Trends in
Ecology & Evolution

CellPress
OPEN ACCESS

Special issue: Animal behaviour in a changing world

Opinion

Social consequences of rapid environmental change

Daniel T. Blumstein [1,*] Loren D. Hayes, [2,*] and Noa Pinter-Wollman [1,*]

While direct influences of the environment on population growth and resilience are well studied, indirect routes linking environmental changes to population consequences are less explored. We suggest that social behavior is key for understanding how anthropogenic environmental changes affect the resilience of animal populations. Social structures of animal groups are evolved and emergent phenotypes that often have demographic consequences for group members. Importantly, environmental drivers may directly influence the consequences of social structure or indirectly influence them through modifications to social interactions, group composition, or group size. We have developed a framework to study these demographic consequences. Estimating the strength of direct and indirect pathways will give us tools to understand, and potentially manage, the effect of human-induced rapid environmental changes.

Highlights

The environment directly influences individual fitness in many species.

The environment influences the adaptive value of sociality both directly and indirectly, influencing individual fitness.

Social relationships are sensitive to anthropogenic environmental changes that include the response to extreme weather, fire, human-created chemicals, etc.

We have developed a framework that permits the study of both direct and indirect pathways by which environmental changes (both natural and artificial) impact fitness and hence population viability.

The framework can be used to identify important targets of management in an increasingly human-altered world.

The Anthropocene is characterized by rapid environmental change

Human-induced environmental changes can be rapid [1] and create novel mismatches between evolved decision rules and the environment, resulting in negative demographic impacts (Figure 1, arrow 1). Anthropogenic effects may act directly and indirectly, through various pathways, to influence demography and population persistence.

One recognized but relatively underexplored pathway involves anthropogenic effects on social behavior. Moss and While [2] and Ruiz-García *et al*. [3] recently offered novel conceptual frameworks for how temperature can impact social evolution and sexual selection, respectively. Blumstein [4] noted that the biosphere impacts the frequency and abundance of resources, which influences the adaptive value of sociality (Box 1) and could have demographic consequences. Fisher *et al*. [5] highlighted three general themes for animal responses to human-induced environmental change: (i) destabilization of **social systems** (see Glossary) due to limited energy availability in arid, variable, polluted, or fragmented habitats; (ii) variability of responses depending on natural history; and (iii) simultaneous changes in multiple environmental factors, resulting in antagonistic or synergistic effects. Komdeur and Ma [6] emphasized that sociality allows for flexible responses and acclimation to environmental change. However, an integrated examination of how the behavioral mechanisms underlying sociality are impacted by anthropogenic effects directly and indirectly, and the demographic consequences of these effects, is still lacking. Such integration into a single framework allows us to dissect the temporal and spatial scales at which various processes occur and uncover feedback between social behavior and anthropogenic changes.

We propose a framework in which sociality is viewed as a trait that can be studied from different interconnected perspectives. The size, composition, and stability of a group [7] can impact the types of social, mating, and parental care interactions within and between social units (Box 1). Social, sexual, and parent–offspring interactions are impacted by the environment in similar

[1]Department of Ecology and Evolutionary Biology, 621 Young Dr. South, University of California, Los Angeles, CA 90095-1606, USA
[2]Department of Biology, Geology, and Environmental Science, University of Tennessee at Chattanooga, Chattanooga, TN 37403, USA

*Correspondence:
marmots@ucla.edu (D.T. Blumstein), loren-hayes@utc.edu (L.D. Hayes), and nmpinter@ucla.edu (N. Pinter-Wollman).

ways because they are forms of social interactions. Therefore, we focus our framework on how social behavior is affected by the environment by examining direct effects on social interactions, or indirect effects through their influence on social structure. Ultimately, we tie the effects on social interactions to demography and population persistence in response to anthropogenic changes (Figure 1).

