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## Review Paper

## Large carnivores living alongside humans: Brown bears in human-modified landscapes

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## ABSTRACT

Expansion of human activities into large carnivore habitats and of large carnivore ranges into anthropogenic settings increase the potential for human-wildlife conflicts. Future carnivore survival and recovery depend on both their ability to adapt to human-modified landscapes and the application of adequate conservation strategies. We review human-related factors that negatively affect brown bears inhabiting human-modified landscapes, aiming to improve human-bear coexistence. Brown bears have triggered much research and a review on this model species should be useful for the conservation-oriented management of many large carnivores. In human-modified landscapes, main threats to bear populations are human settlements, habituation and availability of anthropogenic food, density and traffic load of roads and railways, and recreational and industrial activities. Main effects of coexistence with humans for bears are: increased disturbance, human-bear conflicts and human-caused mortality; behavioural alterations; reduced fitness and genetic diversity; and physiological alterations. To promote bear-human coexistence in human-modified landscapes, we identified nine key elements: reduction of human-induced mortality and use of scientific information for better assessment of new infrastructures; improve education on waste management and bear deterrence methods; safeguard and restore habitat connectivity; mitigate road effects and restrict motorized trail use; adjust viewing activity practices to local conservation status of bear populations and food availability; implement mitigation measures to minimize risk of human-bear encounters; quantify empirically the effects of recreational activities on the energetics and fitness of bears; better dissemination of scientific results and management guidelines; and further research on behavioural reactions of bears to different management regimes and persecution histories.

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## 1. Introduction

Human-modified landscapes are characterized by the widespread presence of people, human activities, and infrastructures. Much of the distribution range of large carnivore species is characterised by high human densities, widespread agricultural activities, livestock raising and urban development, and dense networks of transport infrastructures (Penteriani et al., in press, Chapron et al., 2014). Human-large carnivore coexistence causes large carnivore mortality (Bischof et al., 2009) and multiple human-driven disturbances (Ordiz et al., 2017), affecting the distribution, demography, behaviour, and viability of large carnivore populations (Penteriani et al., 2018; Zarzo-Arias et al., 2018).

The expansion of human activities into large carnivore habitats and the expansion of large carnivore ranges into anthropogenic settings from which they had been absent for decades increase the potential for conflicts with humans (Smith et al., 2010; Woodroffe and Ginsberg, 1998). Therefore, long-term viability of large carnivore populations is largely dependent on their ability to adapt to human-modified landscapes (Støen et al., 2015), which in turn can be promoted by applying adequate long-term management strategies that also permit human development (Mace, 2014). For instance, wildlife may be able to adapt to road presence to some extent, but the process can be facilitated by building crossing structures (Ford et al., 2017). This lies indeed at the core of the human-wildlife coexistence concept, as both humans and wildlife conservation would benefit by reducing conflict and threats (Frank et al., 2019; Mace, 2014).

The brown bear (*Ursus arctos*), one of the most iconic large carnivores, inhabits many human-modified landscapes. Furthermore, brown bears are a model species to understand the interactions between large carnivore populations and people (e.g. (Ordiz et al., 2013, 2012). Although some population ranges have been rather stable or expanding recently (Chapron et al., 2014; Coogan et al., 2018), bears generally avoid humans both spatially and temporally (Støen et al., 2015), and worldwide concern centres on the impact that human presence, activities and infrastructures have on bears (Coogan et al., 2018; Nellemann et al., 2007).

Identification of critical threats for species and ecosystems is a priority in the frame of Conservation Biology, defined as such three decades ago (Soulé, 1985). Here, we review research that has been carried out in this temporal frame and that



**Fig. 1.** Graphical representation and flowchart of the human activities and mechanisms that may affect brown bear populations, and thus bear conservation, in human-modified landscapes. The main effects on brown bears living in human-modified landscapes are shown for each of the nine main threats highlighted in this review, i.e. (from left to right) human settlements, habituation, anthropogenic food, transport infrastructures, hunting and fishing, forestry, industrial activities, viewing practices and recreational activities. All these effects have the potential to impact bear population dynamics and trends. (The icons were downloaded from 123RF ROYALTY FREE STOCK PHOTOS, <http://www.123rf.com>; from left to right: ID26999408 Koon Lay Gan, ID106769666 urfandadshov, ID31805672 Khoon Lay Gan, ID47746316 seamartini and ID36170731 Dejan Jovanovic, ID24965219 Khoon Lay Gan and ID97122068 Руслан Нестеренко, ID31805682 Khoon Lay Gan, ID16542815 soleilc1, ID76348160 Ivan Ryabokon, ID42540725 soleilc1; brown bear picture: V. Penteriani). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

focused on describing the negative effects of human-related factors on brown bears that inhabit human-modified landscapes (Fig. 1). Although the present study is framed in a key topic dealing with the coexistence of a large terrestrial mammal flagship species and people in humanized landscapes, it is worth noting that this kind of approach on this specific topic was largely missing at a global scale. The extensive literature may overwhelm managers in their attempt to synthesize conclusions so as to apply optimum conservation and management strategies. Therefore, summarizing and providing critical appraisal of the existing literature may strengthen and optimize our management tools, to improve human-bear coexistence and help delineate further research and conservation strategies for this species and other large carnivores. By reviewing the available literature, we tested the following hypotheses: (1) Human activities and infrastructures increase bear mortality risk; (2) human activities induce changes in bear behaviour, habitat use and movements, reproduction, and physiology; (3) human infrastructures, such as settlements and roads, limit brown bear population connectivity and reduce genetic diversity; (4) the effects of human activities on bears vary at different spatial and temporal scales; and, (5) different durations of coexistence between brown bears and humans in Europe and North America may help explain some differences in brown bear responses to human activities at the trans-continental scale, with bears in Europe generally showing better adaptation to humans.

## 2. Methods

We conducted the literature review using Elsevier's Scopus database and a broad range of terms that represent the consequences for bears of inhabiting human-modified landscapes. The terms 'bear', 'grizzly' and 'Ursus arctos' were combined with 'agricultural', 'agriculture', 'artificial feeding', 'attack', 'corridor', 'crop', 'damage', 'food-conditioning', 'human', 'human-caused mortality', 'human-dominated landscape', 'human-induced mortality', 'human settlement', 'hunting', 'livestock', 'mitigation', 'nuisance', 'road', 'supplemental feeding', 'tourism' and 'viewing'. The search was done for the title, keywords and abstract of articles in English published between 1980 and the present. We also searched in the literature-cited sections of all retrieved articles. We excluded articles that did not mention presence of people, human activities, and infrastructures in the description of their study areas, as those articles were not carried out in human-modified landscapes). The publications finally included in our review ( $n = 156$ ) were categorized, and then examined, according to different human-related factors: (1) human settlements ( $n = 30$ ); (2) habituation ( $n = 6$ ); (3) anthropogenic foods ( $n = 15$ ); (4) transport infrastructures ( $n = 72$ ); (5) hunting and fishing activities ( $n = 31$ ); (6) forestry ( $n = 10$ ); (7) industrial activities ( $n = 4$ ); (8) viewing practices ( $n = 10$ ) and, (9) other recreational activities ( $n = 7$ ). Publications that addressed several topics were included in more than one category. We were doing a narrative synthesis instead of a meta-analysis because there is large variability among bear studies in sample size, study design, methods of collecting information (e.g., using radio-tracked bears vs. pure observational data) and overall, context. Brown bears inhabit North America and Eurasia and many of the studies revised here did not include fine-scale information on key parameters (i.e., on human-, bear-, and habitat-related variables) as to allow a meta-analysis that could account for the huge variability in those factors across bear populations and continents.

## 3. Results

We organized our results on the basis of different human-related factors that negatively affect brown bears inhabiting human-modified landscapes and described how the effects of each factor seemed to vary across the world.

### 3.1. Human settlements

Human settlements, defined as inhabited single houses, villages or towns (Elfström et al., 2014), decrease brown bear habitat quality due to human disturbance and persecution. Bear habitat selection is negatively affected by human density and proximity in both North America (Mowat et al., 2013; Suring et al., 2006) and Europe (Fernández et al., 2012; Nellemann et al., 2007; Oberosler et al., 2017; Ziólkowska et al., 2016). Avoidance of human settlements may be of particular importance during winter denning (Ciarniello et al., 2005; Petram et al., 2004), when disturbance can cause the loss of cubs and thus lower reproductive success, which in turn can reflect negatively on population trends (Linnell et al., 2000; Swenson et al., 1997a). Increasing the density of settlements decreases bear movements in North America, which may lead to low gene flow and elevated genetic distances (Proctor et al., 2012).

Bear avoidance of human settlements is age and sex dependent. Subadult individuals and females with cubs occur near people or settlements more often than adult males and lone adult females in both North America (Gibeau et al., 2002) and Europe (Kaczensky et al., 2006; Nellemann et al., 2007). Subadults and females with cubs may move into areas closer to human settlements mainly to avoid predation and infanticide by adult males, respectively (Elfström et al., 2014).

Brown bears living close to human settlements employ behavioural strategies to deal with human disturbance, avoiding people at different spatial and temporal scales. Bears become more crepuscular or nocturnal to avoid overlap with human diel activity patterns (Gibeau et al., 2002; Kaczensky et al., 2006; Martin et al., 2010; Oberosler et al., 2017; Ordiz et al., 2014; Schwartz et al., 2010). This behavioural change is particularly common in Europe, probably due to a longer history of persecution than in North America. Habitat selection may also vary with time of day and season according to human-derived

risks, e.g., by selecting slopes and highly concealed resting sites during daylight hours (Martin et al., 2010; Ordiz et al., 2011; Skuban et al., 2017a). Moreover, Scandinavian bears select resting sites further from human settlements in summer and fall (when human activity is high) than in spring (Ordiz et al., 2011). Brown bears inhabiting human-modified landscapes in Europe also select areas with high elevations and rugged terrain, which are associated with better shelter and limited human access (Penteriani et al., in press, Nellemann et al., 2007; Martin et al., 2010; Fernández et al., 2012; Ziólkowska et al., 2016). Contrary, Slovak bears are known to move closer to human settlements in late summer/autumn due to the availability of fruits and especially maize on fields (Skuban et al., 2017a).

