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REVIEW

Evolutionary and ecological traps for brown bears *Ursus arctos* in human-modified landscapes

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ABSTRACT

1. Evolutionary traps, and their derivative, ecological traps, occur when animals make maladaptive decisions based on seemingly reliable environmental cues, and are important mechanistic explanations for declines in animal populations.
2. Despite the interest in large carnivore conservation in human-modified landscapes, the emergence of traps and their potential effects on the conservation of large carnivore populations has frequently been overlooked.
3. The brown bear *Ursus arctos* typifies the challenges facing large carnivore conservation and recent research has reported that this species can show maladaptive behaviours in human-modified landscapes. Here we review, describe and discuss scenarios recognised as evolutionary or ecological traps for brown bears, and propose possible trap scenarios and mechanisms that have the potential to affect the dynamics and viability of brown bear populations.
4. Six potential trap scenarios have been detected for brown bears in human-modified landscapes: 1) food resources close to human settlements; 2) agricultural landscapes; 3) roads; 4) artificial feeding sites; 5) hunting by humans; and 6) other human activities. Because these traps are likely to be of contrasting relevance for different demographic segments of bear populations, we highlight the importance of evaluations of the relative demographic consequences of different trap types for wildlife management. We also suggest that traps may be behind the decreases in brown bear and other large carnivore populations in human-modified landscapes.

INTRODUCTION

Humans are currently one of the most important biotic forces on Earth (Palumbi 2001), as they have transformed nearly every landscape at unprecedented rates and extents (Vitousek et al. 1997). The main or synergistic effects of resource exploitation, habitat destruction, and fragmentation may alter animal foraging ecology and behaviour. Anthropogenic impacts on habitats and animal populations are resulting in worldwide species range contractions and population decreases (e.g. Laliberte & Ripple 2004, Cardillo et al. 2005, Stoner et al. 2013, Fleschutz et al. 2016). This phenomenon is particularly critical for large carnivores, whose widespread decline in numbers and distribution may also have cascading effects on the loss of global biodiversity (Ordiz et al. 2013, Ripple et al. 2014).

Animals base their habitat selection on physical characteristics of the environment (settlement cues) that typically reflect habitat quality, which is expressed as, e.g. food availability, mating opportunities, pressure from predators, as well as on interspecific and intraspecific competition (Schlaepfer et al. 2002, Kristan 2003). Therefore, an individual may base its habitat selection on sound ecological cues but, due to human interferences, these cues may no longer provide the expected fitness effects (Fletcher et al. 2012, Hale et al. 2015, Fig. 1). In human-modified landscapes (also frequently described as human-dominated landscapes), evolutionary, and ecological traps are important factors in the decline of animal populations (Schlaepfer et al. 2002, Robertson et al. 2013, Hale & Swearer 2016). Evolutionary traps, i.e. maladaptive behavioural decisions made regardless of the availability of better options, and important derivatives of them, ecological traps, i.e. maladaptive habitat selection decisions made despite the availability of better habitat, occur when animals make these decisions based on seemingly reliable environmental cues, using these cues to try to maximise their expected fitness (Schlaepfer et al. 2002, Battin 2004a, Robertson et al. 2013). Ecological traps are thus subsumed by evolutionary traps, because habitat selection can be considered a specific case of a behavioural choice in which a given habitat is considered equally attractive as or more attractive than others, despite its lower fitness value. Moreover, for an ecological trap to have persistent effects at the population level, individuals must move from source habitats into the ecological trap (Robertson & Hutto 2006, Lamb et al. 2017). A scenario where environmental cues do not match up with expectations of future fitness can occur through human modification of landscapes or even naturally, so that traps can also occur in pristine areas (Battin 2004b). These habitat alterations engender the emergence of traps resulting from either: 1) attraction for low-fitness options, 2) degraded fitness opportunities without a concomitant decrease in preference, or 3) both attraction and degradation simultaneously (Sih et al. 2011, Robertson et al. 2013, Fig. 1).

Traps are arguably an inevitable consequence of human-induced environmental change, because human alteration of the landscape may occur faster than cues that are shaping individual responses to the landscape can evolve (Robertson et al. 2013, Hale & Swearer 2016). Traps may also occur at a variety of scales (Battin 2004b, Hale & Swearer 2016), from landscape and within-patch levels, including edge effects at the boundary of protected areas (Loveridge et al. 2017), to small-scale site selection, such as the selection of dens and feeding sites. Traps differ from demographic sinks of classical source-sink systems because individuals may occupy trap areas before or at the same time as they occupy high-quality habitats, whereas animals settle in sinks only when all higher quality habitats are already occupied (Battin 2004b). Individuals may select for traps, whereas sinks are not attractive or are even avoided. Distinguishing traps from source-sink systems is a priority in conservation biology, as sinks that are actually traps may attract a considerable portion of the source population, which may lead to overall population decrease or even extinction (Delibes et al. 2001, Kokko & Sutherland 2001, Kristan 2003, Gilroy & Sutherland 2007). Early detection of traps is also important because the identification of apparently favourable habitats is an important step in conservation, and overlooking the possibility that apparently high-quality habitats may represent traps can lead to detrimental management decisions (van der Meer et al. 2013, 2015).