We structure our discussion around the logical flow presented in Figure 1, which illustrates the direct and indirect pathways in which **environmental drivers** influence social interactions and their consequences at both the individual (i.e., fitness) and population (i.e., population growth rate) levels. An increasingly common way to quantify animal social structures is using **social network analysis** (Box 2 and references therein), which formally quantifies a variety of social attributes [8] that may have conservation relevance [9] and can incorporate information about the nature of interactions [10] and the consequences of those interactions, such as the ease with which information or disease can travel among individuals in a group [11,12]. Both an individual's position in a social network [13,14], as well as the social unit's structure [15] may have a variety of fitness consequences (Box 2). In the following sections we illustrate evidence of each of these links and suggest that to properly understand anthropogenic influences on fitness and population biology, we should examine the strength of the direct and indirect pathways and the potential feedback between consequences and drivers.

Environmental drivers directly shape social interactions

Environmental variables directly influence the ways in which individuals interact (Figure 1, arrow 2). Broadly we may wish to classify putative drivers as: (i) reflecting different distributions of environmental parameters (temperature, rainfall, etc.) that might be expected by climate change; (ii) the modification of habitat (e.g., fragmentation, agriculture); and/or (iii) the addition of novel or enhanced stimuli (e.g., chemical, sound, or light pollution). Studies of how different environmental variables influence animal interactions are reviewed in detail by Fisher *et al*. [5]. In the Anthropocene, we expect more extreme droughts, floods, and fires [16,17], all of which might influence how animals move through their environment (e.g., due to habitat loss and fragmentation, or changes to activity patterns) and either create novel interaction opportunities or isolate animals from each other. For example, storms can concentrate individuals who huddle for thermoregulatory benefits or isolate individuals that possess defensible space, such as burrows. Environmental chemicals, particularly non-metabolized pharmaceuticals, can directly modify social predispositions [18]. Indeed, the field of behavioral ecotoxicology capitalizes on the ways in which chemicals modify social behaviors that can be monitored and from which inferences can be drawn about local pollution [19]. **Endocrine disrupting chemicals** found in plastics that leach into water systems mimic steroid hormones and can have direct and indirect effects on social behavior [20,21]. The environment also works indirectly in at least two ways to influence social interactions, by affecting group size and group composition (Figure 1, arrows 3 and 4), which we discuss in following sections.

Environmental drivers indirectly shape social interactions by modifying group size

Environmental variables could influence the nature of interactions indirectly through impacts on group size (Figure 1, arrow 3). A sudden heat wave, or a toxic spill that increases mortality directly reduces the number of individuals that can interact. Droughts may reduce reproductive success, reducing recruitment, which can bias age structure and decrease the number of individuals available for interactions. In obligately social species, modified group sizes have a profound influence on sociality because the number of individuals one interacts with may impact, for example, the amount of social information that is available to them [22]. Additionally, many network statistics

Glossary

Communal breeding: a form of social organization in which reproduction among group members is relatively equitable (low skew) and breeders provide care to nondescendent offspring.

Cooperative breeding: a form of social organization in which reproduction among group members is inequitable (high skew) and nonbreeders provide alloparental care to nondescendent offspring.

Endocrine disrupting chemicals: artificial substances that interfere with the normal function of the endocrine system by resembling the structure of hormones and thus binding to hormone receptors.

Environmental drivers: we use the term broadly to refer to climatic (e.g., precipitation, storms, fires) or other environmental factors (nutrient loading, pollution) whether natural or unnatural, that may influence demography directly or indirectly by affecting social behavior.

Social network analysis: a quantitative tool used to analyze social interactions. Network statistics can describe an individual's position in its group, as well as the overall structure of the group. Such measures may be correlated with fitness and thus are demographically important.

Social system: animal societies, characterized by four interrelated components: social organization, mating system, parental care system, and social structure (Box 1).

Structural equation modeling: when experiments are not logistically or ethically possible, causality can be assessed using formal structural equation models applied to longitudinal datasets. Statistical developments now allow us to conduct path analysis with unbalanced repeated measures data sets and without many assumptions that were historically necessary. Such analyses can be used to identify the relative strength of direct and indirect pathways through which the environment influences demographic parameters and thus ultimately may influence population persistence.

