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REVIEW

Climate change and deer in boreal and temperate regions: From physiology to population dynamics and species distributions

Annika M. Felton[1] | **Hilde Karine Wam**[2] | **Zbigniew Borowski**[3] | **Aksel Granhus**[4] | **Laura Juvany**[1] | **Juho Matala**[5] | **Markus Melin**[5] | **Märtha Wallgren**[6,7] | **Anders Mårell**[8]

[1]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences (SLU), Lomma, Sweden

[2]Department of Wildlife and Rangelands, Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway

[3]Forest Research Institute, Raszyn, Poland

[4]Department of Forest Management, Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway

[5]Natural Resources Unit, Natural Resources Institute Finland (Luke), Joensuu, Finland

[6]Skogforsk (Forestry Research Institute of Sweden), Uppsala, Sweden

[7]Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences (SLU), Umeå, Sweden

[8]INRAE, EFNO, Nogent-sur-Vernisson, France

Correspondence

Annika M. Felton, Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences (SLU), PO Box 190, Lomma SE-234 22, Sweden.
Email: annika.felton@slu.se

Hilde Karine Wam, Department of Wildlife and Rangelands, Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway.
Email: Hilde.Wam@nibio.no

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Abstract

Climate change causes far-reaching disruption in nature, where tolerance thresholds already have been exceeded for some plants and animals. In the short term, deer may respond to climate through individual physiological and behavioral responses. Over time, individual responses can aggregate to the population level and ultimately lead to evolutionary adaptations. We systematically reviewed the literature (published 2000–2022) to summarize the effect of temperature, rainfall, snow, combined measures (e.g., the North Atlantic Oscillation), and extreme events, on deer species inhabiting boreal and temperate forests in terms of their physiology, spatial use, and population dynamics. We targeted deer species that inhabit relevant biomes in North America, Europe, and Asia: moose, roe deer, wapiti, red deer, sika deer, fallow deer, white-tailed deer, mule deer, caribou, and reindeer. Our review (218 papers) shows that many deer populations will likely benefit in part from warmer winters, but hotter and drier summers may exceed their physiological tolerances. We found support for deer expressing both morphological, physiological, and behavioral plasticity in response to climate variability. For example, some deer species can limit the effects of harsh weather conditions by modifying habitat use and daily activity patterns, while the physiological responses of female deer can lead to long-lasting effects on population dynamics. We identified 20 patterns, among which some illustrate antagonistic pathways, suggesting that detrimental effects will cancel out some of the benefits of climate change. Our findings highlight the influence of local variables (e.g., population density and predation) on how deer will respond to climatic conditions. We identified several knowledge gaps, such as studies regarding the potential impact on these animals of extreme weather events, snow type, and wetter autumns. The patterns we have identified in this literature review should help managers understand how populations of deer may be affected by regionally projected futures regarding temperature, rainfall, and snow.

Annika M. Felton and Hilde Karine Wam should be considered joint first authors.

KEYWORDS
herbivore, precipitation, temperature, ungulate, wildlife

1 | INTRODUCTION

Climate change causes far-reaching disruption in nature. The tolerance thresholds of some plants and animals are already exceeded, exemplified by increased heatwaves that can cause local mass mortalities (IPCC, 2022). Impacts from slow-onset processes, such as regional decreases in precipitation, create cascading effects that are increasingly difficult to manage (IPCC, 2022). Observed impacts on wildlife of weather extremes and slow-onset processes include, for example, effects on their physiology and health, reproduction and population dynamics, movement, and migrations, nutritional conditions, as well as shifts in species distributions (Bellard et al., 2012; Parmesan & Yohe, 2003; Urban, 2015). Animals may be able to adapt to climate change to varying extents, through phenotypic (Bonamour et al., 2019) and behavioral (Wong & Candolin, 2014) plasticity, which could potentially speed up the rate of evolution (Hoffmann & Sgrò, 2011; Husby et al., 2011). This adds another layer of complexity to how wildlife species may be affected by climate change.

Twenty-four years ago, researchers gathered at the Abisko research field station in northern Sweden to discuss animal responses to global change in Europe's cold regions (Danell et al., 1999). They predicted that warmer winters would have the greatest impact on animals in these regions through snow characteristics and the timing of melt-off. However, a general lack of detailed data was reported, and the authors emphasized the specific need for more detailed studies. Since then, scientists have published hundreds of studies that potentially link wildlife responses to climate change, and the number of testimonies of ongoing responses is steadily growing. Therefore, there is a need for an updated synthesis. Here, we provide a synthesis of peer-reviewed literature addressing climate responses of deer inhabiting not only the cold regions of Europe but all of the boreal and temperate forest biotopes in the Northern hemisphere. The boreal and temperate forests of the Northern hemisphere are inhabited by the following members of the deer family, Cervidae: moose (*Alces alces*), roe deer (*Capreolus capreolus*), wapiti (*Cervus canadensis*), red deer (*C. elaphus*), sika deer (*C. nippon*), fallow deer (*Dama dama*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), caribou, and reindeer (*Rangifer tarandus*). These deer can have a large impact on ecosystems and societies, on the one hand as damage agents to, for example, agriculture or forestry, and on the other hand as part of culture and as appreciated resources for recreation and hunting (Linnell et al., 2020).

Climate change affects deer initially through an individual physiological or behavioral response, for example, body temperature (Thompson et al., 2019), hormone levels (Spong et al., 2020), and activity (Aublet et al., 2009). The individual response may ultimately show in their body mass (Couturier, Côté, Otto, et al., 2009), reproduction (Ekanayake et al., 2018), or survival (Hurley et al., 2014). Over time, individual responses can aggregate to the population level, interact with other species, and through trophic cascades ultimately affect entire ecosystems (Legagneux et al., 2014). The vulnerability to climate change varies among different species of deer (Zhang et al., 2020). Traits likely to influence the vulnerability are, for example, body size, extent of dietary specialization, or if the species is particularly adapted to the cold. Low phenotypic and behavioral plasticity makes the species more vulnerable to climate change. Importantly, all deer species are consumers and prey simultaneously, thereby modifying both top-down and bottom-up species dynamics and associated landscape use patterns (Bernes et al., 2018; Côté et al., 2004; Persson et al., 2000).

In this review, we synthesize published research on direct associations between deer and the following climatic factors: temperature, rainfall, snow, combined measures (e.g., the North Atlantic Oscillation [NAO]), and extreme events (hurricanes, fire, etc.), in the context of climate change, from studies focused on individuals to populations to species. We do not review the effects of climate on habitat alterations for deer through, for example, forest management, forage, and predation because those are vast topics that require their own targeted reviews. These alterations will mediate patterns locally (Spong et al., 2020) and are, therefore, indirectly part of our review. There is a great complexity involved in detangling the indirect effects of climate on deer through habitat factors such as plants (Parmesan & Hanley, 2015) and forest management (e.g., moose, Johnson & Rea, 2023). We see our present synthesis of literature about the direct effects of climatic conditions on deer physiology, spatial use, and population dynamics as providing just one piece of a complex puzzle, acknowledging that the resilience of deer species to a changing climate will be greatly influenced by all of these facets in combination.

We chose these specific climate factors because they are predicted to change substantially in the boreal and temperate regions of the Northern hemisphere. Deer in this hemisphere live in a vast array of climates, with different degrees of seasonality: For example, moose in the taiga of northern Finland compared with red deer in the dry fringes of temperate northern Spain. The warming of temperatures, which is the driver of all other climate change, is both documented (Morice et al., 2021) and predicted to be stronger in a south–north gradient (Figure S1) and to cause northward shifts of climate zones (King et al., 2018). Although the intensity of changes will vary between regions, some overall predicted patterns include an increased frequency of summer heat waves and decreased frequency of winter cold waves (Figure S1). With warmer temperatures, evaporation will increase, and so will the annual rainfall (Figure S1). However, snowfall is predicted to decrease in certain regions, with shortened duration of the snow season as a consequence (e.g., 17% less snowfall in Eurasia under the SSP2-4.5 scenario, Lin &

Chen, 2022). Consequences that are of particular importance to deer are the earlier green-up in spring and more plant-growing days, which could result in higher forage availability. For example, using 50 years of meteorological observations, Tyler et al. (2021) found that on Finnmarksvidda in northern Norway, the green-up advanced 9.3 days from 1960 to 2018 and the growing season expanded 9.8 days into the autumn. The increase in mean temperature during winter (Oct–Apr) was 2.3°C, and the number of winter days with thawing doubled (Tyler et al., 2021). More examples of these kinds of changes will be treated in detail throughout the result section of our review.

Our synthesis is exploring broad trends rather than specific attributes and includes all identified relevant deer responses to climate factors found in the peer-reviewed literature. We do not quantify the magnitude of any response to any climate change (i.e., it is not a numeric meta-analysis). Instead, we elucidate likely patterns of animal responses to climate change factors and identify important knowledge gaps.

2 | METHODS

2.1 | Definitions of climate factors and deer responses

We organize our review into three broad categories of deer responses to climate factors: physiology (body condition, thermal stress [physiological or behavioral], disease, rut, conception, and gestation), spatial use (activity patterns, daily movements, foraging behavior, migration, and species distribution), and population dynamics (reproduction, sex ratios, mortality, and population size, and density).

Studies included in our review (see below for search terms) associated deer responses with temporal data on: temperature, rainfall, snow, combined measures (e.g., the NAO), and extreme events (hurricanes, fire, etc.). Combined measures merge several variables into simple measures, reducing complex space and time variability, but they may lose details on important local conditions that are likely to have a more direct link to animals living there (Stenseth et al., 2003). In our literature search, we found studies that involved a range of combined measures, of which the most frequent ones were the NAO, several varieties of "winter severity," and the Normalized Difference Vegetation Index (NDVI or NVI).

The NAO represents a dominant atmospheric pattern in the North Atlantic region that affects temperature and precipitation and has considerable influence on ecological processes (Stenseth et al., 2003). For example, NAO index values that are higher than the average indicate an increased likelihood of warmer-than-average temperatures in certain geographic regions. NAO values below the average typically indicate the opposite pattern. The exact patterns vary across seasons and regions, but the ecological relevance is regionally clear as the patterns are directly linked to seasonal weather. For example, higher winter NAO in Scandinavia is associated with higher temperatures and precipitation, but due to altitudinal differences in the temperature, this means less snow and more rain at lower elevations near the coast, but more snow at higher elevations. A more thorough overview is given in Ottersen et al. (2001). "Winter severity" are various indices combined from, for example, temperature, snow, wind, and freezing rain, and are often computed seasonally and regionally (Walker et al., 2019). The NDVI index, on the contrary, is not based on weather variables nor direct vegetation observations but on satellite imagery. It estimates the relative "greenness" of the landscape and therefore has often been used as a proxy for vegetation phenology, amount of biomass and thus also a lump sum availability of forage in a given ecosystem. It can also be used to index the start, intensity, and length of the growing season. However, at its current state of the art it cannot easily be used to differentiate between the nutritional appropriateness of different food types for deer.

