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Commentary

Understanding potential responses of large carnivore to climate change

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Abstract

Large carnivores are essential keystone species in the ecosystems that they inhabit, and the warming climate is harming a majority of the species. Here, we review the literature that spanned the years 1991-2022 on fifteen large carnivore species and their response to climate change via the proxies of (1) habitat alterations; (2) diet profile changes; and (3) behavioural changes. The literature review highlighted that 15 large carnivore species had been taken into account by 164 studies (87 on habitat, 59 on diet, 18 on behaviour) on potential climate change effects in five continents. Eighty-seven studies featured projected or current changes in suitable habitat due to climate change, 59 studies featured projected or current changes in preferred diet due to climate change, and 18 studies covered proposed or current behaviour changes in response to climate change. Of the 87 suitable habitat studies, 66 (78 %) were categorized as negative, i.e., when a potential reduction in resources has been projected. Of the 59 preferred diet studies, 39 (66 %) were categorized as negative. Despite the evidence that information on how large carnivore habitats, diets, and behaviours might be affected by climate change are still scarce for several species and/or geographical areas, most of the available predictions point to an unfortunate truth. Species with habitats susceptible to considerable alterations will probably experience a severe local decline in the next few decades. Loss of suitable habitats and decreased food availability, which has been forecasted for most large carnivores, might also induce these species to shift their home ranges in search of alternative food sources. These may include areas where they are more likely to experience more conflict with humans. Large carnivores require long-term conservation, management strategies, and more research to develop a deeper understanding of climate change's impacts and establish pre-emptive measures ensuring population viability in the following decades.

Introduction

Now, more than ever, knowledge of how animal species and ecological environments respond to climate change is crucial due to the recent increase in human encroachment on natural habitats and the rapid loss of biodiversity (Pimm and Raven, 2000). Climate change has and will continue to alter how our world looks via temperature changes, rising sea levels, and previously suitable habitats becoming unliveable for many species (Davis et al., 2021; Hazra et al., 2002; Pachauri et al., 2014). Global extinction rates have risen, and biodiversity loss is inevitable in many regions worldwide (Ceballos et al., 2015; Brook et al., 2008).

Large carnivores are essential to ecosystems for many reasons. They are often at the top of the food chain model as they are considered the highest energy consumers in most ecological communities (del Rio et al., 2001). Predator species keep prey species under control to preserve the delicate balance in which ecosystems thrive. Overabundant herbivores can decimate primary producers, so natural population control via large carnivore species assists in this maintenance (del Rio et al., 2001; Ripple and Beschta, 2012). Large carnivores are also sometimes known as umbrella species, and conserving their populations and habitats ensures the protection of other species and the ecologic dynamics that are involved in different ecosystems (Kittle et al., 2018).

Large carnivores are diverse in their habitats, diets, and specific behaviours and, as such, may have varying responses to our rapidly changing climate (Fig. 1). The overall claim of researchers has been a resounding conclusion that the loss of many of large carnivore spe-

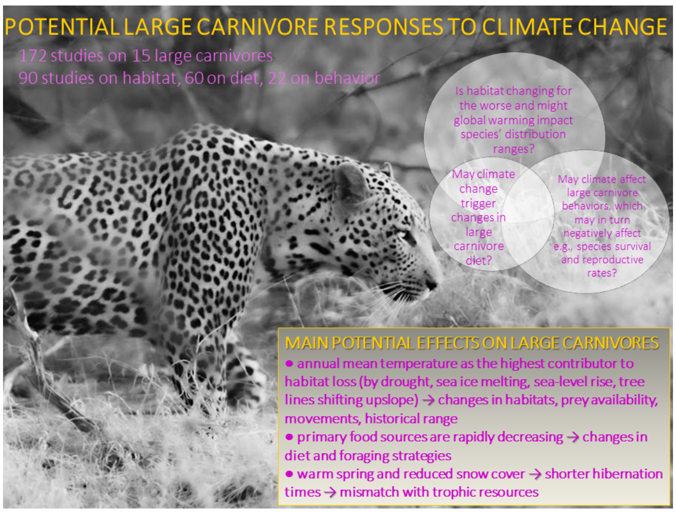

Figure 1 – Synthesis of the review approaches and main potential effects of climate change on large carnivores.

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cies is inevitable due to their extensive range requirements for habitat (Karssene et al., 2017). These studies are vital to understanding the impending changes to future ecosystems, but having the ability to map, model, and predict species' potential responses on a global scale will significantly impact species conservation on a greater geographical scale. The ability to qualify the status or the predicted outcome of the world's large carnivore species due to climate change will be a priority tool for conservationists, NGOs, governmental agencies, and other stakeholders globally.