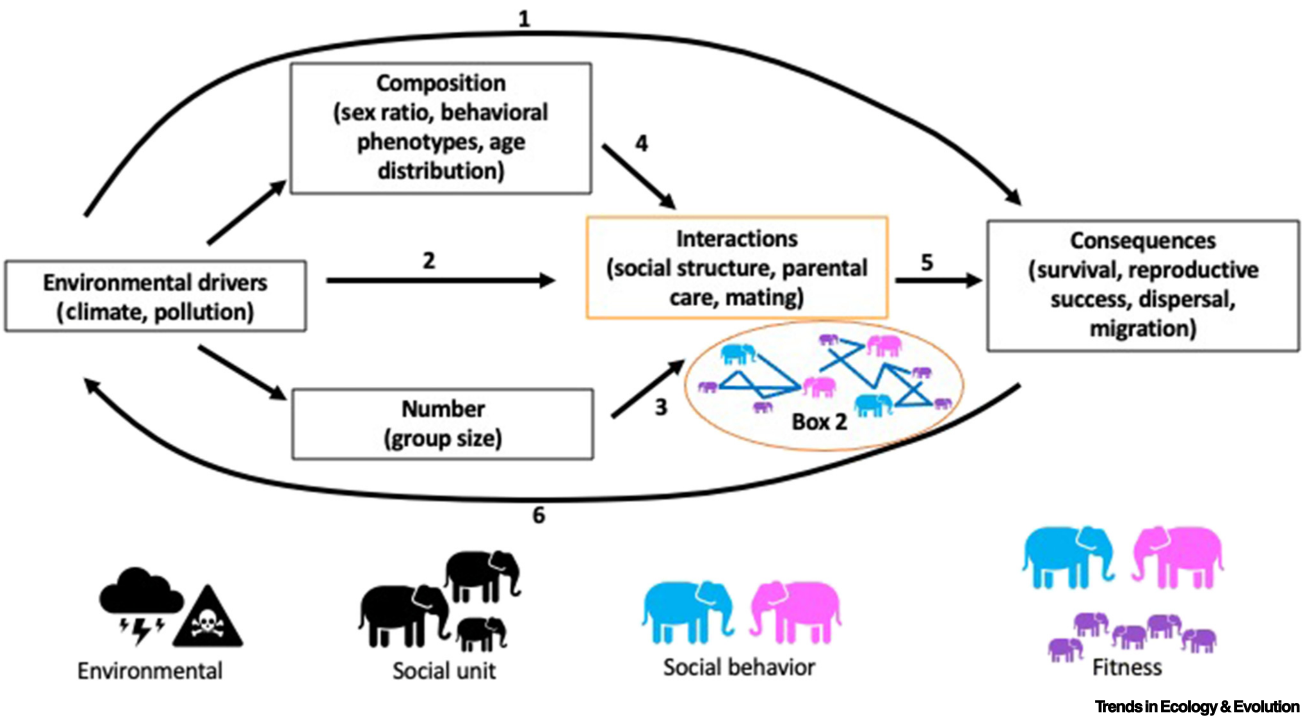

Figure 1. Framework for examining how environmental drivers impact social structure both directly and indirectly to influence fitness consequences and hence population viability. See also Box 2.

are explicitly a function of group size [23] (Box 2) and as group size decreases social complexity often decreases. Changes to group size are likely less important for facultatively social species. For example, facultatively social yellow-bellied marmots (*Marmota flaviventris*) pay costs of social integration (e.g., less social females live longer lives [24] and have higher reproductive success [25] and less social marmots are more likely to survive hibernation [26]). However, obligately social species evolved to benefit from social interactions. Therefore, strong social relationships seem to be associated with increased longevity only in obligately social species [27].

Environmental drivers indirectly shape social interactions by modifying group composition

Environmental variables may influence the nature of interactions indirectly through impacts on the behavioral composition of a social group (Figure 1, arrow 4). Variation among individuals in a group can take many forms, including behavioral, morphological, and demographic [7], and emerge from variation at different levels of organization [28]. In species that have a mechanism of temperature-dependent sex determination [29], heat waves during egg incubation will modify the sex ratio in the population and therefore impact sex-specific social interactions. Temperature can mediate the energy available for key behaviors [30]. Individuals differ in their behavior and variation in behavioral phenotypes within a population is influenced by the environment [31]. High predation or population density can select for individuals with certain behavioral predispositions (e.g., risk aversion), which will subsequently influence the nature and outcomes of social interactions. For example, the loss of an elephant (*Loxodonta africana*) matriarch results in lost information about seldom-used water holes, leading to calves dying in a drought [32]. Differential exposure to environmental chemicals will lead to variation among individuals in behavior, which may result in different social interactions based on whether or not the behavior of individuals was affected by the chemicals in the environment.

