Stronger together? A framework for studying population resilience to climate change impacts via social shielding

Miyako H. Warrington[1,2*], David N. Fisher[3], Jan Komdeur[4], Natalie Pilakouta[5], Michael Griesser[2,6,7,8*]

1 - Department of Biological and Medical Sciences, Oxford Brookes University, Oxford, OX3 0BP, UK

2- Luondu Boreal Field Station, 93391 Arvidsjaur, Sweden

3 - School of Biological Sciences, University of Aberdeen, King's College, Aberdeen, AB24 3FX, UK

4 - Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands

5- Centre for Biological Diversity, School of Biology, University of St Andrews, St Andrews, KY16 9TH, UK

6 - Department of Biology, University of Konstanz, 78457 Konstanz

7 - Centre for the Advanced Study of Collective Behaviour, University of Konstanz, 78457 Konstanz, Germany

8 - Department of Collective Behaviour, Max Planck Institute of Animal Behaviour, 78457 Konstanz, Germany

*Shared corresponding and first authors: Warrington, M.H. (mwarrington@brookes.ac.uk), Michael Griesser (michael.griesser@uni-konstanz.de). All middle authors in alphabetical order, with equal contributions.

Abstract

1. Climate change is driving a rapid increase in the frequency and intensity of extreme climatic events, leading to substantial alterations in climate patterns and other environmental conditions. These changes are often degrading habitats and increasing thermal, water, and nutritional stress for animals, thereby elevating general stress levels and imposing energetic costs.
2. Social behaviours (i.e., interactions between conspecifics) can be crucial for animals in reducing the costs imposed by these changes. Social behaviours can improve resource acquisition, reduce mortality, and provide a social buffer against physiological stress. Furthermore, helping others during reproduction can provide a buffer against reproductive failure under unfavourable environmental conditions. However, these buffering effects remain vaguely defined and it is unclear how to test for their occurrence.
3. This review explores how social behaviours can shield animals from the negative impacts of climate and environmental changes. We examine how social behaviours can provide benefits across key aspects of life, including foraging success, decreasing energetic costs, reproductive success, and the direct reduction of physiological stress.
4. We synthesize these ideas in the social shielding hypothesis and explain its key components, including the proximate mechanisms that drive social behaviours, the levels of behavioural change (individuals to groups to populations), shielding benefits across all life stages (embryo to senescence), and the ultimate consequences of these behavioural changes.
5. We emphasize that social behaviours can shield individuals under unfavourable conditions, favourable conditions, or independent of conditions, and we provide guidance on how to statistically distinguish between these different types of social shielding. These different shielding mechanisms influence how individuals and populations respond to the negative effects of climate and environmental change.
6. This framework can help predict and manage the negative effects of climate change on animals, thus guiding conservation strategies that support biodiversity and animal welfare.

Keywords: climate change, social behaviours, physiological buffering, environmental buffering, cooperative breeding, social shielding hypothesis.

1. Introduction

Our global climate is undergoing rapid changes. Climate change alters many climatic parameters leading to higher mean temperatures, increased unpredictability of precipitation, and increased frequency and intensity of extreme climatic events (Bailey & van de Pol, 2016b; van de Pol et al., 2017). These climatic changes are degrading the environments in which animals live and alter habitats, making them unfavourable or even unsuitable (Fisher et al., 2021). Furthermore, altered climatic conditions and extreme climatic events can increase thermal and water stress which influence physiological responses by increasing the energetic costs of animals (Mitchell et al., 2018). These alterations can lead to a deviation from homeostasis (Schradin et al., 2023) and affect the costs and benefits associated with any given behaviour. Consequently, these rapid environmental changes are negatively affecting key aspects of animal lives, including their behaviour, survival, and reproduction. Moreover, these changes are concurrently occurring alongside other anthropogenic impacts (e.g., chemical pollution, (Gore et al., 2019) that can also affect behaviours and stress responses (Fisher et al., 2021). Therefore, it is critical to understand whether and how species respond to these changes to mitigate their effects and implement effective conservation strategies (LeDee et al., 2021). Here, we focus on the role of social behaviour as an adaptation to climate change.

1.1 Social behaviours: a key adaptation for the response to climate change

Animals can respond and adapt to environmental changes by adjusting their morphology (Ryding et al., 2021), physiology (Moss & While, 2021), and/or behaviour (Fisher et al., 2021). Because behaviours can be immediately altered by changes in environments, they provide some of the first clues that animals are affected by these changes. For example, animals rapidly change their movement patterns in response to human activities (Schrimpf et al., 2021). Therefore, behaviours have been described as the first line of defence to climate change (Van Buskirk, 2012). Species that exhibit a greater degree of behavioural flexibility within and between individuals, e.g., the ability to exploit new resources or settle in new habitats, are more likely to survive, and even thrive, in novel environments (Lowry et al., 2013; Sol et al., 2005). Therefore, altering behaviours can be a crucial aspect of an immediate response to climate change. Social behaviours (i.e. interactions between conspecifics) are ubiquitous and facilitate cooperation, competition, and mating. Due to their close links to survival and reproductive success, changes in social behaviours may be a key mechanism through which animals can offset the effects of unfavourable conditions and therefore cope with climatic changes.

In response to climatic changes, animals can alter both sociality per se (i.e., rate of group formation and splitting, group size and composition) and/or the expression of social behaviours (Blumstein et al., 2023; Fisher et al., 2021; Komdeur & Ma, 2021). Climate change could constrain or enhance the expression of social behaviours. For example, increased temperatures are associated with smaller group sizes in a number of bird species (Fisher et al., 2021). Southern pied babblers (*Turdoides bicolor*) decrease nestling provisioning during heatwaves, leading to reduced nestling condition (Wiley &

Ridley, 2016). Other species respond to these challenges by increasing sociality. In Iberian magpies (*Cyanopica cooki*), some individuals do not breed on their own under challenging weather conditions but instead join other pairs by helping them raise their offspring (Canário et al., 2004). Comparative work suggested that cooperative breeding, where alloparents provide parental care for offspring of other group members (Ben Mocha et al., 2023), is associated with more variable environments (Griesser et al., 2017; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017). In these species, alloparents can mitigate the costs of breeding in years with low levels of precipitation, as allo-parental care can buffer against reproductive failure (Borger et al., 2023; Covas et al., 2008). Therefore, the benefits of social behaviours can allow animals to buffer the negative effects of climate change. Alternatively, climate change could result in increased resource availability or can release animals from environmental stressors, for example, through reduced snow cover that increases food availability for predators (Williams et al., 2015). We therefore expect social behaviour to be highly plastic in response to environmental variation and critical for animals to cope with climatic changes.

Previous studies have hypothesized that climate change can alter social interactions (Blumstein et al., 2023; Fisher et al., 2021; Komdeur & Ma, 2021; Pilakouta et al., 2023; Soravia et al., 2021). However, sociality and social behaviour itself could limit or even buffer the impacts of climate change through different mechanisms. Work in captive animals showed that physical proximity among individuals lowers stress hormone levels, buffering the negative impact of stress (Davitz & Mason, 1955), which has been labelled social buffering (Kikusui et al., 2006). Meanwhile, work in wild birds showed that cooperative breeding can reduce the risk of nest failure under unfavourable conditions (Komdeur & Ma, 2021), which has been labelled environmental buffering (Borger et al., 2023). However, while a common theme is that socially mediated benefits allow animals to cope with the effects of climate change, the ‘environmental buffering’ and 'social buffering' hypotheses remain unintegrated. Integrating these ideas will facilitate comparability of studies testing these hypotheses, allow for standardising or paralleling investigative approaches, and enhance our ability to incorporate knowledge and approaches from multiple disciplines that study these effects.

In this review, we i) give an overview on climatic variables and their effects on social behaviour; ii) describe how social behaviours can buffer animals from climatic impacts; iii) present the novel social shielding hypothesis to standardise the study of buffering effects of social behaviours against impacts of climate and environmental changes; and iv) suggest future avenues for studies to gain knowledge on how to mitigate the negative impacts of climate change.

2. Background: Climate affects social behaviour

Unfavourable climatic conditions have a fundamental effect on social behaviours both directly via changes in resource availability and by having negative physiological consequences, including thermal and water stress (Schradin et al., 2023). Moreover, unfavourable climatic conditions also impact animals indirectly, for example, via changes in resource availability that increase intraspecific and interspecific competition over resources. These changes can negatively affect reproductive success and survival (Halupka et al., 2023; Komdeur & Ma, 2021). However, there are several potential responses that can counteract the negative impacts of climate change and increase the resilience of animal populations in a changing world (Gascoigne et al., 2024).

Assessing the interplay between climate change and social parameters requires suitable climatic parameters (see Supporting Information Box 1). Past studies that examined climatic effects on behaviours have often used coarse climatic measures such as monthly or seasonal averages of temperature and precipitation (Canário et al., 2004; Ebensperger et al., 2014; Layton-Matthews et al., 2021; Warrington et al., 2013). One can also examine the effect of extreme weather events, including floods, heatwaves, droughts and hurricanes (van de Pol et al., 2017). Preferably, climatic measures should be recorded directly in the study site (Bourne et al., 2023; Covas et al., 2008; Warrington et al., 2022), but local weather data are often not available, especially in long-term studies. For example, Siberian jays (*Perisoreus infaustus*) have been studied since 1952 in subarctic boreal forests in Swedish Lapland (Griesser & Lagerberg, 2012). Local weather data are only available from 1996 onward, whereas earlier climatic data are available from more distant weather stations, requiring extrapolations that increase uncertainty in understanding the links between climatic parameters and social behaviours. Furthermore, it is important to keep in mind that climatic events or conditions vary in their immediacy of impact on animals. Some act immediately (e.g., those that cause overheating or dehydration), while others have delayed effects (e.g., via food and water availability in the environment) (Cumming & Bernard, 1997; McKechnie & Dunn, 2019). Consequently, it is important to consider environmental variation at different spatial scales (microclimate vs macroclimate) to identify the key factors to which animals respond.

2.1 The effects of climate change on social behaviours

Social behaviours encompass many different behaviours that are driven and influenced by different abiotic and biotic factors, and anthropogenic factors (Fisher et al., 2021). Many studies have looked at the effects of specific climatic variables on social behaviours (e.g., effect of temperature on social interactions (Moss & While, 2021; Pilakouta et al., 2023). Changing climatic conditions can affect behaviours via changes in chemical reactions driving molecular processes (Moss & While, 2021). For example, increased water or thermal stress can increase the levels of hormones (oxytocin, vasopressin;

(Natochin et al., 2018) that also regulate sociality and cooperation (Griesser et al., 2025), and neurotransmitters that regulate information processing and decision making (Sharma, 2006; Soravia et al., 2021).

Climate change can also affect animal activity and movement patterns by potentially affecting encounter rates, via habitat loss or habitat fragmentation (e.g., changes in movement corridors; (Bergeron et al., 2011; Bichet et al., 2016), and by changing the availability of critical resources including food (Warrington et al., 2013), or nesting-building materials (Mainwaring et al., 2017). Changing climates can create unfavourable conditions that either break apart groups, as organisms face limited resources, or encourage group formation if survival and reproduction are only possible within a group (Pavelka et al., 2003). Therefore, the possible effects of climate change are variable, depending on the ecology of the species, and are further compounded if multiple stressors act in concert. Disruption of social systems could exacerbate the direct negative impacts of changing climates, increasing the need for animals to find ways to mitigate these effects.