Human settlements may also create evolutionary and ecological traps in both Europe and North America (Miller and Tutterrow, 1999; Mowat et al., 2013; Penteriani et al., 2018; Schwartz et al., 2012, 2010; Steyaert et al., 2016). For example, the presence of attractive food (natural or anthropogenic) nearby human settlements may create ecological trap scenarios, as bears may select such areas based on seemingly reliable environmental cues that would report positively on fitness, but due to human interference, increase mortality risk, i.e., decrease fitness. Some individuals move from source habitats into human settlement areas, potentially threatening the long term viability of the population, especially when small (Lamb et al., 2017; Penteriani et al., 2018).

Brown bears using the surroundings of human settlements are often involved in human-bear conflict and experience reduced survival (Lamb et al., 2017; Sato, 2017). Common human-bear conflicts in such areas include damaging property, obtaining human-related foods and human injuries (Qashqaei et al., 2014), which in turn cause retaliatory bear mortality (Gunther et al., 2004; Miller and Tutterrow, 1999). Other sources of bear mortality near human settlements involve the lethal removal of conflict bears (Gunther et al., 2004; Steyaert et al., 2016) and collisions with vehicles and trains (see **Transport infrastructures**).

High human density can cause North American brown bear population declines (Mattson and Merrill, 2004). Indeed, some studies have reported that North American brown bears, cannot exist at human densities  $>7$  people/km<sup>2</sup> (Mattson and Merrill, 2002; Mowat et al., 2013), which might derive from a shorter coexistence of bears and humans in North America, as some European bear populations inhabit areas with much higher human densities (Swenson et al., 2000).

### 3.2. Habituation

Brown bear habituation, a process leading to decreased responsiveness to a repeated negative stimulus, implies that some individuals become more tolerant to human presence or activities (Mattson, 1990; Ordiz et al., 2019). Subadult bears may be more prone to habituation to humans (Mueller et al., 2004), which may also occur because subadults frequently inhabit areas closer to people than do adults (e.g., Nellemann et al., 2007). Bear to human habituation can encourage the exploitation of food and other resources near humans, which can lead to conflicts. Human to bear habituation can also reduce fear of bears, which can also cause conflict if people behave inappropriately or bears associate humans with food (Penteriani et al., 2016). Habituated bears near roads or railways are also more likely to encounter food associated with people and become human-food-conditioned (Herrero et al., 2005) and are more likely to be injured or killed by vehicles or trains. In addition, habituated bears are more likely to be killed legally, removed as potentially dangerous animals, and illegally killed by poachers (Herrero et al., 2005). More subtle, non-visible effects of habituation, e.g., physiological changes incurring energetic costs, can also occur (Herrero et al., 2005; Støen et al., 2015).

### 3.3. Anthropogenic food

The brown bear is an omnivorous generalist, which leads bears to use attractive feeding opportunities available in human-modified landscapes, such as livestock, apiaries, agriculture and human food waste (Bautista et al., 2017; Coogan et al., 2018; Naves et al., 2018). However, bears consuming anthropogenic foods may experience lower protein consumption than optimal during spring (Coogan et al., 2018), which reduces body mass gain (Swenson et al., 2007), causes dietary-induced thermogenesis (Erlenbach et al., 2014), and may translate into lower reproductive success (López-Alfaro et al., 2013). Despite brown bear tolerance to varying dietary macronutrient proportions, populations adapted to consume anthropogenic foods may struggle if such supplies become unavailable (Coogan et al., 2018).

Brown bear use of anthropogenic foods is a great source of human-bear conflict and related bear mortality in North America (Gunther et al., 2004; Wilson et al., 2006), Europe (Bautista et al., 2017; Fernández-Gil et al., 2016; Naves et al., 2018; Steyaert et al., 2016) and Asia (Qashqaei et al., 2014; Sato et al., 2005). This general pattern reinforces the role of attractive anthropogenic foods in human-modified landscapes as ecological traps that may ultimately threaten population viability (Penteriani et al., 2018). Furthermore, the use of garbage by brown bears may increase pathogen infection risk and the ingestion of toxics and foreign bodies (Coogan and Raubenheimer, 2016; Sato, 2017).

### 3.4. Transport infrastructures

Developed countries are crisscrossed by roads, e.g., 50% of land in Europe is within 1.5 km of the nearest road (Torres et al., 2016), which has a cost for wildlife. Because brown bears have large spatial requirements, the effects of transport infrastructure distribution and density are a major concern.

### 3.4.1. Roads

**3.4.1.1. Effects on human induced mortality.** Bears inhabiting human-modified landscapes are frequently killed by vehicles and during human-bear interactions near roads (McLellan, 2015). Road-related mortality varies with sex, age, season and time of day (Kite et al., 2016) (see Supplemental File 1 for detailed road effects). For example, (a) females with cubs suffer higher mortality than females with yearlings (Ciarniello, 2006); (b) mortality particularly affects subadult individuals (Boulanger et al., 2014; Kaczensky et al., 2003; Skuban et al., 2017b), because of their inexperience and their extensive movements during dispersal (Boulanger et al., 2014; Kaczensky et al., 2003; Sawaya et al., 2014); (c) in North America (Graves et al., 2007; Kite et al., 2016) and Slovakia (Skuban et al., 2017b), bears are more frequently killed during autumn, probably as they increase food searching along roads during hyperphagia, whereas in Slovenia road mortality peaks during the mating season, in spring (Kaczensky et al., 2003).

The presence of roads in high quality habitats facilitates human access, which decreases bear density, increases bear mortality, and generates bear displacement (Ciarniello et al., 2007). In North America, the carrying capacity of ecosystems decreases up to 30% where roads are present (Lyons et al., 2018). The home range of bears inhabiting areas with high road density is smaller as a consequence of the reduced movement of individuals (Bischof et al., 2017), which may perceive roads as borders of their home range. Displacement of bears from habitats around roads can also reduce body condition (Mace et al., 1996; McLellan and Shackleton, 1988).

Road density in North America should be kept below 0.6 km/km<sup>2</sup> to promote bear population recovery, because female brown bear survival and reproduction is higher with road densities below that limit (Mace et al., 1996). However, thresholds might be population and area specific, with tolerated values of road density varying between 0.5 and 0.75 km/km<sup>2</sup> (Proctor et al., 2018). In Scandinavia, traffic load may be more important than road density (Elfström et al., 2008), as bears prefer areas with a higher density of roads and lower traffic than *vice versa* (Northrup et al., 2012). When road density increases, females may use poorer habitats to avoid human presence and, thus, suffer higher mortality and lower reproductive success (Mace et al., 1996). This may derive from a longer coexistence between bears and humans in Europe than in North America, with the former being more tolerant to the presence of human infrastructures.

**3.4.1.2. Effects on behaviour.** **3.4.1.2.1. Road avoidance displacement.** In many areas, bears avoid roads to reduce contact with humans and mortality risk (Mace et al., 1996), especially when roads increase human access to bear habitats (Wielgus and Vernier, 2003). Brown bears avoid roads when denning in both Europe and North America. Actually: (a) brown bears avoid denning in areas with a high density of roads (Ciarniello et al., 2005; Elfström et al., 2008), which may cause den abandonment (Elfström and Swenson, 2009); (b) the presence of roads affects den choice, with adult males choosing the dens furthest from roads (Elfström and Swenson, 2009). In North America, the relative probability of den selection dropped by 30% when road densities increased from 0 to 0.6 km/km<sup>2</sup> and by nearly 70% at road densities of ~1 km/km<sup>2</sup>, and road densities of 2.0 km/km<sup>2</sup> are entirely avoided (Pigeon et al., 2014).

**3.4.1.2.2. Use of roads.** Food availability alongside roads can increase the likelihood of bears using road edges and crossing roads, particularly in spring and early summer, when roadsides are rich in herbaceous species (Roever et al., 2008), as well as during the hyperphagia period (Graham et al., 2010; McLellan and Shackleton, 1988). This attraction to roads increases bear mortality in both North America and Europe (Graves et al., 2007; Skuban et al., 2017b). Thus, local abundance of food resources (McLellan and Shackleton, 1988) may transform road networks into evolutionary/ecological traps (Ciarniello et al., 2007; Penteriani et al., 2018).

**3.4.1.3. Barrier effects.** Roads and highways limit individual movement, dispersal and connectivity among bear populations across their worldwide range (Bischof et al., 2017; Kaczensky et al., 2003), increasing the risk of extinction in endangered populations (Karamanlidis et al., 2012; Mateo-Sánchez et al., 2014; Proctor et al., 2012, 2002). This may be due to the combination of bears avoiding areas with high human activity and the high mortality due to vehicle collisions (Proctor et al., 2002). Road permeability for bears is directly related to traffic volumes (Find'o et al., 2018; Proctor et al., 2012), whose effect also varies depending on local factors (Waller and Servheen, 2005).

Isolation of endangered populations could compromise survival by increasing genetic distances (Proctor et al., 2012) and reducing both genetic interchanges and diversity (McCown et al., 2009), which can increase extinction risk due to inbreeding depression (Frankham, 2008). Again, the barrier effect of roads on bears varies depending on sex (Sawaya et al., 2014), age (Waller and Servheen, 2005), season (Graves et al., 2007; Kite et al., 2016) and time of day (Graves et al., 2006) (see Supplemental File 1). For instance, the viability of brown bear populations may locally depend on the survival and dispersal of adult females across highways (Proctor et al., 2012).