Box 1. What is sociality?

Animal social systems consist of four interrelated components: social organization, mating system, care system, and social structure (Figure I) [9]. Delineating these four components of a social system clarifies the unit of observation, such as equating social monogamy to pair-living [64] or including social hierarchies under the umbrella of social organization [5]. This delineation further provides a clear foundation for making predictions about the social underpinnings of variation in individual fitness, such as benefits associated with group size (e.g., dilution) and cooperation (e.g., cooperative defense of young). Because changes in one component of the social system (e.g., death of a key group member) can influence other components (e.g., social, mating, or parental–offspring interactions), a changing environment can impact the survival and reproductive success of individuals through multiple ways (see Figure 1 in main text).

For example, changes in social organization can weaken social interactions [65], result in heightened aggression within groups [66], and impact social hierarchies [67]. Disruption of social relationships could have negative fitness consequences [68] and impact the persistence of populations. Limited evidence suggests that changes in social organization can alter the mating and care systems and, thus, female fitness. The dearth of studies examining links between social organization, mating systems, and care systems indicates an important area of future research.

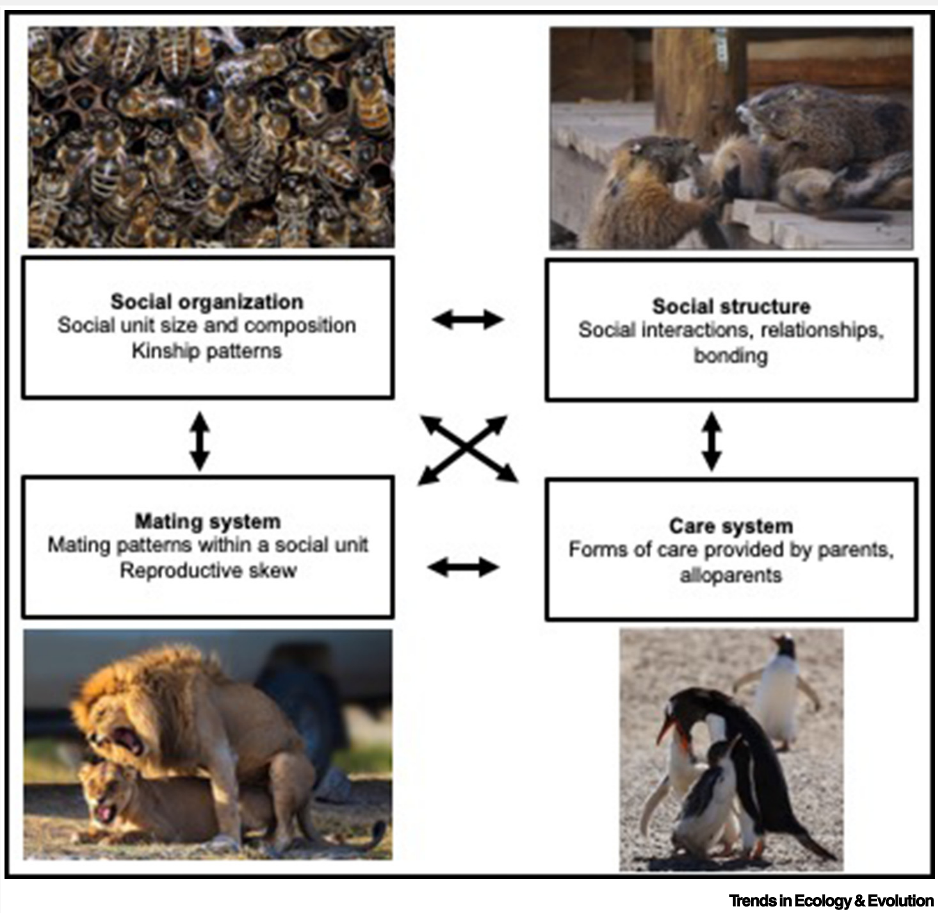

Figure I. Animal social systems following Kappeler [78]. Arrows indicate that social system components are interconnected. Photo credits [start top left, clockwise: *Apis mellifera* by Quartl, CC BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0), via Wikimedia Commons; *Marmota flaviventris*, photo credit Alexandra Jebb; *Pygoscelis papua* by Liam Quinn, Canada, CC BY-SA 2.0 (https://creativecommons.org/licenses/by-sa/2.0), via Wikimedia Commons; and *Panthera leo* by Ankit Gita, (https://creativecommons.org/licenses/by/2.0), via Wikimedia Commons].

Box 2. How can we use social network analysis to examine the social consequences of rapid environmental change?

Studies of social animals have increasingly used social network analysis to quantify and examine changes in sociality [8,69]. Social networks describe interactions among individuals (see Figure 1 in main text) by linking individuals (nodes) that interact with one another (edges). The number of individuals in a group is reflected in the size of the network (i.e., the number of nodes) [23]. Network size impacts certain network measures such as connectivity and diameter but can also be accounted for when quantifying network-level measures such as density and reciprocity [15]. Thus, by using either type of measure, one can ask different types of questions when comparing the social networks of different populations or changes in networks over time. Group composition is reflected in the attributes of the individual, such as age, size, sex, behavior, etc. These attributes can be used to examine the relationship between the social position of individuals and their attributes. Specifically, a wide variety of network centrality measures [8] have been used to quantify the