. 2006a, Bellemain et al. 2006b). Mothers also adjust  
226 their movements and modify their habitat selection to avoid infanticidal males (Steyaert et al.  
227 2013a, Steyaert et al. 2014, Steyaert et al. 2016b). Furthermore, avoiding infanticidal males  
228 restricts foraging behavior and carries a nutritive cost (Steyaert et al. 2013b). The reproductive  
229 costs imposed by constraints on habitat and diet selection to counter SSI risk have not been  
230 estimated in the Scandinavian brown bear, but it has been estimated to decrease female  
231 reproductive success by 6% in a hunted brown bear population in Alberta (Wielgus and Bunnell  
232 1994, Wielgus and Bunnell 2000, Wielgus et al. 2001a).

233 SSI might also have a compensatory effect on population growth by synchronizing  
234 reproduction. Ordiz et al. (2008) discussed that SSI may be a mechanism involved in the  
235 observed reproductive synchrony among female bears whose home ranges centroids were 10-20  
236 km apart. This implies that an increase in reproductive synchrony, due indirectly to harvest,  
237 conceivably could have a positive effect on population growth (Fig. 1), thus somewhat  
238 compensating for the negative effect of harvesting. However, this implication is theoretical and  
239 there is no empirical support for it.

240 Whereas hunting promotes SSI in Scandinavia, hunting can have the opposite effect in  
241 other populations and enhance cub survival (McLellan 2005). Male-biased hunting can reduce  
242 the OSR and may relax male-male competition and eventually reduce SSI risk (Miller et al.  
243 2003, McLellan 2005). Such a mechanism has been suggested in several populations of North  
244 American brown bears (Miller et al. 2003, McLellan 2005, 2015) and black bears (*Ursus*  
245 *americanus*) (Czetwertynski et al. 2007, Obbard and Howe 2008). The role of OSRs in  
246 explaining variation in SSI and the potential effects on population growth rate may thus vary  
247 among bear populations according to local ecological and evolutionary constraints. It should be

248 noted, however, that the occurrence of SSI in North America is a controversial subject. Little  
249 evidence of SSI has been found in several North American black and brown bear populations  
250 (Miller et al. 2003, McLellan 2005, Czetwertynski et al. 2007, Obbard and Howe 2008),  
251 although it has been reported in one study of American black bears (LeCount 1987).

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

267         Reproduction is suppressed in young philopatric female brown bears, with age of  
268 primiparity being higher for philopatric females compared to dispersers (Støen et al. 2006, Ordiz  
269 et al. 2008). Harvesting females could relax reproductive suppression and competition for food,  
270 favoring earlier reproduction and early cub survival (Zedrosser et al. 2009), which is expected to

271 have a positive effect on population growth rate (Fig. 1). Competition among females for  
272 reproduction also occurs after primiparity; the probability of a female brown bear having cubs in  
273 a given year varies in relation with distance to the closest neighboring female and whether or not  
274 the latter has cubs (Ordiz et al. 2008). Thus, dominant pregnant adult female brown bears appear  
275 to inhibit reproduction in their female neighbors, imposing reproductive asynchrony (Ordiz et al.  
276 2008). This reproductive asynchrony may be a factor limiting population growth, suggesting the  
277 existence of a population-regulatory nature that is typically found in social species, rather than  
278 solitary animals (Ordiz et al. 2008).

279         Dispersal in large carnivores has been shown to change due to harvest (e.g., Cooley et al.  
280 2009), which could affect the distribution of females across the landscape (e.g., Robinson et al.  
281 2008); there is some evidence of this in brown bears near the Swedish-Norwegian border  
282 (Bischof and Swenson 2012, Gilroy et al. 2015). The number of bears in Sweden has decreased  
283 in the past few years, due to a higher hunting quota (Swenson et al. 2017) and simultaneously the  
284 number of bears detected in Norway has decreased from 2009 to 2015 (Aarnes et al. 2016). The  
285 increased harvest in Sweden has probably reduced the dispersal of bears from the high-density  
286 areas and provided more vacancies in the nearby peripheral areas in Sweden, such as along the  
287 Norwegian border (Swenson et al. 1998a), which could result in reduced movement of bears into  
288 Norway. However, the effect of altered dispersal and female distribution on  $\lambda$  is still  
289 unknown.