2.2 Previous frameworks assessing benefits of sociality

Animal and human psychologists have observed that the presence of conspecifics buffers individuals against adverse effects, including stress, and facilitates a quicker recovery following stressful events (Davitz & Mason, 1955; Hennessy et al., 2009; Kikusui et al., 2006). These studies focused on hormonal and neural mechanisms and highlighted the important role of sociopositive touch (grooming, preening: touch hereafter), which is associated with an increase in hormones of the oxytocin-vasotocin family that lower the stress response (Kikusui et al., 2006; Rincon et al., 2020). For example, separating squirrel monkeys (*Saimiri sciureus*) infants from their mothers leads to a smaller increase in cortisol (a physiological stress marker) if infants are together with other group members compared to when they are alone (Stanton et al., 1985). These observations are conceptualised in the social buffering hypothesis (Kikusui et al., 2006). Simultaneously, evolutionary biologists have noticed that cooperatively breeding birds are overrepresented in regions with highly variable environments, i.e., in savanna regions in southern Africa or arid regions of Australia (du Plessis et al., 1995; Griesser et al., 2017; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017). This pattern is hypothesized to reflect the benefits of allo-parental care, where, in addition to parents, other group members provide parental care, and thus reduce the risk of reproductive failure particularly in bad years (Borger et al., 2023; Covas et al., 2008). These ideas are combined into the environmental buffering hypothesis (Borger et al., 2023; Komdeur & Ma, 2021). Against this background, we develop the social shielding hypothesis that integrates both the social and environmental buffering hypotheses to describe how social effects allow animals to buffer their lives against climatic and environmental challenges.

2.3 Social behaviours and properties can shield against negative climate impacts

Previous work has shown that social behaviours can shield animals against the negative impacts of climate change (Blumstein et al., 2023; Covas et al., 2008; Komdeur & Ma, 2021; Paniw et al., 2019). These benefits can arise through different mechanisms and differ in how they manifest in relation to climatic conditions (Fig. 1). For example, if food resources become scarce due to climatic changes, animals that live in social groups can benefit from cooperative foraging strategies. For instance, common ravens (*Corvus corax*) that forage in groups and thus share information about food locations tend to be in better body condition than those that forage alone (Heinrich & Marzluff, 1995).

Furthermore, the social properties of groups influence the expression of social behaviours. These properties include group size and composition (e.g., helping vs. non-helping individuals), and the experience level of group members (see Supporting Information Box 2). Changes in social properties lead to changes in social behaviours that can shield individuals, in part or completely, against the negative impacts of climatic conditions (see Fig. 1). We outline the social shielding hypothesis below.

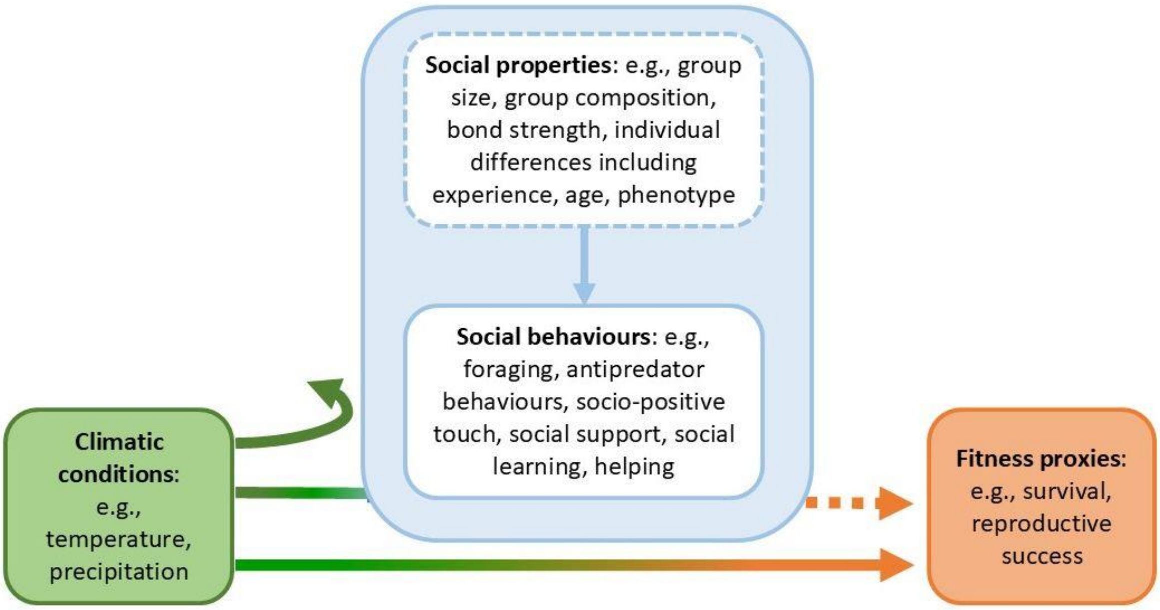

Figure 1. Overview of how social behaviours (blue box) can shield individuals against the effects of climatic conditions (green box). Social properties of groups (e.g., group size) and group members (e.g., bond strength, level of experience; blue dashed-line box) influence the expression of social behaviours (e.g., foraging, touch, helping; blue solid-line box), which together modulate how climatic conditions affect fitness proxies (orange box).

3. Outlining the social shielding hypothesis

The social shielding of climatic conditions differs within and across species. Thus, it is important to assess how precisely social behaviours affect the response to environmental changes. A study on cooperatively breeding white-browed scrubwrens (*Sericornis frontalis*) examined the effect of group size on breeding success (Magrath, 2001). Although young females survive better in groups, older females survive better in pairs. Notably, territory quality only affected young females breeding in low quality territory, reducing breeding success, while this pattern was not found in older females. Thus, the interaction between sociality and habitat quality affects fitness-relevant components in scrubwrens, but social behaviours can buffer the effects of low territory quality (Magrath, 2001). However, this study did not directly test the link between changing climatic conditions and the social benefits of alloparents. Similarly, an exploratory study in Seychelles warblers (*Acrocephalus sechellensis*) examined the association between cooperative breeding and climatic conditions (Borger et al., 2023). This study did not find a shielding effect of alloparents under low precipitation, because multiple climatic variables affected insect food availability, and thus breeding success (see Groenewoud et al. this issue).

We develop our framework based on the insights of these previous studies. Social shielding assesses how changes in a social behaviour affect a fitness proxy depending on the climatic conditions (e.g., how changes in nesting feeding rates of all group members in a cooperative breeder affects breeding success in years with different conditions). However, most studies use a group property (e.g., group size or composition) as their social measure, since these are easier to determine than feeding rates at every nest (Borger et al., 2023). However, the use of such measures has been justified by studies in the same population showing that group properties are linked to behaviours (e.g., group size and feeding rates are positively associated in Seychelles warblers; (van Boheemen et al., 2019).

Social behaviours can modulate the response to environmental and climatic conditions in four different ways, each of which reflects different mechanisms (Fig. 2). Social shielding can occur under favourable conditions only (social facilitation, hereafter), under unfavourable conditions only (social buffering, hereafter), or under all climatic conditions (social advantage, hereafter). Social shielding, however, can also be absent (no social effects hereafter) (Fig. 2). Categorizing the type of social shielding requires assessing the statistical interaction via the difference in the regression slopes between different groups that vary in a social property (e.g., group size, group composition; below we use group size as example) or a social behaviour (e.g., nesting feeding rate) and a climatic parameter (e.g., precipitation, temperature), in relation to a fitness proxy (e.g., number of offspring produced, survival; below we use reproductive success as example). Social facilitation occurs when being in a group with a beneficial social property confers greater advantages, especially under favourable conditions. In contrast, social buffering occurs when being in a group with a beneficial social property confers greater advantages, especially under unfavourable conditions. Alternatively, social advantage occurs when being in a group with a beneficial social property always confers greater advantages independently of the conditions. Finally, a beneficial social property may be unrelated to a fitness proxy, and all groups show a similar response to changes in climatic conditions. Thus, no social effects are present, but groups respond independently of their social situation to changes in climatic conditions.

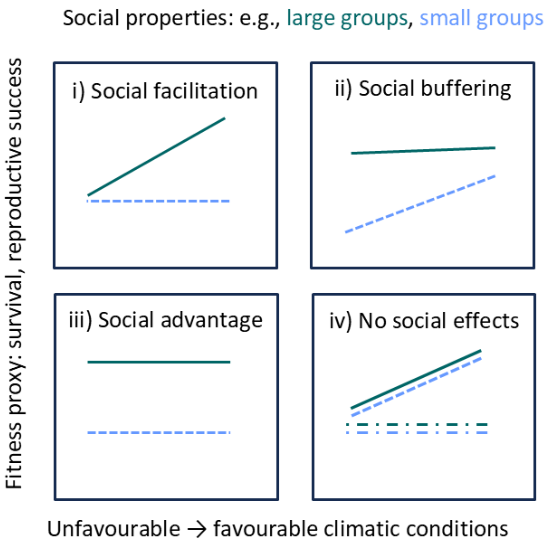

Figure 2. Categorization of the four different types of social shielding. Groups can vary in their response (e.g., a fitness proxy including reproductive success or survival) to changes in climatic conditions depending on social properties of groups (see Fig. 1). Social facilitation (i) occurs when being in a group with a beneficial social property is advantageous, especially under favourable conditions. Social buffering (ii) occurs when being in a group with a beneficial social property is advantageous, especially under unfavourable conditions. Social advantage (iii) occurs when being in a group with a beneficial social property is always advantageous. No social effects (iv) occur when groups independent of their social property respond to environmental conditions.

All three social shielding effects (facilitation, buffering, advantage) can help groups alleviate the impact of changing climatic conditions. Social buffering and social advantage allow groups to have a higher reproductive success (or other fitness proxy measures) under more challenging climatic conditions, directly buffering the impact of challenging conditions. Social facilitation alleviates the negative impacts more indirectly. A higher reproductive success under favourable conditions either compensates for earlier poor performance during unfavourable conditions (Bourne et al., 2020) or creates a buffer for unfavourable conditions experienced later, and could thereby, for example, prevent group extinction. For example, when large groups have a higher breeding success under favourable conditions, then this group has a larger buffer against group extinction during unfavourable conditions that increase mortality (e.g., via reduced resource availability, higher physiological stress levels). We note that the delay in response in social facilitation can still lead to an increased risk of group extinction compared to social buffering or social advantage. Thus, it is important to understand the mechanisms that underlie eco-social effects, because they differ in their potential for stabilising populations.

Our framework complements previous related frameworks that examine other aspects of buffering. Demographic buffering posits that temporal variation in the life history rates that most affect population growth rates should be reduced in the face of increasing environmental variation (Hilde et al., 2020). For example, alloparents could provide demographic buffering by supporting small populations to sustain in the face of climatic challenges (e.g., observed in Red-cockaded woodpeckers *Leuconotopicus borealis*, (Walters et al., 2004). A related type of buffering is life history buffering (Forcada et al., 2008), which focuses on the evolutionary strategies in an organism's life cycle and reproduction that can mitigate environmental risks. However, it remains unknown whether these different types of buffering can support population persistence under increasing environmental variability caused by climate change.

4. Key elements of the social shielding hypothesis

Below, we describe the conceptual outline of the social shielding hypothesis (Fig. 3). Climatic variables can directly affect the proximate mechanisms that underlie the expression of social behaviours (see above), which subsequently influence behavioural interactions within and between groups in a population (Kappeler, 2019). Different species can interact to influence ecosystem dynamics, including mutualisms or between-species competition (Gilman et al., 2010). The consequences of alterations in social behaviours and features include changes in the direct and indirect fitness of individuals, the persistence and turnover of the group, all of which together can affect population growth rates and persistence. We expand on the importance of these components below.