By spanning the available literature on large carnivore species' potential responses to climate change worldwide, we investigated species responses at three levels, i.e., habitat, diet, and behaviour. Each level is associated with a related question and hypothesis (Fig. 1). Results from this research will inform a global perspective of the climate crisis contextualized by large carnivore species frame and may reveal crucial gaps in our knowledge of certain species for future studies.

Question 1 habitat: is habitat suitability changing for the worse, and might global warming impact species' distribution ranges? We expect diverse climatic effects at different elevations, mainly because high elevations are susceptible to more rapid warming effects as global temperatures rise, i.e., large carnivore ranges that either entirely or partially inhabit high elevation ranges could be altered much more rapidly than those living at lower altitudes (Pachauri et al., 2014). Finally, c limate change has varying impacts on ambient temperature, sea-level rise, and other forcings at different latitude locations, e.g., sea ice at lower latitudes faces a faster decline than at higher latitudes (Markus et al., 2009). We thus predict that changes in habitat suitability and availability have the potential to harm most species (*hypothesis 1, H1)*.

Question 2 diet: may climate change trigger changes in large carnivore preferred diet? Prey that makes up large carnivore diet may also be affected by changes in climate (Hebblewhite et al., 2014; O'Farrill et al., 2014; Rode et al., 2020). Prey species are experiencing or projected to experience significant alterations in their habitats and resources, potentially affecting carnivore responses (Hebblewhite et al., 2014). Under this scenario, we hypothesize that large carnivores will become more opportunistic and generalized in their diet because of a generalized decrease in preferred prey availability (*hypothesis 2, H2)*.

Question 3 behaviour: may climate change affect large carnivore behaviours, which may, in turn, negatively affect species survival and reproductive rates? We predict (*hypothesis 3, H3)* that, to follow resource shifts and increasing temperatures, movement changes and alteration of circadian activity may be among the most apparent changes in behaviour (Penteriani et al., 2019), and that temperature change may alter the denning entrance/exit for species that hibernate like polar, brown and American black bears (González-Bernardo et al., 2020). Additionally, as climate change forces some large carnivores to seek new habitats, they may also begin to overlap more frequently among them and with humans, causing potential conflicts.

Methods

The literature review was conducted on Google Scholar, Duke University Library, Web of Science, and SCOPUS databases, including papers available at the time of review, July 2022, by using the following search terms: the combination of the climate change and global warming strings with (a) projection, (b) forecast and (c) status, climate change habitat, global warming habitat, climate change diet, global warming diet, climate change behaviour, global warming behaviour, large carnivore common names, and large carnivore scientific names. Multiple species have several common names (e.g., cougar/puma/mountain lion), so these were searched individually. Literature was selected for relevancy to global climate impact, large carnivore species, and if studies specifically included an observation or projection of the response of species' suitable habitat, preferred diet, or behavioural change. The literature review highlighted that 15 large carnivore species had been taken into account by 164 studies (87 on habitat, 59 on diet, 18 on behaviour) on potential climate change effects in four continents (Fig. 2 and Supplemental Table S1). The literature included peer-reviewed articles, review articles, a paper in conference proceedings, and graduate student dissertation works that spanned 1991–2022. Based on the literature review, effects of climate change on suitable habitat and preferred diet have been separated into four categories: (1) *positive*, when a potential increase in total habitat availability and/or prey abundance/availability has been detected; (2) *negative*, when a potential reduction in these resources has been detected; (3) *unchanged*, when climate change seems not to impact large carnivore resources directly; and (4) *unknown/inconclusive*, when lack of information does not allow reaching clear conclusions.

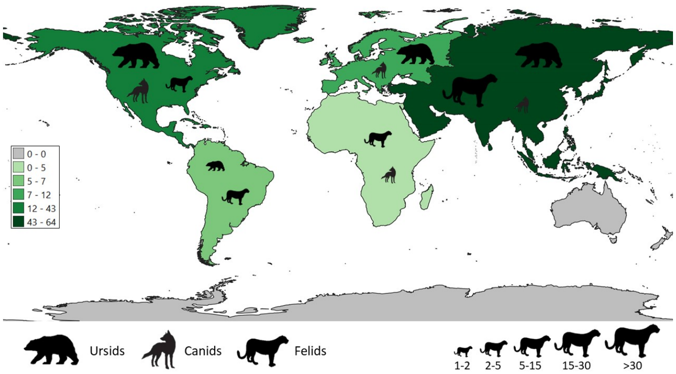

Figure 2 – Map showing the locations of the studies analysed in this review, highlighting which species they refer. The total number of studies per geographical areas is represented on the left legend, ranging from light grey (no studies) to dark green (43–46 studies), whereas the size of the animal represents the number of studies on a given group of species (Ursids, Canids and Felids; black silhouettes of group of species are access free images from Shutterstock).

