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

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Abstract

1. Evolutionary traps, and their derivative, ecological traps, occur when animals make maladaptive choices 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; and (6) other leisure activities. Because these traps are likely 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 of brown bear and other large carnivore populations in human-modified landscapes.

Key words: ecological traps, evolutionary traps, maladaptive choice, source-sink, *Ursus arctos*

Running head: Brown bears and evolutionary/ecological traps

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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). Main and/or synergistic effects of resource exploitation, habitat destruction and fragmentation 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 and 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. 2014a).

Animals base their habitat selection on physical characteristics of the environment (settlement cues) that typically reflect habitat quality, e.g., food availability, mating opportunities, pressure from predators, as well as interspecific and intraspecific competition (Kristan 2003, Schlaepfer et al. 2002). Thus, an individual can 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; Figure 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 and Swearer 2016). Evolutionary traps, i.e., maladaptive *behavioural choices* made regardless of the availability of better options, and an important derivative of them, ecological traps, i.e., maladaptive *habitat selection choices* made despite the availability of better habitat, occur when animals make these choices based on seemingly reliable environmental cues, which an animal uses to presumably maximize its expected fitness (Battin 2004a, Robertson et al. 2013, Schlaepfer et al. 2002). Ecological traps are thus subsumed by evolutionary traps because habitat selection can be considered a specific case of a behavioural choice where a given habitat is considered equally or more attractive than others, despite its lower fitness value. Moreover, to have persistent effects at the population level, individuals should 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, i.e., traps can also occur in pristine areas (Battin, 2004b). These habitat alterations engender the emergence of traps resulting from either (a) attraction for low-fitness options, (b) degraded fitness opportunities without a concomitant decrease in preference or (c) both attraction and degradation simultaneously (Sih et al. 2011, Robertson et al. 2013) (Figure 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 (Hale and Swearer 2016, Robertson et al. 2013). 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 occupy trap areas before or at the same time as high-quality habitats, whereas animals settle in sinks only when all higher-quality habitats are occupied (Battin 2004b). That is, 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 and lead to overall population decrease or even extinction (Delibes et al. 2001, Gilroy and Sutherland 2007, Kokko and Sutherland 2001, Kristan 2003). 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 less for large carnivores (Loveridge et al. 2017, Pitman et al. 2015, Balme et al. 2010, van der Meer et al. 2013). 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 any other group of species because larger carnivores have slow life histories, low densities and small population sizes, and they roam over wide home ranges (Ripple et al. 2014b).

The brown bear as a model species

The brown bear *Ursus arctos* illustrates well the challenges facing large carnivore conservation: an extensive species/population distribution range in combination with wide-ranging individual movements dictate that management of this species involves different spatial scales and heterogeneous habitats (Penteriani et al. in press). Despite a relatively wide distribution, brown bears are selecting particular habitats at various scales, from the landscape level to 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 out of 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 likely increases (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 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 completely avoid novel human threats, which may lead to maladaptive behaviour in human-modified landscapes (Lamb et al. 2017). The interest in brown bears as a model species is also justified because they are hunted for sport across most of their

Holarctic distribution range. Bear survival is often reduced in areas 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 over their distribution range in the near future (Table 1). This information is useful to forecast potential hotspots of conservation and management interest (Figure 1).

Methods

To select articles for our review, we used Google Scholar and 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 literature-cited 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 mostly focused and/or demonstrated effects on bear survival (e.g., increased mortality rates), we always refer to suggested traps as *potential* traps.