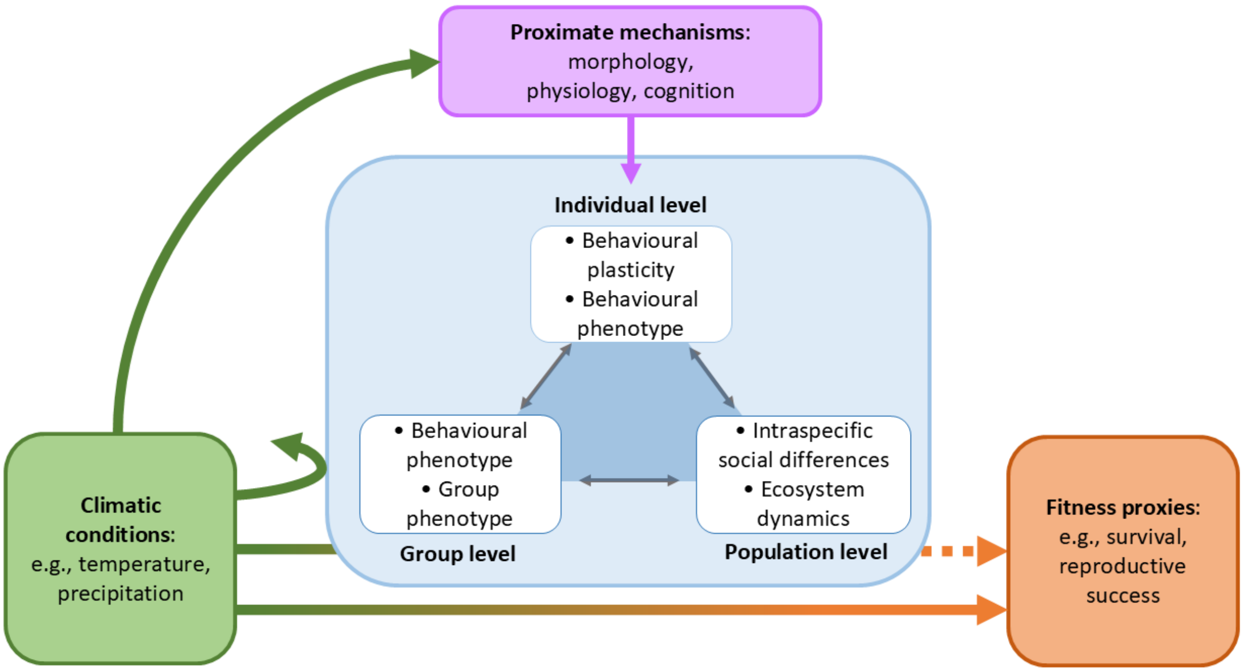

Figure 3. Conceptual outline of the social shielding hypothesis, examining the impact of climatic conditions (green box) on proximate mechanisms driving behaviour (purple box), social behaviours (blue box), and the fitness consequences (orange box). Proximate mechanisms are linked to the behaviour of individuals and the within- and between-individual variation in behaviour. Social behaviours can occur at the intragroup, intergroup, and interspecific levels of interactions. In all contexts, phenotypes and interaction levels of social behaviours can have downstream consequences on direct and indirect fitness, group persistence, group turnover, and population growth rate. These consequences can also affect social behaviours.

4.1 Behavioural changes depend on the proximate mechanisms

Behavioural changes can be influenced by or interact with an individual's morphological, physiological, or cognitive responses to stressors (Moss & While, 2021). Thus, it is important to consider both the mechanisms that are affected by climate change and the behavioural contexts that have been altered. For example, climate change can influence physical features that affect heat dissipation (e.g., appendages, body size or shape (Mitchell et al., 2018; Ryding et al., 2021), which in turn can affect locomotory abilities and movements (Rosalino et al., 2013) that influence foraging, territoriality, and mate-searching behaviours (Fisher et al., 2021). Changes in temperature or water availability can also influence biochemical processes involved in pigment and enzyme production that are critical for the expression of social behaviours (Fisher et al., 2021). Climate change can also act indirectly by changing resource availability, for example food resources that are affected by rainfall (Van Zyl, 1965) that either relieves or increases physiological constraints of social behaviours (Mitchell et al., 2018; Moss & While, 2021).

Energetic limitations and increased stress levels can also influence the production of costly communication signals that can affect social interactions (Prestwich, 1994). Likewise, in some social species, group living allows individuals to gain thermoregulatory benefits, e.g., communal roosting in acorn woodpeckers (*Melanerpes formicivorus*) (du Plessis et al., 1994) or long-tailed tits (*Aegithalos caudatus*) (Bebbington & Hatchwell, 2016), or water regulating benefits, e.g., clustering behaviour in hermit crabs (*Clibanarius symmetricus*) (Peres et al., 2018). Thus, a release from adverse conditions can decrease grouping behaviours, with negative effects on cooperative interactions (Griesser et al., 2025).

4.2 Levels of change: individual, group, population, ecosystem

Changes to the phenotypic expression and limits (Komdeur & Ma, 2021) of individuals' social behaviours can lead to behavioural changes at the group, population, and ecosystem level (Fig. 3). The consequences of behavioural variation at any level can then, in turn, affect an individual's social behaviour. Similarly, behavioural changes at any level can potentially interact with behaviours at all other levels (Cantor et al., 2021). For example, an individual that disperses to another group affects the composition of both groups and influences population structure (Griesser et al., 2014). Consequently, the failure to consider behavioural interactions at all levels limits our ability to predict responses of species to climate change.

The effects of climatic conditions on individual behaviours are numerous and have been described in previous reviews (Blumstein et al., 2023; Fisher et al., 2021; Komdeur & Ma, 2021; Moss & While, 2021; Soravia et al., 2021). Behavioural changes at the group and population level can be measured as changes to social systems features (i.e., social organization, social structure, mating system, care system) and social interactions (Kappeler, 2019). Changing environments can also impact group and population structure if different categories of individuals (e.g., breeding vs. nonbreeding group members) are differently affected by climate change. For example, in species where allo-parental care differs between sexes (e.g., Seychelles warblers, (Komdeur, 1992)), climate change impacts that particularly affect the helping sex can influence the social benefits of group living. Furthermore, nonbreeding group members could be more disadvantaged in unfavourable environments, as breeding group members generally are socially more dominant and have preferential access to resources (Majolo et al., 2012). This could lead to dispersal of helping subordinates during unfavourable conditions (Bateman et al., 2013).

Climate change can alter the ranges and phenology of organisms (Gilman et al., 2010), ecosystem process (e.g., nutrient cycling, carbon sequestration, (Melillo et al., 2002), and ecosystem biochemistry (e.g., acidification of aquatic environments, (Doney et al., 2009), while extreme weather events can alter and cause disturbance regimes (e.g., wildfires, (Turner, 2010)). These changes can influence all organisms living in a community and thus between-species dynamics. Consequently, changes to interspecies interactions can influence how climate change affects organisms because of the costs and benefits associated with these interactions, including predator-prey interactions, competition and mutualisms (Gilman et al., 2010).

In addition, many social species engage in the construction of shelters. For example, fossorial mammals (Davidson et al., 2012), colonial birds (Collias, 1964) and social insects (Queller & Strassmann, 1998) construct and maintain constructions that shield animals against extreme weather conditions. Furthermore, several social species are ecosystem engineers that alter the physical environment (Davidson et al., 2012) and thus, have disproportionate effects on the community. Changes in the behaviours and abundance of these species can have cascading effects on the habitat structure of the ecosystem. For example, aridity drives sociality in mole-rats (Bennett & Faulkes, 2000) via energy benefits associated with shared burrowing and colony tasks. Thus, a change in aridity across the range of mole-rat species could change these social costs and benefits and thus influence social evolution and species resilience to climate change. The burrowing activity of mole rats benefits the ecosystem because their digging increases soil fertility and improves plant growth (Bennett & Faulkes, 2000). Furthermore, their burrows could provide shelter and nesting habitats for other organisms, observed in other African burrowing mammals living in the same habitat (Ewacha et al., 2016). Similarly, many other species that have large effects on their communities are group-living. Therefore, any changes in their behaviours could have an impact on the ecosystem services that they provide (Marjakangas et al., 2023), including pollination (e.g., honeybees *Apis mellifera*, and other colonially living insect pollinators), and seed dispersers (McConkey et al., 2012).

4.3 The importance of behavioural plasticity

Plasticity in social behaviours is critical for the occurrence of social shielding, and plasticity can occur through multiple avenues (Fig. 3). First, individuals can rapidly change their own behaviour in response to environmental change. These within-individual changes can allow individuals to maintain a high body condition, survival rate, and fecundity when exposed to adverse conditions (e.g., a hot spell or drought) that might otherwise lead to desiccation and death. For example, cheetahs (*Acinonyx jubatus*) modify their daily hunting patterns from diurnal to crepuscular on hotter days, to avoid overheating and to conserve energy (Hetem et al., 2019). Second, individuals can change their behaviour in response to changes in their own reproductive status. For example, breeders in Iberian magpies and long-tailed tits that fail with their own breeding attempt become an alloparent at another nest (usually of a related individual) (Bebbington & Hatchwell, 2016; Canário et al., 2004) and increase the breeding success of that nest. Third, individuals may differ in their response to environmental change, leading to between-individual variation within a population. These differences can reflect genetic differences, irreversible developmental plasticity, or phenotypic plasticity (Stager et al., 2024). Individuals can also permanently specialise in particular tasks. For example, eusocial insects exhibit cast differentiation that improves the overall efficiency of the group and supports high reproductive output (Queller & Strassmann, 1998). Fourth, populations living in different environments may express different social behaviours, either due to genetic changes (local adaptation) or due to plasticity. Determining whether among-individual and population variation in behaviours are due to plasticity or genetic factors is important for studying adaptation of social behaviours to climate change impacts. This can be investigated through common garden and reciprocal transplant experiments or by directly examining genetic variation linked to social behaviour and environmental differences (Fisher et al., 2021).

4.4. Consequences of behavioural changes

Consequences of flexibility of social behaviours can occur at the individual, group, or population level and will also be influenced by direct impacts of climate change on population demographic measures (Fig. 3). It is typical to examine effects of climate change on fitness proxies such as reproductive output and survival. Changes in social behaviours can also alter reproductive investment with downstream consequences for fitness. For example, maternal investment in response to climatic variables can be influenced by the presence of alloparents. In superb fairy wrens (*Malurus cyaneus*), mothers receiving help decrease their egg size in cooler, wetter conditions but increase egg size in hotter, dryer conditions compared to mothers receiving no help (Langmore et al., 2016).

Individual survival and reproduction can be influenced by the dynamics and stability of the group. Measuring group dynamics and stability often includes the examination of group persistence and turnover. Group persistence refers to the continued existence of a social group over time. It encompasses the ability of the group to maintain its structure, size, and function despite changes in the environment that might otherwise lead to group dissolution. Group persistence is often linked to habitat stability and availability of resources, as well as the ability to successfully reproduce and raise offspring (Ebensperger et al., 2009; Krause & Ruxton, 2002). Group turnover is defined as the rate at which individuals within a group are replaced by new individuals and is often used to understand how groups respond to environmental changes and stressors (Ebensperger et al., 2009). High turnover rates can indicate frequent changes in group composition, caused by high mortality, emigration, or immigration (Layton-Matthews et al., 2018). It is important to examine changes in group features and their effects on group persistence and turnover because fitness-relevant parameters can be affected by these changes. For example, female African elephants (*Loxodonta africana*) have reduced reproductive rates in groups after the loss of older females (Gobush et al., 2008). Furthermore, it is critical to consider Allee effects (Allee, 1931), whereby a minimal group size or structure is needed to maintain a group or population. In some species, groups cannot be maintained when their size drops below a critical number, leading to group extinction. For example, in African wild dogs (*Lycaon pictus*), smaller packs face difficulties in hunting effectively and are at greater risk of extinction due to decreased cooperative behaviours (Angulo et al., 2018). Similarly, given that density-dependent processes can affect group persistence (Krause & Ruxton, 2002), it is important to examine population persistence in relation to group persistence and/or individual survival.