2.2 | Literature search and screening

We searched for relevant literature with publication month and years January 2000–November 2022 in two databases: Web of Science (https://www.webofscience.com/; The Core Collection) and Scopus (https://www.scopus.com). We used the same nested Boolean (i.e., AND between different groups of search terms, OR within groups of similar search terms and NOT for excluding search terms) search string in the title, abstract, and keywords fields for both Web of Science (TS) and Scopus (TITLE-ABS-KEY) (complete search strings in the Appendix S2). We targeted the relevant deer species for the boreal and temperate forests (i.e., *Alces alces*, *Capreolus capreolus*, *Cervus* spp., *Dama dama*, *Odocoileus* spp., and *Rangifer tarandus*; for distribution maps, see Figure S2), by using a combination of Latin and common names that we combined with geographical constraints based on names of biogeographical regions, countries, and states. We combined this search string with climate-related variables (temperature, precipitation etc., Appendix S2). From here on, we refer to *Cervus elaphus* as red deer, and *C. canadensis* as wapiti. We refer to *R. tarandus* living in Europe and Asia as reindeer but as caribou when living in North America. We restrained the search by language (English) and document type (peer-reviewed papers). Our aim was to be as least exclusive as possible, but this led to some unexpected irrelevant documents. We therefore added exclusion terms to filter out non-targeted biogeographical regions and scientific fields. We did not exclude any topical part of our search because it would be impossible to make a coherent pre-emptive list of terms to exclude.

The search hits from Web of Science and Scopus were merged and cleaned of duplicates, resulting in 8154 unique papers. Screening of papers was conducted using Rayyan (Ouzzani et al., 2016), a free web application for reviewing articles. Decisions on exclusion or inclusion were first made by reading the title and abstract of each article and determining their conformity to the criteria targeted by the search terms: right topic (i.e., in the context of climate change), species (Cervidae excluding semi-domestic reindeer), geography (boreal and temperate zones), language (English), and type of study (new, or new synthesis of, empirical temporal data on deer response to climate). We included papers of migratory caribou residing in forest for larger parts of the year. Note that papers did not have to specify a climate change context to be included. It was sufficient that it contained temporal data on deer and weather variations. Given the controversies surrounding definitions of climate change, rather few papers proclaim having documented climate change and a stricter criterion would have excluded almost all papers.

The robustness of the exclusion criteria and the individual screener divergence of the first screening were tested before the actual screening was done. Fifty randomly drawn papers were reviewed by all authors individually without conferring. The papers were randomly distributed among authors. The discrepancies were rather few (13 out of 50 papers [26%] had at least one person with a different opinion than the others). After discussing each of these cases in detail, the basis for coherent decision-making was improved. To verify the improvement, another control procedure was applied for the remaining screening: 289 papers were each read by two to four authors. The result of this control screening showed 18 (6%) conflicting decisions.

Screening of the remaining 7815 papers was done by the authors one by one and assigned equally among readers according to alphabetic order by the first author of the papers. The first screening finally generated 556 papers possibly relevant for the review. All papers with conflicting decisions in the test and control screenings were included among the 556. The possibly relevant papers were then equally divided between the authors. These papers were read completely and again scrutinized for conformation to criteria, resulting in a final list of 218 papers relevant for review. Data from these papers were then tabulated and systemized per demographics (species, location, season, etc.), deer responses, and climate factor (Felton et al., 2024). Further details on this data collection are specified in Appendix S3. One relevant paper among the 556 was excluded because of printing errors in the results, which could not be interpreted. A detailed overview of sample sizes is given in Table 1. Any papers cited in Section 3 are from our literature search unless marked as a non-review paper (NR, used as a background, for instance). While any search risks missing some relevant papers, we were not able to identify any consistent bias where, for example, papers would have been systematically missed from a given region or a given climatic factor etc. The missing papers are therefore not likely to have affected the conclusions drawn in our review.

3 | RESULTS AND DISCUSSION

The 218 papers in our review covered five genera and eight species of deer (Figure 1). The papers included studies of populations across the entire range of the boreal and temperate zone of the northern hemisphere (Figure 2). However, some regions (like Asia) and some of the deer species were underrepresented (Figure 1; Figure 2; Appendix S3: Figure S2). No relevant papers about *D. dama* were found. In this section, we provide summaries of patterns we found in the literature regarding each deer response and climate factor combination (collated in Table 2). In the text (Sections 3.1–3.4), we do not cite every study that our review included, but all studies relevant for a pattern found are listed in Table 2.

3.1 | Extreme events

Extreme weather events such as flooding, icing of landscapes, hurricanes, and landslides typically affect a range of deer responses all at once, from instant survival to subsequent foraging and breeding.

TABLE 1 Numbers of peer-reviewed papers addressing deer (Cervidae) responses to climate factors in forests of the northern hemisphere, based on a systematic literature search (Web of Science and Scopus, January 2000 until November 2022).

		Climate factor					
Response	*N* (or %) of papers	Temperature	Rainfall	Snow	Combined measures	Extreme events	*N* (or %) of combinations
Physiology (*N*)	76	56	29	28	18	0	131
Physiology (%)	35%	15%	8%	8%	5%	0%	36%
Spatial use (*N*)	92	44	17	45	8	9	123
Spatial use (%)	42%	12%	5%	12%	2%	2%	34%
Population dynamics (*N*)	69	32	24	33	20	3	112
Population dynamics (%)	32%	9%	7%	9%	5%	1%	31%
Total unique papers	218	121	61	100	41	12	-
Climate × response combinations (*N*)		132	70	106	46	12	366
Climate × response combination (%)		36%	19%	29%	13%	3%	-

Note: Combined measures are large-scale patterns like the North Atlantic Oscillations and Normalized Vegetation indices, or local meteorological data merged for example into “winter severity.”

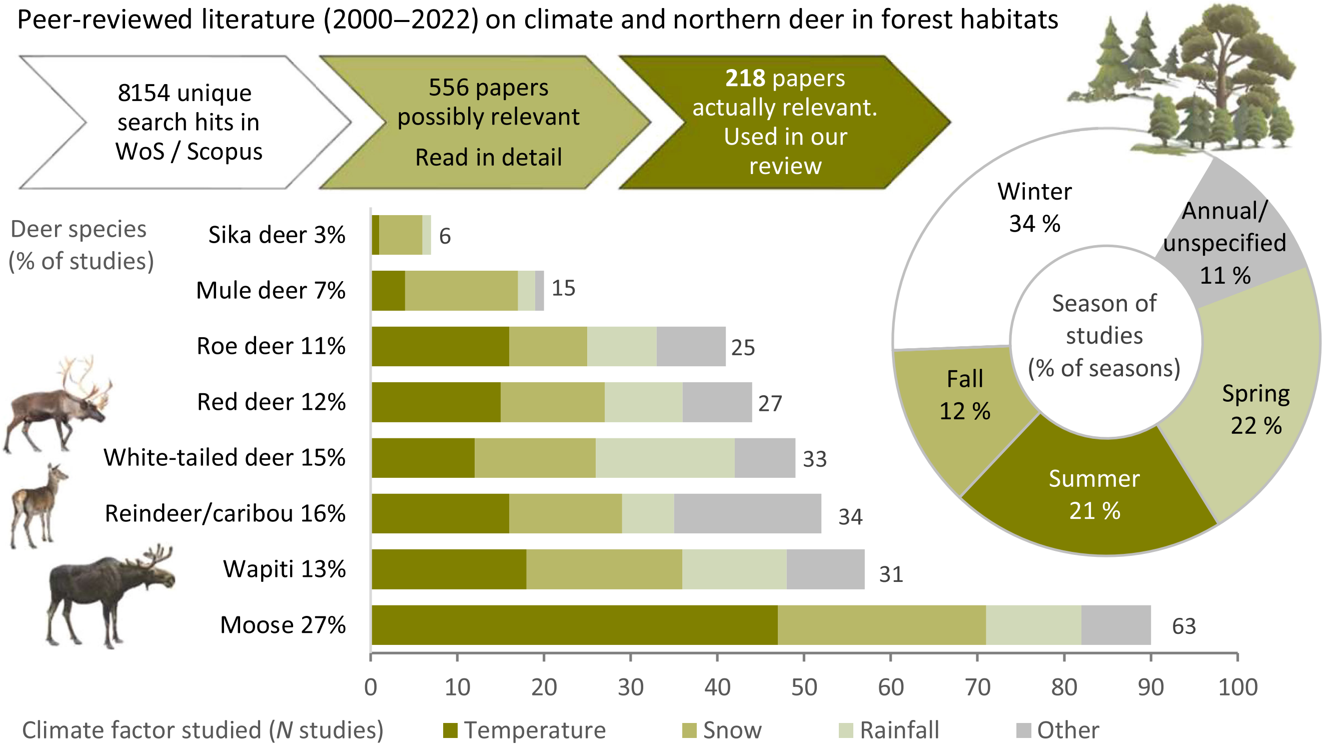

FIGURE 1 Demographics of 218 peer-reviewed papers addressing deer (Cervidae) responses to climate factors in forests of the northern hemisphere, based on a systematic literature search (Web of Science and Scopus, including January 2000–November 2022). Some papers addressed several species, or more than one climate factor for a given species. Numbers to the right of the bars are *N* unique studies with the deer species. Latin names of deer species: Moose (*Alces alces*), roe deer (*Capreolus capreolus*), wapiti (*Cervus canadensis*), red deer (*C. elaphus*), sika deer (*C. nippon*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), caribou, and reindeer (*Rangifer tarandus*).