Results

General results

The literature review has highlighted varying degrees of current and projected response to climate change (Fig. 1 and Supplemental Table S1). Of the 164 studies that met our review criteria, 87 studies featured projected or current changes in suitable habitat due to climate change, 59 studies featured projected or current changes in preferred diet due to climate change, and 18 studies covered proposed or current behaviour changes in response to climate change. Of the 87 suitable habitat studies, 13 (15 %) were categorized as positive, 66 (78 %) were categorized as negative, and 6 (7 %) were categorized as unchanged. No habitat papers had unknown projections for the large carnivores in their studies. Of the 59 preferred diet studies, 9 (15 %) were categorized as positive, 39 (66 %) were categorized as negative, 4 (7 %) were categorized as unchanged, and 7 (12 %) were categorized as unknown/inconclusive (Fig. 3). Fig. 4 (panels 1–15) depicts the habitat and diet response to climate change for each species based on the total response of each species determined for each study (see also Supplemental Table S1).

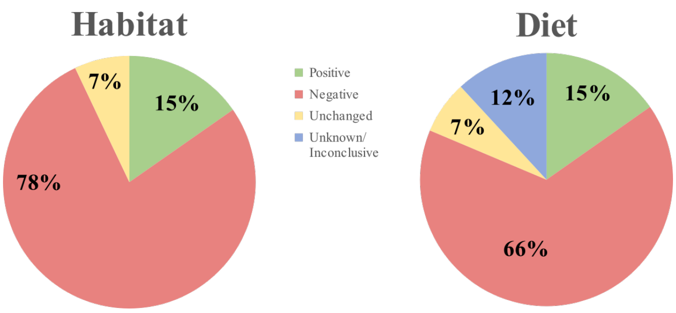

Figure 3 – Percentages of total studies reviewed that were positive, negative, unchanged, or unknown/inconclusive.

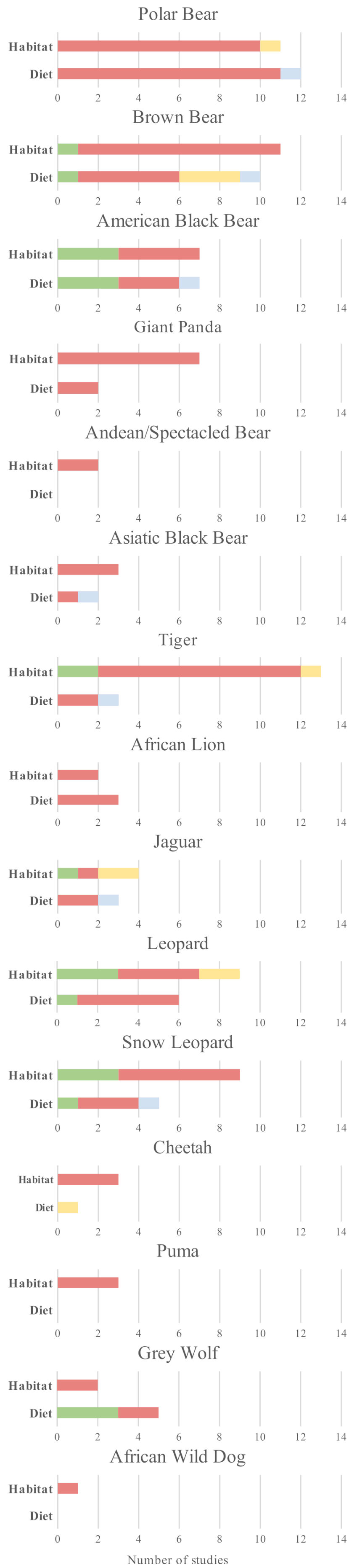

Figure 4 – Synthesis of the potential effects of climate change on habitat and diet of the fifteen study species. Positive effects (green): increase in suitable habitat and/or preferred diet abundance; negative effects (red): reduction in suitable habitat and/or preferred diet abundance; unchanged (yellow): climate change has not directly impacted the loss of suitable habitat and/or preferred diet; unknown/inconclusive (blue): not enough information available to reach a conclusion on the impact of climate change.

Species-specific results

Polar bear *Ursus maritimus*

Changes in habitat

Polar bears depend on sea ice for habitat, foraging, and finding mates (Rode et al., 2020), and suitable polar bear habitat is in total decline, with studies always projecting habitat loss. As the world warms, sea ice rapidly declines due to melting from temperature (Klappstein et al., 2020), the Arctic has lost about 40 % of summer sea ice over the past 40 years, and about 20 % of that loss can be traced directly to climate change (England et al., 2020). The decline is especially notable at lower latitudes, where sea ice reoccurs annually, while higher latitudes lose ice less rapidly due to more permanent ice coverage (Derocher et al., 2004). For example, because of the sea ice decline in these southern regions, the Hudson Bay population of polar bears has been reduced by over 30 % (Klappstein et al., 2020). From 1978 to 1999, studies estimate that total sea ice cover declined by 14 % (Vinnikov et al., 1999).