Results

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

Because of the high nutritional demands of the grizzly (brown) bear, areas with attractive food (natural or anthropogenic) close to human settlements create the conditions for the emergence of an ecological trap bears in the Canadian Rocky Mountains (Lamb et al. 2017). Indeed, when abundant resources occur in the vicinity of humans, anthropogenic mortality (e.g., hunting, management removals due to conflicts with humans, road and railway collisions, and poaching; Gangadharan et al. 2017, Lamb et al. 2017) represents the primary cause of mortality in bears. In the absence of humans, consuming high-energy berries benefits grizzly bears' fitness (McLellan 2011, 2015, Welch et al. 1997), thus representing an attraction for them (McLellan and Hovey 2001, Nielsen et al. 2010, 2003). However, presence of highly attractive habitat patches in close proximity to human settlements created a trap scenario (Robertson et al. 2013, Hale et al. 2015), which intensified 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 an 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) also showed another crucial facet of this trap mechanism, which worsens the severity of the trap: bear mortality was mainly due (68%) to non-hunting sources of human-caused mortality (e.g., collisions with vehicles and trains, illegal kills), a mortality source that 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 primarily are recolonised by young (mainly male) dispersers. Individuals killed in the trap area were on average three 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 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 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, emigrations out of a declining population because of the effect of an ecological trap may create severe conservation problems if source populations are small and 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 for the long-term viability of bear populations, which also highlights the need to maintain the quality of undamaged landscapes that can provide safe refuge 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 of bear populations and bear relocations (Wilson et al. 2005, 2006, Northrup et al. 2012b). In southwestern Alberta, Canada, bear–human conflicts resulted from overlaps in human settlements and agricultural practices with grizzly bear preferred habitats (Northrup et al. 2012b). In this potential trap scenario, where landscapes preferred by bears directly overlapped with areas of high conflict risk, conflicts were more likely to occur in areas with higher human density and vehicle access. The identification of these areas was an essential step in conflict reduction because bears selected private agricultural lands: over the 50% of them were considered as ecological traps at night, when the individuals were most active (Northrup et al. 2012b). Agricultural landscapes may become traps principally when bears were attracted to anthropogenic foods, such as dead cattle and grain 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 compared to 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 GPS fixes were recorded within that land cover type, i.e., bear mortality risk was larger near villages, roads, buildings, and agricultural grounds than in the more utilized forest habitat surrounding agricultural lands (Steyaert et al., 2016b). This showed that mortality risks are not homogenously distributed throughout the landscape, but they are much higher in areas with human activities, like agricultural fields.

Both Northrup et al. (2012) 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 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 localization 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, vary by time of day and season, and be affected by traffic volume. One of the principal factors that have reduced brown bear populations in some areas of North America has been the effects of high mortality related to the 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 determine substantial energy loss (Nielsen et al. 2006, Northrup et al. 2012a). These kinds of behavioural responses could decrease productivity at the population level (Northrup et al. 2012a). As evidence of the possibility that roads may become bear ecological traps, Boulanger and Stenhouse (2014) demonstrated that in Alberta, Canada, sex and age class survival was associated with road density, as 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 two year olds or no cubs at all. 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). Additionally, 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 (e.g., increasing the risk of bears getting killed in vehicle collisions; see also Northrup et al. 2012a) or as an avoidance mechanism against potentially infanticidal adult males, which generally avoid the vicinity of roads (Boulanger and Stenhouse 2014). Thus, females with cubs are attracted to areas close to roads despite higher mortality rates. As mentioned previously, such a trap mechanism may have serious demographic consequences, although the net negative effects of road kill versus juvenile mortality caused by sexually selected infanticide (SSI, i.e., a reproductive strategy of males that can increase their fitness by killing unrelated offspring so as to bring a female into reproductive condition and, thus, increase the chance of the infanticidal male to subsequently reproduce with her; Hrdy 1979) need to be evaluated. Also, 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. Important to note is that even if brown bears exhibit a despotic social organization where adult males may influence the habitat choices of females with cubs (due to the risk they pose due to 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 should not necessarily determine the entrance of bear families in a trap.

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

It is worth noting here that railways can also negatively impact bears as they clearly visit railways to obtain food, but can be killed by trains. For example: (a) 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 (b) the large amount of grain that spills from trains passing through Banff and Yoho National Parks, Canada, attract grizzlies and contribute to increase the number of bear–train collisions (Gangadharan et al. 2017).

Artificial feeding as a potential evolutionary trap mechanism

Artificial feeding of bears, i.e., 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, their feeding behaviour and preferences, denning ecology, and interspecific interactions (Selva et al. 2017, Oro et al. 2013, Krofel & Jerina 2016, Kirby et al. 2017, Krofel et al., 2017, Penteriani et al. 2017). Moreover, physiological problems may be expected when supplementary food is not appropriate for bears (Penteriani et al. 2010, 2017); e.g., 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 could also affect bear nutrition through increased body size and energy requirements, as observed in grizzly bears foraging on garbage dumps (Robbins et al. 2004).