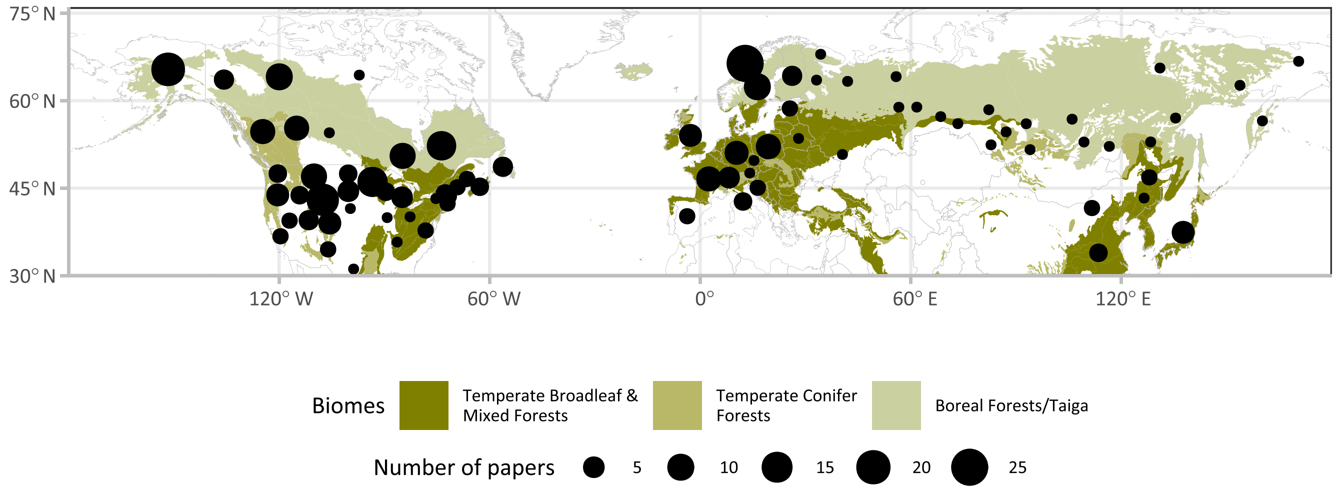

FIGURE 2 Distribution of reviewed studies across temperate and boreal forests of the northern hemisphere. In the map, some dots (the size of which reflects the number of papers, e.g., 5 or 10 papers) are outside forest area because meta-studies included also non-forest species. Only the forest-related data were treated in our review. In the map, studies are summarized at the country level, except for Canada, China, Russia, and United States for which states/provinces were used, and the data were displayed using the country/state/province centroids, which explains why some of the points are outside the actual study zone although the studies were performed within the boreal or temperate forest biome. The extent of the boreal and temperate forest biomes from Dinerstein et al. (2017).

We therefore did not dedicate response-specific sections to extreme events. While drought is an extreme event, we addressed it under rainfall or snow, as it was difficult to separate from "just" low precipitation. Similarly, one paper was about extreme cold, which we addressed under temperature. The remaining papers addressed either storms (*N* = 4) or fire (*N* = 8). They showed an increase in deer food availability (quantity and quality) in tree windfall gaps, leading to shifts in either diet or habitat (PF1, Table 2). However, increased

TABLE 2 General patterns found (PF) while reviewing the literature (published 2000–2022) on deer responses to climate factors in the forests of the northern hemisphere.

Patterns found		Deer species and references
Climate-related extreme events		
PF1	There are yet very few studies on deer and climate-related extreme events. However, it seems clear that forest-dwelling caribou are mostly negatively affected by fire in their winter ranges because it destroys the lichen cover (papers marked *). In contrast, early successional stages caused by windfall or forest fires increase food availability for deer in general (papers marked c)	*Alces alces*: Joly et al. (2012) (c); *Capreolus capreolus*: Moser et al. (2008) (0); Storms et al. (2006) (0); *Cervus canadensis*: Taper and Gogan (2002) (c); Weckerly et al. (2021) (c); *Cervus elaphus*: Krojerova-Prokesova et al. (2010) (c); Storms et al. (2006) (c); *Odocoileus virginianus*: Courbin et al. (2017) (c); *Rangifer tarandus*: Anderson and Johnson (2014) (*0); Barrier and Johnson (2012) (*0); Joly et al. (2012) (*); Konkolics et al. (2021) (*0); Palm et al. (2022) (*0); Silva et al. (2020) (*)
Deer physiology		
PF2	Warmer summers will cause declines in the body condition of deer along all geographical gradients (*), mainly due to heat stress and parasites (see PF5)	*A. alces*: Chen, Holyoak, Liu, Bao, Ma, Dou, Li, Roberts, and Jiang (2022) (*); Ericsson et al. (2002) (0); Herfindal, Sæther, et al. (2006) (*); Herfindal et al. (2020) (*); McCann et al. (2013) (*); Solberg et al. (2007) (0); Spong et al. (2020) (*)[†]; Thompson et al. (2020) (*); Thompson et al. (2019) (*); Veeroja et al. (2008) (0); *C. capreolus*: Kjellander et al. (2006) (*); *C. canadensis*: Millspaugh et al. (2001) (*); *C. elaphus*: Anderwald et al. (2021) (0); Corlatti et al. (2018) (*); Huber et al. (2003) (*); *O. hemionus*: Freeman et al. (2013) (0); *O. virginianus*: Campbell and Wood (2013) (0); *R. tarandus*: Couturier, Côté, Huot, et al. (2009) (0); Couturier, Côté, Otto, et al. (2009) (*0)
PF3	In winter, warmer temperatures per se will likely be non-significant (0) or have minor benefits (*) for deer body condition (less thermal stress of individual or mother), but can be negative (c), for example through parasites (see PF5) and more icy or wetter snow (see PF8)	*A. alces*: Herfindal, Sæther, et al. (2006) (*); Herfindal, Solberg, et al. (2006) (c); Herfindal et al. (2020) (0); Holmes et al. (2021) (*); Solberg et al. (2007) (0); Thompson et al. (2019) (*); Veeroja et al. (2008) (*); *C. capreolus*: Kjellander et al. (2006) (*); Mysterud et al. (2007) (0); *C. canadensis*: Johnson et al. (2013) (*); *C. elaphus*: Anderwald et al. (2021) (*); Corlatti et al. (2018) (*); Huber et al. (2003) (*); Stopher et al. (2014) (*); *O. hemionus*: Freeman et al. (2013) (c); *O. virginianus*: Campbell and Wood (2013) (*0); Garroway and Broders (2005) (*c); Giroux et al. (2014) (0); Giroux et al. (2016) (0); Powell and DelGiudice (2005) (0*); Wolcott et al. (2015) (*); *R. tarandus*: Couturier, Côté, Otto, et al. (2009) (*)
PF4	A warmer spring (earlier green-up) and a longer or greener growing season will enhance deer body condition through improved foraging conditions (*), but not if the spring is also too warm (heat stress through, e.g., molting mismatch), more rapid or spatially more homogenous, or drier (c). It is unknown whether plant phenology changes faster than deer can adapt their calving dates	*A. alces*: Ericsson et al. (2002) (*); Herfindal, Sæther, et al. (2006) (*0); Herfindal, Solberg, et al. (2006) (c); Herfindal et al. (2020) (*); Holmes et al. (2021) (c); Van de Vuurst et al. (2021) (c); *C. capreolus*: Cao et al. (2022) (c); Douhard et al. (2013) (c); Mysterud et al. (2007) (0); Pettorelli et al. (2006) (*0); *C. canadensis*: Middleton et al. (2013) (c); Stewart et al. (2005) (0); *C. elaphus*: Martinez-Jauregui et al. (2009) (*0); Moyes et al. (2011) (*0); Mysterud et al. (2001) (*); Mysterud et al. (2008) (*); Nussey et al. (2005) (*); Pettorelli et al. (2005) (*); Stopher et al. (2014) (*); *O. hemionus*: Searle et al. (2015) (c); *O. virginianus*: Campbell and Wood (2013) (0); McGraw et al. (2022) (*0); *R. tarandus*: Chen et al. (2018) (*c); Couturier, Côté, Huot, et al. (2009) (*); Couturier, Côté, Otto, et al. (2009) (*)
PF5	Warmer temperatures (all seasons) will lead to increased parasite exposure and infection in northern deer (*), but not of all kinds everywhere (0 or c)	All deer species in the study area: Härkönen et al. (2010) (*); *A. alces*: Hoy et al. (2021) (*); Jones et al. (2019) (*); Madslien et al. (2011) (*); Malmsten et al. (2019) (*); Verocai et al. (2012) (*); *C. capreolus*: Bariod et al. (2022) (0); *C. elaphus*: Handeland et al. (2019) (*0); *O. virginianus*: Dumas et al. (2022) (*); Elias et al. (2021) (*); Jacques et al. (2017) (*); Maskey et al. (2015) (*); Pickles et al. (2013) (*c); Sleeman et al. (2009) (*); *R. tarandus*: Ball et al. (2001) (*); Haider et al. (2018) (*); Laaksonen et al. (2009) (*); Verocai et al. (2012) (*)
PF6	Warmer temperatures negatively affect deer mass or size through generational flow-on effects (e.g., delayed conception or birth due to less body fat of mothers or smaller-sized fathers), and via, for example, birth asynchrony and plant phenology (*). However, there are many, and partly antagonistic, pathways (0 or c)	*A. alces*: Neumann et al. (2020) (*); Solberg et al. (2007) (0); Veeroja et al. (2013) (*); Veeroja et al. (2008) (*); *C. capreolus*: Chirichella et al. (2019) (*)[§]; Hagen et al. (2021) (0); Rehnus et al. (2020) (*); *C. canadensis*: Middleton et al. (2013) (*); *C. elaphus*: Corlatti et al. (2018) (0), Moyes et al. (2011) (c); Stopher et al. (2014) (*c); *O. virginianus*: Campbell and Wood (2013) (0c)

TABLE 2 (Continued)