Changes in diet

Polar bear prey relies on consistent ice habitat, and due to a decline in ice habitat, preferred prey abundance is also declining. The main habitat (thinner, annually ephemeral sea ice; Derocher et al., 2004) of primary prey species, ringed (*Pusa hispida)* and bearded (*Erignathus barbatus)* seals, is expected to decline due to climate change (Smith et al., 1991). Some polar bear populations are forced to the shores earlier in the season due to earlier ice break up, and they must replace ringed seals with a terrestrial food source (Molnár et al., 2010). Polar bears use shore habitat more frequently as sea ice abundance declines, and they are becoming more opportunistic in their diets: (a) some polar bears move to areas overlapping with lesser snow geese and eat their eggs for energy (Prop et al., 2015; Rockwell and Gormezano, 2009); and (b) other terrestrial species occur in their diet, e.g., caribou and snow geese (Gormezano and Rockwell, 2013).

Changes in behaviour

Movement. The three most influential factors affecting polar bear movement are changes in time of freezing and break-up of sea ice, loss of preferred spring habitat, and rising habitat fragmentation (Pilfold et al., 2017; Sahanatien and Derocher, 2012). Polar bear movements due to the ice drift speed in Beaufort, Barents, and Chuckchi Seas have recently increased, which increased energy expenditure in response (Klappstein et al., 2020).

Denning. Female polar bears that rely on the land near the shore for denning must journey from the ice in time to dig their dens (Derocher et al., 2004) and, consequently, these females incur a higher energetic cost of walking and swimming (Derocher et al., 2004). As a result, a reduction in offspring numbers and offspring body size has been linked to these declining sea ice conditions (Molnár et al., 2011; Rode et al., 2010).

Brown bear *Ursus arctos*

Changes in habitat

Most studies projected a decline in preferred habitats in Central Asia and the Asian Highlands, the Hindu Kush Himalayan Region, Nepal, Alberta, and Northern Spain (Dar et al., 2021; Dai et al., 2019, 2021; Penteriani et al., 2018; Su et al., 2018; Pigeon et al., 2016b), where the annual mean temperature was the highest contributor to habitat loss (Su et al., 2018). One study on brown bears in Alberta, Canada, predicts that a rise in temperature and alterations of forest cover will negatively impact thermoregulation for male bears, a rise in ambient temperature projected to hinder male brown bears' ability to stay cool (Pigeon et al., 2016a). In the Cantabrian Mountains, brown bears are expected to experience significant reductions in historical range by 2050 and are anticipated to be displaced to more 'humanized' regions Penteriani et al. (2019).

Changes in diet

Predicted changes in brown bear diet for the species are inconclusive due to their generalist profile. However, some local case studies are more worrying. In the Greater Yellowstone Ecosystem, one primary bear food source, the whitebark pine *Pinus albicaulis*, is rapidly decreasing (Koteen, 2002), with brown bears having to find analogous food sources to replace high caloric density pine seeds (Keane et al., 2017). In the Cantabrian mountains, the expectation exists that bears will move to more seed and meat energy sources to satisfy their diets (Penteriani et al., 2019; Rodríguez et al., 2007).

Changes in behaviour

Movement. With climate change, polar and brown bears are overlapping more often, showing some hybridization events (Penteriani and Melletti, 2020). Changes in movement patterns and displacements that are the result of the movements of polar and brown bears due to changes in climate regimes have the potential to increase hybridization events in the future.

Denning. Because temperature will rise, warmer springs may become more frequent, meaning climate change could permanently alter hibernation times (Evans et al., 2016). Warmer springs and reduced snow cover may cause shorter hibernation times (Pigeon et al., 2016b). The sensitivity of brown bears to changes in climatic factors during hibernation might negatively affect their ability to cope with global climate change (Delgado et al., 2018).

American black bear *Ursus americanus*

Changes in habitat

American black bears are a famously opportunistic species, and this adaptable species is projected to continue to increase in population despite the impact of climate change. Though, three out of six studies concerning habitat project a decline in suitable habitat at the southern fringes of the American black bear's range (Mexican and south Florida populations, which are susceptible to sea-level rise) (Davis et al., 2021; Lara-Díaz et al., 2018; Murphy et al., 2017; Whittle, 2009), these losses should not outweigh the overall gain of suitable habitat, which is expected to increase overall bear range (Deb et al., 2020).

Changes in diet

Three (Bonin et al., 2020; Bastille-Rousseau et al., 2018; Ditmer et al., 2018) out of seven studies project a positive outcome in the northern range of black bear habitat, whereas another three (Lara-Díaz et al., 2018; Laufenberg et al., 2018; Murphy et al., 2017) project a negative outcome in conjunction with diminishing suitable habitat and sea-level rise. In terms of natural food resources, black bear diets are expected to have an increase in resources and food availability (Bastille-Rousseau et al., 2018).