In many countries, especially in Europe, artificial feeding of bears is recommended or even compulsory (Kavčič et al. 2013, 2015). This management measure should, among other purposes, 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 indicate that artificial feeding in different natural and management settings may 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). This is likely caused by 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 from the intensity of bear hunting in relation to increased food availability (see Garshelis et al. 2017 for synthesis). Moreover, well planned and regulated artificial feeding in the framework of adaptive management can help decrease conflicts (Garshelis et al. 2017) and maintain a higher density of bears, possibly leading to sustainable species preservation.

Moreover, artificial feeding, as observed for black bears *Ursus americanus*, might: (a) contribute substantially to bear diets (Kirby et al. 2017); (b) drive bears to increase their use of these developed areas according to physiological demands for food (e.g., hyperphagia and natural food shortage years; Baruch-Mordo et al. 2014, Johnson et al. 2015); and (c) induce females to train their cubs to seek artificial foods (Mazur and Seher, 2008). Food from artificial feeding sites can represent one of the most important food sources for brown bears as well (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 choice might potentially have negative effects on (a) individual health and (b) cubs learning food habits, if the artificial feeding sites are frequented by females with cubs (Penteriani et al. 2010, 2017). Additionally, artificial feeding sites may artificially increase local bear density and/or increase reproduction (Jerina et al. 2013), alter bear movements (Selva et al. in press) and increase the frequency of interactions among the bears (Krofel et al. 2016), which may engender intraspecific competition, aggressive encounters and perhaps also infanticide risk (Ben-David et al. 2004). Thus, the use of feeding sites may in certain settings represent a maladaptive behavioural choice, because the artificial food is considered equally or more attractive than other resources despite a lower fitness value in terms of survival, health and behaviour, ensnaring individuals in a trap.

Hunting and ecological traps for females with cubs and young bears

Bear hunting is not necessarily related 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, we propose here that bear hunting might engender a subtle trap mechanism that determines maladaptive choices based on seemingly reliable environmental cues by females with cubs.

The hunting of adult brown bear males 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 in order 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: (a) 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, (b) by removing adult males from the population, hunters destabilize the spatial organization of the population for at least two years after a male has been killed (Leclerc et al. 2017).

Females with cubs avoid males during the mating season as a counterstrategy to SSI (Dahle and Swenson 2003, Steyaert et al. 2013), e.g., females avoid habitat types frequented by males and select for habitat close to humans (Steyaert et al., 2016), which can have a negative effect on the quality of their diet (Steyaert et al., 2013) and may reduce 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 due to the risk of infanticide might experience an additional negative effect, i.e., the increased risk of SSI because of the arrival of new 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 potential 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 different bear populations (e.g., Palomero et al. 2007, Swenson et al. 1997, Wielgus et al. 1994), whereas it seems to be less common or absent in some other bear ranges (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 bear hunting as an ecological trap in relation to the occurrence of SSI and habitat selection of females with cubs may also differ across the distribution range of the species.

Potential for other trap mechanisms

After centuries of persecution, human activities are likely perceived by bears as a predation risk that oblige them to increase 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 and 2012). This trade-off 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), while others have been under protection for decades, e.g., brown bears 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 it happens when bear populations are subjected to bear-viewing activities (Penteriani et al. 2017), may face an increased mortality risk. Indeed, losing fear to humans may increase 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, proper management of ecotourism practices is urgent (see Penteriani et al. 2017).

Another human activity that has the potential to represent a trap mechanism attracting bears to areas with potentially high mortality rates is the reindeer husbandry of the Sámi people, the indigenous people of northern Fennoscandia. The Sámi allow their reindeer herds to move across large distances, in an area that covers approximately half of the area of Scandinavia, for instance, overlapping with brown bears (Hobbs et al. 2012, Sivertsen et al. 2016). Reindeer calving grounds may attract bears because 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 as bears are in a physiological state in which they need protein (Sivertsen et al. 2016). In this context, due to the high predation rates of bears on reindeer neonates (Sivertsen et al. 2016), removal of bears increases to reduce predation, which decreases the number of reindeer that can be harvested by the Sámi (Hobbs et al. 2012). This trap mechanism may be exacerbated by human alteration of landscapes such as forest harvesting and road construction. Indeed, effects of human-caused land-use changes can influence reindeer–brown bear behavioural interactions and, in turn, vulnerability to bear predation (Sivertsen et al. 2016). Suggested mitigation measures to reduce bear predation include: (a) fencing, keeping reindeer females in enclosures during calving and some weeks afterwards (Hobbs et al. 2012), which may help to reduce bear attraction to reindeer calving grounds; (b) zoning for carnivore conservation and reindeer herding in different areas (Ordiz et al. 2017); and (c) minimizing forestry activities in the main reindeer calving ranges in reindeer herding districts (Sivertsen et al. 2016).