### 3.4.2. Railways

Railways cause bear mortality throughout their distribution range (Kaczensky et al., 2003; Waller and Servheen, 2005). Bears are attracted to railways: (a) to feed on spilled grain (Gangadharan et al., 2017; Murray et al., 2017) and sulphur pellets (Hopkins et al., 2014) that fall from trains transporting agricultural products (Waller and Servheen, 2005); (b) because the

edge effect of railway structures increases light and temperature, favouring fruit production (Pollock et al., 2017); and (c) because of the presence of ungulates foraging on railway verges and carcasses of animals killed by trains (Hopkins et al., 2014; Murray et al., 2017).

### 3.5. Hunting and fishing activities

High harvest rates cause population decline (Bischof et al., 2009; Mattson and Merrill, 2002) and fragmentation in both North America and Europe. Beyond limits considered as sustainable (McLellan et al., 2017), harvests can threaten population survival (Lortkipanidze, 2010), with young males being the most vulnerable cohort (McLellan et al., 2017).

Fecundity, litter size and cub survival are smaller in hunted populations (Gosselin et al., 2017, 2014; Swenson et al., 1997b; Wielgus and Bunnell, 2000). As observed mainly in European populations, removing adult males triggers a reorganization of the social and spatial structure of a bear population (Leclerc et al., 2017): immigration of younger and unrelated males increases infanticide of unrelated offspring, which decreases recruitment and may reduce population growth rates. The observed adaptive behaviour in European populations may derive from a longer history of persecution (Swenson et al., 1997b) (but see McLellan, 2005). Natality rate can also decrease due to lower mean age of males caused by the harvest of adult individuals (Frank et al., 2017; Milner et al., 2007).

The sex ratio and age structure of bear populations may change when hunted. For example, by killing older females the population-wide age of females decreases and so does population growth, because young females generally have smaller litters with lower survival (Frank et al., 2017). The harvest of bears can also decrease dispersal movements and the colonization of new areas because young animals can occupy the territories left behind by the animals killed nearby (Frank et al., 2017). Thus, hunting activities may influence home range dynamics and the social structure of bear populations (Frank et al., 2018). Bears killed for recreational purposes are generally shot further from villages than in management removals (Steyaert et al., 2016) and a spatial heterogeneity in hunting pressure could produce source–sink dynamics, with lower recruitment in areas of high hunting-derived mortality (Gosselin et al., 2017). All the effects mentioned above can lead to lowered population growth, population decline (Gosselin et al., 2014) and even extinction of small populations (Wielgus et al., 2001).

Prolonged historical hunting, occurring in Europe as opposed to North America, can modify life-history traits in relation to cub survival and litter size. For example, cubs that remain longer with their mothers have higher chances of surviving than independent yearlings, because the hunting of bear families is prohibited (Zedrosser et al., 2013). Thus, hunting pressure could select for prolonged maternal care, which promotes slow life histories that may have demographic consequences (Bischof et al., 2018; Van De Walle et al., 2018; Zedrosser et al., 2011). Also, females with earlier primiparity may be selected for the same reason (Krofel et al., 2012).

Solitary bears may increase their metabolic rates and stress (Støen et al., 2015) and become more wary and nocturnal during the hunting season (Swenson, 1999) in order to avoid hunters, particularly in Europe. Bears decrease foraging efficiency in the morning during the autumn hunting season, when the risk of getting shot is highest, spending more time vigilant and foraging in lower quality food patches (Hertel et al., 2016b). For bears, the hyperphagia period is critical to store fat, so documented alterations in optimal activity patterns and habitat displacement during hyperphagia, when foraging is the key bear behaviour, may result in poorer body condition and lower reproductive success (Hertel et al., 2016b; Ordiz et al., 2012).

The hunting of other species can also affect brown bears. For example, drive hunting of wild boars with dogs in central-southern Europe is an important source of disturbance during hyperphagia, reducing bear foraging efficiency and increasing bear mortality (Maiorano et al., 2015). Moose hunting in Scandinavia can cause bear den abandonment and may favour bear attacks on humans in autumn, when bears experience a pre-denning physiological state that may prevent them from running away and charge more often than they do earlier in the year (Sahlén et al., 2015). Hunting of ungulates in North America modifies brown bear autumn distribution, because bears exploit carcasses left by hunters and, consequently, human-bear contact increases, as does bear mortality (Haroldson et al., 2004).

Fishing for salmon in North America is decreasing salmon availability for bears to eat, which can increase fitness costs by means of increased cortisol and testosterone levels (Bryan et al., 2013) and can also affect bear population numbers and ecosystem health (Levi et al., 2012). The same situation has occurred in Japan, where salmon overfishing has prompted a change in brown bear diet from fish to deer (Matsubayashi et al., 2015). Sport fishing can also displace bears from salmon spawning sites, creating potential food-stress situations (Olson et al., 1998).

### 3.6. Forestry

Brown bear reactions to forest disturbances have been mainly studied in North America and northern Europe. Forest clearings can be attractive foraging areas, but they are yet another form of human alteration of bear habitats (Boulanger et al., 2013; Stewart et al., 2012). Locally, bears may avoid forest harvests (but see Wielgus and Vernier, 2003), forest clearings (Frackowiak et al., 2014), and forested roads within harvested areas (Wielgus and Vernier, 2003), which may reduce available habitat. Moreover, the use of harvested forests increases mortality risk due to increased human-bear interactions and increased road density (Gaulton et al., 2011; Stewart et al., 2012; Wielgus and Vernier, 2003). Indeed, (a) higher human access via forestry roads brings humans and bears into closer contact, which increases bear mortality (Ciarniello et al., 2009); and (b) logging increases forestry road network density and, again, bear mortality (Ciarniello et al., 2009; Gaulton et al., 2011; Stewart

et al., 2012) (see Roads). Forested areas with low human alteration are crucial for maintaining habitat suitability and connectivity (Ziółkowska et al., 2016), yet human-caused fragmentation and isolation can generate significant genetic divergence (Straka et al., 2012).

Forestry can also modify the distribution and abundance of berries, as shown in Scandinavia (Hertel et al., 2016a), because (1) clear-cutting may reduce bilberry plant coverage, which is higher in mature forests than in clear-cuts, and (2) dense young forests with little light incidence are not productive bilberry habitats. Something similar occurs with ant availability in clear-cuts (Frank et al., 2015). Thus, because short harvest rotation times and denser forest stands that increase economic income might negatively affect bilberry and hardmast availability for bears, commercial forestry might alter the distribution and abundance of food, consequently altering bear foraging patterns.

### 3.7. Industrial activities

Effects of industrial activities have mostly been studied on North American brown bears. Industrial activities can threaten wildlife by means of direct mortality, encounters with humans, habitat fragmentation, and a decreased habitat quality as a result of pollution, noise, and light disturbances (Richardson, 2017). Pipelines and other oil and gas features are generally avoided, probably because of increased human activity (McKay et al., 2014). Seismic cutlines to prospect for oil and gas reservoirs change the size and distance between vegetation patches, which makes habitat less favourable for bears (Linke et al., 2005). Industrial activities also require road building, which increases bear mortality in North America (McLellan, 2015) and potentially in Europe (see Roads).

### 3.8. Viewing practices

The practice of brown bear viewing (i.e., organized viewing of wild bears) is developed all around the world (Penteriani et al., 2017b). However, it is in areas where bear populations are endangered and with little optimal habitat that bear viewing may be more costly for bears, as an additional disturbance factor in human-modified landscapes and because of the higher number of people that can participate in such activities, compared to more remote areas.

Here, in view of the recent review by Penteriani et al., 2017b, we only provide a synthesis of the potential negative effects of bear viewing. Because bear viewing frequently occurs in sensitive places where bears congregate for mating, rearing cubs and/or feeding, behavioural, physiological and ecological aspects related to brown bears may be involved. Brown bears may leave areas that are crucial for them and/or reduce activity during the daytime (Rode et al., 2007, 2006). Moreover, human disturbance can affect bear foraging patterns, mating behaviour, space use and activity, which may in turn affect bear survival and fitness (Fortin et al., 2016; Rode et al., 2006). When temporary and non-regulated viewing occurs, e.g., targeting females with cubs or bear aggregations during mating and hyperphagia (Penteriani et al., 2017b; Ruiz-Villar et al., 2019), brown bears may face additional risks (see also Herrero et al., 2005), e.g., close proximity of bears and people may encourage illegal acts such as poaching. Additionally, viewing sites can represent sources of physiological stress because of human presence. Indeed, because human presence and human activities affect brown bear rhythms of activity (Ordiz et al., 2014, 2012) and may act as a stressor (Støen et al., 2015), bear viewing can add to the existing level of disturbance induced by people in human-modified landscapes.

In some areas, brown bear viewing is associated with the presence of artificial feeding points, which attract bears to increase viewing opportunities (Penteriani et al., 2017b). The provision of artificial food might impact negatively on bears (Penteriani et al., 2010, Penteriani et al., 2017b) by: (a) interfering with daily/seasonal movements; (b) disrupting denning behaviour; (c) increasing the possibility of creating food-conditioned bears; and (d) providing bears with food that may be nutritionally unfavourable.

### 3.9. Other recreational activities

Recreational activities may be perceived as a nuisance by brown bears, whose levels of activity in otherwise suitable habitats are inversely related to the amount of human recreation (Fortin et al., 2016; Nellemann et al., 2007). As a general rule, brown bears may (a) switch from diurnal to crepuscular/nocturnal activity (Ordiz et al., 2013); (b) reduce the use of areas closer to people; and (c) experience reduced foraging efficiency (Fortin et al., 2016; Nellemann et al., 2007). Thus, recreational activities can potentially reduce survival, decrease nutritional intake, displace bears, and reduce reproduction (Coleman et al., 2013; Fortin et al., 2016), besides inducing physiological responses such as increased stress (Støen et al., 2015).