Patterns found		Deer species and references
PF7	The outcome of more rainfall in the growing season on deer physiology will highly depend on location. It can be negative (N) or beneficial (B), depending mainly on whether plants are normally water limited, or if parasites in the area benefit from moist conditions. Drought (D) will likely always be bad (only one study), as the benefit of less parasites do not counter the setback from poorer forage conditions	*A. alces*: Ericsson et al. (2002) (0); Herfindal et al. (2020) (N*); Holmes et al. (2021) (B*); Solberg et al. (2007) (0); *C. capreolus*: Bariod et al. (2022) (N*); Chirichella et al. (2019) (0); Hagen et al. (2021) (0); *C. canadensis*: Johnson et al. (2013) (B*); Johnson et al. (2019) (B*); Stewart et al. (2005) (B*); *C. elaphus*: Anderwald et al. (2021) (B*); Huber et al. (2003) (0); Vicente et al. (2004) (N*); *O. hemionus*: Freeman et al. (2013) (0); *O. virginianus*: Campbell and Wood (2013) (N*0); Dumas et al. (2022) (N*); Jacques et al. (2017) (N*); Maskey et al. (2015) (N*); Peterson et al. (2019) (D*); Sleeman et al. (2009) (N*); Wolcott et al. (2015) (B*)
PF8	Deer physiology (e.g., higher body mass or fat, less susceptible to disease, earlier birth, higher pregnancy rates) can be enhanced by reduced snow depth (*), but often such benefits are not observed (0 or c). It is unknown whether less snow in the future means a different type of snow (e.g., more wet or crusty snow)	*A. alces*: Ericsson et al. (2002) (0); Herfindal, Sæther, et al. (2006) (*0); Herfindal et al. (2020) (*); Holmes et al. (2021) (*); Hoy et al. (2021) (0); Rosenblatt et al. (2021) (*); Veeroja et al. (2008) (*); *C. capreolus*: Chirichella et al. (2019) (*); Mysterud et al. (2007) (0); *C. canadensis*: Johnson et al. (2013) (*); Merkle et al. (2018) (*); *C. elaphus*: Anderwald et al. (2021) (*); Corlatti et al. (2018) (0); Huber et al. (2003) (*); Martinez-Jauregui et al. (2009) (*0); Mysterud et al. (2001) (*); Mysterud et al. (2008) (*); Pettorelli et al. (2005) (*c); *O. hemionus*: Freeman et al. (2013) (*); Searle et al. (2015) (c); *O. virginianus*: Campbell and Wood (2013) (*0); Cotterill et al. (2020) (0); Garroway and Broders (2005) (*); Giroux et al. (2014) (0); Giroux et al. (2016) (0); Mech (2007) (0); Powell and DelGiudice (2005) (*0); *R. tarandus*: Adams (2005) (*); Chen et al. (2018) (0); Couturier, Côté, Huot, et al. (2009) (0); Couturier, Côté, Otto, et al. (2009) (*0)
Deer spatial use		
PF9	Warmer winters (W*) will likely increase the home range and daily activity of temperate deer species, while warmer spring/summers (S*) are more likely to affect both temperate and boreal species, who will alter their activity to avoid heat stress and parasites which leads to smaller home ranges	*A. alces*: Alston et al. (2020) (S*); Burkholder et al. (2022) (W0*); Ditmer et al. (2018) (S*); Dussault et al. (2004) (S*); Herfindal et al. (2017) (S*); Jennewein et al. (2020) (S*); McCann et al. (2013) (S*); McCann et al. (2016) (S0); Melin et al. (2014) (S*); Montgomery et al. (2019) (S*); Street et al. (2016) (S*); Street et al. (2015) (S*, W*); Teitelbaum et al. (2021) (S*, W0); Thompson et al. (2021) (S*); van Beest et al. (2011) (S0, W*0); van Beest et al. (2012) (S*, W0); Wattles et al. (2018) (S*); *C. capreolus*: Stache et al. (2013) (S0, W0); *C. canadensis*: Porter et al. (2002) (W*); *C. elaphus*: Kamler et al. (2007a) (W*0, S*0); Kamler et al. (2007b) (W*0, S*0); Prebanić and Ugarković (2015) (S*); Rivrud et al. (2010) (S*, W*); *O. virginianus*: Courbin et al. (2017) (W*); DelGiudice et al. (2013) (0); Gilbert et al. (2022) (W*); *R. tarandus*: Beguin et al. (2013) (S0, W0); Leclerc et al. (2019) (W*); Witter, Johnson, Croft, Gunn, and Poirier (2012) (S*c)
PF10	Warmer springs and autumns, per se and through shortened snow cover, will change the timing and routes of migrations (*), advancing it in spring and delaying it in autumn. In the long term, this may shift migratory deer to become resident	*C. capreolus*: Ramanzin et al. (2007) (*); *C. canadensis*: Rickbeil et al. (2019) (*); Eggeman et al. (2016) (*0); Middleton et al. (2013) (*0); Van Dyke (2007) (*); *C. elaphus*: Malnar et al. (2015) (*); Pettorelli et al. (2005) (*); *C. nippon*: Igota et al. (2004) (*); Takii et al. (2012) (*); *O. virginianus*: Fieberg et al. (2008) (*0); Grovenburg et al. (2011) (*0); Sabine et al. (2002) (*0); *R. tarandus*: Gurarie et al. (2019) (*0); Le Corre et al. (2017) (*0); Wittmer et al. (2006) (*0)
PF11	Warmer temperatures will likely shift deer species' distribution ranges northward (*) due to heat stress or changes in the relative abundance of forest habitat types. However, there are still few studies on this topic	*A. alces*: Dou et al. (2013) (*); Chen, Holyoak, Liu, Bao, Ma, Dou, and Jiang (2022) (*); *C. capreolus*: Büntgen et al. (2017) (*0); Benjamin et al. (2022) (*0); *C. elaphus*: Büntgen et al. (2017) (*0); *C. nippon*: Honda (2009) (0); *O. virginianus*: Kennedy-Slaney et al. (2018) (*)
PF12	Heavy rainfall temporarily reduces deer activity (*), but increased rainfall in general will likely have minor (0) or even positive (c) effects on activity and home range size compared with other more important climate or non-climate factors	*A. alces*: Ditmer et al. (2018) (c); van Beest et al. (2011) (*0); *C. capreolus*: Stache et al. (2013) (0); Benjamin et al. (2022) (*0); *C. elaphus*: Kamler et al. (2007a) (0*); Kamler et al. (2007b) (0); Rivrud et al. (2010) (*c)

(Continues)

TABLE 2 (Continued)

Patterns found		Deer species and references
PF13	Reduced snow cover will lead to increased movements, larger home ranges, and access to habitats with different or higher forage quality and may even change the social organization of the deer (*) (e.g., smaller group sizes in winter). However, it is unknown whether less snow in the future means a different type of snow (e.g., more wet or crusty snow)	*A. alces*: Burkholder et al. (2022) (0*); Kittle et al. (2008) (*); Månsson et al. (2017) (*); Poole and Stuart-Smith (2006) (*); Stephenson et al. (2006) (*); van Beest et al. (2011) (*); Van Moorter et al. (2013) (*); *C. capreolus*: Stache et al. (2013) (*0); Ramanzin et al. (2007) (*); *C. canadensis*: Merkle et al. (2018) (*); Poole and Mowat (2005) (*); *C. elaphus*: Kamler et al. (2007a) (*); Kamler et al. (2007b) (0); Kittle et al. (2008) (*); Pettorelli et al. (2005) (*); Rivrud et al. (2010) (*); *C. nippon*: Igota et al. (2004) (*); Sakuragi et al. (2003) (*0); *O. hemionus*: Gilbert et al. (2017) (*); Sawyer et al. (2017) (*0); Serrouya and Robert (2008) (*); Anton et al. (2022) (*0); Poole and Mowat (2005) (*); *O. virginianus*: Courbin et al. (2017) (*); DelGiudice et al. (2013) (*0); Kittle et al. (2008) (*); Massé and Côté (2012) (*); Morrison et al. (2003) (*); *R. tarandus*: Kinley et al. (2003) (*); Jung et al. (2019) (*)
PF14	Shortened snow cover duration and shallower snow depth caused by milder winters will likely shift distribution ranges of deer northward and/or to higher elevations (*), but anthropogenic land use may be an important constraint	*A. alces*: Poole and Stuart-Smith (2006) (*); *C. nippon*: Honda (2009) (*); Kaji et al. (2000) (*); Ohashi et al. (2016) (*0); *O. virginianus*: Dawe et al. (2014) (*); Dawe and Boutin (2016) (*); Kennedy-Slaney et al. (2018) (*); Pickles et al. (2013) (*); *R. tarandus*: Beguin et al. (2013) (0)
Deer population dynamics		
PF15	Milder winters will likely lead to no effect (0) or only a slight increase (*) in deer survival rates (W), but this can be countered by heat stress-induced mortality due to abnormally high temperatures at any season (H; also see PF16)	*A. alces*: Joly et al. (2017) (W*0); Lenarz et al. (2009) (H*); *C. capreolus*: Davis et al. (2016) (W*0); Warchałowski et al. (2015) (W*); *C. canadensis*: Griffin et al. (2011) (W0); Wang et al. (2002) (W*); *C. elaphus*: Stopher et al. (2014) (W0); Warchałowski et al. (2015) (W*); *O. hemionus*: Gilbert et al. (2007) (W*); *O. virginianus*: Michel et al. (2018) (W0)
PF16	Extreme temperatures and warmer summers will reduce recruitment partly through direct effects on female natality and young survival (F), but more importantly, these effects may be exacerbated or overruled by climate-driven time-lag effects (T), for instance via female body condition	*A. alces*: Brown (2011) (F0); Grøtan et al. (2009) (F*0c, T*); Holmes et al. (2021) (T*); Johnson et al. (2013) (F0, T*); Joly et al. (2017) (T*); Monteith et al. (2015) (F0, T*); Selas et al. (2011) (T*); *C. canadensis*: Griffin et al. (2011) (F0, T*); Starns et al. (2014) (F0); Wang et al. (2002) (F*); *C. elaphus*: Moyes et al. (2011) (F0); Stopher et al. (2014) (F*c); *O. hemionus*: Gilbert and Raedeke (2004) (F0); *O. virginianus*: Warbington et al. (2017) (F0); *R. tarandus*: Bastille-Rousseau et al. (2018) (F0, T*)
PF17	Warmer temperatures and increased temperature variability will affect deer population growth rate and abundance (W), but the overall outcome of different antagonistic effects on vital rates is unclear and difficult to determine because of complex interactions through, for example, density-dependent effects (DD)	*A. alces*: Brown (2011) (W*, DD*); Chen, Holyoak, Liu, Bao, Ma, Dou, and Jiang (2022) (W*); Dou et al. (2013) (W*, DD*); Priadka et al. (2022) (W*c, DD*)[¶]; *C. capreolus*: Gaillard et al. (2013) (W*, DD0); Grøtan et al. (2005) (W0); *C. canadensis*: Schooler et al. (2022) (W*); Starns et al. (2014) (W0, DD*); Wang et al. (2006) (DD*); Wang et al. (2002) (W*, DD*); *C. elaphus*: Stopher et al. (2014) (W*, DD0); *O. hemionus*: Gilbert et al. (2007) (W*, DD*); *R. tarandus*: Bastille-Rousseau et al. (2018) (W0)
PF18	Increased rainfall (R) will likely be beneficial to deer's vital rates and population dynamics, most probably through indirect effects on forage quantity and quality, while extreme rainfall (E) and drought (D) in spring and summer will likely reduce deer recruitment and may even modify offspring sex ratio (S)	*A. alces*: Holmes et al. (2021) (D*); Monteith et al. (2015) (D*); Ruprecht et al. (2020) (R*); *C. capreolus*: Hagen et al. (2022) (S0); Hamel et al. (2009) (D*); *C. canadensis*: Creel and Creel (2009) (R*0); Cunningham et al. (2009) (D*); Johnson et al. (2013) (R*); Johnson et al. (2019) (R*); Middleton et al. (2013) (D*); Starns et al. (2014) (R0); Taper and Gogan (2002) (R*); Vucetich et al. (2005) (R*); Weckerly et al. (2021) (R*); *C. elaphus*: Griffin et al. (2011) (R*); Stopher et al. (2014) (Rc); *O. hemionus*: Gilbert and Raedeke (2004) (E*); *O. virginianus*: Michel et al. (2018) (R*); Tosa et al. (2018) (D*); Warbington et al. (2017) (R0c); *R. tarandus*: Bastille-Rousseau et al. (2018) (R*c)