Discussion

Beyond the interest of trap mechanisms for evolutionary and population ecology, traps have clear conservation implications. It is crucial to pay attention to habitat choices in bear populations, in order to recognise cases where a mismatch between preferences and habitat quality could lead to population declines. Because cue-response relationships in wild animals will be difficult to change, increasing the actual quality of the trap area by decreasing the level of anthropogenic mortality is likely to be the best solution to mitigate the impact of the trap or to transform it in 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 individuals (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 (Figure 1), i.e., the type of interventions used to restore the trap will depend on the target(s) of human disturbances: (a) if the habitat quality is high, human effects need to be reduced to increase habitat suitability, which may turn the trap into a source; otherwise, (b) if the habitat quality of the trap is low, but human modification has increased its attractiveness, efforts should be made to reduce trap attractiveness, which would turn it into a sink. Therefore, restricting human access and/or modifying habitat quality to make areas where bears can easily encounter humans less attractive or accessible to bears need to be considered (Nielsen et al. 2006). In some cases such modifications will be difficult to implement, but some (e.g., changes in artificial feeding regimes) could be done relatively easily with adjustments in bear management.

Considering the possibility that brown bears may occupy exclusively either source or trap habitats is unrealistic because of their large home ranges (Schwartz et al. 2006). Actually, bears may include safe 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. Additionally, landscape utilization is also dynamic because it depends on the complex life cycle and social structure of brown bears. Landscape use may change with seasons, food availability and distribution, seasonal and long-term intra-specific interactions, e.g., during mating seasons and owing to the spatial structure of individuals across the landscape depending on their sex and age, and other environmental factors.

Fully understanding mortality risk for an individual requires information about the likelihood that (a) mortality will occur at a given location and (b) 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 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 is required to reliably identify a trap. Additionally, 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 the right 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 also 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 along park boundaries generated territorial vacuums that were filled by the immigration of male lions *Panthera leo* from the protected area (Loveridge et al. 2007, 2009, 2017). Hunting areas 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, which did not present the obvious cues to trigger avoidance. However, if hunting mortality hot spots across 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 United States, most bears in North America live outside of protected areas, where human growth across landscapes is increasing (McLellan, 2015). Even in the lower 48 US states, brown bears are increasing out of protected areas and it is expected that 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 of the species in some human-modified lands (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 of protected areas. Zones outside protected areas frequently represent population traps because of humans killings, and most deaths 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, where they are exposed to different management regimes (Penteriani et al. in press).

Negative consequences of traps are exacerbated when safe areas are small, with 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 also 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 area, which is likely 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, Pitman et al. 2015, van der Meer et al. 2013). 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., 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 recognizing traps for brown bear conservation and management, the trap mechanisms, locations and effects are still largely overlooked and more information on demographic effects and the reproductive side of fitness is required. This lack of knowledge may engender serious negative consequences on bear populations worldwide and reduce the effectiveness of conservation actions because trap mechanisms are frequently subtle and difficult to distinguish. If 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 realistically 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 the unexpected decreases of brown bear and other large carnivore populations in human-modified landscapes. Focusing research on this topic will help forecast potential hotspots for carnivore conservation and management in a global scenario of increasing human populations and partial carnivore recoveries.