Changes in behaviour

Foraging. Due to the large distribution range of the species, climate effects may vary locally. In Mexico, for example, black bears experience a higher temperature than the more northern populations of black bears (Lara-Díaz et al., 2018). As temperatures rise, black bears might decrease their daily activity and maintain foraging activity during the crepuscular hours of the day at dawn and dusk (Lara-Díaz et al., 2018). In contrast, a study with northern populations of black bears (e.g., the Newfoundland black bear) projected that higher spring precipitation would increase forage quality, reducing the movement behaviour of black bears (Bastille-Rousseau et al., 2018).

Denning. One study on black bears in Colorado found that increased annual temperatures are correlated with shorter hibernation periods, which leads to increased length in the active season (Johnson et al., 2018). Decreasing the hibernation duration could negatively affect bear fitness and increase the frequency of potential human-bear conflicts as their active season lengthens.

Giant panda *Ailuropoda melanoleuca*

Changes in habitat

Giant pandas will experience a total decline in suitable habitats (Songer et al., 2012). Studies reviewed estimate that the total suitable habitat for giant pandas in their current range is expected to decline between 52.9–71.5 % (Songer et al., 2020; Li et al., 2015). In addition, four studies focusing on individual populations of giant pandas found that regardless of what mountain range giant pandas reside in, a total decline in suitable habitat is projected (Zhang et al., 2018; Li et al., 2017; Shen et al., 2015; Fan et al., 2014). Other habitat negative impacts include corridor degradation, habitat fragmentation, and an increase in the average elevation of giant panda habitat from 2576m to up to 2997m under the RCP 8.5 scenario, which could increase energy expenditure for giant pandas finding food and potential mates (Li et al., 2015).

Changes in diet

Regarding the projection of preferred diet availability, bamboo availability is projected to decline drastically. Projections showed a complete loss of suitable habitat for giant pandas in the Qinling Mountains by the end of the twenty-first century due to the extreme loss of three species of preferred understory bamboo species (Tuanmu et al., 2013). With bamboo being the primary component of giant pandas' preferred diet, impacts of climate change on bamboo species distribution will have profound effects on giant pandas. Moreover, as climate change increases the average elevation of suitable habitats, bamboo foraging at higher elevations could also increase energy expenditure (Li et al., 2015).

Andean bear *Tremarctos ornatus*

Changes in habitat

For the Andean bear, negative suitable habitat responses are expected (Guerrero-Casado and Zambrano, 2020; Meza Mori et al., 2020). As temperatures increase, suitable habitat for Andean bears is expected to decline, with increasing habitat fragmentation and degradation resulting in a potential decrease in mating and population numbers. Projections for the Andean bear in 2050 and 2070 claim that there will be a decrease in overall suitable habitat over time (Meza Mori et al., 2020), and, while climate is a factor, the expected reduction in habitat availability could be mainly due to anthropogenic activities.

Asiatic black bear *Ursus thibetanus*

Changes in habitat

Studies concerning the Iranian and Hindu Kush Himalayan populations project suitable habitat decline for the Asiatic black bear by 2070 (Zahoor et al., 2021; Morovati et al., 2020; Farashi and Erfani, 2018). Habitat fragmentation and drought are two main drivers of suitable habitat loss projected in Iran (Farashi and Erfani, 2018). Specifically, habitat is projected to decline by 5% (Farashi and Erfani, 2018) to 10% (Morovati et al., 2020) or a shift of suitable habitat to higher elevations in the Himalayas (Zahoor et al., 2021).

Changes in diet

Negative outcomes are expected for diet, mainly due to potential frost damage incurred by hard-mast vegetation (Honda, 2013). Late frosts have also been shown to increase human-wildlife conflict as bears seek human food sources to supplement the loss of their preferred diet (Honda, 2013).

Changes in behaviour

Changes in movement behaviour, such as the Himalayan population moving to higher elevations, can increase human-wildlife conflict as bears overlap with human activity . Similarly, with late Spring frosts in Japan, bears may alter their foraging behaviour to include human resources in their diets, increasing human-wildlife conflict .

Tiger *Panthera tigris*

Changes in habitat

Tiger habitat is in an almost overall total decline in response to climate change (Rather et al., 2020; Mukul et al., 2019; Bargali and Ahmed, 2018; Devi et al., 2018; Shevade et al., 2017; Thapa et al., 2016; Guha et al., 2015; Rahim et al., 2015; Tian et al., 2014; Loucks et al., 2009). The majority of studies projecting a negative response were performed in the Sundarbans, a mangrove area in the delta formed by the confluence of the Ganges, Brahmaputra, and Meghna Rivers in the Bay of Bengal, and cited sea-level rise as the main factor triggering the decline of suitable tiger habitat (Mukul et al., 2019).The Sundarbans region is especially vulnerable, with predictions of almost 50 % loss by 2050 and a 96 to 98 % loss by 2070 (Mukul et al., 2019; Rahim et al., 2015; Loucks et al., 2009). However, in the Russian Far East, one study projects an increase in suitable habitats farther north from their historical range (Tian et al., 2014). In contrast, another study suggests that tiger habitat will remain essentially unchanged (Hebblewhite et al., 2014). Another region that may experience an increase in suitable tiger habitat is north-western North Korea, where range shifts are expected to also move upwards in a changing climate context (Tian et al., 2014).