290

### 291 **Behavioral indirect effects from hunting**

292         Wildlife are generally sensitive to human-induced disturbances (e.g., see George and  
293 Crooks 2006 and references therein). Bears are no exception and generally avoid people and

294 their activities [e.g., Peyton et al. (1998) for Andean bears *Tremarctos ornatus*; Goodrich and  
295 Berger (1994) and Stillfried et al. (2015) for American black bears; Fortin et al. (2016) for North  
296 American brown bears; Nellemann et al. (2007) and Ordiz et al. (2013b) for Scandinavian brown  
297 bears]. Here we review the effects caused by the disturbance of hunting on bears' behavior and  
298 their potential effects on population growth.

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

309         An important question is whether the consequences of hunter-caused disturbances are  
310 great enough to influence population growth. To maximize food intake, foraging bears select  
311 locations providing the highest energetic gain (Hertel et al. 2016a) or forage at times when prey  
312 detection is easiest (MacHutchon et al. 1998) and prey are most vulnerable (Klinka and  
313 Reimchen 2002, 2009). For instance, brown bears are very efficient in preying on Pacific salmon  
314 (*Oncorhynchus* spp.) and reindeer calves (*Rangifer tarandus*) at night (Klinka and Reimchen  
315 2002, Ordiz et al. 2017), whereas bears forage in the best berry habitat patches during the  
316 crepuscular and light hours (McLellan and McLellan 2015, Hertel et al. 2016b). Because bears

317 have a limited period to acquire resources prior to hibernation, any alteration to their foraging  
318 behavior may have negative effects on their body condition and fitness (Hertel et al. 2016b).

319         Hunting can be perceived by bears as a predation risk (Ordiz et al. 2011, Sahlén et al.  
320 2015, Steyaert et al. 2016b), forcing them to increase vigilance at the expense of foraging  
321 activity during the hunting season and therefore suggesting that a human-induced landscape of  
322 fear exists in our hunted population of brown bears (Sahlén et al. 2015, Støen et al. 2015,  
323 Steyaert et al. 2016a). Similar findings have been reported in ungulates (Lone et al. 2014) and  
324 other large carnivores (Oriol-Cotterill et al. 2015), including black bears (Laske et al. 2011,  
325 Stillfried et al. 2015). Hunting can thus induce behavioral changes that may carry nutritional  
326 costs due to decreased energy intake and/or increased energy expenditure (Lima and Dill 1990).

327 During the hunting season in Sweden, bears reduce their foraging activity and, even while  
328 foraging, pay a nutritional cost by using less productive berry patches when mortality risk is  
329 highest (Hertel et al. 2016b). Foraging activity and efficiency remain unaffected during less risky  
330 times, so bears appear to be unable to compensate for lost foraging opportunities (Hertel et al.  
331 2016b). Efficient foraging is particularly important in critical phases of energy expenditure or  
332 weight gain, e.g., during lactation or preparation for hibernation (Farley and Robbins 1995,  
333 López-Alfaro et al. 2013). In years of food shortage, bears may not be able to trade off forage  
334 intake with antipredation behaviors (Johnson et al. 2015), which might make them more  
335 vulnerable to hunting.

336         No study, however, has yet documented quantitatively that these recreational-caused  
337 effects on behavior depress food intake to the point that it decreases bear reproduction or  
338 survival (Fortin et al. 2016) (Fig. 1). This may be because bears seem to be flexible in exhibiting  
339 compensatory foraging in disturbance-free periods (Ayres et al. 1986, Beckmann and Berger

340 2003) or switching to alternative food resources away from risky areas (Rode et al. 2007).  
341 Nevertheless, the topic warrants further research.