However, few studies have identified traps for mammals (Schlaepfer et al. 2002, Robertson & Hutto 2006, Hale & Swearer 2016), and even fewer for large carnivores (Balme et al. 2010, van der Meer et al. 2013, Pitman et al. 2015, Loveridge et al. 2017). Despite the interest in large carnivore conservation in human-modified landscapes, the emergence of traps and their potential effects on the conservation of large carnivore populations has frequently been overlooked. Trap effects are potentially worse in large carnivores than in other groups of species, because the larger carnivores have slow life histories, low densities, and small population sizes, and they roam over wide home ranges (Ripple et al. 2014).

The brown bear as a model species

The brown (or grizzly) bear *Ursus arctos* illustrates well the challenges facing large carnivore conservation: an extensive geographical range (both for the species and for populations) in combination with wide-ranging individual movements dictate that management of this species involves different spatial scales and heterogeneous habitats

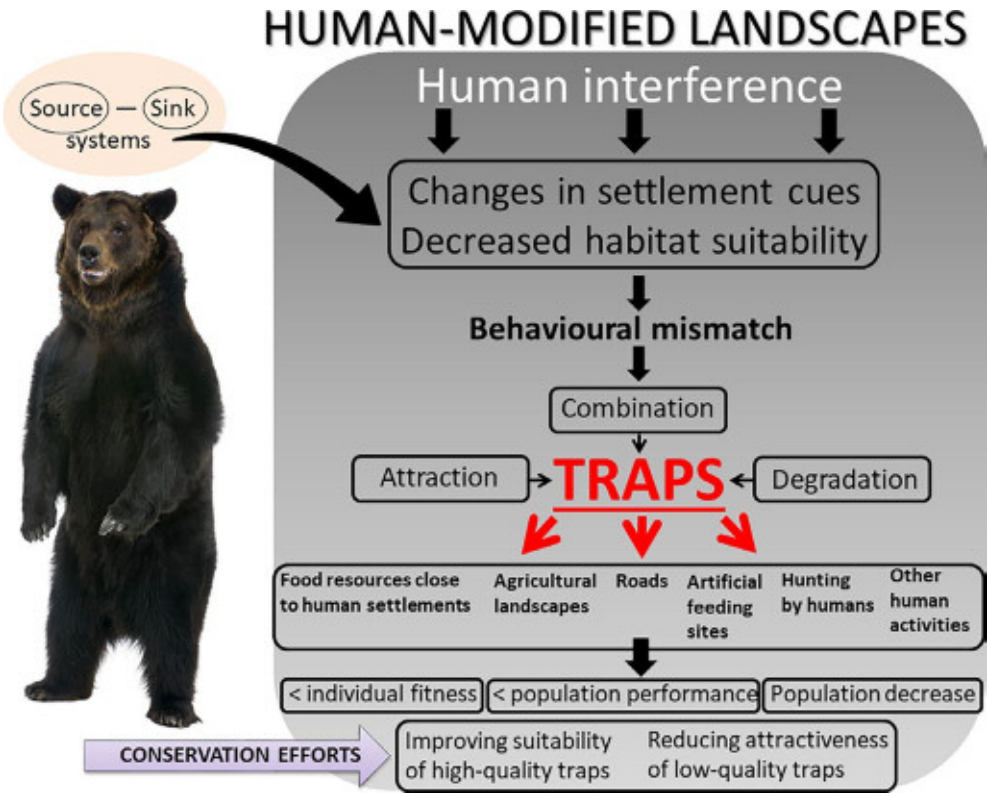

Fig. 1. Graphical representation of evolutionary and ecological trap scenarios and mechanisms that may affect brown bear populations in human-modified landscapes. Traps occur when, because of human interference, the suitability of high-quality habitats is decreased and/or settlement cues are altered, so that the attractiveness of low-quality habitat is increased and unsuitable habitats are preferred. This process may also affect the original properties and attractiveness of source–sink systems. Habitat alterations provoked by humans may: cause brown bears to select relatively low-fitness options (Behavioural mismatch), engender the emergence of traps resulting from either increased preference for low-fitness options (Attraction), provide degraded fitness opportunities without a concomitant decrease in preference (Degradation), or result in both attraction and degradation simultaneously (Combination). To date, six potential trap scenarios for brown bears have been detected in human-modified landscapes: 1) food resources close to human settlements; 2) agricultural landscapes; 3) roads; 4) artificial feeding sites; 5) hunting by humans, and 6) other human activities. Traps principally influence individual fitness and population performance and viability. Depending on the quality of the trap habitat, conservation efforts should mainly be focussed on improving the suitability of high-quality traps or on reducing the attractiveness of low-quality traps. This conceptual framework is an elaboration of graphical representations from Sih et al. (2011), Robertson et al. (2013), and van der Meer et al. (2015; the brown bear photo was downloaded from http://www.123rf.com, Image ID 7119875, Eric Isselee). [Colour figure can be viewed at wileyonlinelibrary.com]