North American riparian habitats, which are seasonally important for brown bears (Machutcheon and Wellwood, 2002a), are frequently used by people for recreational travel and camping. Here, concerns exist on the potential negative effects that increasing human use of rivers may have on bears (Machutcheon and Wellwood, 2002a). Indeed, bear-human interactions in river valleys can displace bears from riparian habitats, changing bear rhythms of activity and, if a conflicting situation occurs (e.g., a bear attack), it may lead to the killing or translocation of bears (Machutcheon and Wellwood, 2002a).

Finally, brown bears are either found in lower abundance or are less active around trails used for motorized recreational activities (Ladle et al., 2018a, 2018b). Such an avoidance of areas of interest to motorized recreationists might affect the foraging ability of bears.

#### 4. Conclusions and management implications

Our review and summary of the available information supports our five hypotheses concerning the effects of human disturbance on bears inhabiting human-dominated landscapes. Flexibility in the daily activity or movement patterns of brown bears may help them inhabit human-modified landscapes (Zarzo-Arias et al., 2018), but behavioural adaptations alter optimal foraging and resting routines (Ordiz et al., 2017). Human activities displace bears from their preferred areas and, therefore, limiting human activities spatially (Coleman et al., 2013b) and temporally (Schwartz et al., 2010) seems crucial for the long-term conservation of bears in human-modified landscapes. In the short-term, this need can be particularly important for small and endangered bear populations, but behavioural responses also matter in increasing bear populations, where some individuals may be more prone to interact with humans and our activities. Avoiding or at least reducing such potential interactions between large carnivores and humans is crucial to favour coexistence in human-dominated landscapes.

We recommend to also reviewing both potential positive effects of human-activities for bears (e.g., some types of forestry may increase food productivity for bears), and bear effects on human activities (e.g., bears seasonally feeding on fish may affect recreational human activities) to build fully integrated management strategies that allow large carnivore conservation and development of some human activities.

Nine crucial points arise from our literature review, suggesting that they should be addressed to promote human-brown bear coexistence in human-modified landscapes:

1. Bears have high mortality rates in areas near human activity and infrastructure. The conservation of populations affected by the rapidly expanding development of human access into wilderness areas and the recovery of bear populations expanding into human-modified landscapes may be compromised. Indeed, human-induced mortality is the primary factor threatening brown bear and other large carnivore populations viability (e.g., Eberhardt et al., 1994; Woodroffe and Ginsberg, 1998). Given the clear impact of human infrastructure on the population dynamics and behaviour of bears and other large carnivores, rigorous environmental assessments are needed when planning new infrastructures.
2. Increased effort in education about waste management and bear deterrence methods in areas adjacent to bear habitats may reduce habituation and food conditioning and, therefore, human bear conflicts and bear mortality (Marley et al., 2017; Sato, 2017).
3. Future management efforts should be aimed at safeguarding and restoring the connectivity of bear habitats in order to preserve genetic variation of subpopulations and to support gene flow among them (Straka et al., 2012).
4. Mitigation options to reduce negative road effects include limiting access and reclaiming roads no longer needed. Restricting motorized trail use will also allow bears to make the best use of foraging opportunities and reduce required investment in avoidance behaviours (Ladle et al., 2018a, 2018b). Moreover, wildlife crossing structures, particularly overpasses and open-span bridges (Ford et al., 2017), placed in optimal areas may allow sufficient gene flow and prevent isolation problems (Find'o et al., 2018; Sawaya et al., 2014). Access of bears from protected areas to such structures must be safeguarded.
5. Impacts of bear viewing are highly context and population dependent (Penteriani et al., 2017b; Zarzo-Arias et al., 2018), thus requiring local assessments and regulation. Suitability, locations, and schedules of bear viewing need to be evaluated on the basis of the conservation status of bear populations, local bear behaviour, and annual availability of key food resources, ensuring that wildlife watchers do not prevent bears from foraging in optimal areas.
6. Regulation of camping sites and implementation of mitigation measures to minimize risk to people and bears are needed to (Machutcheon and Wellwood, 2002a, 2002b): (1) reduce the possibility of bears becoming conditioned to human food; (2) confine human impacts to bear habitat of the lowest quality; (3) place campsites in open areas that provide good visibility and are not surrounded by dense vegetation; and (4) restrict people camping alone, to reduce the risk of bear attacks (Garrote et al., 2017; Machutcheon and Wellwood, 2002b; Penteriani et al., 2016, Penteriani et al., 2017a).
7. While empirical studies support the fact that nutritional intake can decline in bears exposed to recreational activities, there is no data regarding the impacts of recreation in terms of bear energetic costs and fitness at the population level, which can thus represent an important area of future research, for both bears (Fortin et al., 2016) and other large carnivores. Managers must ensure that human recreation occurs without interfering wildlife, to avoid both disturbance and potential changes in wildlife behaviour, which ultimately pays off in management and conservation challenges if animals lose fear to people and/or suffer fitness costs.
8. As suggested by Coogan et al. (2018a), the complex set of factors acting upon bears in human-modified landscapes requires multi-scale and interdisciplinary approaches to their conservation and management. Moreover, because administrative and political rules govern management policies, it is crucial that scientific results have a societal impact, i.e., good applied science should be communicated in a way that non-specialists can understand (Coogan et al., 2018). This would facilitate a better understanding by the public of the management regulations that in some circumstances may, for instance, limit access to areas heavily used by bears. People may assume those regulations more positively if they understand that they are crucial for large carnivore conservation. This is particularly important now that several large carnivore populations are recovering former ranges in human-dominated landscapes (Chapron et al., 2014). Further recovery likely requires that policy-makers and the public continue to recognize the value of wilderness areas as strongholds for biodiversity conservation (Gilroy et al., 2015).



9. The longer historical coexistence of bears and humans in Europe than in North America may imply differences in behavioural responses to human activities at the trans-continental scale (Fortin et al., 2016; Zedrosser et al., 2011). Further differences occur among populations in each continent, suggesting that bear behavioural responses may reflect both the long-term effects of persecution and the effects of alternative management regimes nowadays. Therefore, further empirical research should address the potential variation of bear and other large carnivore behavioural reactions in response to different long-term histories and present management, e.g., comparing how animals react in areas where they are hunted vs. where they are fully protected.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e00937>.

### References

- Bautista, C., Naves, J., Revilla, E., Fernández, N., Albrecht, J., Scharf, A.K., Rigg, R., Karamanlidis, A.A., Jerina, K., Huber, D., Palazón, S., Ciucci, P., Groff, C., Dutsov, A., Seijas, J., Quenette, P.I., Olszańska, A., Shkvyria, M., Adamec, M., Ozolins, J., Jonozović, M., Selva, N., 2017. Patterns and correlates of claims for brown bear damage on a continental scale. *J. Appl. Ecol.* 54, 282–292. <https://doi.org/10.1111/1365-2664.12708>.
- Bischof, R., Swenson, J.E., Yoccoz, N.G., Myrsterud, A., Gimenez, O., 2009. The magnitude and selectivity of natural and multiple anthropogenic mortality in hunted brown bears. *J. Anim. Ecol.* 78, 656–665. <https://doi.org/10.1111/j.1365-2656.2009.01524.x>.
- Bischof, R., Steyaert, S.M.J.G., Kindberg, J., 2017. Caught in the mesh: roads and their network-scale impediment to animal movement. *Ecography* 40, 1369–1380. <https://doi.org/10.1111/ecog.02801>.
- Bischof, R., Bonenfant, C., Rivrud, I.M., Zedrosser, A., Friebe, A., Coulson, T., Myrsterud, A., Swenson, J.E., 2018. Regulated hunting re-shapes the life history of brown bears. *Nat. Ecol. Evol.* 2, 116–123. <https://doi.org/10.1038/s41559-017-0400-7>.
- Boulanger, J., Cattet, M., Nielsen, S.E., Stenhouse, G., Cranston, J., 2013. Use of multi-state models to explore relationships between changes in body condition, habitat and survival of grizzly bears *Ursus arctos horribilis*. *Wildl. Biol.* 19, 274–288. <https://doi.org/10.2981/12-088>.
- Boulanger, J., Stenhouse, G.B., Margalida, A., 2014. The impact of roads on the demography of grizzly bears in Alberta. *PLoS One* 9, 1–22. <https://doi.org/10.1371/journal.pone.0115535>.
- Bryan, H.M., Darimont, C.T., Paquet, P.C., Wynne-Edwards, K.E., Smits, J.E.G., 2013. Stress and reproductive hormones in grizzly bears reflect nutritional benefits and social consequences of a salmon foraging niche. *PLoS One* 8, 1–10. <https://doi.org/10.1371/journal.pone.0080537>.
- Chapron, G., Huber, D., Andrén, H., López-bao, J.V., Adamec, M., Linnell, J.D.C., Boitani, L., Swenson, J.E., Salvatori, V., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346 (80), 17–20. <https://doi.org/10.1126/science.1257553>.
- Ciarnello, L.M., Boyce, M.S., Heard, D.C., Seip, D.R., 2007. Components of grizzly bear habitat selection: density, habitats, roads, and mortality risk. *J. Wildl. Manag.* 71, 1446–1457. <https://doi.org/10.2193/2006-229>.
- Ciarnello, L.M., 2006. Demography and Habitat Selection by Grizzly Bears (*Ursus arctos* L.) in Central British Columbia. *Dep. Biol. Sci. Univ. Alberta*.
- Ciarnello, L.M., Boyce, M.S., Heard, D.C., Seip, D.R., 2005. Denning behavior and den site selection of grizzly bears along the Parsnip river, British Columbia, Canada. *Ursus* 16, 47–58.
- Ciarnello, L.M., Boyce, M.S., Seip, D.R., Heard, D.C., 2009. Comparison of grizzly bear *Ursus arctos* demographics in wilderness mountains versus a plateau with resource development. *Wildl. Biol.* 15, 247–265. <https://doi.org/10.2981/08-080>.
- Coleman, T.H., Schwartz, C.C., Gunther, K.A., Creel, S., 2013. Influence of overnight recreation on grizzly bear movement and behavior in Yellowstone National Park. *Ursus* 24, 101–110. <https://doi.org/10.2192/URSUS-D-12-00024.1>.
- Coogan, S.C., Raubenheimer, D., 2016. Might macronutrient requirements influence grizzly bear-human conflict? Insights from nutritional geometry. *Ecosphere* 7, 1–15. <https://doi.org/10.1002/ecs2.1204>.
- Coogan, S.C., Coops, N.C., Janz, D.M., Cattet, M.R.L., Kearney, S.P., Stenhouse, G.B., Nielsen, S.E., 2018a. Towards grizzly bear population recovery in a modern landscape. *J. Appl. Ecol.* 1–7. <https://doi.org/10.1111/1365-2664.13259>.
- Coogan, S.C., Raubenheimer, D., Stenhouse, G.B., Coops, N.C., Nielsen, S.E., 2018b. Functional macronutritional generalism in a large omnivore, the brown bear. *Ecol. Evol.* 8, 2365–2376. <https://doi.org/10.1002/ece3.3867>.
- Eberhardt, L.L., Blanchard, B.M., Knight, R.R., 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Can. J. Zool.* 72, 360–363. <https://doi.org/10.1139/z94-049>.
- Elfström, M., Swenson, J.E., 2009. Effects of sex and age on den site use by Scandinavian brown bears. *Ursus* 20, 85–93. <https://doi.org/10.2192/09GR005.1>.
- Elfström, M., Swenson, J.E., Ball, J.P., 2008. Selection of denning habitats by Scandinavian brown bears *Ursus arctos*. *Wildl. Biol.* 14, 176–187. [https://doi.org/10.2981/0909-6396\(2008\)14\[176:SODHBS\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2008)14[176:SODHBS]2.0.CO;2).
- Elfström, M., Zedrosser, A., Stoen, O.G., Swenson, J.E., 2014. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. *Mamm. Rev.* 44, 5–18. <https://doi.org/10.1111/j.1365-2907.2012.00223.x>.
- Erlénbach, J.A., Rode, K.D., Raubenheimer, D., Robbins, C.T., 2014. Macronutrient optimization and energy maximization determine diets of brown bears. *J. Mammal.* 95, 160–168. <https://doi.org/10.1644/13-MAMM-A-161>.
- Fernández, N., Selva, N., Yuste, C., Okarma, H., Jakubiec, Z., 2012. Brown bears at the edge: modeling habitat constrains at the periphery of the Carpathian population. *Biol. Conserv.* 153, 134–142. <https://doi.org/10.1016/j.biocon.2012.04.013>.