TABLE 2 (Continued)

Patterns found		Deer species and references
PF19	Reduced snow cover duration and depth will likely lead to less mortality (M), higher recruitment through birth rates or calf survival (B), and increased population growth (G), because of less snow-induced malnutrition, or easier escape from predation. However, it is unknown whether less snow in the future means a different type of snow (e.g., more wet or crusty snow)	*A. alces*: Brown (2011) (B0, G0); Debow et al. (2021) (Bc)[††]; Grøtan et al. (2009) (B*0); Joly et al. (2017) (B0, M*0); Ruprecht et al. (2020) (Gc); Selas et al. (2011) (B*); Vucetich and Peterson (2004) (G0); *C. capreolus*: Grøtan et al. (2005) (G*); Gula (2004) (M0); Warchałowski et al. (2015) (M*); *C. canadensis*: Creel and Creel (2009) (G*); Hebblewhite (2005) (M*); Horne et al. (2019) (M*); Johnson et al. (2013) (B*0); Mech et al. (2001) (M*); Taper and Gogan (2002) (M0, B0, G0); *C. elaphus*: Gula (2004) (M0); Mysterud et al. (2000) (B*); Warchałowski et al. (2015) (M*); *O. hemionus*: Anton et al. (2022) (M*); Gilbert et al. (2020) (B*, M*); Hurley et al. (2017) (M*); Jackson et al. (2021) (M*); Schuyler et al. (2019) (Mc); *O. virginianus*: DelGiudice et al. (2002) (M*); Kautz et al. (2020) (M*); Patterson and Power (2002) (B*, G*); Simard et al. (2010) (B*0, M0, Gc); *R. tarandus*: Bastille-Rousseau et al. (2018) (B0c); Hegel, Mysterud, Huettmann, and Stenseth (2010) (B0); Jenkins and Barten (2005) (B0)
PF20	General trends in weather patterns due to climate change will likely lead to small and slow changes in deer population dynamics that will be overshadowed in most cases by strong local factors such as population density and age structure, forage availability and nutritional quality, altitude, topography and predation (*)	*A. alces*: Chen, Holyoak, Liu, Bao, Ma, Dou, and Jiang (2022) (*); De Jager et al. (2020) (*); Post and Forchhammer (2001) (*) (2019); *C. capreolus*: Davis et al. (2016) (*); Grøtan et al. (2005) (*); Hagen et al. (2022) (*); Heurich et al. (2012) (*); *C. canadensis*: Hebblewhite (2005) (*); Middleton et al. (2013); Post et al. (2009) (*); Schooler et al. (2022) (*); Taper and Gogan (2002) (*); *C. elaphus*: Mysterud et al. (2000) (*); Pelletier et al. (2012) (*); Post et al. (2009) (*); *O. virginianus*: Garroway and Broders (2007) (*0); Kautz et al. (2020) (*); Simard et al. (2010) (*); *R. tarandus*: Bastille-Rousseau et al. (2013) (*); Bastille-Rousseau et al. (2018) (*); DeMars et al. (2021) (*); Hegel, Mysterud, Huettmann, and Stenseth (2010) (*); Hegel, Mysterud, Ergon, et al. (2010) (*); Jenkins and Barten (2005) (*); Joly et al. (2011) (*); Mahoney et al. (2016) (*); Post et al. (2009) (*)

Note: Studies with supporting evidence (*) are listed for each PF, and so are studies that report non-significant (0) or contradictory (c) findings. Furthermore, the specification of results in relation to the PF stated may be indexed by various letters explained in the PF text. More than one mark means the pattern applied variously to sex- or age groups, between seasons, between vectors (e.g., more than one parasite was studied), or between responses (e.g., a significant result for reproduction but not for mortality).

[†] Study uses annual temperature sum, but it can be inferred that summer is the main seasonal driver of the pattern found.

[§] Positive up to a 23°C threshold (normal temperatures), then shifts to negative.

[¶] Positive effect of warmer spring temperature on population density, but later onset of frost in the fall had the opposite effect.

[††] Winter survival of moose calves was positively correlated with snow depth. The authors suggest this result was spurious as max snow depth coincided with max tick engorgement.

food availability due to windfall did not change the diet composition for roe deer in Switzerland (Moser et al., 2008).

The fire studies mainly showed negative effects by the destruction of food habitats for caribou (PF1). Caribou was shown to avoid burnt areas in their winter ranges due to the lack of lichens (Anderson & Johnson, 2014; Barrier & Johnson, 2012) and because lichens take a long time to recover in burnt areas (Joly et al., 2012). However, fire can also have some positive effects. Silva et al. (2020) showed that while caribou avoided burnt sites in winter and autumn, they increased their use of recently burnt (<5 years) areas during the calving season. Similarly, Taper and Gogan (2002) reported short-term benefits of recent fire for population growth rates of wapiti in the Yellowstone National Park, likely due to modifications in food availability (see also moose in Joly et al., 2012).

3.2 | Deer physiology

Here, we focus on 76 papers addressing physiological responses of deer to climate change. Body condition was most often indexed by body mass, but some measured fat or protein reserves, antler size, or length of jawbone. Reproductive responses were mainly calving dates, but also the number of ovulated eggs and antler cast dates. There were surprisingly few studies measuring physiological stress per se, but they encompassed hormones, respiration, and body temperature. Stress is also indicated by habitat use or activity, which in our review are covered under spatial use. Importantly, in several of the studies of physiology the climate effect was accentuated by higher deer density (Kjellander et al., 2006; Moyes et al., 2011; Nussey et al., 2005; Stewart et al., 2005).

3.2.1 | Physiological responses to warmer temperatures

We found no strong physiological responses to warmer winters (PF3 in Table 2). A few papers showed that body condition improved, but it rarely could be pinned to temperature per se because it often covaried with snow conditions. In contrast, warmer summers consistently showed negative associations with deer body condition, and this applied to deer of all body sizes (PF2). Interestingly, one paper showed that there can be marked individual differences within a species in their behavioral plasticity to buffer heat stress in summer and thermal stress in winter (moose, van Beest & Milner, 2013).

In spring, the effects of warmer temperatures on body condition possibly follow a latitudinal gradient (PF4), being neutral or positive at higher latitudes but negative at lower latitudes (Herfindal et al., 2020; Martinez-Jauregui et al., 2009) (see also Douhard et al., 2013). The potential benefits (e.g., earlier vegetation green-up, Pettorelli et al., 2005) are likely countered by increasing heat stress or a too rapid plant phenology more south. Warmer springs can also combine with unusually low precipitation to halt the green-up irrespective of latitude (Holmes et al., 2021; Middleton et al., 2013). Because deer are adapted to a normal cycle of seasonality, earlier springs means that the timing of births can become mismatched for deer to reap the highs of the plant phenology (Neumann et al., 2020; Rehnus et al., 2020).

Our review suggests three reasons why warmer summers adversely affect the physiology of northern deer: (i) thermal stress, (ii) foraging, and (iii) parasites. Importantly, there is an interplay between the three that can start to spiral with climate change. For example, the level of thermal stress is linked to habitat availability (access to thermal refugia; Gilbert et al., 2022), and to the individual's body condition at the time of stress (McCann et al., 2013; Thompson et al., 2019). Also, foraging raises the body temperature. While animals can reduce feeding to reduce heat stress, the benefit is countered by the lower food intake, and subsequently, by altered gut microbiota (Chen, Holyoak, Liu, Bao, Ma, Dou, Li, et al., 2022). Especially moose seem susceptible to heat stress, and possibly red deer/wapiti (PF2). Vapor pressure (Thompson et al., 2020) and wind (McCann et al., 2013) oppositely modulate thermal stress in moose, and both of these factors may increase with a warming climate. Captive moose showed heat stress at 17°C without wind and at 24°C with wind (McCann et al., 2013). In winter, moose have a larger inner buffer to cope with temperature changes than it has in summer (Thompson et al., 2019). From this, we can postulate that warmer winters will be less of a thermal benefit than warmer summers will be a setback to moose (see also Mysterud et al., 2008).

One major way northern deer become more health compromised with climate change is through parasites, because parasites generally thrive in warmer temperatures (Härkönen et al., 2010). All papers addressing these aspects showed or predicted higher exposure and/or infestation of at least one parasite with warmer climate (PF5). However, one should not assume that warmer temperatures mean more of all parasites everywhere. Many factors determine parasite development. For example, forest caribou in Bathurst, Canada, have been less exposed to mosquitos from 1957 to 2008 (Witter, Johnson, Croft, Gunn, & Poirier, 2012), but increasingly exposed to black and oestrid flies.

Finally, several reproductive pathways mediate the effects of warming temperatures on body condition (PF6). Changes in the length of seasons influence the timing of the reproductive cycle, which may affect entire cohorts (Stopher et al., 2014; Wolcott et al., 2015). While a longer or greener growing season in combination with a shorter winter sounds like good news to northern herbivores, our review had a large body of countering evidence. For example, Chirichella et al. (2019) found implantation success to increase with warmer summers for Italian roe deer, though with a threshold (mean daily July temperature 23°C) above which the implantation rate instead started to fail. Warmer summers also negatively influenced pregnancy rates of red deer in Italy (Corlatti et al., 2018). Interestingly, females may not always be the most affected ones: Warmer temperatures affected body mass only in male white-tailed deer (negatively so, and with 1–2 years of time lag) in Virginia, USA (Campbell & Wood, 2013), possibly because male progeny require more maternal resources. While male antler size has increased and conception times advanced for red deer on the Island of Rhum due to more growing days (Moyes et al., 2011), the situation may be different for the more cold-adapted moose, where a warmer September has delayed the rut and conception in Estonia (Veeroja et al., 2013).