(Penteriani et al. in press). Despite a relatively wide distribution, brown bears select particular habitats at various scales, from at the landscape level to at very fine scales (Nellemann et al. 2007, Ordiz et al. 2011). This may create conditions for the development of maladaptive behaviour in human-modified landscapes, even if substantial variation in this hierarchical habitat selection has the potential to create escape routes from maladaptive behaviours. Like most large carnivores, brown bears are frequently involved in conflicts related to human safety, damages to crops, and livestock depredation, often leading to the retaliatory killing of problem individuals (Can et al. 2014, Darimont et al. 2015). In human-modified landscapes, bear habitats commonly juxtapose with those favoured by humans, where the frequency and lethality of contact between bears and humans is likely to increase (Mattson & Merrill 2002). As apex consumers, brown bears are highly vulnerable to traps because they do not have any natural predators, at least when they are adult individuals. This may reduce their vigilance in the face of a novel human threat. Bears adjust their daily activity patterns and habitat choice to avoid hunting pressure (Ordiz et al. 2011, 2012), and human settlements and human activities may have a stress effect on bears (Støen et al. 2015). However, bears may not be able to avoid novel human threats completely, which may lead to maladaptive behaviour in human-modified landscapes (Lamb et al. 2017). Interest in brown bears as a model species is also justified because they are hunted for sport in most of their Holarctic geographical range. Bear survival is often reduced in areas

Table 1. The different scenarios that have been recognised as evolutionary or ecological traps for brown bears, as well as possible trap scenarios and mechanisms that have the potential to affect the dynamics and viability of brown bear populations. For each trap, details are given of: 1) the attractive resource triggering the trap, 2) the effects on bears (at both the individual level and at the population level), 3) the bears that may most easily fall into the trap, and 4) the expected severity of the demographic impact of the trap.

Trap	Attractive resource	Effects	Individuals most likely to be attracted	Expected demographic impacts
Food resources close to human settlements	Anthropogenic food	Increased human-caused mortality Increased habituation to humans	Young individuals	Variable
	Refuge from adult males	Increased human-caused mortality Increased habituation to humans	Females with cubs	Severe
Agricultural landscapes	Food	Increased human-caused mortality	Variable	Variable
Roads	Food	Increased human-caused mortality	Young individuals	Variable
	Refuge from adult males	Increased human-caused mortality	Females with cubs	Severe
Artificial feeding sites	Anthropogenic food	Increased habituation to humans Negative physiological impacts Disruption of social stability	Variable	Low
Hunting by humans	—	Increased human-caused mortality Disruption of social stability	Females with cubs	Severe
Other human activities: reindeer husbandry	Easy prey	Increased human-caused mortality	Females with cubs	Severe

closer to human settlements and infrastructures, and this pattern holds for both North America (Lamb et al. 2017) and Europe (Steyaert et al. 2016b).

Here we review, describe and discuss scenarios that have been recognised as evolutionary or ecological traps for brown bears, and propose possible trap scenarios and mechanisms that have the potential to affect the dynamics and viability of brown bear populations throughout their geographical range in the near future (Table 1). This information can be used to forecast potential hotspots of conservation and management interest (Fig. 1).

METHODS

To select articles for our review, we used Google Scholar and the Thomson Reuters 'Web of Science' databases. We conducted the literature review (summer 2017) using a broad range of search terms that represent the variety of ways in which both 'traps' and 'brown bear' may be included. Thus, the terms 'bear' and 'grizzly' were combined with the following terms (in alphabetical order): 'ecological trap', 'evolutionary trap', 'maladaptive', 'source-sink', and 'trap'. We also searched in the reference sections of all recorded articles. Ideally, to demonstrate a trap mechanism on animal fitness, studies should take into account both survival and reproduction, as they can have offsetting effects on the severity of a trap or its existence. To be conservative, and given that the reproductive component of fitness was often ignored in the reviewed bear studies, which were mostly focused on or demonstrated effects on bear survival (e.g. increased mortality rates), we refer to suggested traps as potential traps.

RESULTS

Our search only yielded in total eight specific papers on ecological and evolutionary traps for brown bears, published between 2002 and 2017, and carried out in North America ($n = 7$) and Europe ($n = 1$). However, our review revealed that six potential ecological and evolutionary traps for bears can be identified: 1) food resources close to human settlements; 2) agricultural landscapes; 3) roads; 4) artificial feeding sites; 5) hunting by humans; and 6) other human activities.

Human settlements, abundant food, and the possible emergence of ecological traps

Because of the high nutritional demands of the brown bear, areas with attractive food (natural or anthropogenic) close to human settlements may create the conditions for the emergence of ecological traps for bears in the Canadian Rocky Mountains (Lamb et al. 2017). Indeed, when abundant resources occur in the vicinity of humans, anthropogenic mortality (via, e.g. hunting, management removals due to conflicts with humans, road and railway collisions, and poaching; Gangadharan et al. 2017, Lamb et al. 2017) is the primary mortality in bears. In the absence of humans, consuming high-energy berries benefits bears' fitness (Welch et al. 1997, McLellan 2011, McLellan 2015), thus berries are attractive for them (McLellan and Hovey 2001, Nielsen et al. 2003, Nielsen et al. 2010). However, the presence of highly attractive habitat patches in close proximity to human settlements can create a trap scenario (Robertson et al. 2013, Hale

et al. 2015), which intensifies demographic loss in source populations. Increased mortality and food associated with proximity to human settlements: 1) caused a bear population decline of 8% per year inside and 1.5% outside the trap area; 2) reduced survival and compensation in recruitment to prevent population decline; and 3) caused immigration of individuals into the trap area from contiguous locations at a ratio of ten bears entering the trap and dying for every bear leaving the trap and dying. Lamb et al. (2017) showed another crucial facet of this trap mechanism, which worsens the severity of the trap: 68% of bear mortality was caused by humans, but not related to hunting (it was caused by, e.g., collisions with vehicles and trains, illegal kills). This mortality source cannot be mitigated through regulatory policies, as is done with hunting.