- Fernández-Gil, A., Naves, J., Ordiz, A., Quevedo, M., Revilla, E., Delibes, M., 2016. Conflict misleads large carnivore management and conservation: Brown bears and wolves in Spain. *PLoS One* 11, e0151541. <https://doi.org/10.1371/journal.pone.0151541>.
- Find'o, S., Skuban, M., Kajba, M., Chalmers, J., Kalaš, M., 2018. Identifying attributes associated with brown bear (*Ursus arctos*) road-crossing and roadkill sites. *Can. J. Zool.* 97, 156–164. <https://doi.org/10.1139/cjz-2018-0088>.
- Ford, A.T., Barreto, M., Clevenger, A.P., 2017. Road mitigation is a demographic filter for grizzly bears. *Wildl. Soc. Bull.* 41, 712–719. <https://doi.org/10.1002/wsb.828>.
- Fortin, J.K., Rode, K.D., Hilderbrand, G.V., Wilder, J., Farley, S., Jorgensen, C., Marcot, B.G., 2016. Impacts of human recreation on brown bears (*Ursus arctos*): a review and new management tool. *PLoS One* 11, 1–26. <https://doi.org/10.1371/journal.pone.0141983>.
- Frackowiak, W., Theuerkauf, J., Pirga, B., Gula, R., 2014. Brown bear habitat selection in relation to anthropogenic structures in the Bieszczady Mountains, Poland. *Biologia* 69, 926–930. <https://doi.org/10.2478/s11756-014-0386-4>.
- Frank, S.C., Steyaert, S.M.J.G., Swenson, J.E., Storch, I., Kindberg, J., Barck, H., Zedrosser, A., 2015. A “clearcut” case? Brown bear selection of coarse woody debris and carpenter ants on clearcuts. *For. Ecol. Manage.* 348, 164–173. <https://doi.org/10.1016/j.foreco.2015.03.051>.
- Frank, S.C., Ordiz, A., Gosselin, J., Hertel, A., Kindberg, J., Leclerc, M., Pelletier, F., Steyaert, S.M.J.G., Støen, O.-G., Van De Walle, J., Zedrosser, A., Swenson, J.E., 2017. Indirect effects of bear hunting: a review from Scandinavia. *Ursus* 28, 150–164. <https://doi.org/10.2192/URSUS-D-16-00028.1>.
- Frank, S.C., Leclerc, M., Pelletier, F., Rosell, F., Swenson, J.E., Bischof, R., Kindberg, J., Eiken, H.G., Hagen, S.B., Zedrosser, A., 2018. Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting. *J. Anim. Ecol.* 87, 247–258. <https://doi.org/10.1111/1365-2656.12767>.
- Frank, B., Glikman, J.A., Marchini, S., 2019. *Human-wildlife Interactions: Turning Conflict into Coexistence*. Cambridge University Press.
- Frankham, R., 2008. Inbreeding and extinction: island populations. *Conserv. Biol.* 22, 665–675. <https://doi.org/10.1111/j.1523-1739.1998.96456.x>.
- Gangadharan, A., Pollock, S., Gilhooly, P., Friesen, A., Dorsey, B., St Clair, C.C., 2017. Grain spilled from moving trains create a substantial wildlife attractant in protected areas. *Anim. Conserv.* 20, 391–400. <https://doi.org/10.1111/acv.12336>.
- Garrote, P.J., Delgado, M.M., López-Bao, J.V., Fedriani, J.M., Bombieri, G., Penteriani, V., 2017. Individual attributes and party affect large carnivore attacks on humans. *Eur. J. Wildl. Res.* 63, 80. <https://doi.org/10.1007/s10344-017-1142-1>.
- Gaulton, R., Hilker, T., Wulder, M.A., Coops, N.C., Stenhouse, G., 2011. Characterizing stand-replacing disturbance in western Alberta grizzly bear habitat, using a satellite-derived high temporal and spatial resolution change sequence. *For. Ecol. Manage.* 261, 865–877. <https://doi.org/10.1016/j.foreco.2010.12.020>.
- Gibeau, M.L., Clevenger, A.P., Herrero, S., Wierzchowski, J., 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biol. Conserv.* 103, 227–236.
- Gilroy, J.J., Ordiz, A., Bischof, R., 2015. Carnivore coexistence: value the wilderness. *Science* 347 (80), 382. <https://doi.org/10.1126/science.347.6220.382-a>.
- Gosselin, J., Zedrosser, A., Swenson, J.E., Pelletier, F., 2014. The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. *Proc. R. Soc. B Biol. Sci.* 282, 20141840. <https://doi.org/10.1098/rspb.2014.1840>.
- Gosselin, J., Leclerc, M., Zedrosser, A., Steyaert, S.M.J.G., Swenson, J.E., Pelletier, F., 2017. Hunting promotes sexual conflict in brown bears. *J. Anim. Ecol.* 86, 35–42. <https://doi.org/10.1111/1365-2656.12576>.
- Graham, K., Boulanger, J., Duval, J., Stenhouse, G., 2010. Spatial and temporal use of roads by grizzly bears in west-central Alberta. *Ursus* 21, 43–56. <https://doi.org/10.2192/09GR010.1>.
- Graves, T.A., Farley, S., Goldstein, M.L., Servheen, C., 2007. Identification of functional corridors with movement characteristics of brown bears on the Kenai Peninsula, Alaska. *Landsc. Ecol.* 22, 765–772. <https://doi.org/10.1007/s10980-007-9082-x>.
- Graves, T.A., Farley, S., Servheen, C., Reviewed, P., 2006. Frequency and distribution of highway crossings by Kenai Peninsula brown bears. *Wildl. Soc. Bull.* 34, 800–808. [https://doi.org/10.2193/0091-7648\(2006\)34\[800:fadohc\]2.0.co;2](https://doi.org/10.2193/0091-7648(2006)34[800:fadohc]2.0.co;2).
- Gunther, K.A., Haroldson, M.A., Frey, K., Cain, S.L., Copeland, J., Schwartz, C.C., 2004. Grizzly bear-human conflicts in the Greater Yellowstone ecosystem, 1992–2000. *Ursus* 15, 10–22. [https://doi.org/10.2192/1537-6176\(2004\)015<0010:GBCITC>2.0.CO;2](https://doi.org/10.2192/1537-6176(2004)015<0010:GBCITC>2.0.CO;2).
- Haroldson, M.A., Schwartz, C.C., Cherry, S., Moody, D.S., 2004. Possible effects of Elk harvest on fall distribution of grizzly bears in the greater yellowstone ecosystem. *J. Wildl. Manage.* 68, 129–137. [https://doi.org/10.2193/0022-541X\(2004\)068\[0129:PEOHO\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2004)068[0129:PEOHO]2.0.CO;2).
- Herrero, S., Smith, T., Debrun, T.D., Gunther, K., Matt, C.A., 2005. From the Field: Brown bear habituation to people — safety, risks, and benefits. *Wildl. Soc. Bull.* 33, 362–373.
- Hertel, A.G., Steyaert, S.M.J.G., Zedrosser, A., Mysterud, A., Støen, O.G., Steyaert, S.M.J.G., Swenson, J.E., 2016a. Bears and berries: species-specific selective foraging on a patchily distributed food resource in a human-altered landscape. *Behav. Ecol. Sociobiol.* 70, 831–842. <https://doi.org/10.1007/s00265-016-2106-2>.
- Hertel, A.G., Zedrosser, A., Mysterud, A., Støen, O.G., Steyaert, S.M.J.G., Swenson, J.E., 2016b. Temporal effects of hunting on foraging behavior of an apex predator: do bears forego foraging when risk is high? *Oecologia* 182, 1019–1029. <https://doi.org/10.1007/s00442-016-3729-8>.
- Hopkins, J.B., Whittington, J., Clevenger, A.P., Sawaya, M.A., St Clair, C.C., 2014. Stable isotopes reveal rail-associated behavior in a threatened carnivore. *Isot. Environ. Health Stud.* 50, 322–331. <https://doi.org/10.1080/10256016.2014.922555>.
- Kaczynsky, P., Gossow, H., Knauer, F., Krze, B., Jonozovic, M., Adamic, M., 2003. The impact of high speed, high volume traffic axes on brown bears in Slovenia. *Biol. Conserv.* 111, 191–204. [https://doi.org/10.1016/S0006-3207\(02\)00273-2](https://doi.org/10.1016/S0006-3207(02)00273-2).
- Kaczynsky, P., Huber, D., Knauer, F., Roth, H., Wagner, A., Kusak, J., 2006. Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia. *J. Zool.* 269, 474–485. <https://doi.org/10.1111/j.1469-7998.2006.00114.x>.
- Karamanlidis, A.A., Straka, M., Drosopoulou, E., de Gabriel Hernando, M., Kocijan, I., Paule, L., Scouras, Z., 2012. Genetic diversity, structure, and size of an endangered brown bear population threatened by highway construction in the Pindos Mountains, Greece. *Eur. J. Wildl. Res.* 58, 511–522. <https://doi.org/10.1007/s10344-011-0598-7>.
- Kite, R., Nelson, T., Stenhouse, G., Darimont, C., 2016. A movement-driven approach to quantifying grizzly bear (*Ursus arctos*) near-road movement patterns in west-central Alberta, Canada. *Biol. Conserv.* 195, 24–32. <https://doi.org/10.1016/j.biocon.2015.12.020>.
- Krofel, M., Jonozović, M., Jerina, K., 2012. Demography and mortality patterns of removed brown bears in a heavily exploited population. *Ursus* 23, 91–103. <https://doi.org/10.2192/URSUS-D-10-00013.1>.
- Ladle, A., Nielsen, S.E., Avgar, T., Wheatley, M., Stenhouse, G.B., Boyce, M.S., 2018a. Grizzly bear response to spatio-temporal variability in human recreational activity. *J. Appl. Ecol.* 56, 1–12. <https://doi.org/10.1111/1365-2664.13277>.
- Ladle, A., Steenweg, R., Shepherd, B., Boyce, M.S., 2018b. The role of human outdoor recreation in shaping patterns of grizzly bear-black bear co-occurrence. *PLoS One* 13, 1–16. <https://doi.org/10.1371/journal.pone.0191730>.
- Lamb, C.T., Mowat, G., McLellan, B.N., Nielsen, S.E., Boutin, S., 2017. Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. *J. Anim. Ecol.* 86, 55–65. <https://doi.org/10.1111/1365-2656.12589>.
- Leclerc, M., Frank, S.C., Zedrosser, A., Swenson, J.E., Pelletier, F., 2017. Hunting promotes spatial reorganization and sexually selected infanticide. *Sci. Rep.* 7, 1–6. <https://doi.org/10.1017/S0021932080006128>.
- Levi, T., Darimont, C.T., MacDuffee, M., Mangel, M., Paquet, P., Wilms, C.C., 2012. Using grizzly bears to assess harvest-ecosystem tradeoffs in salmon fisheries. *PLoS Biol.* 10, e1001303. <https://doi.org/10.1371/journal.pbio.1001303>.
- Linke, J., Franklin, S.E., Huettmann, F., Stenhouse, G.B., 2005. Seismic cutlines, changing landscape metrics and grizzly bear landscape use in Alberta. *Landsc. Ecol.* 20, 811–826. <https://doi.org/10.1007/s10980-005-0066-4>.
- Linnell, J.D.C., Swenson, J.E., Andersen, R., Barnes, B., 2000. How vulnerable are denning bears to disturbance? *Wildl. Soc. Bull.* <https://doi.org/10.2307/3783698>.
- López-Alfaro, C., Robbins, C.T., Zedrosser, A., Nielsen, S.E., 2013. Energetics of hibernation and reproductive trade-offs in brown bears. *Ecol. Model.* 270, 1–10. <https://doi.org/10.1016/j.ecolmodel.2013.09.002>.
- Lortkipanidze, B., 2010. Brown bear distribution and status in the South Caucasus. *Ursus* 21, 97–103. <https://doi.org/10.2192/09GR017.1>.