3.2.2 | Physiological responses to rainfall changes in growing season

We found some examples of deer physiology responding positively to increased rainfall in the growing season (PF7, Table 2). In wapiti, wetter summers can lead to cascading effects between body conditions and reproduction (e.g., higher body fat in mothers and earlier calving dates, Johnson et al., 2019). Dry springs are related to lower body mass of calves and fewer calves per cow in moose, but only if combined with relatively high spring temperatures (Holmes et al., 2021). Interestingly, Wolcott et al. (2015) suggest that in white-tailed deer, mothers in high condition can even interpret more rainfall as a cue of favorable conditions, and thereby allocate their body resources so that it induces conception or birth. More rainfall is expected to be beneficial mainly in regions where plants are normally water limited (Herfindal et al., 2020), which is not so frequent in the habitats of northern deer (but see Anderwald et al., 2021). In other areas, or where parasites benefit from moist conditions, increased rainfall can instead reduce body condition. For example, increased infection rates of meningeal worms in Dakota US (Jacques et al., 2017; Maskey et al., 2015) and nasopharyngeal bot flies in Iberia Spain (Vicente et al., 2004) both increased with more rainfall (but see also Sleeman et al., 2009).

3.2.3 | Physiological responses to changed precipitation and snow in winter

Snowfall in contrast to rainfall is predicted to generally decline (Figure S1), although there will of course be local deviations. However, most of the studies in our review looked at the opposite pattern, demonstrating a general pattern of decreased body condition with increased snow depth. Either way, this suggests the direct benefits of less snow for deer physiology (PF8, Table 2). In deep snow, deer expend more energy for movement, leaving less for maintenance and growth. Deep snow can therefore have strong negative repercussions on body condition, which has been shown for white-tailed deer in Canada (Garroway & Broders, 2005). The deeper the snow, the longer it also takes to melt in spring and uncover fresh forage. Increased snow depth can also be associated with higher stress levels (Hoy et al., 2021; Rosenblatt et al., 2021) or higher risk of disease as individuals tend to aggregate more closely (Merkle et al., 2018).

A few studies highlighted complex pathways of physiological effects of snow. Although only two winters were involved, Giroux et al. (2016) showed how the influence of snow can interact with habitat and diet shifts to modulate the outcome for deer: use of balsam fir stands negatively affected the body mass of white-tailed deer on Anticosti in the milder winter, but positively in the harsher winter when access to the better forage was no longer available. Two long time-series studies reveal (a) how conditions in other seasons can override the influence of winter precipitation, such as access to field crops for roe deer in Poland (1982–2002, Mysterud et al., 2007), or (b) how winter conditions affect summer conditions, which in turn had the stronger effect on the body mass of red deer in Norway (1965–1998, Mysterud et al., 2001).

We note a lack of research into the effects of a complete lack of snow in wintertime on deer physiology, for example, via effects on the vegetation in regions where snow cover has been the norm. Neither did we find studies that assess the likelihood of less snow being associated with different snow types for the forest-dwelling northern deer, such as wetter, icier, or more layered snow, as documented for artic reindeer living above the tree line (Hansen et al., 2011, NR).

3.2.4 | Studies of physiology using combined measures of climate

The studies using combined climate measures showed complex links between benefits and setbacks for deer physiology, and the only clear patterns were found in the papers that used the NDVI to address the synchrony of green-up across space or over time. The other papers ranged too broad in topics. The NDVI papers presented evidence of an overriding positive trend between body condition and earlier green-up in spring despite an expected increasing mismatch between plant phenology and birth dates (Section 3.2.1). The trend could be strong. For example, for every increment of 0.1 of June NDVI, calf autumn body mass of forest-dwelling caribou in Canada increased by up to 6 kg (Couturier, Côté, Otto, et al., 2009). It is important to note, however, that the positive effects of earlier green-up can be lost if the duration of spring becomes faster and more simultaneous across a region, resulting in a shorter temporal and spatial window of access to fresh vegetation (Herfindal, Sæther, et al., 2006; Middleton et al., 2013; Searle et al., 2015). This unfortunate increased spring synchrony is more likely to occur more south and at lower elevations, where there is less seasonality even without climate change (Neumann et al., 2020).

3.3 | Deer spatial use

Here, we consider behavioral responses to climate change at various spatial scales. The 92 studies addressed a wide range of responses: from individual foraging behaviors, daily activity patterns, and movement rates, through habitat use and selection to migration and distribution shifts.

3.3.1 | Responses in spatial use to warmer temperatures

We found clear evidence of spatial responses of deer to warmer temperatures at different scales from daily activity patterns and habitat use to migration patterns and, ultimately, shifts in distribution ranges. As short-term responses to high summer temperatures, deer reduced heat stress by shifting their daily activities toward the cooler times of the day (PF9, Table 1, Dussault et al., 2004; Montgomery et al., 2019). Likewise, deer sought out habitats that provided thermal shelter such as dense and mature coniferous stands (e.g., Gilbert et al., 2022; Melin et al., 2014) as well as wetlands and moist forest habitats (Herfindal et al., 2017; McCann et al., 2016). During warm summer days, insect harassment may exacerbate the need to modify habitat use (Laaksonen et al., 2009; Witter, Johnson, Croft, Gunn, & Gillingham, 2012). Consequently, deer largely responded to warmer summer temperatures by reducing their home range size (Kamler et al., 2007b; Rivrud et al., 2010).

The response of red deer to winter temperatures was shown as higher activity during the warmest hours (Kamler et al., 2007b) and larger home ranges during the warmest winters (Rivrud et al., 2010). In addition, wapiti and white-tailed deer showed increased use of denser forest stands at colder conditions even though such forests provide less forage (Courbin et al., 2017; Porter et al., 2002). Above results suggest that these deer species might benefit from warmer winter conditions due to easier movements and access to forage. In some cases, the other factors overshadowed the effects of temperature (Beguin et al., 2013). For example, warmer winter temperatures influenced caribou to decrease their residency time (Leclerc et al., 2019), while movement patterns (home range size) of moose in Southern Norway was largely unaffected (van Beest et al., 2011).

van Beest et al. (2011) suggest this lack of effect may be due to the proximity of the study population to the species' southern distribution limit, which could have made them relatively resilient to temperature.

Long-term responses at larger spatial scales to warmer temperatures will likely include altered migration patterns (PF10), albeit it is unclear whether net outcomes are positive or negative. For example, caribou was found to start migrating earlier with warming springs since 2000, but also to prolong their migration routes when the weather during the migration continued to be warmer and wetter than usual (due to energetic costs, Le Corre et al., 2017). Furthermore, we found a general, but not exclusive, trend of distribution ranges shifting northward in response to warmer temperatures (PF11), which is a field still lacking in studies. Northward shifts in the distributions of animal species may redraw the scene for multi-species interactions more than any of the other deer responses (Kennedy-Slaney et al., 2018).

3.3.2 | Responses in spatial use to rainfall changes in the growing season

Relatively few papers dealt with the effect of changed rainfall patterns on deer spatial use (Table 1). Generally, the effects of rainfall seemed to be less important than those of other climate and non-climate factors (PF12, Table 2), though extreme events such as heavy rainfall could trigger inactivity. Also, a couple of studies indicate that an overall increase in rainfall can cause a shift of strategies within deer populations from migratory to resident, for example by making migration energetically costlier (PF10). This is likely to happen at least in deer populations that today display mixed migration strategies such as in wapiti (Middleton et al., 2013).

3.3.3 | Responses in spatial use to changed precipitation and snow in winter

Snow is a strong determinant of deer ecology in the boreal and temperate zone, and expectedly showed up often in our review of deer spatial use. We found a high share of evidence that snow avoidance explained deer foraging patterns, habitat use, and movements from smaller-scale daily activity to larger-scale distribution and seasonal migrations. In areas where climate change means less snow, snow clearly will become less of a constraint to deer. It seems, however, that the strength and type of effect of snow varied between the different deer species as well as between the regions they were occupying: mountainous or non-mountainous areas (Igota et al., 2004), the type of forest cover available (DelGiudice et al., 2013) or whether the deer species were migratory or non-migratory by nature (Fieberg et al., 2008; Le Corre et al., 2017). We even found that snow affected social organization (PF13), indicating that less snow means smaller groups (Jung et al., 2019; Månsson et al., 2017). Thereby, changed snow conditions is likely to change both intra- and interspecific interactions among deer. Deer generally increased daily activity and movement (PF13) in response to lower snow depths (Stache et al., 2013; Van Moorter et al., 2013). This undoubtedly can cause them to advance the area used, given that the opposite normally occurs in times of deeper snow (Ramanzin et al., 2007; van Beest et al., 2011, but see also Anton et al., 2022; Burkholder et al., 2022). We must await future studies to bring forth what happens over long-term declines in snow depths. However, it is a long-established fact that lower snow depths often come at the cost of greater predation risk (Kittle et al., 2008), which can dampen the deer advancement into new areas.

Expectedly, several studies in our review highlight how snow greatly influences deer migration (PF10). The timing of snowfall in the fall and snow melt in the spring is part of what triggers migratory movements in deer (Rickbeil et al., 2019; Sabine et al., 2002), thereby will a warming climate delay the fall migration into winter ranges and advance the spring migration into summer ranges. In the long term, reduced snow cover in winter ranges could drive deer populations to become resident (Fieberg et al., 2008; Malnar et al., 2015; Ramanzin et al., 2007). Ultimately, reduced snow cover will likely—in concert with other factors such as vegetation changes—push deer distribution ranges northward and to higher elevations (PF14) as was shown for sika deer (Kaji et al., 2000) and white-tailed deer (Kennedy-Slaney et al., 2018), though these shifts will most likely be restrained by human land use (Beguin et al., 2013; Ohashi et al., 2016).

3.3.4 | Studies of spatial use using combined measures of climate

All studies using combined measures of climate corroborate the above-mentioned results that milder winters with less snow will likely push deer distribution northward and to higher elevations (PF14).

3.4 | Deer population dynamics

Here, we review 69 papers about the associations between climate change and population dynamics, including effects on population size, density, and growth rate as well as demographic parameters related to survival (or mortality) and reproduction (e.g., birth rates/natality, fecundity, and recruitment).

3.4.1 | Responses in population dynamics to warmer temperatures

We found that temperature affected both survival and reproduction, with milder winter temperatures being favorable, while temperatures creating heat stress in any season had negative effects (PF15 and PF16, Table 2). For example, deer of all species exposed to very low winter temperatures experienced higher mortality rates (Davis et al., 2016; Gilbert et al., 2007; Joly et al., 2017). However, five of the nine studies found no effect of winter temperatures on survival (PF15). Temperature indirectly affects reproduction through female body conditions (see Section 3.2) and through modifications in migratory behavior (see Section 3.3). Furthermore, several studies found yearly or seasonal time lags (PF16), most likely operating through forage quality, when testing for effects of temperature on reproduction (birth rate, fecundity, and recruitment), of which moose in particular seems to be a model species for the research (Brown, 2011; Monteith et al., 2015).