The combination of highly attractive food resources and high anthropogenic mortality creates unoccupied spaces that are primarily recolonised by young (mainly male) dispersing bears. Individuals killed in the trap area were on average 3 years younger than those killed outside (Lamb et al. 2017). This age- and sex-skewed composition of the individuals in these trap areas suggests that dispersing juvenile males are the best candidates to occupy vacant risky areas. In areas with few females and many young males, the reproductive potential of the population is low (Lamb et al. 2017). Attractive food may provide little motivation for dispersers to move out of the trap area, and the longer the bears stay in the trap, the more likely they are to be killed by humans. On the other hand, if the trap is an apparently suitable area, younger bears may not be motivated to move into other areas with fewer human settlements where competition for mates, food, and space may confront them with older bears inhabiting these safer areas (Nellemann et al. 2007). This type of trap has the potential to have severe demographic consequences for slowly reproducing species like the brown bear (Table 1).

Finally, emigration from a declining population because of the effect of an ecological trap may create severe conservation problems if source populations are small and if the landscapes in which the trap is acting are exceptionally attractive (Lamb et al. 2017). Because of the large home ranges of brown bears and the movement of young individuals, the effects of localised mortality in a trap area might result in negative demographic consequences for areas far from traps (Table 1). Thus, addressing these subtle and insidious sources of mortality is an essential step towards achieving long-term viability of bear populations; this also highlights the need to maintain the quality of undamaged landscapes that can provide safe refuges from human expansion and associated human–bear conflicts (Lamb et al. 2017).

Agricultural landscapes as ecological traps

Agricultural lands represent an extremely conflictual human-modified landscape for bears, where they compete with humans for space and resources, resulting in conflicts that frequently end in damage to human property, bears being killed in defence of life or property, government-supported reduction in bear populations, and bear relocations (Wilson et al. 2005, 2006, Northrup et al. 2012b). In southwestern Alberta, Canada, bear–human conflicts result from overlaps in human settlements and agricultural practices with habitats preferred by brown bears (Northrup et al. 2012b). In this potential trap scenario, where landscapes preferred by bears directly overlap with areas of high conflict risk, conflicts are more likely to occur in areas with higher human density and vehicle access. The identification of these areas is an essential step in conflict reduction, because bears select private agricultural lands: over 50% of them were considered to be ecological traps for bears at night, when the individuals are most active (Northrup et al. 2012b). Agricultural landscapes may become traps principally when bears are attracted to anthropogenic foods, such as dead cattle and grain in storage containers (Mattson & Merrill 2002, Wilson et al. 2005, 2006).

Steyaert et al. (2016b) revealed a similar mechanism in central Sweden, where nutritious oat crops attract bears and expose them to a higher hunting risk than they experience in non-agricultural habitats. Up to 8.4% of the bears were killed in agricultural lands, although these areas covered <0.5% of the study area and only 1% of all bear telemetry fixes were recorded within that land cover type, i.e. bear mortality risk was larger near villages, roads, buildings, and in agricultural land than in the more heavily utilised forest habitat surrounding the agricultural land (Steyaert et al. 2016b). This shows that mortality risks for bears are not homogenously distributed throughout the landscape, but they are much higher in areas with human activities, like agricultural land, than in other areas.

Both Northrup et al. (2012b) and Steyaert et al. (2016b) contend that it is crucial to identify potential ecological traps and how they work, to be able to focus on effective mitigation efforts in such areas. Once traps have been identified, agricultural stakeholders can be involved in management policies to ensure implementation of husbandry practices that limit potential conflicts, e.g. proper storage of attractants, grazing of cattle in lower risk areas and improved livestock protection (Northrup et al. 2012b, Treves et al. 2016). Trap identification and localisation is facilitated by the availability of geo-referenced bear mortality and human-bear interaction data, preferably over long periods.