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Table legend

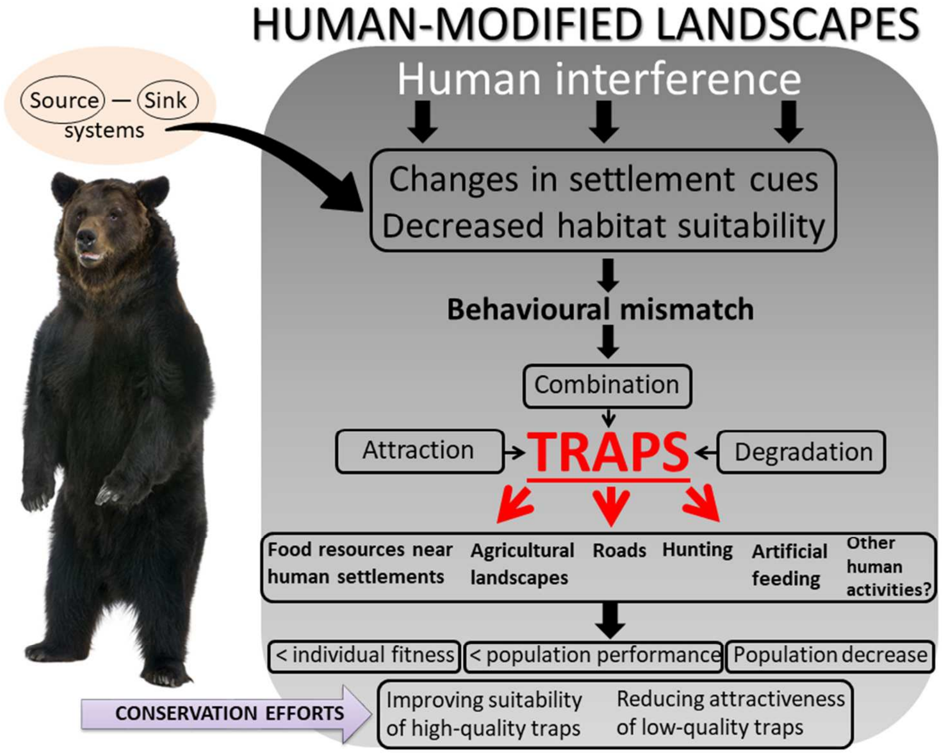
Table 1. The different scenarios that have been recognised as evolutionary or ecological traps for brown bears, as well as possible trap scenarios and mechanisms that have the potential to affect the dynamics and viability of brown bear populations. For each trap are detailed (a) the attractive resource triggering the trap, (b) the effects on bears (at both the individual and population levels), (c) the bear class that may more easily fall into the trap and the expected severity of the demographic impact of the trap.

Trap	Attractive resource	Effects	Attracted individuals	Likely demographic impacts
Human settlements	Anthropogenic food	Increased human caused mortality Increased habituation to humans	Mainly young males	Variable
	Refuge from adult males	Increased human caused mortality Increased habituation to humans	Females with cubs	Severe
Roads	Food	Increased human caused mortality	Mainly young males	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

Agricultural areas	Food	Increased human caused mortality	Variable	Variable
Reindeer husbandry	Easy prey	Increased human caused mortality	Females with cubs	Severe

Figure legend

Figure 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 have been 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. The 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), degraded fitness opportunities without a concomitant decrease in preference (Degradation), or both attraction and degradation simultaneously (Combination). To date, six potential trap scenarios for brown bears have been detected in human-modified landscapes: (1) important food resources close to human settlements; (2) agricultural landscapes; (3) roads; (4) hunting for habitat selection cues of females with cubs and young bears; (5) artificial feeding points and (6) other leisure activities. Traps principally influence individual fitness and population performance and viability. Depending on the quality of the trap habitat, conservation efforts should mainly focus on improving the suitability of high-quality traps or 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 123RF ROYALTY FREE STOCK PHOTOS, http://www.123rf.com, Image ID 7119875, Eric Isselee).



Graphical representation of 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 have been 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. The 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), degraded fitness opportunities without a concomitant decrease in preference (Degradation), or both attraction and degradation simultaneously (Combination). To date, six (five demonstrated and one potential) trap scenarios for brown bears have been detected in human-modified landscapes (see main text): (1) important food resources close to human settlements; (2) agricultural landscapes; (3) roads; (4) hunting for habitat selection cues of females with cubs and young bears; (5) artificial feeding points and (6) other leisure activities. Traps principally influence individual fitness and population performance and viability. Depending on the quality of the trap habitat, conservation efforts should mainly focus on improving the suitability of high-quality traps or 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 123RF ROYALTY FREE STOCK PHOTOS, http://www.123rf.com, Image ID 7119875, Eric Isselee).

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