Whether the above-mentioned seasonal effects of temperature on vital rates translate into effects on population abundance and growth rate remains unclear (PF17). This is probably because of antagonistic effects between seasons, but it is also inherently difficult to detect indirect influences through density dependency (Wang et al., 2006) and predation (Bastille-Rousseau et al., 2018). Surprisingly, we only found one study that explicitly elucidated the complex effects of temperature on population dynamics through the different vital rates. Gaillard et al. (2013) used life table response experiments to show that the observed decrease in population growth of roe deer during warmer springs was mainly influenced by a reduction in recruitment. The authors attribute this to indirect climate-driven mortality of fawns through reduced maternal conditions.

3.4.2 | Responses in population dynamics to rainfall changes in the growing season

While it is ambiguous whether the effects of warming temperatures on the vital rates manifest into effects on population dynamics (Section 3.4.1), most reviewed papers support that increased rainfall will likely benefit the deer's vital rates and population dynamics (PF18, Table 2). However, some studies also document higher fawn mortality (Gilbert & Raedeke, 2004; Warbington et al., 2017), suggesting that the net effect on population dynamics can depend more on local conditions, such as predator abundance and habitat type, than on rainfall.

Extreme rainfall and drought in summer is likely to decrease deer reproduction (PF18). In roe deer, drier summers in the year of birth led to lower lifetime reproductive success (Hamel et al., 2009). In wapiti, both low precipitation in spring (Taper & Gogan, 2002) and late summer (Johnson et al., 2019) were associated with lower population growth rate and offspring recruitment the following year, respectively. Similarly, the calf: cow ratio of Swedish moose declined with decreasing spring precipitation, but only when low rainfall coincided with a higher-than-average spring temperature (Holmes et al., 2021).

In contrast, red deer experienced lower recruitment during years with higher rainfall in populations on Isle of Rum in Scotland (Stopher et al., 2014), where relatively cool and moist summers are the normal. High precipitation together with cold temperatures during fawning was also shown to negatively affect mule deer recruitment (Gilbert & Raedeke, 2004), mediated by higher deer density and lower available forage in the previous year. Whether forage plants are normally water limited seems to be a key mediator on the outcomes of more rainfall on vital rates, given its effects on body condition (Section 3.2). Yet, forage and population dynamics were seldom simultaneously addressed in the reviewed studies. The net effects of rainfall on deer recruitment also seem to frequently interact with predation and diseases, which can both enhance and counteract the negative effect of low rainfall and drought on deer recruitment (Bastille-Rousseau et al., 2018; Griffin et al., 2011; Tosa et al., 2018).

A less apparent influence of precipitation is how it may affect offspring sex ratio, as shown by Cunningham et al. (2009) in their study of wapiti in Montana (47 years of data, 1961–2007). Higher annual precipitation and a lower drought index led to a higher share of female fetuses, but only at lower population densities, where precipitation improved the nutritional status of the mother (contradicting the original Trivers-Willard hypothesis).

3.4.3 | Responses in population dynamics to changed precipitation and snow in winter

The depth of snow in winter is one of the most important climate factors affecting deer survival and reproduction, and our review showed that reduced duration and depth of snow will likely increase survival rates and reproduction of deer populations (PF19, Table 2). As for snow and spatial use (Section 3.3), this is to some extent based on transposed evidence, because many studies focused on the effects of more snow rather than less snow. Indeed, we found strong evidence that increased snow fall, snow depth or snow density decreased survival rates in deer (Gula, 2004; Hurley et al., 2017), and this was associated with malnutrition (Gilbert et al., 2020; Kautz et al., 2020) or increased predation (DelGiudice et al., 2002; Horne et al., 2019; Mech et al., 2001). The effects of snow on reproduction were less clear and showed both negative and no effects (PF19).

We further found evidence that the effects of snow on vital rates translated into enhanced population growth rates following reduced snow cover (PF19). However, density dependency acting on the vital rates and other important factors may cancel out the potential benefits. In most cases, density dependence operated in winters when snow conditions were more severe (Creel & Creel, 2009; Patterson & Power, 2002; Taper & Gogan, 2002), indicating that the importance of density-dependent effects due to snow conditions will likely diminish with climate change.

3.4.4 | Studies of population dynamics using combined measures of climate

Studies using combined climate measures showed weak responses of deer population dynamics (PF20, Table 2). Large-scale meteorological oscillations may vary at local scales due to the modifying effects of topography and altitude. This may explain contrasting responses and asynchrony among deer populations along latitudinal, longitudinal, and altitudinal gradients (Grøtan et al. 2005; Hegel, Mysterud, Ergon, et al., 2010; Joly et al., 2011; Mysterud et al., 2000). Moreover, population responses to other local factors often overshadowed the effects of general weather patterns. The two most important such factors seem to be density dependence (Simard et al., 2010) and predation (Mahoney et al., 2016), which may both be enhanced by extreme weather (Hebblewhite, 2005; Middleton et al., 2013). These interactive effects are likely to further depend on temporal forage availability (De Jager et al., 2020; Post & Forchhammer, 2001) and even be affected by time-lag effects, as described in Section 3.2. It therefore seems likely to expect pronounced variation at the species level in the strength and direction of population responses to a warming climate (Post et al., 2009). This makes it difficult to detect and differentiate weaker responses to climate from stronger responses to other factors, even though the climate can still be an important determinant in these cases. Interestingly, combined measures have also been used to show higher genetic diversity in caribou populations inhabiting regions that have remained climatically more stable over the past 21 thousand years, as compared to less climatically stable regions (Yannic et al., 2014, NR).

4 | CONCLUSIONS

Since the millennium shift, a plethora of studies has shed valuable light on what the effects of climate change are likely to be on the deer inhabiting the world's cold regions. Before the millennium shift, it was predicted that warmer winters would have the greatest impact on animals in these regions (Danell et al., 1999). Our updated review, including not only the coldest regions of Europe but all temperate and boreal forest landscapes at northern latitudes, confirms that milder winters and less snowfall indeed will be of great significance. However, our review also highlights that the effects of temperature and rainfall during other seasons are likely to be even stronger. In fact, we suggest that unfavorable summer conditions will become the main driving factor of deer responses to climate change. Here, we will summarize the main patterns found by our review (Figure 3), suggest further research based on identified knowledge gaps, and discuss relevant management implications.

4.1 | Is climate change overall good or bad for northern deer?

Our review illustrates how a great deal of complexity is involved in answering this question. However, it also revealed several patterns that point to what we can expect to happen. First, our results suggest that the predicted increase in the frequency of summer heat waves will likely cause trouble for the northern deer. This is because higher than normal summer temperatures are generally negative for their physiology due to realized heat stress (PF2 in Table 2) and parasitism (PF5), and consequently also for their reproduction (PF6 and PF16). Hotter summers are also linked to smaller home ranges, due to altered activity patterns (PF9). Notably, heat stress, sickness, and foraging interact with each other, and the outcome for the animals can spiral with climate change. The poorer the animals' health status is at the time of stress, the worse the effects of the heat wave will be (McCann et al., 2013; Thompson et al., 2019). Deer may reduce their body temperature by foraging less, but the benefit is then countered by the lower food intake. Like summers, warmer springs may also result in a poorer physiological state, but mainly if those springs simultaneously become shorter or drier (PF4). In general, summers and springs with more rainfall (falling evenly across the season) are likely to be beneficial for deer body condition, vital rates, and recruitment (PF7 and PF18), at least in regions where the forage plants are water limited (PF7), but possibly not for migrating deer (PF10). However, while rainfall is predicted to increase during the growing season in some regions (e.g., Europe, Figure S1), it is expected to fall more irregularly and in more concentrated bursts, thus possibly alternating with more extreme drought.

Warmer winters are also predicted to become more common. For the regions where this means less snow, deer will move more easily and have better access to forage (PF13), which should result in improved body condition (PF8), lower mortality (both via better nutrition and predator escape) (PF 19), higher birth rates and calf survival (PF19), and larger home ranges (PF13). Higher population growth rates are expected as a result (PF19). However, while the positive influence of less snowfall appears to be clear, other factors associated with warmer winters (longer growing season, changed snow texture, parasite exposure, disease transmission, etc.) seem to be more influential than the benefit of easier locomotion (PF3, PF5, PF8, and PF15).

Sometimes, it is hard to evaluate whether the documented responses by deer to climate change will result in good or bad outcomes for the species in the long term. For example, several studies show significant alterations to migration timing and routes due to warmer temperatures, changed rainfall, and snow (PF10). It is possible that migratory populations could become resident due to these changes. But is this good or bad for the species? It is similarly unclear whether the effects of warmer temperatures on deer vital rates (PF15 and PF16) translate into positive or negative effects on population abundance and growth. Different seasonal effects may act together or cancel each other out depending on regional and environmental differences, and there are multiple pathways through indirect effects incorporating not only density-dependent effects, but often also time lags.