Roads as potential ecological traps

The ecological effects of roads represent a pressing issue in animal conservation (Trombulak & Frissel 2000), and bears are no exception among affected species (e.g. Bischof et al. 2017, Skuban et al. 2017, Lamb et al. 2018). Roads fragment habitats and can affect bear behaviour, survival, reproduction, and population viability (Northrup et al. 2012a, Boulanger & Stenhouse 2014, Skuban et al. 2017). Moreover, the relationship between roads and bears can be complex, because road effects may often be area- and/or sex-specific, may vary by time of day and season, and may be affected by traffic volume. One of the principal factors that have reduced brown bear populations in some areas of North America has been mortality related to human access into bear habitat by roads (Schwartz et al. 2006, Boulanger & Stenhouse 2014). Nielsen et al. (2006) and Northrup et al. (2012a) suggested that roads may cause habitat loss, alter movement patterns and, consequently, can become ecological traps for brown bears. For example proximity to roads with high traffic volume might increase nutritional and psychological stress, whereas displacement from better areas can result in substantial energy loss (Nielsen et al. 2006, Northrup et al. 2012a). These kinds of behavioural responses may decrease productivity at the population level (Northrup et al. 2012a). As evidence of the possibility that roads may become ecological traps for bears, Boulanger and Stenhouse (2014) demonstrated that in Alberta, Canada, sex and age class survival was associated with road density. Subadult bears were the most exposed to road-based mortality, and females with cubs-of-the-year and/or yearlings had lower survival than females with 2-year-old cubs or no cubs. Frequent bear mortality near roads was also demonstrated by McLellan (2015). Indeed, most fatalities may occur near roads from which bears are killed (Mace et al. 1996, McLellan 2015), and new roads may increase the number of bears poached: bigger road networks could improve the effectiveness of poachers searching for bears (McLellan 2015). In addition, roads may fragment bear populations as a result of the high mortality around roads (Proctor et al. 2012, Boulanger & Stenhouse 2014, Skuban et al. 2017).

A possible mechanism of roads acting as ecological traps could be the attraction of females with cubs-of-the-year to roads due to higher forage availability (increasing the risk of bears being killed in vehicle collisions; see also Northrup et al. 2012a) or as an avoidance mechanism against potentially infanticidal adult males. Males may kill offspring in sexually selected infanticide (SSI: a reproductive strategy by which males can increase their fitness by killing unrelated offspring so as to bring the mother into reproductive condition, thus increasing the chance of the infanticidal male to subsequently reproduce with her; Hrdy 1979). Males generally avoid the vicinity of roads (Boulanger & Stenhouse 2014), so females with cubs may be attracted to areas close to roads despite higher mortality rates. Such a trap mechanism may have serious demographic consequences, although the net negative effects of road kills vs. juvenile mortality caused by SSI still needs to be evaluated.

Bears often choose to forage along roadsides in spring (Nielsen et al. 2002), which highlights a probable mismatch between perceived habitat quality and real fitness benefits. Even if brown bears exhibit a despotic social organisation where adult males may influence the habitats chosen by females with cubs (as females seek to avoid SSI; Nellemann et al. 2007, Elfström et al. 2014) and cause females with cubs to select areas closer to roads more often than other bears, displacements of females with cubs triggered by adult males may not necessarily result in the entrance of bear families in a trap.

Road development in critical bear areas should be limited under specific, local thresholds (Nielsen et al. 2006, Boulanger & Stenhouse 2014, Lamb et al. 2018), or should require strict control of human access, as well as the deactivation and re-vegetation of roads in areas where temporary extraction of resources has concluded (Nielsen et al. 2006). In addition, the spatial distribution of individual bears, coupled with measures of road densities, should be used to evaluate land management decisions (Boulanger & Stenhouse 2014, Ordiz et al. 2014, Skuban et al. 2017).

As well as roads, railways can also negatively impact bears, as they visit railways to obtain food, but can be killed by trains. For example: 1) in Slovenia, ca. 40% of all bear traffic mortality is caused by railways, e.g. when bears are searching for the carrion of railway-killed ungulates (Kaczensky et al. 2003, Krofel et al. 2012); and 2) the large amount of grain that spills from trains passing through Banff and Yoho National Parks, Canada, attract brown bears to railways, which results in bear–train collisions (Gangadharan et al. 2017).

Artificial feeding as a potential evolutionary trap mechanism

Artificial feeding of bears, e.g. baiting for hunting or viewing purposes, and diversionary feeding for diverting bears from human settlements, is controversial, because it can alter movement patterns and the spatial distribution of individuals, feeding behaviour and preferences, denning ecology, and interspecific interactions (Oro et al. 2013, Krofel & Jerina 2016, Kirby et al. 2017, Krofel et al. 2017, Penteriani et al. 2017, Selva et al. 2017). Moreover, physiological problems may be expected when supplementary food is not appropriate for bears (Penteriani et al. 2010, 2017); bait for hunting may consist of high-calorie foods,

which can include high-sugar foods, such as cookies, donuts, and candies (Kirby et al. 2017). Artificial feeding may also affect bear nutrition by leading to increased body size and energy requirements, as observed in brown bears foraging on garbage dumps (Robbins et al. 2004).

In many countries, especially in Europe, artificial feeding of bears is recommended (Kavčič et al. 2013, 2015). This management measure should, among other things, divert the bears from people and thus decrease conflict rates. Conversely, the feeding of bears is strongly discouraged or even forbidden in other parts of the world, especially in North America (Kavčič et al. 2013, Garshelis et al. 2017). It is commonly believed that bears that associate artificial feeding with people lose their natural caution and often become a nuisance (Kavčič et al. 2013). Recent studies indicates that artificial feeding in different natural and managed settings may in fact increase, not affect, or decrease conflict rates (Kavčič et al. 2013, Steyaert et al. 2014, Stringham & Bryant 2015, Bautista et al. 2016, Garshelis et al. 2017, Morehouse & Boyce 2017). Variation in the effects of feeding is likely to be caused by variation in a number of factors, such as annual or seasonal fluctuations of food availability, the spatial arrangement of feeding sites, the type of artificial food and the way in which this food is provided (e.g. hand feeding vs. automatic feeders), and probably also by the intensity of bear hunting in relation to increased food availability (see Garshelis et al. 2017 for a synthesis). Moreover, well-planned and regulated artificial feeding in the framework of adaptive management can help to decrease conflicts (Garshelis et al. 2017) and maintain a higher density of bears, possibly leading to sustainable species conservation.