342

### 343 **Human-induced selection and potential evolutionary effects**

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

357 Hunter selectivity does not depend only on animal morphology, but also on the hunting  
358 methods used, harvest intensity, and management regulations (Mysterud 2011). For example,  
359 harvest could select for behavioral traits (Leclerc et al. 2017b) and restrictions limiting hunting  
360 to daylight hours could select for more nocturnal bears. In addition, it has been suggested that the  
361 long persecution period of brown bears in Europe might explain why bears are generally more  
362 nocturnal in Europe than in North America (Swenson 1999, Ordiz et al. 2011).



363           Legal protection of family groups is a common practice in bear management strategies in  
364 North America and Europe, including Sweden, and has often been stressed as a factor explaining  
365 bias in hunting data and differential vulnerability of age and sex classes to hunting (McLellan  
366 and Shackleton 1988, Kohlmann et al. 1999, Krofel et al. 2012, Leclerc et al. 2016a). The main  
367 consequence of legally protecting family groups is the protection of adult females with offspring  
368 and the increased selective harvest of males and solitary females (Solberg et al. 2000, Zedrosser  
369 et al. 2013, Rughetti and Festa-Bianchet 2014). Because females may gain a fitness benefit  
370 through increased survival when associating longer with dependent offspring (Zedrosser et al.  
371 2013, Leclerc et al. 2016a), legal protection of family groups can select for longer periods of  
372 maternal care (Van de Walle et al. unpublished data). The strength of this selective pressure  
373 depends on harvest intensity, but also on the duration of maternal care and the timing of the  
374 hunting period (before or after weaning time; McLellan and Shackleton 1988), which varies  
375 among bear populations. Nevertheless, in Scandinavia we have witnessed a general increase in  
376 the average duration of maternal care in recent years (Leclerc et al. 2016a), which may have  
377 adverse consequences on recruitment and population growth rate. On the other hand, protecting  
378 adult females, i.e., the demographic parameter depicting the greatest elasticity on population  
379 growth, should also result in a higher population growth (Van de Walle et al. unpublished data;  
380 Knight and Eberhardt 1985, Gosselin et al. 2015), potentially compensating for reduced  
381 reproductive output.

382           Even in the absence of apparent selectivity by hunters or hunting regulation, there is  
383 usually heterogeneity in individual vulnerability to hunting. Bolder and more active individuals  
384 are more frequently caught in traps or killed by hunters in several species (Biro and Post 2008,  
385 Ciuti et al. 2012, Leclerc et al. 2017b). In Sweden, hunters do not kill bears randomly within the

386 landscape, but generally kill them closer to human infrastructure (Steyaert et al. 2016a). In  
387 addition, the individual differences in habitat selection patterns found in Scandinavia (Leclerc et  
388 al. 2016b) could lead to different levels of vulnerability to hunting. Because behaviors are often  
389 heritable, we could expect evolutionary changes in response to harvest-induced selection  
390 (Postma 2014, Dochtermann et al. 2015). For example, it was suggested that the wariness of  
391 brown bears in Scandinavia may be an adaptation resulting from the long-term human  
392 persecution that almost eradicated the species by 1930 (Swenson et al. 1995).

393         Even in the absence of age, sexual, morphological, and behavioral selectivity, high  
394 mortality rates can exert selective pressure on life history traits (Festa-Bianchet 2003, Olsen et al.  
395 2004). Because higher mortality rates select for reproduction at smaller size and younger age  
396 (Stearns 1992), hunting can select for larger investment in reproduction (Festa-Bianchet 2003,  
397 Law 2007, Darimont et al. 2009) and accelerate life histories (Servanty et al. 2011). Centuries of  
398 brown bear persecution in Europe may have selected for faster life histories, potentially  
399 explaining why females there reproduce earlier and produce more cubs relative to their body  
400 mass compared to their North American counterparts (Zedrosser et al. 2011). This “ghost of  
401 persecution past” may explain why the historically heavily persecuted Swedish population has  
402 one of the fastest life histories documented (reviewed in Nawaz et al. 2008) and can now sustain  
403 relatively high levels of harvest.