social position of animals. The formation of social interactions can be studied by using generative models (as detailed in [70]). Thus, using social network analysis provides the quantitative tools to quantify sociality and therefore to dissect changes in sociality in response to environmental changes. The analysis of temporal changes in social networks is a growing field of study and different approaches have been proposed to study network dynamics in animal behavior, including time ordered analysis [71], dynamic community analysis [72], stochastic actor-oriented models [73], multilayer networks [10], and others.

Social network analysis further allows connecting social behavior with demographic processes, as reviewed in [60], and shown empirically in equids [74]. Examining the feedback between demographic consequences of changes in sociality due to environmental changes can be done with the help of social network analysis. Different types of networks (spatial and social) can be linked using multilayer networks [75]. Modeling changes in group size and composition with agent-based models [70] can be used to simulate, for example, the loss of individuals and determine the extent to which sociality facilitates or hinders resilience to environmental changes.

Social interactions have demographic consequences

The integration of group size, composition, and social interactions results in fitness consequences, which can impact population resilience (Figure 1, arrow 5). Cooperative relationships can reduce physiological stress during periods of social unrest [33], lower the risk of predation [34], and promote social foraging [35], which can enhance resource acquisition [36]. By contrast, conflict over resources and mates can drive social instability and have negative fitness consequences to some group members. Social interactions that reduce conflict among group members [13] can maintain social hierarchies and enhance the success of groups. The threat of conflict between groups can facilitate strong cooperative relationships among group members, which are critical to keeping or expanding territories.

There is need to develop methods to uncover how sociality shapes the fitness consequences of environmental conditions. The evolution of group-living has repeatedly been associated with harsh environments [37–40] that favor reduced social conflict and increased cooperation [41]. Alloparental care in **cooperative breeders** enhances reproductive success [42]. **Communal breeding** enhances reproductive success under conditions of high rainfall [41] and low food availability [43], but not in hot years with drought [44]. Survival benefits of group-living in harsh environments differ between males and females [45] and changes to the environment drive shifts from peaceful to aggressive interactions within or among groups [46]. As described later, there may be fitness consequences of specific social attributes. The challenge remains to identify whether the nature and strength of environmental drivers' effect on fitness is direct or indirect, though social relationships are important. **Structural equation modeling** [47,48], because it permits the evaluation of direct and indirect pathways, may be particularly useful to estimate the strength of these putative drivers on specific demographic traits.