Artificial feeding, as observed in black bears *Ursus americanus*, may: 1) contribute substantially to bear diets (Kirby et al. 2017); 2) drive bears to increase their use of developed areas where feeding takes place according to physiological demands for food (e.g. hyperphagia and natural food shortage years; Baruch-Mordo et al. 2014, Johnson et al. 2015); and 3) induce females to train their cubs to seek artificial foods (Mazur & Seher 2008). Food from artificial feeding sites can represent one of the most important food sources for brown bears (Kavčič et al. 2015), and a large proportion of bears at least occasionally use artificial feeding sites if these are available (Krofel & Jerina 2016). Bears may interpret food at artificial feeding sites as the best available option and, thus, focus on it instead of preferring to forage for natural foods (but see Jerina et al. 2012, 2015, Kavčič et al. 2015, for an opposite result at the population level). This decision may have negative effects on individual health and on cubs learning food habits, if the artificial feeding sites are frequented by females with cubs (Penteriani et al. 2010, 2017). In addition, feeding sites may artificially increase local bear density, lead to increased reproduction (Jerina et al. 2013), alter bear movements (Selva et al. 2017), and increase the frequency of interactions among bears (Krofel et al. 2016), which may engender intraspecific competition, aggressive encounters and perhaps also lead to increased risk of SSI (Ben-David et al. 2004). Thus, the use of feeding sites may in certain settings represent a maladaptive behavioural decision, because the artificial food is considered equally attractive to or more attractive than other resources, despite a lower fitness value in terms of survival, health, and behaviour, ensnaring individuals in a trap.

Hunting by humans and ecological traps for females with cubs and young bears

Hunting of bears by humans is not necessarily related to or exclusive to human-modified landscapes, but its practice is more frequent in those areas where human densities are higher. Even though this leisure activity has never been evaluated under the perspective of a trap mechanism for bears, we propose here that hunting bears might engender a subtle trap mechanism that determines maladaptive decisions, based on seemingly reliable environmental cues, by females with cubs.

The hunting of adult male brown bears can disrupt locally stable social structures. When an adult male is removed, one or more immigrating males replacing the dead individual may kill existing cubs to reproduce (Swenson et al. 1997, Leclerc et al. 2017). Thus, the removal of adult males through hunting can increase the risk of SSI. Besides the direct demographic effects of hunting males, SSI increases cub mortality and as such can decrease brown bear population growth (Swenson et al. 1997). Therefore, disruption of the social structure may exacerbate the demographic effects of hunting (Table 1), increasing demographic variability and ultimately affecting population size (Leclerc et al. 2017).

Hunting also has relatively wide spatial and temporal effects on bear populations because: 1) the killing of an adult male has the potential to reduce the survival of cubs within 25 km of the harvested male (Gosselin et al. 2017) and, 2) by removing adult males from the population, hunters destabilise the spatial organisation of the population for at least two years after each male has been killed (Leclerc et al. 2017).

Female brown bears with cubs avoid males during the mating season, as a counterstrategy to SSI (Dahle & Swenson 2003, Steyaert et al. 2013a, b), e.g. females avoid habitat types frequented by males and select habitat close to humans (Steyaert et al. 2016a), which may have a negative effect on the quality of their diet (Steyaert et al. 2013a, b), and may reduce their reproductive output (Wielgus

& Bunnell 2000). Therefore, by increasing the risk of SSI, hunting pressure might trigger a trap mechanism which is additive to the effect of male avoidance. That is, in areas where bear hunting is allowed, females already settling in less favourable habitats to avoid the risk of SSI might experience an additional negative effect, i.e. the increased risk of SSI because of the arrival of new male individuals following the removal of resident males. The death of resident males, which were the potential mates the year before den emergence with cubs, and the consequent immigration of new males (the potentially infanticidal bears), can be two facets of a process relatively difficult to detect for mother bears (Gosselin et al. 2017).

SSI in brown bears has been documented in some populations (e.g. by Wielgus et al. 1994, Swenson et al. 1997, Palomero et al. 2007), but it seems to be less common or absent in other populations (McLellan 2005). Therefore, the potential effects of SSI on bear population growth rates may vary among bear populations depending on local ecological and evolutionary constraints. Accordingly, the role of hunting bears as an ecological trap in relation to the occurrence of SSI and habitat selection of females with cubs may also differ throughout the geographical range of the species.