5. How to test for social shielding

Researchers have investigated the relationship between environmental conditions and social structures across species and within populations. Across species, researchers investigated the occurrence of social shielding by relating aspects of a species' typical environment (e.g., variability in annual precipitation) to elements of their social structure (e.g., occurrence of cooperative breeding, (Griesser et al., 2017; Jetz & Rubenstein, 2011)). These comparative studies usually used average values of climatic parameters of the whole distribution range, but did not assess the effect of an interaction between a social parameter and environmental conditions on a fitness proxy. They neither assessed whether the association between the occurrence of cooperative breeding and environmental variability reflects that cooperative species outcompete noncooperatively breeding species in these environments, or whether cooperate species do better in adverse conditions irrespective of between-species competition. Consequently, these studies are unable to assess social shielding (Borger et al., 2023), but nonetheless provide important insights. At the between-species level, cooperatively breeding birds are more abundant under more variable climatic conditions (Griesser et al., 2017; Jetz & Rubenstein, 2011), but assessing the precise mechanism underlying this pattern is only possible if detailed data on group size, environmental, and fitness parameters are available (Ben Mocha et al., 2024). Notably, these interspecific studies contrast with findings from within-population studies (Borger et al., 2023). When formulated at the individual level, one can test how particular social behaviours or group compositions can give fitness benefits under specific environmental conditions (Borger et al., 2023; Covas et al., 2008). The interaction between social traits and environmental conditions when fitness components are regressed on these factors is precisely the prediction of the social shielding hypothesis (Fig. 3). This approach requires individual-level data on behaviour, fitness, and environmental conditions, and can be performed using a linear regression fitting model.

However, if we are interested in whether plasticity in social behaviour itself brings fitness benefits, we need another approach, as the individual-level analysis described above only shows that individual variation in behaviour, in combination with variation in the environment, is associated with variation in a fitness-related trait. Therefore, this approach does not give insight into whether a change in behaviour was key. To test whether individual (or group) plasticity in behaviour itself is associated with a fitness proxy, we need to estimate selection on social plasticity. The latter can be achieved using bivariate mixed-effect models (Dingemanse & Dochtermann, 2013), with both the behaviour of interest and a fitness component as response variables (Hadfield et al., 2010). For the behavioural trait, the environmental variable(s) of interest is fitted as a fixed effect, along with both individual-level (or group-level if looking at the responses of entire groups) random intercepts and random slopes for that variable. Crucially, the covariances between the fitness component and both the individual intercepts and individual slopes are then estimated, the latter indicating whether plasticity in response to the environmental variable is associated with differential fitness (for an example with a life-history trait, see (Brommer et al., 2005)). As far as we are aware, this type of analysis has yet to be performed for social behaviours that require a well-studied species with detailed individual data available across different environmental conditions.

5.1 The role of variance within and between groups of key traits for social shielding

Social shielding depends on the variance in key traits that facilitate fitting into the species' niche (Fig. 4). Climate change will likely shift ecological niches via the availability of key resources, for example food, or via climatic changes such as different ambient temperatures. Evidently, groups that do not fall within the species niche will likely go extinct (e.g., group G3 in Fig. 4). Trait variance among all group members can ensure groups fit their niche if the variance overlaps with the niche.

Although variance in traits matters, it depends on the specific traits whether variance on the group level or on the individual level matters. For some traits, all group members need to fit the niche, for example, the thermal tolerance of individuals. Under this scenario, all individuals of G2a will survive, while the two right individuals of G2b would die as they do not fall within the required niche. In contrast, other traits benefit other group members, for example knowledge about the location of key resources (Wato et al., 2018), or the foraging niche of workers in eusocial mole rats (Bennett & Faulkes, 2000). Similarly, the level of experience of key group members (i.e., breeders) influences the reproductive output for the whole group (Hatchwell et al., 1999). For these traits, it is critical that phenotypes within the group cover the entire required range, but not that any one individual covers that range (e.g., the two left individuals of G2b). Figure 4 also illustrates the role of key group members for group persistence. Losing specific individuals can lead to group extinction (see above for the example in elephants, G2c). The latter example can also explain the occurrence of Allee effects, which can lead to group extinction after the loss of key group members.

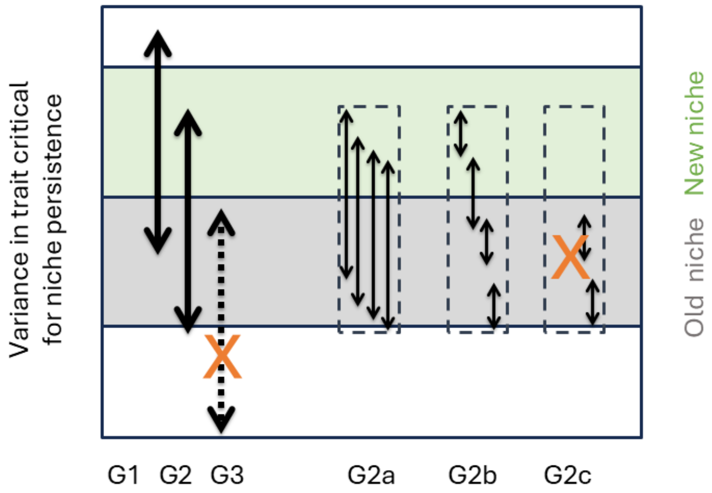

Figure 4. Trait variance among individuals with groups can differ in relation to the climatic niche and the consequence of niche shifts caused by climate change. Trait variance among all group members can ensure that groups fit into their niche if the variance overlaps with the niche. In this example, groups (G) 1 & 2 will persist in the old and new niche, while G3 will go extinct in the new niche (indicated with orange cross). The variance of group members can be similar to the variance of the group (G2a) or different (G2b). Loss of key group members can lead to group extinction (G2c). In G1-3, an arrow refers to a group; in G2a-c, an arrow refers to an individual.

6. Social shielding through life

Social shielding can occur at different stages during ontogeny and can reflect either a reactive response to past and current conditions or a proactive response to anticipated conditions (Fig. 5). At the embryo stage, social shielding can occur through maternal effects (e.g., by providing additional resources under unfavourable conditions), while other group members could support the mothers' investment into her offspring at this stage. In cooperatively breeding birds, the presence of alloparents can lead to a reduction of a mother's investment, e.g., superb fairywren female breeders receiving allo-parental help reduce egg volume (Russell et al., 2007), because allo-parental care can offset the offspring costs of hatching from a smaller egg.

After birth or hatching, caregivers can shield young through increased parental provisioning (Covas et al., 2008), and by protecting them from predators (Griesser et al., 2006). Across species, parental care patterns are related to the pace of life where some species only provide parental care during a short time, with accompanied short shielding periods. In other species, care is extended well into adulthood (Uomini et al., 2020), creating ample opportunities for caregiver shielding outside the reproductive context (Covas & Griesser, 2007), e.g., against the negative effects of harsh climatic conditions.

After independence, social partners can provide social shielding to subadults and adults via the mechanisms described in Section 2.2. For example, female wild baboons (*Papio cynocephalus)* with strong social bonds have a higher lifetime reproductive success and increased longevity (Alberts, 2019). This difference has been suggested to reflect the positive effect of social bonds on the reduction of adverse early life conditions both directly (via long-term negative physiological effects) and indirectly (via a negative impact on social relationships later in life) (Alberts, 2019). Furthermore, social shielding could occur on different temporal scales, from short-term to long-term help, with effects being seen immediately (Van de Ven et al., 2020), or with delayed effects. For example, alloparents can affect the survival and future reproductive success of breeders (Hammers et al., 2019; Magrath, 2001). Therefore, it is important to design studies testing for social shielding effects at different temporal scales.

6.1 Reactive versus proactive shielding

Changes in social behaviours can occur after climatic changes or events and therefore help limit their negative impacts. We refer to this type of response as reactive shielding. For example, sandgrouse (*Pterocles sp*.) increase parental provisioning of water to young in warmer and drier conditions, and meerkat (*Suricata suricatta*) alloparents increase provisioning of young on hotter days (Van de Ven et al., 2020), shielding offspring against negative climatic effects (Cad & Maclean, 1967). Reactive shielding can also alleviate negative social events, which has been labelled the 'tend and befriend' strategy (Taylor et al., 2000). After stressful events, individuals seek and receive behaviours that lower their stress levels and decrease recovery time. In primates, grooming is often used to achieve this (Cheney & Seyfarth, 2009) because grooming increases hormones of the oxytocin-vasotocin family that buffer out stress responses (Griesser et al., 2025).

Contrastingly, behavioural change could reflect anticipation of future impact, such as the befriend part of the 'tend and befriend' stress response, which refers to the formation and maintenance of social bonds that can help in future stress responses. Although shielding can be informed by past conditions, it could also anticipate future needs, such as by giving resources in the present time to prepare for future events. We refer to this type of buffering as proactive shielding, and this has been observed in some cooperatively breeding birds (Arnold et al., 2001; Komdeur et al., 1997). For example, Superb fairy-wren (*Malurus cyaneus*) mothers without alloparents laid larger eggs (more nutrients for developing young) under unfavourable (hotter) conditions, compared to mothers with alloparents (Langmore et al., 2016), indicating a potential proactive response to climate change effects that cannot be offset by alloparents. Social moulding effects (maternal and allo-parental) have also been shown in social insects. In hymenopterans, queens can determine the sex of offspring (genetically via haplodiploidy) and the caste development of workers is determined by the diet developing larvae are fed by colony members (Slater et al., 2020).

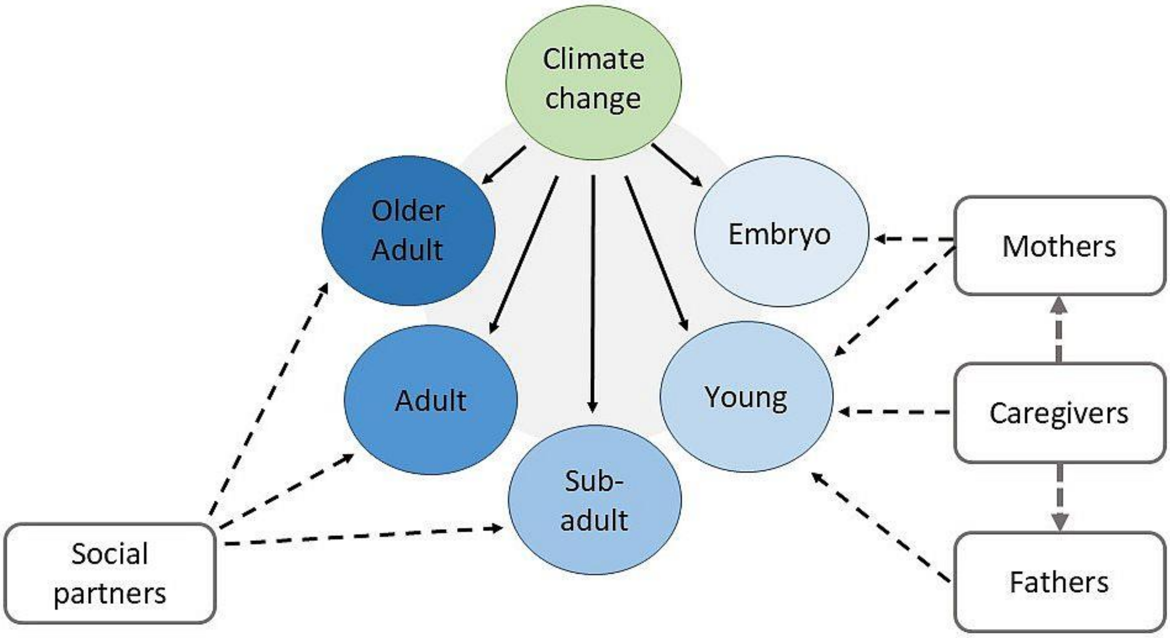

Figure 5. Social effects (dashed arrows) of climatic conditions at different ontogenic stages; these effects can be reactive or proactive processes. These effects can be mediated via parent(s) or caregivers (e.g., mother receiving resources from other group members) or occur directly (e.g., offspring receiving resources from parents and other group members). At the embryonic stage, climate change impacts will vary depending on embryo type (oviparous vs. viviparous) and may differ from climatic effects felt by born young and adults.

7. Implications for conservation

Several previous reviews examined general features of organisms that can influence their vulnerability to the negative impacts of climate change (Boyles et al., 2011; da Silva et al., 2023; Paniw et al., 2021). This information will allow for planning conservation and climate action initiatives (Buchholz et al., 2019; LeDee et al., 2021; Marjakangas et al., 2023). Although the response of animals to climate change is predicted to depend on many organismal features, examining social behaviours is useful in the conservation of vulnerable animals (Berger-Tal & Saltz, 2016). There are several types of information, including reproduction, survival, disease, and human-wildlife conflict, that will help in designing effective conservation strategies for social animals, which could include more involved ecological rescue strategies (LeDee et al., 2021), such as focusing on conserving larger groups rather than smaller groups. One must consider the impacting weather variables, the level of social response, and the specific mechanisms driving the response. However, an assessment of the overall consequence of specific conservation measures for population persistence and viability is ultimately what is needed when conserving a species (Berger-Tal & Saltz, 2016).