Changes in diet

Projections showed a decline in the abundance of preferred prey availability (Qi et al., 2020; Hebblewhite et al., 2014). For example, in the Russian Far East, moose represents an important prey species for tigers, but moose numbers are projected to decline (Hebblewhite et al., 2014). One study in China anticipates increased competition for resources as tiger suitable habitat in this region overlaps with leopard suitable habitat (Qi et al., 2020).

Changes in behaviour

As sea-level rise decimates mangrove habitat, some tigers may shift their ranges or increase their movement to establish new home ranges (Mukul et al., 2019). Vegetation decline in the Sundarbans may also alter the foraging behaviours of tigers that may have to rely on a hunting behaviour other than ambushing prey due to lack of vegetation cover (Rather et al., 2020).

African lion *Panthera leo*

Changes in habitat

Habitat decline is projected in the southern range of African lion distribution (Kotze et al., 2020; Peterson et al., 2014). In the Okavango Delta, the ecosystem is subject to a wet and dry season, and animals are acclimated to the changing precipitations and the environment's response in terms of prey availability or vegetation abundance. However, climate change is impacting the level of precipitation in this region: dry seasons are becoming longer and more severe, leading to a decline in prey availability (Kotze et al., 2020). Because of this, lion ranges are shrinking, causing crowding and competition with other lions (Kotze et al., 2020).

Changes in diet

Negative potential responses are predicted, and the common factor for the decline in preferred diet abundance was increased drought in southern Africa, which has increased stress on lion prey species (Kotze et al., 2020; Trinkel, 2013; Bissett et al., 2012).

Prey species' abundance in southern Africa is closely linked to water availability and overall precipitation (Bissett et al., 2012).It is projected that c limate change will cause a decrease in annual precipitation and an increase in drought persistence which could cause a total decrease in prey species abundance (Peterson et al., 2014). A decrease in prey availability due to overcrowding of lions has also been forecasted (Bissett et al., 2012; Trinkel, 2013).

Jaguar *Panthera onca*

Changes in habitat

Jaguars are projected to experience a mix of outcomes regarding habitat. Out of a total of four studies, two forecasted that habitat would be unchanged because the climate is projected not to affect habitat in Central America or that jaguar's high dispersion capacity allows for adaptability to more fragmented habitat (Zanin et al., 2021; Olsoy et al., 2016), one concluded a total increase (Blair et al., 2012), and one concluded a total decrease for suitable jaguar habitat (79 % decline in the suitable habitat of jaguars due to a lack of crucial waterholes in projected scenarios; O'Farrill et al., 2014). Overall, the species will experience a negative habitat response because the total habitat may be unchanged, but climate change is projected to create fragmentation of key habitat areas throughout Central and South America, which is not wholly suitable for the species. (Zanin et al., 2021; Olsoy et al., 2016).

Changes in diet

A decline in preferred diet abundance has been forecasted for jaguars (Cuyckens et al., 2015; O'Farrill et al., 2014). For example, Mexico will lose vital waterholes in various scenarios, which will not only impact jaguars if persistent, but prey populations that rely on water sources for survival could decline in response to rising ambient temperatures (O'Farrill et al., 2014).

Leopard *Panthera pardus*

Changes in habitat

Results are inconclusive given that the positive effects on leopards in China, India, and Asia (Rather et al., 2020; Buzzard and Bleisch, 2017; Lovari et al., 2013a), contrast with no effects for China, Russian Far East, and Nepal (Qi et al., 2020; Thapa et al., 2016) and negative results forecasted for Iran (from 12 to 24 % of current suitable habitat might be lost; (Khosravi et al., 2021; Ashrafzadeh et al., 2019; Ebrahimi et al., 2017).

Changes in diet

Of the projections evaluated, leopard diet will have a negative response (Khosravi et al., 2021; Qi et al., 2020; Ebrahimi et al., 2017; Khorozyan et al., 2015; Lovari et al., 2013b) but see (Buzzard and Bleisch, 2017). The principal causes identified are future drought, which might be causing prey decline that could significantly impact the diet (Ebrahimi et al., 2017). Another negative response would be increased competition with other large carnivores, such as the tiger in China and the Russian Far East or snow leopards along the Himalayas (Qi et al., 2020; Lovari et al., 2013b).