404         Although evolution was once thought to be a process occurring over a very long time  
405 including many generations, recent studies show that evolution can occur over just a few  
406 generations (Olsen et al. 2004, Kvalnes et al. 2016, Pigeon et al. 2016) and influence ecological  
407 processes (Pelletier et al. 2009). Human-induced selection has the potential to cause rapid  
408 phenotypic changes (Darimont et al. 2009) and hard-to-reverse evolutionary changes in exploited

409 populations (Palumbi 2001, Olsen et al. 2004, Pigeon et al. 2016). Therefore, it represents one of  
410 the most pervasive effects of hunting, warranting caution when making management decisions  
411 (Festa-Bianchet 2003, Jørgensen et al. 2007).

412

### 413 **Concluding remarks**

414 Usually managers focus on the effects of direct harvest mortality on vital rates and  
415 population growth rate (e.g., Miller 1990) and rarely consider indirect effects of hunting (Milner  
416 et al. 2007, Pauli and Buskirk 2007, Ordiz et al. 2013a). In this review, we show both statically  
417 supported evidence and reason to suspect that indirect effects of hunting can have measurable  
418 effects on a population's growth rate (Fig. 1). We have concentrated on the Scandinavian  
419 population of brown bears, because it is a particularly well studied system since the 1980's, but  
420 we suggest that indirect effects of hunting on population dynamics is likely a general  
421 phenomenon. In addition, hunting can cause human-induced selection, which may further affect  
422 vital rates and population growth in the long-term. Our focus on brown bears alone has excluded  
423 the indirect and potential evolutionary effect of bear harvest on community and ecosystems  
424 processes. Hunting bears and other large carnivores also could affect their ecological role in an  
425 ecosystem (Ordiz et al. 2013a) and indirectly affect other species in the trophic network. For  
426 example, Scandinavian bears can have a strong, lasting effect on the behavior of their prey  
427 species, such as moose (*Alces alces*) (Sahlén et al. 2016) and may affect the expansion patterns  
428 and predation rates of other large carnivores, such as the gray wolf (*Canis lupus*) (Ordiz et al.  
429 2015, Tallian et al. 2017). Such information on interspecific interactions is also useful for  
430 management, for instance, to adjust hunting quotas of ungulates that are both hunted and  
431 predated upon by bears and sympatric wolves (Jonzén et al. 2013).

432           The main point of our review is to stress that indirect effects of harvest deserve more  
433 attention by managers, because they can influence population growth rates. Some of the effects  
434 have been documented and most certainly exist (Fig. 1), but indirect and evolutionary effects are  
435 generally more difficult to document and quantify than direct effects of harvest. We found two  
436 quantitative estimates of indirect effects of hunting on bears on  $\lambda$ ; an increased mortality of  
437 cubs of the year due to SSI in brown bears in Scandinavia (Swenson et al. 1997, Swenson et al.  
438 2001, Gosselin et al. 2015, Gosselin et al. 2017), and a reduced reproductive rate of female  
439 grizzly bears in Alberta, due to females selecting less productive sites as a counter strategy to  
440 SSI (Wielgus et al. 2001b).

441           In societies where wildlife management is an important public issue, e.g., where wildlife  
442 populations are managed under the public trust doctrine (Batcheller et al. 2010, Treves et al.  
443 2017), the public may increasingly require that managers not only document the direct,  
444 numerical effects of management decisions, but also their indirect and potential human-induced  
445 selection effects. Although research on indirect effects of hunting on fitness is difficult and  
446 requires long-term monitoring of individuals in a population that has experienced different  
447 harvest rates, it is an important responsibility for managers to carry out or fund research on this  
448 topic. Long-term monitoring of harvest effects on bears also provides opportunities for managers  
449 to make informed decisions while considering uncertainty (Regehr et al. 2017). As we await the  
450 outcome of such research, managers of bear populations should apply the cautionary principle  
451 and assume that indirect effects do exist and have a potential impact on bear population structure  
452 and growth that may differ from that predicted by harvest models based on direct effects alone.