Other human activities with potential for trap mechanisms

After suffering centuries of persecution, bears are likely to perceive human activity as a predation risk that obliges them to increase their vigilance instead of foraging, e.g. during the hunting season and the times of day when humans are in the forest (Ordiz et al. 2011, 2012). The trade-off between foraging and vigilance suggests the presence of a human-induced 'landscape of fear' for large carnivores in human-modified landscapes (Ordiz et al. 2013, Støen et al. 2015, Steyaert et al. 2016b). However, some bear populations have come under hunting pressure relatively recently (Zedrosser et al. 2011), whereas others have been under protection for decades (e.g. brown bear populations in Spain and Italy), and simultaneously some human recreational activities focusing on bears, i.e. ecotourism, have intensified lately. An eventual reduction in the aversion to humans by large carnivores may potentially create a trap, where animals that often face non-aggressive human presence in their immediate surroundings, as happens when bear populations are subjected to bear-viewing activities (Penteriani et al. 2017), may face an increased mortality risk. Indeed, losing their fear of humans may lead to increased bear presence close to human settlements and infrastructures because of habituation, i.e. the loss of human avoidance and escape responses (Smith et al. 2005). Therefore, strategies for the management of ecotourism practices are urgently needed (see Penteriani et al. 2017).

Reindeer husbandry by the Sámi people indigenous to northern Fennoscandia has the potential to represent a trap mechanism by attracting bears to areas with potentially high mortality rates. The Sámi allow their reindeer herds to move over large distances, in an area that covers approximately half of the area of Scandinavia and overlaps with areas used by brown bears (Hobbs et al. 2012, Sivertsen et al. 2016). Reindeer calving grounds may attract bears. Reindeer calve just at the time when bears are emerging from winter dens, and reindeer neonates can be an important component of the bear diet when bears are in a physiological state in which they need protein (Sivertsen et al. 2016). In this context, high predation rates of bears on reindeer neonates (Sivertsen et al. 2016) decreases the number of reindeer that can be harvested by the Sámi (Hobbs et al. 2012), so bears are removed. This trap mechanism may be exacerbated by human alteration of landscapes by forest harvesting and road construction. Indeed, effects of human-caused land-use changes can influence reindeer–brown bear behavioural interactions and, in turn, increase reindeer vulnerability to bear predation (Sivertsen et al. 2016). Suggested mitigation measures to reduce bear predation include: 1) fencing, to keep reindeer females in enclosures during calving and for some weeks afterwards (Hobbs et al. 2012), which may help to reduce bear attraction to reindeer calving grounds; 2) zones for carnivore conservation and reindeer herding in different areas (Ordiz et al. 2017); and 3) minimising forestry activities in the main reindeer calving ranges in reindeer herding districts (Sivertsen et al. 2016).

DISCUSSION

Beyond interest in trap mechanisms for evolutionary and population ecology, traps have clear conservation implications. It is crucial to pay attention to the habitat choices available to bear populations, to recognise cases where a mismatch between preferences and habitat quality could lead to population declines. Because cue-response relationships in wild animals are difficult to change, increasing the actual quality of the trap area by decreasing the level of anthropogenic mortality is likely to be the best way to mitigate the impact of a trap or to transform it into a source area (van der Meer et al. 2013).

Thus, when managing potential trap habitats, it is crucial to consider the habitat quality as perceived by individual animals (Patten & Kelly 2010). Creating high-quality habitats from previous traps without the right cues will be of little use, while allowing poor-quality habitats to appear suitable might be damaging to the entire population (Kokko & Sutherland 2001). As suggested by van der Meer et al.

(2015), the quality of the trap habitat guides the type of intervention (Fig. 1), i.e. the type of interventions used to restore the trap will depend on the target(s) of human disturbances. If the habitat quality is high, human effects need to be reduced to increase habitat suitability, which may turn the trap into a source. In contrast, if the habitat quality in the trap is low, but human modification has increased its attractiveness, efforts should be made to reduce trap attractiveness, to turn it into a sink. Therefore, restricting human access or modifying habitat quality to make areas where bears can easily encounter humans less attractive or less accessible to bears needs to be considered (Nielsen et al. 2006). Some modifications will be difficult to implement, but others (e.g. changes in artificial feeding regimes) could be implemented relatively easily with adjustments in bear management.

Brown bears are unlikely to occupy exclusively either source or trap habitats, because of their large home ranges (Schwartz et al. 2006). Actually, bears may include safe areas and trap areas within their annual or life ranges (Knight et al. 1988). As highlighted by Schwartz et al. (2006), survival for bears and the viability of bear populations are the result of multiple survival probabilities, depending on the number, size, and spatial locations of traps in the landscape contained within bear home ranges, and the amount of time each individual spends at any particular location in the landscape. In addition, landscape utilisation is dynamic, because it depends on the complex life cycle and social structure of brown bears. Landscape use may change with seasons, with food availability and distribution, with seasonal and long-term intraspecific interactions (e.g. during mating seasons), and, owing to the spatial structure of individuals across the landscape, may depend on their sex and age, and on other environmental factors.