Identifying which climatic effects can be mitigated through social shielding, and which cannot due to their disruption of normal physical or physiological functions (Moss & While, 2021), is essential for guiding conservation initiatives. When social shielding is possible, human intervention can be used as a form of ecological rescue. For example, critically endangered Vancouver Island marmots (*Marmota vancouverensis*) live in smaller groups in managed and fragmented forests compared to groups that live in natural forests. Marmots in smaller groups experience increased mortality through increased risk of predation due to a loss of group vigilance (Brashares et al., 2010), limiting the opportunities for populations to recover (Graham et al., 2024). Consequently, translocations of individuals have been used to increase group size in managed forests to alleviate these negative effects (Brashares et al., 2010). Effectively identifying when animals are and are not socially shielded against environmental change will therefore help design effective management interventions. The types and levels of social response creating any shielding effects will likely vary between species. Thus, studies examining whether group-living in general (Griesser et al., 2017; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017), or specific group traits or behaviour contexts (Covas & Griesser, 2007; Van de Ven et al., 2020), have shielding effects will be useful in designing conservation measures.

The general consequences for population persistence and viability can be examined using population models, of which there are many different types (Buckley & Kingsolver, 2012; Johnston, et al., 2019). Population models should be used to predict population changes and estimate the effectiveness of conservation measures (LeDee et al., 2021). Furthermore, our framework can inform theoretical models assessing environmental effects, giving insights into the environmental conditions under which individuals should form groups and cooperate. This modified approach would be useful in predicting adaptation to rapidly changing environmental conditions (Forster et al., 2024).

8. Moving forward

Our framework highlights that social behaviours have the potential to shield animals against the negative impacts of changing climatic conditions through different mechanisms. Insights into specific mechanisms will be critical in designing effective conservation strategies. For example, in animals that exhibit social facilitation, the temporal patterns of unfavourable and favourable periods in combination with the life history of the species will determine whether a population is able to recover after unfavourable periods. A review of studies that assessed social shielding of cooperatively breeding species in relation to climatic conditions (Warrington et al. this issue) showed that populations show a mix of social benefits, facilitation or buffering. So far, social buffering has been documented the least, which could reflect the climatic parameters that previous studies have focused on, or the lack of an experimental and statistical framework that can distinguish among the different forms of social shielding. However, animals may be less likely to be able to socially mitigate the effects of increasingly stressful climatic conditions, for example, heat stress and desiccation (Griffith, 2019; Henen, 1997), as these forms of stress often affect all group members equally. However, in species with alloparental care, an increased number of alloparents can buffer some negative impacts of climate change, such as those that lead to a reduction in food resources. Therefore, it is critical to assess the impact of a variety of climatic factors (e.g., temperature and precipitation) in concert, to understand how changing climatic conditions impact animals. Furthermore, quantitative genetic approaches will allow us to understand the heritability of social traits and their association with other traits that are under selection. We suggest that investigating the heritability of social traits is a fruitful avenue for future research and will provide opportunities to predict the phenotypic change of social behaviours in response to global climate change.

8.1 Conclusions

Rapid changes in climatic parameters and an increase in extreme weather events due to climate change are affecting habitats and organisms and altering behavioural patterns in many animal species. These changes can often be negative by decreasing the available resources and energy that can increase physiological stress. These changes are particularly detrimental when combined with other anthropogenic impacts, including pollution. Animal social behaviours, which can offer adaptive responses to environmental changes, can be a mechanism to mitigate the negative effects of climate change. Social behaviours provide immediate physiological stress relief, improve resource acquisition, and enhance survival through cooperative behaviours, potentially buffering animals against adverse conditions.

The social shielding framework outlines how social behaviours can support animals in dealing with changing climatic conditions, which is vital for conservation efforts and valuable in understanding how climate change affects evolutionary trajectories (Hoffmann & Sgrò, 2011). This includes identifying specific climatic variables that impact social behaviours, the mechanisms driving these changes, and the resulting consequences at the individual, group, and population levels. Empirical and theoretical studies on social shielding can inform conservation strategies, helping to preserve biodiversity and improve animal welfare. By integrating knowledge across disciplines and standardising investigative approaches, we can better predict and manage the impacts of climate change on social animals, ultimately aiding in their survival and adaptation in rapidly changing environments.

Box 1 - How to describe and analyse climatic parameters

Studying the effects of climatic parameters on social parameters requires selecting climatic parameters. Meteorological stations usually measure temperature, precipitation, snow depth (where relevant), humidity, wind speed, air pressure, sunshine, often on an hourly basis. This raises the question of how to select and transform these data into biologically meaningful parameters.

Calculating parameters: Climate can be assessed as absolute values, averages over longer time periods, the temporal predictability or unpredictability of these parameters, and their temporal variability. Predictability is either assessed via the constancy of parameters (i.e., no change in a parameter), their contingency (i.e., a repeatable pattern in a parameter), or a combination of both (Colwell, 1974). To assess the effects of climate change on social parameters, some authors use measurements of parameter anomalies, e.g., number of days of extreme heat, drought, or precipitation (van de Pol et al., 2017).

Selecting parameters: Some authors select specific raw parameters in their studies, e.g., monthly or annual precipitation and temperature measures (D'Amelio et al., 2022; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017), while others combine multiple measures via a principal component analysis (PCA) and use the resulting PCs in their analyses (Cornwallis et al., 2017; Griesser et al., 2017). Selecting specific parameters can be useful but must be based on an in-depth knowledge of what is of relevance for a specific species, as this approach can lead to choosing unrepresentative or irrelevant parameters. In contrast, PCA approaches can lead to very different parameter sets used across studies, limiting comparability (Cornwallis et al., 2017; Griesser et al., 2017; Jetz & Rubenstein, 2011). Importantly, large scale comparative studies usually use mean climatic values over the whole distribution range and relate that to biological data that have been sampled at different populations

(Cornwallis et al., 2017; Griesser et al., 2017; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017). This can increase the statistical noise of comparative studies and limit the ability to detect biological patterns. Furthermore, selecting climate data from particular time periods (referred to as climate windows), such as seasonal averages, can create a bias, especially in species with prolonged or aseasonal breeding where breeding could be more linked to availability of key resources. For example, African ungulates are often constrained by water availability (Ogutu et al., 2014). Thus, one could use a climate window analysis (Bailey & van de Pol, 2016a) to select the strongest periods of climatic sensitivity.

Terminological issues: Across studies, authors can use terms in an inconsistent or conceptually incorrect manner. For example, the term 'harshness' describes the effect of climate on the energy expenditure of animals but has been used as a description for habitats exhibiting extremes in climatic variables (Schradin et al., 2023). However, the same climate can be harsh for some species, but not others. For example, species that hibernate are not affected by winter the same way as species that do not hibernate and often experience energy shortages during winter (Turbill et al., 2011). Although the term harshness is widely used in comparative studies (Cornwallis et al., 2017; Jetz & Rubenstein, 2011), it is better avoided.

Immediate vs delayed effects: While temperature effects often are immediate and direct, via effects on physiology of individuals (McKechnie & Dunn, 2019), precipitation effects can be either direct via water stress or dehydration (McKechnie & Dunn, 2019), or delayed via changes in food availability (Cumming & Bernard, 1997). Importantly, different parameters require different time lags when assessing their impact on animals across different timescales (daily vs weekly vs longer timescales). Moreover, habitat structure can buffering against unfavourable weather conditions (e.g., reduced snow depth increases mortality of marmots during hibernation, (Johnston et al., 2021), thereby altering the conditions animals are exposed to.

Box 2: The importance of social properties for social shielding

Social properties, such as group size, age of group members, social bonds (network and bond strength), and helping behaviours, significantly influence animals' responses to changing climates by shaping their social behaviours and opportunities to adapt. Individuals in larger groups often experience reduced predation risk through shared vigilance and predator mobbing (Carlson & Griesser, 2022; Caro, 2005), increased hunting success with larger or riskier prey (MacNulty et al., 2014), and enhanced information sharing about food and predators (Griesser, 2008). However, intermediate group sizes can be optimal in certain contexts, like reducing food competition among baboons (Markham et al., 2015).

More experienced (i.e., older) group members, can share valuable knowledge during predator encounters, provide social learning opportunities (Griesser & Suzuki, 2017) and improve decision-making (Conradt & Roper, 2003). This knowledge transfer helps groups to adapt quickly to new environments, including finding alternative food sources when resources are scarce (Jaeggi et al., 2010). We note that several nuances of information sharing can differentially affect fitness proxies. For example, the context of information can vary in how easily it is shared within a group, such as knowledge of favourable foraging locations. Moreover, individuals differ in their social phenotypes, for example the observable social behaviours and interactions of an individual within a group (Cote et al., 2008), which can be beneficial in varying social and environmental settings (Webster & Ward, 2011).

Additionally, the social relationship among individual group members is important for a variety of social behaviours. Increased social bond strength shields individuals against challenging situations via direct reduction of stress and support during conflicts, or access to resources including mating opportunities (Gerber et al., 2022; Seyfarth & Cheney, 2012; Silk et al., 2010). In many social animals, closely bonded individuals frequently engage in touch. As detailed above, touch reduces physiological stress via increasing oxytocin levels (Griesser et al., 2025; Kikusui et al., 2006).

Finally, individuals can also engage in helping that directly benefit other group members. Helping can occur in diverse contexts and can also contribute towards how individuals cope with climatic challenges. For example, in cooperatively breeding species, alloparents can help increase offspring production and survival in challenging conditions via increased offspring provisioning (Covas et al., 2008). Moreover, alloparental care allows breeders to conserve energy in raising their offspring, which provides a buffer that can reduce mortality rates in female breeders, especially later in life (Hammers et al., 2019; van Boheemen et al., 2019).

These social benefits, tied to various group properties (e.g., size and composition), can help individuals cope with environmental challenges, such as reduced resources during droughts or scarcity (Wato et al., 2018). By directly or indirectly lowering predation risk, improving foraging efficiency, and aiding with physiological demands, group living can alleviate the immediate impacts of climatic stressors and support quicker recovery from stressful events. Over time, these advantages can enhance individual survival and reproductive success.

Acknowledgements

The climate emergency and protection of nature is something we all take to heart, and we thank every person that has given us inspiration to continue our work in this regard. This review was inspired by a symposium on behavioural responses to climate change at the 2023 Behaviour Conference in Bielefeld, Germany, organised by NP and DF and attended by MHW, MG, and JK among others. MHW's attendance at the conference was supported by an Animal Behaviour Society (ABS) conference attendance grant and childcare grant. MHW was supported by an Oxford Brookes University Emerging Leaders Research Fellowship. MG was supported by a Heisenberg Grant GR 4650/2-1 and a project grant FP 589/20 by the German Research Foundation DFG. NP's attendance at the conference was supported by an Animal Behaviour Society (ABS) childcare grant. DF's attendance at the conference was supported by NERC grant NE/X013227/1.

Conflicts of interest

None.

Author contributions

NP and DF organized the conference symposium that gave rise to this review. All authors refined the ideas; MHW and MG reviewed literature and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Statement on inclusion

Our study was a review and framework development based on ideas in the published literature. As such, there was no local data collection. However, the geographical distribution of the key studies used to develop our framework was selected as geographically diverse as possible, and include studies in regions of the global south and on islands that are being heavily impacted by global climate change. We note that our study does not include authors originating or currently based at institutions in the global south, reflecting that the conference that gave rise to this paper was held in Europe. However, co-authors have worked for periods of times in the global south, and come from diverse cultural backgrounds.