There are feedbacks between fitness consequences and environmental drivers

Social living may buffer the effects of environmental changes, creating a potential for feedback between the consequences of social behavior and environmental change (Figure 1, arrow 6). Living in groups can promote social flexibility necessary to respond to a changing climate or other environmental perturbations [6]. Furthermore, many social species are known for niche construction [49]. Social insects construct or excavate nests that can buffer changes in temperature, humidity, and exposure to predators [50], all of which have fitness consequences. An inclusive view of niche construction [51] suggests that movement allows animals to construct their niche, by changing where they live. Through movements and physical modifications to the environment, some animals can shape where they live and change the impacts induced by changes to the environment [52]. Environmental changes that impact the ways in which animals construct their niche (e.g., through changes to social interactions), may lead to either an exacerbation of the effects of environmental changes or a reduction in their effect [53]. If environmental changes impact social behavior in a way that reduces a society's ability to construct its niche, or if niche construction is fixed and does not respond to environmental change [54], then the construction will become less effective at buffering environmental change, eventually leading to a mismatch between the environment and the constructed niche. However, if the environment impacts social behavior in a way that leads animals to adjust their niche construction to mitigate the effects of environmental changes [55], then social behavior could lead to increased resilience in a changing world. Thus, niche construction can mediate the feedback between environmental changes and the demographic and fitness consequences of social interactions.

Responses to environmental change will differ across systems, spatial and temporal scales, and according to the magnitude of the perturbation

How environmental conditions impact social structure will differ across taxa and socio-ecological contexts, just as it differs across individuals [31]. Species differ in the environmental changes they experience (e.g., aquatic vs. terrestrial), different altitudes and latitudes, etc. Differences in the social structure among species will result in different impacts of environmental changes, with more loosely social species being impacted differently than tight social groups [27]. Thus, both the natural history and the ecological setting of a species need to be taken into consideration when evaluating the effects of environmental changes on social structure. There could also be synergistic and cumulative effects of a variety of impacts and developing frameworks to understand these effects is essential.

The spatial extent of an environmental perturbation could determine the way it impacts social structure. The Anthropocene is characterized by more extreme weather; in many parts of the world this will lead to droughts that will be followed by fires, in other parts of the world this will lead to more frequent and intense storms and flooding. For example, large wildfires (Box 3) and extreme storms may impact entire populations [56]. Such impacts at the population level may alter both groups sizes and composition, by changing which, and how many, animals are available to form groups, as well as the kind of interactions among remaining individuals [57]. By contrast, local perturbations, like logging and urbanization, might impact only parts of a population or only some individuals in a social group. By influencing a subset of individuals in a population, environmental disruptions at small spatial scales might impact who interacts with whom and the ways in which individuals interact but potentially have a smaller impact on group size and composition. The size of an impact needs to be scaled to the space used by the focal species [52]. A local change for certain species might be considered global for species with small distributions [58].

When and for how long an environmental perturbation occurs can impact how it influences social behavior. The extent to which a perturbation impacts organisms likely depends on the timing relative to species-specific life histories [59]. For example, exposure to endocrine disrupting chemicals within a critical developmental window can alter neural pathways underlying sociosexual behaviors and disrupt social interactions [21]. The effect of an environmental change on dispersing juveniles may be greater than on established adults. Habitat fragmentation and loss

Box 3. Wildfires: a worked example of anthropogenically driven environmental change

Wildfires are an emerging human-induced environmental change with far reaching impacts on the natural world [76]. The impacts of wildfires range across spatial and temporal scales. Immediate impacts include the impairment or removal of individuals from a population. Long-lasting effects include the removal of suitable habitat and potentially adding barriers to succession and habitat recovery. For example, after wildfires there is an increased risk of mudslides that can change landscapes, impacting the recovery of the habitat to its previous structure. Spatially, wildfires have been growing over the past decades, impacting larger and larger areas and, therefore, a greater number of animals.