453

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465

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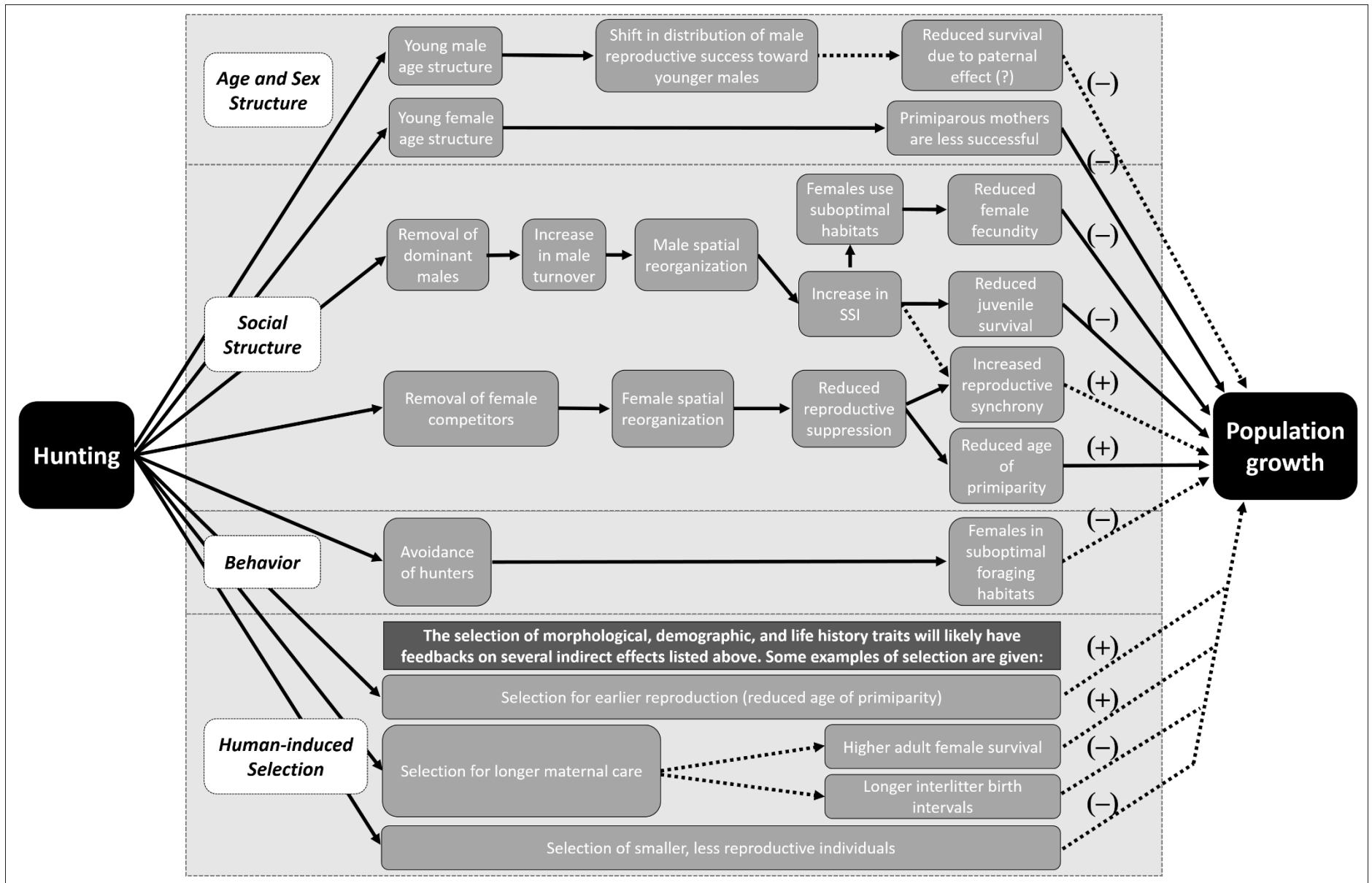
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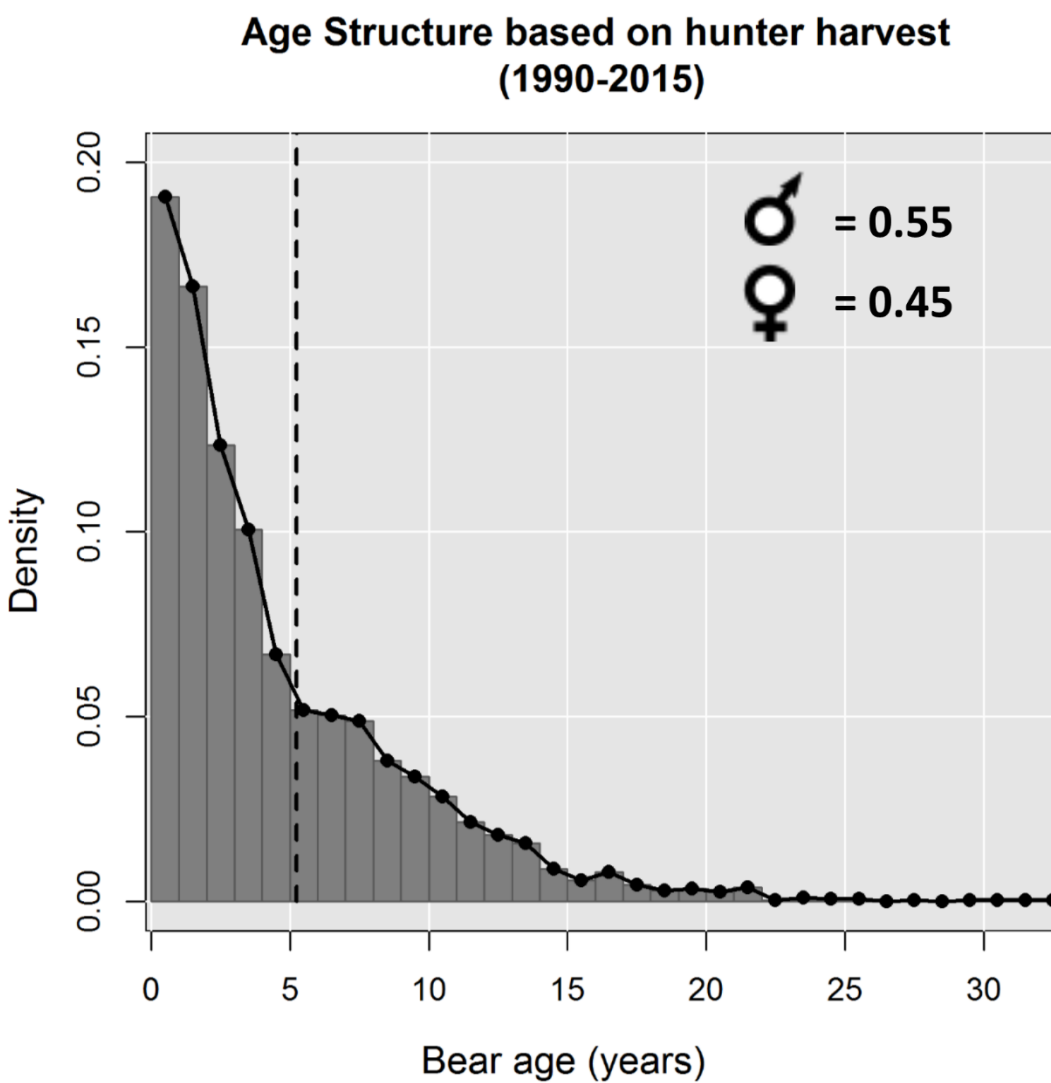
856 Fig. 1. A summary of the indirect effects on population growth of bear hunting discussed in this  
857 paper. The solid arrows show relationships that have been documented statistically and the  
858 dotted arrows show potential relationships. Effects on population growth are noted in  
859 parentheses along the lines directly connecting with the "Population growth" box. This figure  
860 was inspired from Milner et al. (2007).

861





863 Fig. 2. The age structure of hunter-killed brown bears in Sweden during 1990-2015. The vertical  
864 dotted line shows the mean age of bears (~5 years) killed. The frequencies of males and females  
865 harvested are shown.



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