References

Alberts, S. C. (2019). Social influences on survival and reproduction: Insights from a long-term study of wild baboons. *Journal of Animal Ecology*, *88*(1), 47–66. https://doi.org/10.1111/1365-2656.12887

Allee, W. C. (1931). *Animal aggregations, a study in general sociology*. The University of Chicago Press.

Angulo, E., Luque, G. M., Gregory, S. D., Wenzel, J. W., Bessa-Gomes, C., Berec, L., & Courchamp, F. (2018). Allee effects in social species. *Journal of Animal Ecology*, *87*(1), 47–58. https://doi.org/10.1111/1365-2656.12759

Arnold, K. E., Griffith, S. C., & Goldizen, A. W. (2001). Sex-biased hatching sequences in the cooperatively breeding noisy miner. *Journal of Avian Biology*, *32*(3), 219–223. https://doi.org/10.1111/j.0908-8857.2001.320303.x

Bailey, L. D., & van de Pol, M. (2016a). climwin: An R Toolbox for Climate Window Analysis. *PLOS ONE*, *11*(12), Article 12. https://doi.org/10.1371/journal.pone.0167980

Bailey, L. D., & van de Pol, M. (2016b). Tackling extremes: Challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology*, *85*(1), 85–96. https://doi.org/10.1111/1365-2656.12451

Bateman, A. W., Ozgul, A., Nielsen, J. F., Coulson, T., & Clutton-Brock, T. H. (2013). Social structure mediates environmental effects on group size in an obligate cooperative breeder, Suricata suricatta. *Ecology*, *94*(3), 587–597. https://doi.org/10.1890/11-2122.1

Bebbington, K., & Hatchwell, B. J. (2016). Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. *Behavioral Ecology*, *27*(2), 652–659.

Ben Mocha, Y., Scemama de Gialluly, S., Griesser, M., & Markman, S. (2023). What is cooperative breeding in mammals and birds? Removing definitional barriers for comparative research. *Biological Reviews*, *98*(6), 1845–1861. https://doi.org/10.1111/brv.12986

Ben Mocha, Y., Woith, M., Drobniak, S. M., Markman, S., Frisoni, F., Baglione, V., Boersma, J., Cousseau, L., Covas, R., Braga de Miranda, G. H., Dey, C. J., Doutrelant, C., Gula, R., Heinsohn, R., Kingma, S. A., Li, J., Middleton, K.-M., Radford, A. N., Restrepo, C., … Griesser, M. (2024). Advancing cooperative breeding research with a peer-reviewed and "live" Cooperative-Breeding Database (Co-BreeD). *bioRxiv*, 1–46. https://doi.org/10.1101/2024.04.26.591342

Bennett, N. C., & Faulkes, C. G. (2000). *African Mole-Rats: Ecology and Eusociality*. Cambridge University Press.

Bergeron, P., Réale, D., Humphries, M. M., & Garant, D. (2011). Anticipation and tracking of pulsed resources drive population dynamics in eastern chipmunks. *Ecology*, *92*(11), 2027–2034. https://doi.org/10.1890/11-0766.1

Berger-Tal, O., & Saltz, D. (2016). *Conservation behavior: Applying behavioral ecology to wildlife conservation and management* (Vol. 21). Cambridge University Press.

Bichet, C., Allainé, D., Sauzet, S., & Cohas, A. (2016). Faithful or not: Direct and indirect effects of climate on extra-pair paternities in a population of Alpine marmots. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1845), 20162240. https://doi.org/10.1098/rspb.2016.2240

Blumstein, D. T., Hayes, L. D., & Pinter-Wollman, N. (2023). Social consequences of rapid environmental change. *Trends in Ecology & Evolution*, *38*(4), 337–345.

Borger, M. J., Richardson, D. S., Dugdale, H., Burke, T., & Komdeur, J. (2023). Testing the environmental buffering hypothesis of cooperative breeding in the Seychelles warbler. *Acta Ethologica*, *26*(3), 211–224. https://doi.org/10.1007/s10211-022-00408-y

Bourne, A. R., Cunningham, S. J., Spottiswoode, C. N., & Ridley, A. R. (2020). Compensatory breeding in years following drought in a desert-dwelling cooperative breeder. *Frontiers in Ecology and Evolution*, *8*, 190. https://doi.org/10.3389/fevo.2020.00190

Bourne, A. R., Ridley, A. R., & Cunningham, S. J. (2023). Helpers don't help when it's hot in a cooperatively breeding bird, the Southern Pied Babbler. *Behavioral Ecology*, arad023. https://doi.org/10.1093/beheco/arad023

Boyles, J. G., Seebacher, F., Smit, B., & McKechnie, A. E. (2011). Adaptive Thermoregulation in Endotherms May Alter Responses to Climate Change. *Integrative and Comparative Biology*, *51*(5), 676–690. https://doi.org/10.1093/icb/icr053

Brashares, J. S., Werner, J. R., & Sinclair, A. R. E. (2010). Social 'meltdown' in the demise of an island endemic: Allee effects and the Vancouver Island marmot. *Journal of Animal Ecology*, *79*(5), 965–973. https://doi.org/10.1111/j.1365-2656.2010.01711.x

Brommer, J. E., Merilä, J., Sheldon, B. C., & Gustafsson, L. (2005). Natural selection and genetic variation for reproductive reaction norms in a wild bird population. *Evolution*, *59*(6), 1362–1371. https://doi.org/10.1111/j.0014-3820.2005.tb01785.x

Buchholz, R., Banusiewicz, J. D., Burgess, S., Crocker-Buta, S., Eveland, L., & Fuller, L. (2019). Behavioural research priorities for the study of animal response to climate change. *Animal Behaviour*, *150*, 127–137. https://doi.org/10.1016/j.anbehav.2019.02.005

Buckley, L. B., & Kingsolver, J. G. (2012). Functional and Phylogenetic Approaches to Forecasting Species Responses to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, *43*(Volume 43, 2012), 205–226. https://doi.org/10.1146/annurev-ecolsys-110411-160516

Cad, T. J., & Maclean, G. L. (1967). Transport of Water by Adult Sandgrouse to Their Young. *The Condor*, *69*(4), 323–343. https://doi.org/10.2307/1366197

Canário, F., Matos, S., & Soler, M. (2004). Environmental Constraints and Cooperative Breeding in the Azure-Winged Magpie. *The Condor*, *106*(3), 608–617. https://doi.org/10.1093/condor/106.3.608

Cantor, M., Maldonado-Chaparro, A. A., Beck, K. B., Brandl, H. B., Carter, G. G., He, P., Hillemann, F., Klarevas-Irby, J. A., Ogino, M., & Papageorgiou, D. (2021). The importance of individual-to-society feedbacks in animal ecology and evolution. *Journal of Animal Ecology*, *90*(1), 27–44.

Carlson, N. V., & Griesser, M. (2022). Mobbing in animals: A thorough review and proposed future directions. *Advances in the Study of Behavior*, *54*, 1–41. https://doi.org/10.1016/bs.asb.2022.01.003

Caro, T. (2005). *Antipredator defenses in birds and mammals*. Chicago University Press.

Cheney, D. L., & Seyfarth, R. M. (2009). Chapter 1 Stress and Coping Mechanisms in Female Primates. In *Advances in the Study of Behavior* (Vol. 39, pp. 1–44). Academic Press. https://doi.org/10.1016/S0065-3454(09)39001-4

Collias, N. E. (1964). The Evolution of Nests and Nest-Building in Birds. *American Zoologist*, *4*(2), 175–190. JSTOR. https://www.jstor.org/stable/3881291

Colwell, R. K. (1974). Predictability, Constancy, and Contingency of Periodic Phenomena. *Ecology*, *55*(5), 1148–1153.

Conradt, L., & Roper, T. J. (2003). Group decision-making in animals. *Nature*, *421*(6919), Article 6919. https://doi.org/10.1038/nature01294

Cornwallis, C. K., Botero, C. A., Rubenstein, D. R., Downing, P. A., West, S. A., & Griffin, A. S. (2017). Cooperation facilitates the colonization of harsh environments. *Nature Ecology & Evolution*, *1*(3), Article 3.

Cote, J., Dreiss, A., & Clobert, J. (2008). Social personality trait and fitness. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1653), Article 1653. https://doi.org/10.1098/rspb.2008.0783

Covas, R., du Plessis, M. A., & Doutrelant, C. (2008). Helpers in colonial cooperatively breeding sociable weavers Philetairus socius contribute to buffer the effects of adverse breeding conditions. *Behavioral Ecology and Sociobiology*, *63*(1), 103–112. https://doi.org/10.1007/s00265-008-0640-2

Covas, R., & Griesser, M. (2007). Life history and the evolution of family living in birds. *Proceedings of the Royal Society B-Biological Sciences*, *274*(1616), 1349–1357. https://doi.org/10.1098/rspb.2007.0117

Cumming, G., & Bernard, R. (1997). Rainfall, food abundance and timing of parturition in African bats. *Oecologia*, *111*, 309–317.

da Silva, C. R. B., Beaman, J. E., Youngblood, J. P., Kellermann, V., & Diamond, S. E. (2023). Vulnerability to climate change increases with trophic level in terrestrial organisms. *Science of The Total Environment*, *865*, 161049. https://doi.org/10.1016/j.scitotenv.2022.161049

D'Amelio, P. B., Ferreira, A. C., Fortuna, R., Paquet, M., Silva, L. R., Theron, F., Doutrelant, C., & Covas, R. (2022). Disentangling climatic and nest predator impact on reproductive output reveals adverse high-temperature effects regardless of helper number in an arid-region cooperative bird. *Ecology Letters*, *25*(1), Article 1. https://doi.org/10.1111/ele.13913

Davidson, A. D., Detling, J. K., & Brown, J. H. (2012). Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment*, *10*(9), 477–486. https://doi.org/10.1890/110054

Davitz, J. R., & Mason, D. J. (1955). Socially facilitated reduction of a fear response in rats. *Journal of Comparative and Physiological Psychology*, *48*(3), 149–151.

Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*(1), 39–54. https://doi.org/10.1111/1365-2656.12013

Doney, S. C., Fabry, V. J., Feely, R. A., & Kleypas, J. A. (2009). Ocean acidification: The other CO2 problem. *Annual Review of Marine Science*, *1*(1), 169–192. https://doi.org/10.1146/annurev.marine.010908.163834

du Plessis, M. A., Siegfried, W. R., & Armstrong, A. J. (1995). Ecological and Life-History Correlates of Cooperative Breeding in South-African Birds. *Oecologia*, *102*(2), 180–188.

du Plessis, M. A., Weathers, W. W., & Koenig, W. D. (1994). Energetic benefits of communal roosting by acorn woodpeckers during the nonbreeding season. *The Condor*, *96*(3), 631–637. https://doi.org/10.2307/1369466

Ebensperger, L. A., Chesh, A. S., Castro, R. A., Tolhuysen, L. O., Quirici, V., Burger, J. R., & Hayes, L. D. (2009). Instability Rules Social Groups in the Communal Breeder Rodent Octodon degus. *Ethology*, *115*(6), 540–554. https://doi.org/10.1111/j.1439-0310.2009.01635.x

Ebensperger, L. A., Villegas, Á., Abades, S., & Hayes, L. D. (2014). Mean ecological conditions modulate the effects of group living and communal rearing on offspring production and survival. *Behavioral Ecology*, *25*(4), 862–870. https://doi.org/10.1093/beheco/aru061

Ewacha, M. V. A., Kaapehi, C., Waterman, J. M., & Roth, J. D. (2016). Cape ground squirrels as ecosystem engineers: Modifying habitat for plants, small mammals and beetles in Namib Desert grasslands. *African Journal of Ecology*, *54*(1), 68–75. https://doi.org/10.1111/aje.12266

Fisher, D. N., Kilgour, R. J., Siracusa, E. R., Foote, J. R., Hobson, E. A., Montiglio, P.-O., Saltz, J. B., Wey, T. W., & Wice, E. W. (2021). Anticipated effects of abiotic environmental change on intraspecific social interactions. *Biological Reviews*, *96*(6), 2661–2693. https://doi.org/10.1111/brv.12772