The scale, both spatial and temporal, at which a wildfire impacts the environment can have different implications for social animals. Particular individuals might be less likely to survive a fire, for example, if they move more slowly than others. Young animals or individuals caring for offspring might not be able to escape a wildfire as fast as speedy adults that are not caring for young. Removal of particular individuals from the population based on their behavior can lead to changes in the sex ratio and/or behavioral composition of a population and therefore impact group size and composition and the consequences of sociality. Even if the composition of a population is not impacted directly or immediately by a wildfire, the long-term environmental impacts left in the wake of a fire could alter the ability of animals to form groups and interact. For example, by creating open habitats that some individuals might be less likely to cross than others or through the loss of food sources that might have greater impacts on individuals with higher metabolic needs.

The spatial scale of a wildfire can further determine its impact on social behavior [76]. Smaller fires might remove a few individuals from a population or a group, thus impacting the size and composition of a group. Larger fires may decimate entire groups and separate populations, alerting the ways in which animals leave and join groups and potentially opening habitats into which surviving groups can expand. Indirectly, smoke from wildfires could affect social interactions (e.g., song bird communication) and animal movements far beyond the fire zone [77].

Finally, through niche construction, social animals that live in underground burrows may be more resilient to wildfires and variation among groups in nest construction may result in differential survival after a fire.

With the growing frequency of wildfire throughout the world, uncovering the impacts of wildfires on social behavior and the ability of sociality to potentially buffer the impact of fires is critical for conservation efforts.

of suitable territory will impact how dispersing individuals search for a new home and where they settle [52], thus impacting with whom they will interact and form social bonds. Changes that occur during particular seasons, such as when animals search for mates, will have a greater impact on both immediate social behavior and long-term population structure than changes that occur at other times of year [60]. The impact of slow changes to the environment, such as gradual increases in average temperature over time or accumulation of toxins, may alter population structure [59], which will influence group composition and size. Such slow acting changes may not be immediately apparent when examining social interactions. By contrast, rapid environmental changes, like poisonings or novel diseases, that remove individuals from the population or alter their behavior, will have immediate impacts on social interactions with or without longer term consequences for group composition and size [60].

The magnitude of an environmental perturbation can influence how social interactions are impacted. For example, loud urban sounds can profoundly interrupt the communication of social species and thus their immediate interactions [61]. Oil spills can affect the spacing between social marine animals [62], which could, in turn, influence communication and social cohesion. Other disruptors may have smaller magnitudes that are only impactful after accumulation, such as chemicals that at small amounts have no or little impact but in large amounts after accumulation can lead to physiological changes [18]. While a single stressor may have limited impact alone, combined with others there may be cumulative impacts that have significant deleterious effects [63].

Concluding remarks

We have outlined a framework that links environmental variation to demographic changes through social behavior. We highlight the importance of examining the direct and indirect impacts of environmental changes on social structure by dissecting influences on group membership,

Outstanding questions

What are the relative strengths of direct and indirect pathways by which the environment influences demographic parameters, and hence population viability, through social behavior?

Are some social structures more resilient to environmental perturbations than others?

Are social relationships less susceptible to natural variation in environmental drivers (e.g., patterns of precipitation) than to human-induced environmental drivers (e.g., novel anthropogenically created chemicals)?

Can insights about the ways in which environmental factors influence sociality be used to buffer its effects on demography and population viability?

How will climate variation impact developmental pathways underlying interindividual variation in behavior?

Does social flexibility promote resilience in changing climates?

How do environmentally driven disruptions to social relationships impact mating and parental care?

What is the role of key individuals in the resilience of social groups to environmental perturbations?

To what extent are species with different breeding systems (e.g., cooperative breeding, communal breeding) at risk of extinction due to changing climate?

Under what conditions does niche construction reduce or exacerbate the effects of environmental change on social behavior?

size, and social interactions. The relationship between environmental changes and social behavior has important consequences both at the individual and population levels. These consequences may allow social species to overcome environmental changes and even lead to feedback that alters the environmental change. The impact of environmental change on the outcomes of social behavior should be considered within the ecological context of each species and account for the spatial and temporal scales of disruption. Future work (see Outstanding questions) uncovering the strength of the direct and indirect pathways acting through sociality on individual fitness and hence population viability may have concrete conservation management implications.

Author contributions

All authors conceived and wrote this paper.

Declaration of interests

No interests are declared.

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