Changes in behaviour

As suitable habitats and ranges shift and diet profiles change, leopard behaviour is also expected to change, and an increase in human conflict may arise for some leopard populations as climate change impacts suitable leopard habitats. Large habitat patch size and strong habitat connectivity of Sri Lankan leopards were associated with a decrease in leopard-human conflict, both of which are drivers that may be in decline (Kittle et al., 2018).

Snow leopard *Panthera uncia*

Changes in habitat

Out of nine studies regarding snow leopard habitat, six of them (Shen, 2020; Aryal et al., 2016; Li et al., 2016; Aryal et al., 2014; Lovari et al., 2013a; Forrest et al., 2012) were negative (increased habitat fragmentation) and located in the Himalayas, Bhutan, Myanmar, Nepal, the Hengduan Mountain Region, as well as the species as a whole. Three studies in the Himalayas, Kazakhstan, Mongolia, Russia, and China (Buzzard and Bleisch, 2017; Farrington and Li, 2016; Li et al., 2016) were positive. While global surface temperature warms at a rate of 0.12C per decade, the temperature has increased faster in snow leopard range, specifically with warming rates ranging from 0.16C to 0.90C in the Himalayas (Farrington and Li, 2016). Similarly, glacier cover, permafrost, wetlands, and pasturelands have decreased in abundance within snow leopard range, contributing to a sharp decline in currently available, suitable habitats (Farrington and Li, 2016). As the climate changes, the available habitat range is changing and tree lines shifting to higher elevations will reduce total habitat suitability in the Himalayas by 30 % (Forrest et al., 2012). Eighty percent of snow leopard habitat in Bhutan, Myanmar, and Nepal might be lost, with 24 % of that decline occurring in Nepal alone (Aryal et al., 2016; Li et al., 2016). However, it is also predicted that snow leopard habitat will increase by 58 % in the seven northernmost range states while decreasing in southern lying Nepal (23 % decline) and Bhutan (55 % decline) (Farrington and Li, 2016).

Changes in diet

Blue-horned sheep are a common prey species for snow leopards, and there is a prediction that their numbers will decline in response to climate change (Aryal et al., 2016). Additionally, prey species in the Hengduan Mountain Region will decrease in population due to a decrease in grassland habitat (Shen, 2020). As predicted by multiple studies, conflict with common leopards is expected to increase as snow leopard habitat changes and ranges shift (Lovari et al., 2013a). Only one study based in China predicts a positive response in preferred diet profiles of snow leopards as it projects an increase in potential diet variation as prey species shift their ranges due to changing vegetation in a warming climate (Buzzard and Bleisch, 2017).

Changes in behaviour

As the tree line shifts upslope in the Trans-Himalaya region, snow leopards might follow prey species that shift their ranges, driving a change in movement and foraging behaviour (Aryal et al., 2014). An increase in potential competition with other large carnivores may also drive a change in snow leopard spatial or temporal activity to avoid direct conflict with other species like the leopard (Lovari et al., 2013a,b).

Cheetah *Acinonyx jubatus*

Changes in habitat

A negative response of suitable habitat in response to climate change has been forecasted for the cheetah population in Iran (Khosravi et al., 2021; Shams et al., 2019; Morovati et al., 2017), e.g., habitat decline by 42 % by 2070 (Khosravi et al., 2021). A decrease in rainfall leading to drought conditions makes for a highly arid climate which is projected to increase as ambient temperatures rise (Shams et al., 2019), leading to severe degradation of suitable cheetah habitats (Morovati et al., 2017).

Changes in diet

There are insufficient studies on the impacts of climate change on the preferred diet for the cheetah. However, one study suggested that the availability of the preferred prey for Iranian cheetahs would be unaffected (Khosravi et al., 2021).

Puma *Puma concolor*

Changes in habitat

Projections show negative impacts on suitable habitats for the Florida population of pumas directly attributed to sea-level rise (Pearlstine et al., 2010; Whittle, 2009).

Grey wolf *Canis lupus*

Changes in habitat

Projections shows a decline in suitable habitats for the grey wolf in Turkey and the Netherlands (Suel et al., 2018; Potiek et al., 2012). However, the highly mobile nature of wolves will help their tolerance to their changing environments (Suel et al., 2018).

Changes in diet

Prey increase abundance have been projected at Canada and the Netherlands (Barber et al., 2018; Dawe and Boutin, 2016; Potiek et al., 2012). British Columbia, Canada, is currently experiencing an explosion in the white-tailed deer population and grey wolf population is increasing in response and is expected to increase by 2050 (Dawe and Boutin, 2016). In Alberta, Canada, white-tailed deer population is currently out-competing the caribou, and there is a projected total increase in preferred diet abundance by 2080 (Barber et al., 2018); and in the Netherlands, prey availability is projected to increase by 2100 (Potiek et al., 2012). On the contrary, other studies project prey decline in the Yukon and Eureka, Canada (Hegel et al., 2010) (Mech, 2004). Caribou s in the east-central Yukon are projected to decline (Hegel et al., 2010), and the High Arctic population of wolves in Eureka is experiencing a high rate of herbivore mortality at higher elevations, which is projected to continue with climate change (Mech, 2004).