Forcada, J., Trathan, P. N., & Murphy, E. J. (2008). Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology*, *14*(11), 2473–2488. https://doi.org/10.1111/j.1365-2486.2008.01678.x

Forster, P. M., Smith, C., Walsh, T., Lamb, W. F., Lamboll, R., Hall, B., Hauser, M., Ribes, A., Rosen, D., Gillett, N. P., Palmer, M. D., Rogelj, J., von Schuckmann, K., Trewin, B., Allen, M., Andrew, R., Betts, R. A., Borger, A., Boyer, T., … Zhai, P. (2024). Indicators of Global Climate Change 2023: Annual update of key indicators of the state of the climate system and human influence. *Earth System Science Data*, *16*(6), 2625–2658. https://doi.org/10.5194/essd-16-2625-2024

Gascoigne, S. J., Kajin, M., & Salguero-Gómez, R. (2024). Criteria for buffering in ecological modeling. *Trends in Ecology & Evolution*, *39*(2), 116–118. https://doi.org/10.1016/j.tree.2023.11.006

Gerber, L., Connor, R. C., Allen, S. J., Horlacher, K., King, S. L., Sherwin, W. B., Willems, E. P., Wittwer, S., & Krützen, M. (2022). Social integration influences fitness in allied male dolphins. *Current Biology*, *32*(7), Article 7. https://doi.org/April 11, 2022 ª 2022 Elsevier Inc. https://doi.org/10.1016/j.cub.2022.03.027

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, *25*(6), 325–331. https://doi.org/10.1016/j.tree.2010.03.002

Gobush, K. S., Mutayoba, B. M., & Wasser, S. K. (2008). Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of adult female African elephants. *Conservation Biology*, *22*(6), 1590–1599. https://doi.org/10.1111/j.1523-1739.2008.01035.x

Gore, A. C., Krishnan, K., & Reilly, M. P. (2019). Endocrine-disrupting chemicals: Effects on neuroendocrine systems and the neurobiology of social behavior. *SBN/ICN Meeting 2018*, *111*, 7–22. https://doi.org/10.1016/j.yhbeh.2018.11.006

Graham, L. H., Leishman, E. M., Demers, K., Whiteside, D. P., & McAdie, M. (2024). Factors Associated with Reproductive Success in Captive Vancouver Island Marmots (Marmota vancouverensis). *Animals*, *14*(3), 387. https://doi.org/10.3390/ani14030387

Griesser, M. (2008). Referential calls signal predator behavior in a group-living bird species. *Current Biology*, *18*(1), 69–73. https://doi.org/10.1016/j.cub.2007.11.069

Griesser, M., Bennett, N. C., Burkart, J. M., Hart, D. W., Uomini, N., & Warrington, M. H. (2025). The power of caring touch: From survival to prosocial cooperation. *Trends in Ecology & Evolution*, *40*(4).

Griesser, M., Drobniak, S. M., Nakagawa, S., & Botero, C. A. (2017). Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLOS Biology*, *15*(6), e2000483. https://doi.org/10.1371/journal.pbio.2000483

Griesser, M., Halvarsson, P., Sahlman, T., & Ekman, J. (2014). What are the strengths and limitations of direct and indirect assessment of dispersal? Insights from a long-term field study in a group-living bird species. *Behavioral Ecology and Sociobiology*, *68*(3), 485–497. https://doi.org/10.1007/s00265-013-1663-x

Griesser, M., & Lagerberg, S. (2012). Long-term effects of forest management on territory occupancy and breeding success of an open-nesting boreal bird species, the Siberian jay. *Forest Ecology and Management*, *271*, 58–64. https://doi.org/10.1016/j.foreco.2012.01.037

Griesser, M., Nystrand, M., & Ekman, J. (2006). Reduced mortality selects for family cohesion in a social species. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1596), 1881–1886. https://doi.org/10.1098/rspb.2006.3527

Griesser, M., & Suzuki, T. N. (2017). Naïve juveniles are more likely to become breeders after witnessing predator mobbing. *American Naturalist*, *189*(1), 58–66. https://doi.org/10.1086/689477

Griffith, S. C. (2019). Cooperation and coordination in socially monogamous birds: Moving away from a focus on sexual conflict. *Frontiers in Ecology and Evolution*, *7*, 455. https://doi.org/10.3389/fevo.2019.00455

Hadfield, J. D., Wilson, A. J., Garant, D., Sheldon, B. C., & Kruuk, L. E. B. (2010). The Misuse of BLUP in Ecology and Evolution. *The American Naturalist*, *175*(1), 116–125. https://doi.org/10.1086/648604

Halupka, L., Arlt, D., Tolvanen, J., Millon, A., Bize, P., Adamík, P., Albert, P., Arendt, W. J., Artemyev, A. V., Baglione, V., Bańbura, J., Bańbura, M., Barba, E., Barrett, R. T., Becker, P. H., Belskii, E., Bolton, M., Bowers, E. K., Bried, J., … Halupka, K. (2023). The effect of climate change on avian offspring production: A global meta-analysis. *Proceedings of the National Academy of Sciences*, *120*(19), e2208389120. https://doi.org/10.1073/pnas.2208389120

Hammers, M., Kingma, S. A., Spurgin, L. G., Bebbington, K., Dugdale, H. L., Burke, T., Komdeur, J., & Richardson, D. S. (2019). Breeders that receive help age more slowly in a cooperatively breeding bird. *Nature Communications*, *10*(1), 1301. https://doi.org/10.1038/s41467-019-09229-3

Hatchwell, B. J., Russell, A. F., Fowlie, M. K., & Ross, D. J. (1999). Reproductive success and nest-site selection in a cooperative breeder: Effect of experience and a direct benefit of helping. *Auk*, *116*(2), 355–363. https://doi.org/10.2307/4089370

Heinrich, B., & Marzluff, J. (1995). Why ravens share. *American Scientist*, *83*(4), 342–349. https://www.jstor.org/stable/29775481

Henen, B. T. (1997). Seasonal and annual energy budgets of female desert tortoises (Gopherus agassizii). *Ecology*, *78*(1), 283–296. https://doi.org/10.1890/0012-9658(1997)078[0283:SAAEBO]2.0.CO;2

Hennessy, M. B., Kaiser, S., & Sachser, N. (2009). Social buffering of the stress response: Diversity, mechanisms, and functions. *Hormones & Social Behavior*, *30*(4), 470–482. https://doi.org/10.1016/j.yfrne.2009.06.001

Hetem, R. S., Mitchell, D., De Witt, B. A., Fick, L. G., Maloney, S. K., Meyer, L. C., & Fuller, A. (2019). Body temperature, activity patterns and hunting in free-living cheetah: Biologging reveals new insights. *Integrative Zoology*, *14*(1), 30–47. https://doi.org/10.1111/1749-4877.12341

Hilde, C. H., Gamelon, M., Sæther, B.-E., Gaillard, J.-M., Yoccoz, N. G., & Pélabon, C. (2020). The demographic buffering hypothesis: Evidence and challenges. *Trends in Ecology & Evolution*, *35*(6), 523–538. https://doi.org/10.1016/j.tree.2020.02.004

Hoffmann, A. A., & Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, *470*(7335), 479–485.

Jaeggi, A. V., Dunkel, L. P., Van Noordwijk, M. A., Wich, S. A., Sura, A. A. L., & Van Schaik, C. P. (2010). Social learning of diet and foraging skills by wild immature Bornean orangutans: Implications for culture. *American Journal of Primatology*, *72*(1), Article 1. https://doi.org/10.1002/ajp.20752

Jetz, W., & Rubenstein, D. R. (2011). Environmental Uncertainty and the Global Biogeography of Cooperative Breeding in Birds. *Current Biology*, *21*(1), 72–78. https://doi.org/10.1016/j.cub.2010.11.075

Johnston, A. N., Christophersen, R. G., Beever, E. A., & Ransom, J. I. (2021). Freezing in a warming climate: Marked declines of a subnivean hibernator after a snow drought. *Ecology and Evolution*, *11*(3), Article 3. https://doi.org/10.1002/ece3.7126

Johnston, A. S., Boyd, R. J., Watson, J. W., Paul, A., Evans, L. C., Gardner, E., & Boult, V. (2019). Predicting population responses to environmental change from individual-level mechanisms: Towards a standardized mechanistic approach. *Proceedings of the Royal Society B*, *286*(1913), 20191916. https://doi.org/10.1098/rspb.2019.1916

Kappeler, P. M. (2019). A framework for studying social complexity. *Behavioral Ecology and Sociobiology*, *73*(1), 13.

Kikusui, T., Winslow, J. T., & Mori, Y. (2006). Social buffering: Relief from stress and anxiety. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1476), 2215–2228. https://doi.org/10.1098/rstb.2006.1941

Komdeur, J. (1992). Importance of Habitat Saturation and Territory Quality for Evolution of Cooperative Breeding in the Seychelles Warbler. *Nature*, *358*(6386), 493–495.

Komdeur, J., Daan, S., Tinbergen, J., & Mateman, C. (1997). Extreme adaptive modification in sex ratio of the Seychelles warbler’s eggs. *Nature*, *385*(6616), 522–525.

Komdeur, J., & Ma, L. (2021). Keeping up with environmental change: The importance of sociality. *Ethology*, *127*(10), 790–807. https://doi.org/10.1111/eth.13200

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.

Langmore, N. E., Bailey, L. D., Heinsohn, R. G., Russell, A. F., & Kilner, R. M. (2016). Egg size investment in superb fairy-wrens: Helper effects are modulated by climate. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843), 20161875. https://doi.org/10.1098/rspb.2016.1875

Layton-Matthews, K., Griesser, M., Coste, C. F. D., & Ozgul, A. (2021). Forest management affects seasonal source-sink dynamics in a territorial, group-living bird. *Oecologia*, *196*(2), 399–412. https://doi.org/10.1007/s00442-021-04935-6

Layton-Matthews, K., Ozgul, A., & Griesser, M. (2018). The interacting effects of forestry and climate change on the demography of a group-living bird population. *Oecologia*, *186*(4), 907–918. https://doi.org/10.1007/s00442-018-4100-z

LeDee, O. E., Handler, S. D., Hoving, C. L., Swanston, C. W., & Zuckerberg, B. (2021). Preparing Wildlife for Climate Change: How Far Have We Come? *The Journal of Wildlife Management*, *85*(1), 7–16. https://doi.org/10.1002/jwmg.21969

Lowry, H., Lill, A., & Wong, B. B. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, *88*(3), 537–549. https://doi.org/10.1111/brv.12012

Lukas, D., & Clutton-Brock, T. (2017). Climate and the distribution of cooperative breeding in mammals. *Royal Society Open Science*, *4*(1), 160897. https://doi.org/10.1098/rsos.160897

MacNulty, D. R., Tallian, A., Stahler, D. R., & Smith, D. W. (2014). Influence of Group Size on the Success of Wolves Hunting Bison. *PLOS ONE*, *9*(11), Article 11. https://doi.org/10.1371/journal.pone.0112884

Magrath, R. D. (2001). Group breeding dramatically increases reproductive success of yearling but not older female scrubwrens: A model for cooperatively breeding birds? *Journal of Animal Ecology*, *70*(3), 370–385. https://doi.org/10.1046/j.1365-2656.2001.00498.x

Mainwaring, M. C., Barber, I., Deeming, D. C., Pike, D. A., Roznik, E. A., & Hartley, I. R. (2017). Climate change and nesting behaviour in vertebrates: A review of the ecological threats and potential for adaptive responses. *Biological Reviews*, *92*(4), 1991–2002. https://doi.org/10.1111/brv.12317

Majolo, B., Lehmann, J., de Bortoli Vizioli, A., & Schino, G. (2012). Fitness-related benefits of dominance in primates. *American Journal of Physical Anthropology*, *147*(4), 652–660. https://doi.org/10.1002/ajpa.22031

Marjakangas, E., Santangeli, A., Kujala, H., Mammola, S., & Lehikoinen, A. (2023). Identifying ‘climate keystone species’ as a tool for conserving ecological communities under climate change. *Diversity and Distributions*, *29*(11), 1341–1354. https://doi.org/10.1111/ddi.13764

Markham, A. C., Gesquiere, L. R., Alberts, S. C., & Altmann, J. (2015). Optimal group size in a highly social mammal. *Proceedings of the National Academy of Sciences*, *112*(48), Article 48. https://doi.org/10.1073/pnas.1517794112

McConkey, K. R., Prasad, S., Corlett, R. T., Campos-Arceiz, A., Brodie, J. F., Rogers, H., & Santamaria, L. (2012). Seed dispersal in changing landscapes. *Biological Conservation*, *146*(1), 1–13. https://doi.org/10.1016/j.biocon.2011.09.018

McKechnie, A. E., & Dunn, P. (2019). Physiological and morphological effects of climate change. In *Effects of climate change on birds* (Vol. 120). Oxford University Press Oxford, UK.