- Lyons, A.L., Gaines, W.L., Singleton, P.H., Kasworm, W.F., Proctor, M.F., Begley, J., 2018. Spatially explicit carrying capacity estimates to inform species specific recovery objectives: grizzly bear (*Ursus arctos*) recovery in the North Cascades. *Biol. Conserv.* 222, 21–32. <https://doi.org/10.1016/j.biocon.2018.03.027>.
- Mace, G.M., 2014. Whose conservation? *Science* 345 (80), 1558–1560. <https://doi.org/10.1126/science.1254704>.
- Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J., Zuuring, H., 1996. Relationship among grizzly bears, roads and habitat in the Swan Mountains, Montana. *J. Appl. Ecol.* 33, 1395–1404.
- Machutcheon, A.G., Wellwood, D.W., 2002a. Assessing the risk of bear-human interaction at river campsites. *Ursus* 13, 293–298.
- Machutcheon, A.G., Wellwood, D.W., 2002b. Reducing bear-human conflict through river recreation management. *Ursus* 13, 357–360.
- Maiorano, L., Boitani, L., Monaco, A., Tosoni, E., Ciucci, P., 2015. Modeling the distribution of Apennine brown bears during hyperphagia to reduce the impact of wild boar hunting. *Eur. J. Wildl. Res.* 61, 241–253. <https://doi.org/10.1007/s10344-014-0894-0>.
- Marley, J., Hyde, A., Salkeld, J.H., Prima, M.C., Parrott, L., Senger, S.E., Tyson, R.C., 2017. Does human education reduce conflicts between humans and bears? An agent-based modelling approach. *Ecol. Model.* 343, 15–24. <https://doi.org/10.1016/j.ecolmodel.2016.10.013>.
- Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allainé, D., Swenson, J.E., 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). *Can. J. Zool.* 88, 875–883. <https://doi.org/10.1139/Z10-053>.
- Mateo-Sánchez, M.C., Cushman, S.A., Saura, S., 2014. Connecting endangered brown bear subpopulations in the Cantabrian Range (north-western Spain). *Anim. Conserv.* 17, 430–440. <https://doi.org/10.1111/acv.12109>.
- Matsubayashi, J., Morimoto, J.O., Tayasu, I., Mano, T., Nakajima, M., Takahashi, O., Kobayashi, K., Nakamura, F., 2015. Major decline in marine and terrestrial animal consumption by brown bears (*Ursus arctos*). *Sci. Rep.* 5, 1–8. <https://doi.org/10.1038/srep09203>.
- Mattson, D.J., 1990. Human impacts on bear habitat use. *Bears Their Biol. Manag.* 8, 33–56. <https://doi.org/10.2307/3872901>.
- Mattson, D.J., Merrill, T., 2002. Extirpations of grizzly bears in the contiguous United States, 1850–2000. *Conserv. Biol.* 16, 1123–1136. <https://doi.org/10.1046/j.1523-1739.2002.00414.x>.
- McCown, J.W., Kubilis, P., Eason, T.H., Scheick, B.K., 2009. Effect of traffic volume on American black bears in central Florida, USA. *Ursus* 20, 39–46. <https://doi.org/10.2192/08GR004R2.1>.
- McKay, T., Sahlén, E., Støen, O.-G., Swenson, J.E., Stenhouse, G.B., 2014. Wellsite selection by grizzly bears *Ursus arctos* in west–central Alberta. *Wildl. Biol.* 20, 310–319. <https://doi.org/10.2981/wlb.00046>.
- McLellan, B.N., 2005. Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus* 16, 141–156. [https://doi.org/10.2192/1537-6176\(2005\)016\[0141:SSIGB\]2.0.CO;2](https://doi.org/10.2192/1537-6176(2005)016[0141:SSIGB]2.0.CO;2).
- McLellan, B.N., 2015. Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *J. Wildl. Manag.* 79, 749–765. <https://doi.org/10.1002/jwmg.896>.
- McLellan, B.N., Shackleton, D.M., 1988. Grizzly bears and resource-extraction Industries : effects of roads on behaviour, habitat use and demography. *J. Appl. Ecol.* 25, 451–460.
- McLellan, B.N., Mowat, G., Hamilton, T., Hatter, I., 2017. Sustainability of the grizzly bear hunt in British Columbia, Canada. *J. Wildl. Manag.* 81, 218–229. <https://doi.org/10.1002/jwmg.21189>.
- Miller, S.D., Tutterrow, V.L., 1999. Characteristics of nonsport mortalities to Brown and black bears and human injuries from bears in Alaska. *Ursus* 11, 239–252.
- Milner, J.M., Nilsen, E.B., Andreassen, H.P., 2007. Demographic side effects of selective hunting in ungulates and carnivores. *Conserv. Biol.* 21, 36–47. <https://doi.org/10.1111/j.1523-1739.2006.00591.x>.
- Mowat, G., Heard, D.C., Schwarz, C.J., 2013. Predicting grizzly bear density in western North America. *PLoS One* 8, 13–17. <https://doi.org/10.1371/journal.pone.0082757>.
- Murray, M.H., Fassina, S., Hopkins, J.B., Whittington, J., Clair, C.C.S., 2017. Seasonal and individual variation in the use of rail-associated food attractants by grizzly bears (*Ursus arctos*) in a national park. *PLoS One* 12, 1–16. <https://doi.org/10.1371/journal.pone.0175658>.
- Mattson, D.J., Merrill, T., 2004. A model-based appraisal of habitat conditions for grizzly bears in the Cabinet–Yaak region of Montana and Idaho. *Ursus* 15, 76–89. [https://doi.org/10.2192/1537-6176\(2004\)015<0076:AMAHC>2.0.CO;2](https://doi.org/10.2192/1537-6176(2004)015<0076:AMAHC>2.0.CO;2).
- Mueller, C., Herrero, S., Gibeau, M.L., 2004. Distribution of subadult grizzly bears in relation to human development in the Bow River Watershed, Alberta. *Ursus* 15, 35–47. [https://doi.org/10.2192/1537-6176\(2004\)015<0035:DOSGBI>2.0.CO;2](https://doi.org/10.2192/1537-6176(2004)015<0035:DOSGBI>2.0.CO;2).
- Naves, J., Ordiz, A., Fernández-Gil, A., Penteriani, V., Delgado, M. del M., López-Bao, J.V., Revilla, E., Delibes, M., 2018. Patterns of brown bear damages on apiaries and management recommendations in the Cantabrian Mountains , Spain. *PLoS One* 13, 1–18. <https://doi.org/10.1371/journal.pone.0206733>.
- Nellemann, C., Støen, O.G., Kindberg, J., Swenson, J.E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B.P., Martin, J., Ordiz, A., 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biol. Conserv.* 138, 157–165. <https://doi.org/10.1016/j.biocon.2007.04.011>.
- Northrup, J.M., Pitt, J., Muhly, T.B., Stenhouse, G.B., Musiani, M., Boyce, M.S., 2012. Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. *J. Appl. Ecol.* 49, 1159–1167. <https://doi.org/10.1111/j.1365-2664.2012.02180.x>.
- Obersoler, V., Groff, C., Iemma, A., Pedrini, P., Rovero, F., 2017. The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. *Mamm. Biol.* 87, 50–61. <https://doi.org/10.1016/j.mambio.2017.05.005>.
- Olson, T.L., Squibb, R.C., Gilbert, B.K., 1998. Brown bear diurnal activity and human use: a comparison of two salmon streams. *Ursus* 10, 547–555.
- Ordiz, A., Støen, O.-G., Delibes, M., Swenson, J.E., 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* 166, 59–67. <https://doi.org/10.1007/s00442-011-1920-5>.
- Ordiz, A., Støen, O.G., Sæbø, S., Kindberg, J., Delibes, M., Swenson, J.E., 2012. Do bears know they are being hunted? *Biol. Conserv.* 152, 21–28. <https://doi.org/10.1016/j.biocon.2012.04.006>.
- Ordiz, A., Støen, O.G., Sæbø, S., Sahlén, V., Pedersen, B.E., Kindberg, J., Swenson, J.E., 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. *J. Appl. Ecol.* 50, 306–314. <https://doi.org/10.1111/1365-2664.12047>.
- Ordiz, A., Kindberg, J., Sæbø, S., Swenson, J.E., Støen, O.-G., 2014. Brown bear circadian behavior reveals human environmental encroachment. *Biol. Conserv.* 173, 1–9. <https://doi.org/10.1016/j.biocon.2014.03.006>.
- Ordiz, A., Sæbø, S., Kindberg, J., Swenson, J.E., Støen, O.G., 2017. Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation? *Anim. Conserv.* 20, 51–60. <https://doi.org/10.1111/acv.12284>.
- Ordiz, A., Moen, G.K., Sæbø, S., Stenset, N., Swenson, J.E., Støen, O.-G., 2019. Habituation, sensitization, or consistent behavioral responses? Brown bear responses after repeated approaches by humans on foot. *Biol. Conserv.* 232, 228–237. <https://doi.org/10.1016/j.biocon.2019.01.016>.
- Penteriani, V., Delgado, M.M., Melletti, M., 2010. Don't feed the bears! *Oryx* 44, 169–170. <https://doi.org/10.1017/S003060530003194X>.
- Penteriani, V., Delgado, M. del M., Pinchera, F., Naves, J., Fernández-Gil, A., Kojola, I., Härkönen, S., Norberg, H., Frank, J., Fedriani, J.M., Sahlén, V., Støen, O.-G., Swenson, J.E., Wabakken, P., Pellegrini, M., Herrero, S., López-Bao, J.V., 2016. Human behaviour can trigger large carnivore attacks in developed countries. *Sci. Rep.* 6, 20552. <https://doi.org/10.1038/srep20552>.
- Penteriani, V., Bombieri, G., Fedriani, J.M., López-Bao, J.V., Garrote, P.J., Russo, L.F., Delgado, M.M., 2017a. Humans as prey: coping with large carnivore attacks using a predator-prey interaction perspective. *Hum. Wildl. Interact.* 11, 192–207.
- Penteriani, V., López-Bao, J.V., Bettega, C., Dalerum, F., Delgado, M. del M., Jerina, K., Kojola, I., Krofel, M., Ordiz, A., 2017b. Consequences of brown bear viewing tourism: a review. *Biol. Conserv.* 206, 169–180. <https://doi.org/10.1016/j.biocon.2016.12.035>.
- Penteriani, V., Delgado, M.D.M., Krofel, M., Jerina, K., Ordiz, A., Dalerum, F., Zarzo-Arias, A., Bombieri, G., 2018. Evolutionary and ecological traps for brown bears *Ursus arctos* in human-modified landscapes. *Mamm. Rev.* 48, 180–193. <https://doi.org/10.1111/mam.12123>.
- Penteriani, V., Zarzo-Arias, A., Delgado, M.M., Dalerum, F., Gurarie, E., Peón Torre, P., Sánchez Corominas, T., Vázquez V.M., Vázquez García, P., Ordiz, A., n.d. *In press*. Do Brown Bear Females with Cubs Settle in Risky Areas in Spatially Confined Populations? the Case of the Cantabrian Mountains, Spain.