Fully understanding mortality risk for an individual requires information about the likelihood that mortality will occur at a given location and that the animal will use this particular location, i.e. the level of exposure to that mortality risk. For example a high-risk location may either be one that is infrequently visited by an individual, but where the likelihood of mortality is high, or one in which the chance of dying is lower, but where an individual spends substantial amounts of time (Loveridge et al. 2017). On the other hand, it is important to note that studies on traps have almost exclusively been focused on mortality, which is just one component of individual fitness. When analysing the effects of traps on animal populations, it is important to consider also the reproductive component of fitness and how it could offset some of the negative effects of increased mortality. Thus, trap identification can be costly, particularly if data on reproduction, mortality, and habitat selection are required to identify traps reliably. In addition, bears might show adaptation to misleading cues over time through the turnover of individuals falling in the trap. That is, over time, individual turnover may result in a population of individuals that are 'trap-averse' and that are better at matching cues with fitness expectations. Indeed, individual variation is often overlooked in studies on trap mechanisms, which prevalently use population level parameters, but in situations with high inter-individual variation in habitat selection (e.g. Leclerc et al. 2016, Lesmerises & St-Laurent 2017), a trap is less likely to persist (Battin 2004b).

The removal of individuals from trap areas may create vacancies, attracting new individuals from neighbouring regions. This 'vacuum effect' has already been documented in carnivores and may cause edge effects to extend within large protected areas (Balme et al. 2010). For example hunting of lions *Panthera leo* by humans along protected area boundaries generated territorial vacuums that were filled by the immigration of male lions from the protected area (Loveridge et al. 2007, 2009, 2017). Areas used for hunting by humans are therefore typical ecological traps, with both a high level of use and a high risk of mortality, that may lead to maladaptive habitat selection by large carnivores. For lions, this occurred because these areas contained relatively intact habitat, good prey populations, and low human presence, so they did not present the obvious cues to trigger avoidance. However, if hunting mortality hotspots in the landscape are sustainably managed (with sustainable hunting quotas and rigorous monitoring of populations), they may both ensure the conservation of intact natural habitat important for wildlife and play a crucial role as buffer areas around protected areas (Loveridge et al. 2017).

Although protected areas have been crucial for the conservation of brown bears in the USA, most bears in North America live outside protected areas, where human population growth throughout landscapes is increasing (McLellan 2015). Even in the lower 48 states of the USA, numbers of brown bears are increasing outside protected areas, and it is expected that in future, bear distribution will largely overlap with human-modified landscapes (McLellan 2015). Similar trends are observed in Europe as a result of the continuous increase in populations of brown bears in some human-modified areas (Chapron et al. 2014). As noted above, traps of anthropogenic origin are largely connected with human activities outside protected areas. Thus, for effective brown bear conservation, it is important to know how, when and where traps may arise, and what factors may have a negative influence on bears, both inside and outside protected areas. Zones outside protected areas frequently represent population traps because of killing by humans, and most deaths of bears occur beyond park boundaries, mainly when reserves are small relative to

bear home ranges (Schwartz et al. 2006). Similar dynamics may occur when bear populations are shared by several countries, in each of which they are exposed to different management regimes (Penteriani et al. in press).

Negative consequences of traps are exacerbated when safe areas are small, and have lower habitat suitability and higher human densities than traps. The worldwide increase of the human population has intensified fragmentation of habitats available to wide-ranging large carnivores (Crooks et al. 2017), frequently constraining animals to live in closer vicinity to humans (Woodroffe 2000, Inskip & Zimmermann 2009). By crossing into non-protected areas, animals generally come closer to humans and may be accidentally or deliberately killed by them (van der Meer et al. 2013). Although this may suggest that protected areas may offer little conservation value, research on cougars *Puma concolor* has shown that, when human-mediated mortality is widespread, safe areas may harbour carnivore populations and may have greater conservation value than previously supposed (Stoner et al. 2013). Similar trap scenarios have been detected for other carnivores. Leopards *Panthera pardus* in the Limpopo Province, South Africa, and African wild dogs *Lycoan pictus* in Hwange National Park, Zimbabwe, select high-quality habitat within buffer zones of protected areas, which is likely to be maladaptive due to the fitness costs associated with the increasing risk of human-induced mortality in farming areas (where the likelihood of conflict is high; Balme et al. 2010, van der Meer et al. 2013, Pitman et al. 2015). Indeed, trap areas put apparently safe populations close to sources of human-mediated mortality: fitness-enhancing favourable ecological conditions attract individuals unable to perceive the higher mortality risk posed by humans (e.g. via road traffic and shooting).

Despite 1) the potential of human-modified landscapes as primary areas for trap occurrence, 2) the number of scenarios that may trigger the emergence of traps, and 3) the crucial importance of recognising traps for brown bear conservation and management, the trap mechanisms, locations, and effects are still largely overlooked, and more information on demographic effects and on the reproductive side of fitness is required. The lack of knowledge may engender serious negative consequences on bear populations worldwide, and may reduce the effectiveness of conservation actions because trap mechanisms are frequently subtle and difficult to distinguish. If traps are not detected promptly, conservation practices may not be implemented in time to reverse the fate of individuals and populations. There are several brown bear populations that remain understudied and, given that brown bears are long-lived, long-term studies will be required to see if traps are severe enough to endanger populations, especially those that are under hunting pressure or in areas characterised by landscape change. More effort should thus be put into the consideration that traps may be behind unexpected decreases in brown bear and other large carnivore populations in human-modified landscapes. Focusing research on this topic will help us to forecast potential hotspots for carnivore conservation and management in a global scenario of increasing human populations and partial carnivore recoveries.

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