Changes in behaviour

The North Atlantic Oscillation is a climatic event that has caused an increase in winter snow in this region in some years. In response to the increase in snow, wolf pack sizes have increased on Isle Royale (Post et al., 1999). As a result, increased moose kills by the larger packs of wolves at a higher frequency have been observed (Post et al., 1999). As climate change continues to alter weather patterns in regions such as the Isle Royale, grey wolf hunting behaviour may change in response.

African wild dog *Lycaon pictus*

Changes in habitat

African wild dogs occupies extensive range but tend to fill these large swaths of territory in low density (Woodroffe and Ginsberg, 1999). This tendency puts this species at risk of the negative effects of habitat fragmentation, including a loss of genetic diversity. As habitat becomes increasingly fragmented, populations will have a more challenging time dispersing to find potential mates and seeking and establishing new territories (Jones et al., 2016). It is projected that by 2050, African wild dog range will be diminished by 43.7 %, which will significantly impact population numbers (Jones et al., 2016).

Discussion

Information on the impact of climate change on large carnivore habitats, diets, and behaviours is still scarce for several species and/or geographical areas, though most of the available predictions point to an unfortunate truth. Species with habitats susceptible to considerable alterations will probably experience a severe local decline in the next few decades (Davis et al., 2021; Hazra et al., 2002; Pachauri et al., 2014).

Current information seems to support H1; that is, most species would be negatively impacted by the effect of global warming on habitat suitability (Fig. 4). The American black bear is the only species for which positive outcomes from a changing climate have been potentially highlighted (Bastille-Rousseau et al., 2018; Bonin et al., 2020; Ditmer et al., 2018). While some species may become more generalized in their diets (as suggested by H2), like polar bears exploiting terrestrial prey resources (Gormezano and Rockwell, 2013), there is not enough information to support this hypothesis to date. Actually, competition for prey would increase as polar bear hunting territory becomes more concentrated, and younger or subordinate bears could suffer as older or more dominant bears monopolize the hunting grounds (Derocher et al., 2004). Finally, we predicted behavioural changes in response to changing climate in the form of circadian activity to optimize the tasks associated with daily needs (H3). While there was an impact on denning behaviour for hibernating species, movement behaviour, and foraging behaviour, only American black bears had a formal study on changes in their circadian activity (Lara-Díaz et al., 2018), so we lack data projecting behavioural adaptations of large carnivores to the changing climate.

Loss of suitable habitats and decrease in food availability, which have been forecasted for most large carnivores (Fig. 4) might induce these species to shift their common range of distribution to find alternative food sources and, as a result, move to areas where they are more likely to experience conflicts with humans (Penteriani et al., 2019)) (Fig. 1). However, direct anthropogenic impacts on suitable habitat, preferred diet, and behaviour have not been taken into account as an additional factor potentially reinforcing the negative effects of climate change, and that can contribute to an even greater decline of large carnivores during the 21st century. Future large carnivore survival and recovery under climate change scenarios will depend on their ability to adapt to the combination of climate changes and human-related factors that negatively affect these species, such as anthropogenic food, density, and traffic load of roads and railways, as well as recreational and industrial activities (e.g., Bischof et al., 2018; Frank et al., 2019; Loveridge et al., 2017; Morales-González et al., 2020; Penteriani et al., 2018). Incorporating direct anthropogenic effects like hunting, retaliation killing, and human-wildlife conflicts with the impact of climate change on large carnivores would allow a more accurate projection for the future of these essential species.

Increased distances between suitable habitats e.g., during denning and/or reproduction and autumn/winter food, due to landscape alterations because of the warming climate may expose animals to more significant risks than before (e.g., car collisions, increased energy consumption) because of the longer distances they need to cover among seasons (e.g., Ashrafzadeh et al., 2022; Penteriani et al., 2019). Establishing good predictions of habitat loss, diet and behavioural variations over the whole distribution range of a species will better inform future and long-term conservation management plans and aid population viability, and will allow for more holistic conservation management plans that will help maintain worldwide biodiversity.

Climate projections represent a useful first step and plausible null model to rely on for future large carnivore conservation, rather than assuming that their current distribution will remain unaffected. Using climate projections in conjunction with conservation actions intending to maintain large carnivores in their current range and/or restore them to their historical ranges will strengthen the positive impacts of this work. In the future, conservation management practices should be encouraged to prioritize areas identified as potentially suitable for large carnivore species as a consequence of climate change.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Summary of reviewed papers by species.