- Petram, W., Knauer, F., Kaczensky, P., 2004. Human influence on the choice of winter dens by European brown bears in Slovenia. *Biol. Conserv.* 119, 129–136. <https://doi.org/10.1016/j.biocon.2003.07.021>.
- Pigeon, K.E., Nielsen, S.E., Stenhouse, G.B., Côté, S.D., 2014. Den selection by grizzly bears on a managed landscape. *J. Mammal.* 95, 559–571. <https://doi.org/10.1644/13-MAMM-A-137>.
- Pollock, S.Z., Nielsen, S.E., Clair, C.C., 2017. A railway increases the abundance and accelerates the phenology of bear-attracting plants in a forested, mountain park. *Ecosphere* 8, e01985. <https://doi.org/10.1002/ecs2.1985>.
- Proctor, M.F., McLellan, B.N., Strobeck, C., 2002. Population fragmentation of grizzly bears in southeastern British Columbia, Canada. *Ursus* 13, 153–160.
- Proctor, M.F., Paetkau, D., McLellan, B.N., Stenhouse, G.B., Kendall, K.C., MacE, R.D., Kasworm, W.F., Servheen, C., Lausen, C.L., Gibeau, M.L., Wakkinen, W.L., Haroldson, M.A., Mowat, G., Apps, C.D., Ciarniello, L.M., Barclay, R.M.R., Boyce, M.S., Schwartz, C.C., Strobeck, C., 2012. Population fragmentation and inter-ecosystem movements of grizzly bears in Western Canada and the Northern United States. *Wildl. Monogr.* 180, 1–46. <https://doi.org/10.1002/wmon.6>.
- Proctor, M.F., McLellan, B., Stenhouse, G.B., Mowat, G., Lamb, C.T., Boyce, M.S., 2018. Resource Roads and Grizzly Bears in British Columbia, and Alberta, Canadian Grizzly Bear Management Series, Resource Road Management. Trans-border Grizzly Bear Project. <https://doi.org/10.13140/RG.2.2.11780.83846>.
- Qashqaei, A.T., Karami, M., Etamad, V., 2014. Wildlife conflicts between humans and Brown bears, *Ursus arctos*, in the central Zagros, Iran. *Zool. Middle East* 60, 107–110. <https://doi.org/10.1080/09397140.2014.914711>.
- Richardson, M.L., 2017. Daily and monthly activity of Brown bears (*Ursus arctos*) near a proposed industrial Project in coastal British Columbia. *West. North Am. Nat.* 77, 118–123. <https://doi.org/10.3398/064.077.0113>.
- Rode, K.D., Farley, S.D., Robbins, C.T., 2006. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biol. Conserv.* 133, 70–80. <https://doi.org/10.1016/j.biocon.2006.05.021>.
- Rode, K.D., Farley, S.D., Fortin, J., Robbins, C.T., 2007. Nutritional consequences of experimentally introduced tourism in Brown bears. *J. Wildl. Manag.* 71, 929–939. <https://doi.org/10.2193/2006-075>.
- Roever, C.L., Boyce, M.S., Stenhouse, G.B., 2008. Grizzly bears and forestry. I: road vegetation and placement as an attractant to grizzly bears. *For. Ecol. Manage.* 256, 1253–1261. <https://doi.org/10.1016/j.foreco.2008.06.040>.
- Ruiz-Villar, H., Morales-González, A., Bombieri, G., Zarzo-Arias, A., Penteriani, V., 2019. Characterization of a brown bear aggregation during the hyperphagia period in the Cantabrian Mountains, NW Spain. *Ursus*.
- Sahlén, V., Friebe, A., Sæbø, S., Swenson, J.E., Støen, O.G., 2015. Den entry behavior in Scandinavian brown bears: implications for preventing human injuries. *J. Wildl. Manag.* 79, 274–287. <https://doi.org/10.1002/jwmg.822>.
- Sato, Y., 2017. The future of urban Brown bear management in Sapporo, Hokkaido, Japan: a review. *Mamm. Stud.* 42, 17–30. <https://doi.org/10.3106/041.042.0102>.
- Sato, Y., Mano, T., Takatsuki, S., 2005. Stomach contents of brown bears *Ursus arctos* in Hokkaido. *Wildl. Biol.* 11, 133–144. [https://doi.org/10.2981/0909-6396\(2005\)11\[133:SCOBBU\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2005)11[133:SCOBBU]2.0.CO;2).
- Sawaya, M.A., Kalinowski, S.T., Clevenger, A.P., 2014. Genetic connectivity for two bear species at wildlife crossing structures in Banff National Park. *Proc. R. Soc. B* 281, 20131705.
- Schwartz, C.C., Cain, S.L., Podrutzny, S., Cherry, S., Frattaroli, L., 2010. Contrasting activity patterns of sympatric and Allopatric black and grizzly bears. *J. Wildl. Manag.* 74, 1628–1638. <https://doi.org/10.2193/2009-571>.
- Schwartz, C.C., Gude, P.H., Landenburger, L., Haroldson, M.A., Podrutzny, S., 2012. Impacts of rural development on Yellowstone wildlife: linking grizzly bear *Ursus arctos* demographics with projected residential growth. *Wildl. Biol.* 18, 246–257. <https://doi.org/10.2981/11-060>.
- Skuban, M., Find'o, S., Kajba, M., 2017a. Bears napping nearby: daybed selection by brown bears (*Ursus arctos*) in a human-dominated landscape. *Can. J. Zool.* 96, 1–11. <https://doi.org/10.1139/cjz-2016-0217>.
- Skuban, M., Findo, S., Kajba, M., Koreň, M., Chamers, J., Antal, V., 2017b. Effects of roads on brown bear movements and mortality in Slovakia. *Eur. J. Wildl. Res.* 63, 1–9. <https://doi.org/10.1007/s10344-017-1138-x>.
- Smith, D.W., Bangs, E.E., Oakleaf, J.K., Mack, C., Fontaine, J., Boyd, D., Jimenez, M., Pletscher, D.H., Niemeyer, C.C., Meier, T.J., Stahler, D.R., Holyan, J., Asher, V.J., Murray, D.L., 2010. Survival of colonizing wolves in the northern rocky mountains of the United States, 1982–2004. *J. Wildl. Manag.* 74, 620–634. <https://doi.org/10.2193/2008-584>.
- Soulé, M.E., 1985. What is conservation biology? A new synthetic discipline addresses the dynamics and problems of perturbed species, communities, and ecosystems. *Bioscience*.
- Stewart, B.P., Nelson, T.A., Wulder, M.A., Nielsen, S.E., Stenhouse, G., 2012. Impact of disturbance characteristics and age on grizzly bear habitat selection. *Appl. Geogr.* 34, 614–625. <https://doi.org/10.1016/j.apgeog.2012.03.001>.
- Steyaert, S.M.J.G., Zedrosser, A., Elfström, M., Ordiz, A., Leclerc, M., Frank, S.C., Kindberg, J., Støen, O.-G., Brunberg, S., Swenson, J.E., 2016. Ecological implications from spatial patterns in human-caused brown bear mortality. *Wildl. Biol.* 22, 144–152. <https://doi.org/10.2981/wlb.00165>.
- Støen, O.G., Ordiz, A., Evans, A.L., Laske, T.G., Kindberg, J., Frøbert, O., Swenson, J.E., Arneemo, J.M., 2015. Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). *Physiol. Behav.* 152, 244–248. <https://doi.org/10.1016/j.physbeh.2015.09.030>.
- Straka, M., Paule, L., Ionescu, O., Štofik, J., Adamec, M., 2012. Microsatellite diversity and structure of Carpathian brown bears (*Ursus arctos*): consequences of human caused fragmentation. *Conserv. Genet.* 13, 153–164. <https://doi.org/10.1007/s10592-011-0271-4>.
- Swenson, J.E., 1999. Does hunting affect the behavior of brown bears in Eurasia? *Ursus* 11, 157–162.
- Swenson, J.E., Sandegren, F., Brunberg, S., Wabakken, P., 1997a. Winter den abandonment by brown bears *Ursus arctos*: causes and consequences. *Wildl. Biol.* 3, 35–38. <https://doi.org/10.2981/wlb.1997.005>.
- Swenson, J.E., Sandegren, F., Söderberg, A., Bjärval, A., Franzén, R., Wabakken, P., 1997b. Infanticide caused by hunting of male bears. *Nature* 386, 450–451. <https://doi.org/10.1111/mms.12278>.
- Swenson, J.E., Gerstl, N., Dahle, B., Zedrosser, A., 2000. Action Plan for the Conservation of the Brown Bear in Europe (*Ursus arctos*).
- Swenson, J.E., Adamić, M., Huber, D., Stokke, S., 2007. Brown bear body mass and growth in northern and southern Europe. *Oecologia* 153, 37–47. <https://doi.org/10.1007/s00442-007-0715-1>.
- Suring, L.H., Farley, S.D., Hilderbrand, G.V., Goldstein, M.I., Howlin, S., Erickson, W.P., 2006. Patterns of landscape use by female brown bears on the Kenai Peninsula, Alaska. *J. Wildl. Manag.* 70, 1580–1587. [https://doi.org/10.2193/0022-541x\(2006\)70\[1580:polubf\]2.0.co;2](https://doi.org/10.2193/0022-541x(2006)70[1580:polubf]2.0.co;2).
- Torres, A., Jaeger, J.A.G., Alonso, J.C., 2016. Assessing large-scale wildlife responses to human infrastructure development. *Proc. Natl. Acad. Sci. Unit. States Am.* 113, 8472–8477. <https://doi.org/10.1073/pnas.1522488113>.
- Van De Walle, J., Pigeon, G., Zedrosser, A., Swenson, J.E., Pelletier, F., 2018. Hunting regulation favors slow life histories in a large carnivore. *Nat. Commun.* 9, 1100. <https://doi.org/10.1038/s41467-018-03506-3>.
- Waller, J.S., Servheen, C., 2005. Effects of transportation infrastructure on grizzly bears in northwestern Montana. *J. Wildl. Manag.* 69, 985–1000. [https://doi.org/10.2193/0022-541x\(2005\)069\[0985:eotiog\]2.0.co;2](https://doi.org/10.2193/0022-541x(2005)069[0985:eotiog]2.0.co;2).
- Wielgus, R.B., Bunnell, F.L., 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. *Biol. Conserv.* 93, 145–154.
- Wielgus, R.B., Vernier, P.R., 2003. Grizzly bear selection of managed and unmanaged forests in the Selkirk Mountains. *Can. J. For. Res.* 33, 822–829. <https://doi.org/10.1139/x03-003>.
- Wielgus, R.B., Sarrazin, F., Ferriere, R., Clobert, J., 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biol. Conserv.* 98, 293–303. [https://doi.org/10.1016/S0006-3207\(00\)00168-3](https://doi.org/10.1016/S0006-3207(00)00168-3).
- Wilson, S.M., Madel, M.J., Mattson, D.J., Graham, J.M., Merrill, T., 2006. Landscape conditions predisposing grizzly bears to conflicts on private agricultural lands in the western USA. *Biol. Conserv.* 130, 47–59. <https://doi.org/10.1016/j.biocon.2005.12.001>.

- Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280 (80), 2126–2128. <https://doi.org/10.1126/science.3420403>.
- Zarzo-Arias, A., Delgado, M. del M., Ordiz, A., García Díaz, J., Cañedo, D., González, M.A., Romo, C., Vázquez García, P., Bombieri, G., Bettega, C., Russo, L.F., Cabral, P., García González, R., Martínez-Padilla, J., Penteriani, V., 2018. Brown bear behaviour in human-modified landscapes: the case of the endangered Cantabrian population, NW Spain. *Glob. Ecol. Conserv.* 16, e00499 <https://doi.org/10.1016/j.gecco.2018.E00499>.
- Zedrosser, A., Steyaert, S.M.J.G., Gossow, H., Swenson, J.E., 2011. Brown bear conservation and the ghost of persecution past. *Biol. Conserv.* 144, 2163–2170. <https://doi.org/10.1016/j.biocon.2011.05.005>.
- Zedrosser, A., Pelletier, F., Bischof, R., Festa-bianchet, M., Jon, E., Jon, E., 2013. Determinants of lifetime reproduction in female brown bears : early body mass , longevity , and hunting regulations. *Ecology* 94, 231–240. <https://doi.org/10.2307/23435685>.
- Ziółkowska, E., Ostapowicz, K., Radeloff, V.C., Kuemmerle, T., Sergiel, A., Zwijacz-Kozica, T., Zięba, F., Śmietana, W., Selva, N., 2016. Assessing differences in connectivity based on habitat versus movement models for brown bears in the Carpathians. *Landsc. Ecol.* 31, 1863–1882. <https://doi.org/10.1007/s10980-016-0368-8>.