Melillo, J. M., Steudler, P., Aber, J. D., Newkirk, K., Lux, H., Bowles, F., Catricala, C., Magill, A., Ahrens, T., & Morrisseau, S. (2002). Soil warming and carbon-cycle feedbacks to the climate system. *Science*, *298*(5601), 2173–2176. https://doi.org/10.1126/science.107415

Mitchell, D., Snelling, E. P., Hetem, R. S., Maloney, S. K., Strauss, W. M., & Fuller, A. (2018). Revisiting concepts of thermal physiology: Predicting responses of mammals to climate change. *Journal of Animal Ecology*, *87*(4), 956–973. https://doi.org/10.1111/1365-2656.12818

Moss, J. B., & While, G. M. (2021). The thermal environment as a moderator of social evolution. *Biological Reviews*, *96*(6), 2890–2910. https://doi.org/10.1111/brv.12784

Natochin, Y. V., Golosov, D. V., & Shakhmatova, E. I. (2018). New functional role of oxytocin–participation in osmoregulation. *Reports of the Academy of Sciences*, *479*(6), 712–715.

Ogutu, J. O., Piepho, H.-P., & Dublin, H. T. (2014). Responses of phenology, synchrony and fecundity of breeding by African ungulates to interannual variation in rainfall. *Wildlife Research*, *40*(8), Article 8. https://doi.org/10.1071/WR13117

Paniw, M., James, T. D., Ruth Archer, C., Römer, G., Levin, S., Compagnoni, A., Che-Castaldo, J., Bennett, J. M., Mooney, A., Childs, D. Z., Ozgul, A., Jones, O. R., Burns, J. H., Beckerman, A. P., Patwary, A., Sanchez-Gassen, N., Knight, T. M., & Salguero-Gómez, R. (2021). The myriad of complex demographic responses of terrestrial mammals to climate change and gaps of knowledge: A global analysis. *Journal of Animal Ecology*, *90*(6), 1398–1407. https://doi.org/10.1111/1365-2656.13467

Paniw, M., Maag, N., Cozzi, G., Clutton-Brock, T., & Ozgul, A. (2019). Life history responses of meerkats to seasonal changes in extreme environments. *Science*, *363*(6427), 631–635.

Pavelka, M. S., Brusselers, O. T., Nowak, D., & Behie, A. M. (2003). Population reduction and social disorganization in Alouatta pigra following a hurricane. *International Journal of Primatology*, *24*, 1037–1055.

Peres, P. A. S., Ferreira, A. P., & Leite, F. P. P. (2018). Expanding the “shell exchange market” hypothesis for clustering behavior in intertidal hermit crabs: Mating and tide as proximate factors. *Journal of Experimental Marine Biology and Ecology*, *500*, 100–104. https://doi.org/10.1016/j.jembe.2017.12.019

Pilakouta, N., O’Donnell, P. J., Crespel, A., Levet, M., Claireaux, M., Humble, J. L., Kristjánsson, B. K., Skúlason, S., Lindström, J., Metcalfe, N. B., Killen, S. S., & Parsons, K. J. (2023). A warmer environment can reduce sociability in an ectotherm. *Global Change Biology*, *29*(1), 206–214. https://doi.org/10.1111/gcb.16451

Prestwich, K. (1994). The energetics of acoustic signaling in anurans and insects. *American Zoologist*, *34*(6), 625–643. https://doi.org/10.1093/icb/34.6.625

Queller, D. C., & Strassmann, J. E. (1998). Kin selection and social insects. *Bioscience*, *48*(3), 165–175. https://doi.org/10.2307/1313262

Rincon, A. V., Deschner, T., Schülke, O., & Ostner, J. (2020). Oxytocin increases after affiliative interactions in male Barbary macaques. *Hormones and Behavior*, *119*, 104661. https://doi.org/10.1016/j.yhbeh.2019.104661

Rosalino, L. M., Martin, P. S., Gheler-Costa, C., Lopes, P. C., & Verdade, L. M. (2013). Allometric relations of Neotropical small rodents (Sigmodontinae) in anthropogenic environments. *Zoological Science*, *30*(7), 585–590. https://doi.org/10.2108/zsj.30.585

Russell, A. F., Langmore, N. E., Cockburn, A., Astheimer, L. B., & Kilner, R. M. (2007). Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science*, *317*(5840), 941–944. https://doi.org/10.1126/science.1146037

Ryding, S., Klaassen, M., Tattersall, G. J., Gardner, J. L., & Symonds, M. R. E. (2021). Shape-shifting: Changing animal morphologies as a response to climatic warming. *Trends in Ecology & Evolution*, *36*(11), 1036–1048. https://doi.org/10.1016/j.tree.2021.07.006

Schradin, C., Makuya, L., Pillay, N., & Rimbach, R. (2023). Harshness is not stress. *Trends in Ecology & Evolution*, *38*(3), 224–227. https://doi.org/10.1016/j.tree.2022.12.005

Schrimpf, Des Brisay Paulson G., Johnston Alison, Smith Adam C., Sánchez-Jasso Jessica, Robinson Barry G., Warrington Miyako H., Mahony Nancy A., Horn Andrew G., Strimas-Mackey Matthew, Fahrig Lenore, & Koper Nicola. (2021). Reduced human activity during COVID-19 alters avian land use across North America. *Science Advances*, *7*(39), eabf5073. https://doi.org/10.1126/sciadv.abf5073

Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of Psychology*, *63*, 153–177. https://doi.org/10.1146/annurev-psych-120710-100337

Sharma, H. S. (2006). Hyperthermia influences excitatory and inhibitory amino acid neurotransmitters in the central nervous system. An experimental study in the rat using behavioural, biochemical, pharmacological, and morphological approaches. *Journal of Neural Transmission*, *113*(4), 497–519. https://doi.org/10.1007/s00702-005-0406-1

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, *20*(15), Article 15. https://doi.org/10.1016/j.cub.2010.05.067

Slater, G. P., Yocum, G. D., & Bowsher, J. H. (2020). Diet quantity influences caste determination in honeybees (Apis mellifera). *Proceedings of the Royal Society B*, *287*(1927), 20200614.

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences*, *102*(15), 5460–5465.

Soravia, C., Ashton, B. J., Thornton, A., & Ridley, A. R. (2021). The impacts of heat stress on animal cognition: Implications for adaptation to a changing climate. *WIREs Climate Change*, *12*(4), e713. https://doi.org/10.1002/wcc.713

Stager, M., Velotta, J. P., Cheviron, Z. A., & Senner, N. R. (2024). Assessing the evidence for treating developmental plasticity and phenotypic flexibility as different phenomena. *Functional Ecology*, *00*, 1–13. https://doi.org/10.1111/1365-2435.14590

Stanton, M. E., Patterson, J. M., & Levine, S. (1985). Social influences on conditioned cortisol secretion in the squirrel monkey. *Psychoneuroendocrinology*, *10*(2), 125–134.

Taylor, S. E., Klein, L. C., Lewis, B. P., Gruenewald, T. L., Gurung, R. A., & Updegraff, J. A. (2000). Biobehavioral responses to stress in females: Tend-and-befriend, not fight-or-flight. *Psychological Review*, *107*(3), 411–429. https://doi.org/10.1037/0033-295x.107.3.411

Turbill, C., Bieber, C., & Ruf, T. (2011). Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1723), Article 1723. https://doi.org/10.1098/rspb.2011.0190

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, *91*(10), 2833–2849. https://doi.org/10.1890/10-0097.1

Uomini, N., Fairlie, J., Gray, R. D., & Griesser, M. (2020). Extended parenting and the evolution of cognition. *Philosophical Transactions of the Royal Society B*, *375*(1803), 20190495. http://dx.doi.org/10.1098/rstb.2019.0495

van Boheemen, L. A., Hammers, M., Kingma, S. A., Richardson, D. S., Burke, T., Komdeur, J., & Dugdale, H. L. (2019). Compensatory and additive helper effects in the cooperatively breeding Seychelles warbler (Acrocephalus sechellensis). *Ecology and Evolution*, *9*(5), 2986–2995. https://doi.org/10.1002/ece3.4982

Van Buskirk, J. (2012). Behavioural plasticity and environmental change. In U. Candolin & B. B. M. Wong (Eds.), *Behavioural Responses to a Changing World: Mechanisms and Consequences* (pp. 145–158). Oxford University Press. https://doi.org/10.1093/acprof:osobl/9780199602568.003.0011

van de Pol, M., Jenouvrier, S., Cornelissen, J. H. C., & Visser, M. E. (2017). Behavioural, ecological and evolutionary responses to extreme climatic events: Challenges and directions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1723), 20160134. https://doi.org/10.1098/rstb.2016.0134

Van de Ven, T. M. F. N., Fuller, A., & Clutton-Brock, T. H. (2020). Effects of climate change on pup growth and survival in a cooperative mammal, the meerkat. *Functional Ecology*, *34*(1), 194–202. https://doi.org/10.1111/1365-2435.13468

Van Zyl, H. M. (1965). The vegetation of the SA Lombard Nature Reserve and its utilisation by certain antelope. *African Zoology*, *1*(1), 55–71. https://doi.org/10.1080/00445096.1965.11447299

Walters, J. R., Passinelli, Gilberto, Cooper, C. B., Schiegg, Karin, & Daniels, S. J. (2004). Conservation biology. In *Ecology and Evolution of Cooperative Breeding in Birds* (pp. 197–209). Cambridge University Press.

Warrington, M. H., Beaulieu, S., Vos, S., Jellicoe, R., Bennett, N. C., & Waterman, J. M. (2022). Personalities are not associated with different reproductive tactics in male Cape ground squirrels, Xerus inauris. *Animal Behaviour*, *193*, 63–74. https://doi.org/10.1016/j.anbehav.2022.08.014

Warrington, M. H., Rollins, L. A., Raihani, N. J., Russell, A. F., & Griffith, S. C. (2013). Genetic monogamy despite variable ecological conditions and social environment in the cooperatively breeding apostlebird. *Ecology and Evolution*, *3*(14), 4669–4682. https://doi.org/10.1002/ece3.844

Wato, Y. A., Prins, H. H., Heitkönig, I. M., Wahungu, G. M., Ngene, S. M., Njumbi, S., & Van Langevelde, F. (2018). Movement patterns of African elephants (Loxodonta africana) in a semi-arid savanna suggest that they have information on the location of dispersed water sources. *Frontiers in Ecology and Evolution*, *6*, 167. https://doi.org/10.3389/fevo.2018.00167

Webster, M. M., & Ward, A. J. W. (2011). Personality and social context. *Biological Reviews*, *86*(4), Article 4. https://doi.org/10.1111/j.1469-185X.2010.00169.x

Wiley, E. M., & Ridley, A. R. (2016). The effects of temperature on offspring provisioning in a cooperative breeder. *Animal Behaviour*, *117*, 187–195. https://doi.org/10.1016/j.anbehav.2016.05.009

Williams, C. M., Henry, H. A. L., & Sinclair, B. J. (2015). Cold truths: How winter drives responses of terrestrial organisms to climate change. *Biological Reviews*, *90*(1), 214–235. https://doi.org/10.1111/brv.12105