Will the pros outweigh the cons for the northern deer, or will there be a net negative? Considering that northward and altitudinal shifts of some species' distribution are to be expected (PF11, PF14), due to their marginal habitats becoming unsustainable, cons will certainly outweigh the pros for some populations in the long term. Moose, for example, the biggest and most cold-adapted deer

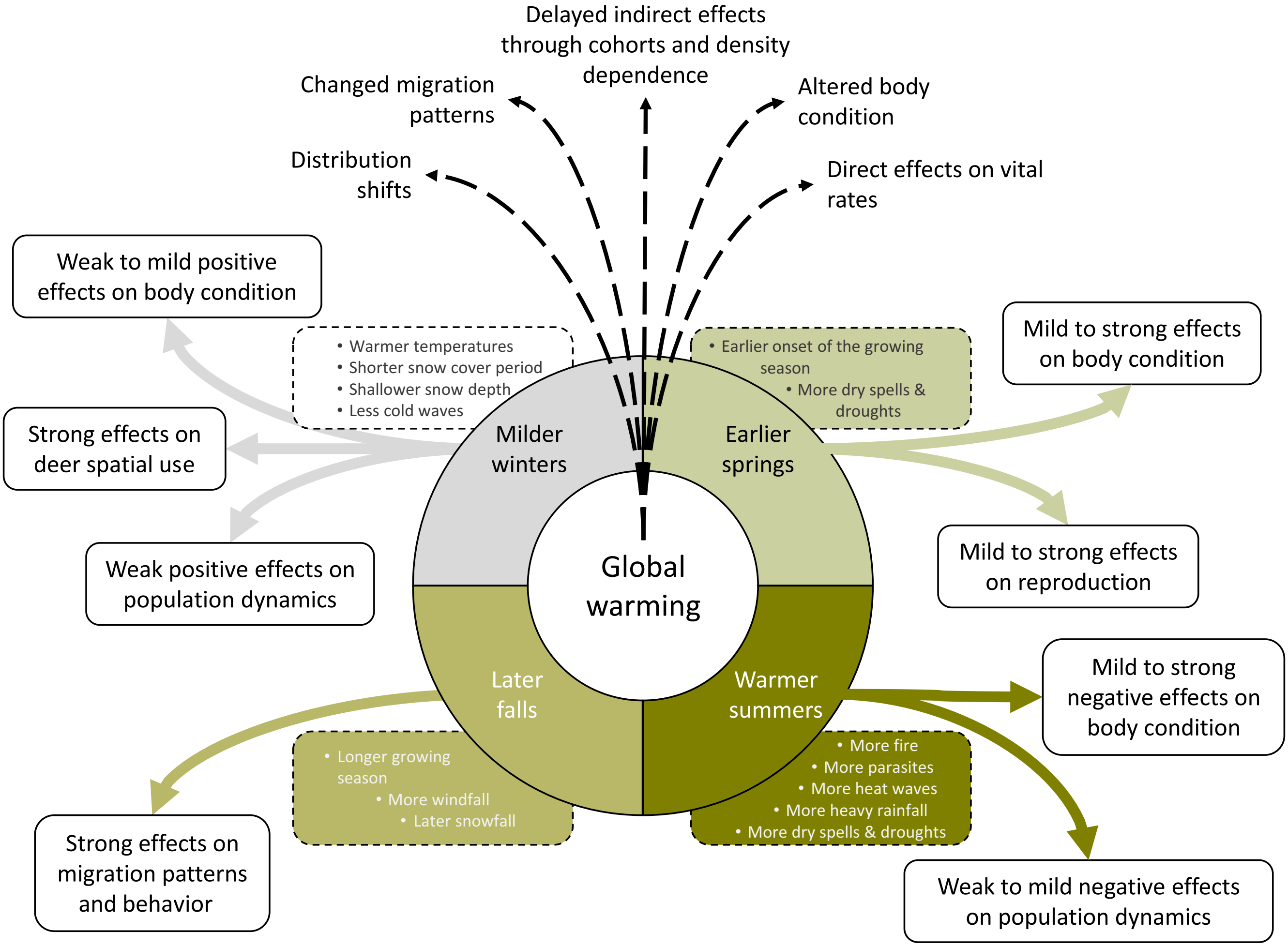

FIGURE 3 Summary of the patterns found in the systematic literature review ($N=218$) of effects on deer physiology, spatial use and population dynamics of climate variables within the forests of the northern hemisphere, in the context of climate change. For specific descriptions of these findings, see Table 2.

apart from reindeer/caribou, and most frequently found in our review (Figure 1), appears to be particularly sensitive to heat stress (Section 3.3). Moose are already more negatively affected by a warming climate in the southern parts of their range than in the northern parts (e.g., their calf production, Holmes et al., 2021). This illustrates how short-term physiological responses to temperature and precipitation (likely compounded by effects on forage) can aggregate to the population level. The American Shiraz population of moose (*Alces alces shirasi*), which lives in the species' southern range, is expected to not persist over the next 50 years, due to thermoregulatory costs (Murray et al., 2006, NR). Surprisingly, however, it has been found that this species has changed its habitat selection and now appears in open habitats where they have not previously been observed (Maskey & Sweitzer, 2019, NR).

The net outcome of climate change hinges on the behavioral plasticity of individuals. Although no study explicitly tested for phenotypic plasticity by controlling for genotypes, we found indirect evidence of several types of phenotypic plasticity among deer in response to climate-related environmental variability in the short and long term. For example, we found strong evidence of deer adapting their spatial use, from daily (PF12) and seasonal habitat use (PF9 and PF13) to shifts in migratory behavior (PF8) and distribution ranges (PF11 and PF14) in response to several climatic factors. Another important phenomenon was morphological plasticity through changes in deer body attributes (mass, antler size, etc.) (PF2, PF6, and PF8) with possible cascading effects on population dynamics partly through delayed density-dependent effects.

4.2 | The importance of local aspects

Irrespective of which climate change factor is in play for any given animal response, our review highlighted that local aspects, such as population density, predation, habitat availability, forage quality, inter-species competition, altitude, and topography always must be considered. For example, higher population density of roe deer relative to habitat productivity may exacerbate the negative influence on body mass of a warmer spring/summer (Douhard et al., 2013; Kjellander et al., 2006). Density dependence and predation appear to be the two most important local factors interacting with how climate change affects deer population dynamics (Section 3.4). To complicate matters even more, the interactive effects of predation and climate are likely to be temporally variable and dependent on the forage (De Jager et al., 2020; Post & Forchhammer, 2001). Finally, whether the animals have access to certain kinds of habitats in their home range will also mediate the effects that climate may have on them. For example, local populations with access to shade or wetlands may be better able to buffer warmer temperatures due to climate change (Section 3.2.1). Considering that local aspects are of such importance for any predictions of future responses by a given deer population, it raises the question of how useful combined climate measures, such as NAO or AO, are for such purposes. They may have more value in retrospective analyses (understanding historical patterns), than in predicting and mitigating potential future consequences for deer. The local aspects simply seem to override the large scale. However, we emphasize that our review is limited to the observed climatic conditions at the various study locations at the time of the study, and extrapolations cannot easily be made to more severe future climatic conditions. Nevertheless, we suggest that local conditions will always influence outcomes for a given deer population.

4.3 | Identified knowledge gaps

We have identified several knowledge gaps related to potential climate change effects on deer species inhabiting boreal and temperate forests of the northern hemisphere, when it comes to physiology, spatial use, and population dynamics. There is a general lack of research regarding the potential impact on these animals of (1) extreme weather events, (2) wetter autumns, and (3) snow type (e.g., whether less snow means wetter or crustier snow). There are also gaps regarding how, or if, migration routes and timing will be affected for other species than caribou and how warmer temperatures ultimately affect population dynamics. For example, it is known that many small adult males in a population may lead to delayed conception times, and consequently, later birth dates and smaller body mass (Solberg et al., 2007). Therefore, one of many promising paths for future research about the ultimate effects on population dynamics is to find out whether warming temperatures overall produce smaller deer, and whether this in turn is beneficial or detrimental to not only the population but also the species. Finally, we were surprised that forage and population dynamics seldom were addressed simultaneously in our reviewed studies, considering that the characteristics of the forage (whether they are water limited or not) seem to be a key mediator in the effects of changing precipitation patterns on deer vital rates, via its influence on deer body condition.

Irrespective of which responses are studied, we strongly suggest that research on deer and climate change take confounding factors into account, such as including multiple seasons, because the effects of season may cancel each other out. It is also important to be diligent about proximate and ultimate climate variables in one's interpretations. Because temperature drives all other weather, one cannot assign insignificance to temperature in a study unless all weather variables are addressed. We did not review studies of indirect influences of climate through habitat factors such as forage, which undoubtedly have large underlying mediating effects on the patterns found in this review. Importantly, we do not believe this created bias in our findings, because they are based on the observed ultimate result irrespective of the underlying pathways. Nevertheless, it is highly valuable to learn more about the indirect factors as well, and we therefore emphasize that there is a need to synthesize the scientific literature relating to the effects of climate variables on key deer forage plant species and other habitat factors in temperate and boreal forest ecosystems.

4.4 | Management implications

In managed forests, balancing timber production with habitat provision for deer represents a major and longstanding challenge. Currently, this challenge also combines with the need to prepare suitable management options in a warmer climate. In addition to being important contributors to biodiversity, deer can cause economic losses to forestry (Liberg et al., 2010; Reimoser & Putman, 2011) or affect public health through road accidents and zoonoses (Linnell et al., 2020). There have been significant increases in deer population densities across extensive regions of the northern hemisphere during the last decades (Apollonio et al., 2017; Linnell et al., 2020), while at the same time, reductions have been observed regarding the fitness of these populations (this review). If this is the ultimate outcome of current climate change, conflicts between different interest groups will continue to increase, particularly in highly managed landscapes where non-commercial vegetation is relatively sparse. The patterns identified in this literature review should help managers understand how populations of deer may be affected by regionally projected futures regarding temperature, rainfall, and snow (Table 2). Our synthesis may also be of help when prioritizing possible nature conservation actions, such as safeguarding the provision of certain habitat types (wetlands as thermal refuges, Thompson et al., 2021). However, because the patterns we have identified are complex, sometimes species specific and almost always dependent on local environmental factors, actions may need to be considered on a case-by-case basis. Based on our findings, we highlight the importance of wildlife monitoring programs that include measures of local-scale environmental variability when providing data for integrated game and forest management and projection of long-term regional effects of climate change.

AUTHOR CONTRIBUTIONS

Annika M. Felton: Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; validation; writing – original draft; writing – review and editing. **Hilde Karine Wam:** Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing

– review and editing. **Zbigniew Borowski:** Conceptualization; data curation; investigation; methodology; writing – original draft; writing – review and editing. **Aksel Granhus:** Conceptualization; data curation; investigation; methodology; writing – original draft; writing – review and editing. **Laura Juvany:** Conceptualization; data curation; investigation; methodology; writing – original draft; writing – review and editing. **Juho Matala:** Conceptualization; data curation; investigation; methodology; writing – original draft; writing – review and editing. **Markus Melin:** Conceptualization; data curation; investigation; methodology; writing – original draft; writing – review and editing. **Märtha Wallgren:** Conceptualization; data curation; investigation; methodology; validation; writing – original draft; writing – review and editing. **Anders Mårell:** Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

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ORCID

Annika M. Felton https://orcid.org/0000-0001-5066-1358
Hilde Karine Wam https://orcid.org/0000-0003-1224-7249
Zbigniew Borowski https://orcid.org/0000-0003-4109-5205
Aksel Granhus https://orcid.org/0000-0002-1713-9928
Laura Juvany https://orcid.org/0000-0002-2552-6047
Juho Matala https://orcid.org/0000-0002-5867-5057
Markus Melin https://orcid.org/0000-0001-7290-9203
Märtha Wallgren https://orcid.org/0000-0002-3172-4496
Anders Mårell https://orcid.org/0000-0002-3328-4834

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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