

Anticipated effects of abiotic environmental change on intraspecific social interactions

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ABSTRACT

Social interactions are ubiquitous across the animal kingdom. A variety of ecological and evolutionary processes are dependent on social interactions, such as movement, disease spread, information transmission, and density-dependent reproduction and survival. Social interactions, like any behaviour, are context dependent, varying with environmental conditions. Currently, environments are changing rapidly across multiple dimensions, becoming warmer and more variable, while habitats are increasingly fragmented and contaminated with pollutants. Social interactions are expected to change in response to these stressors and to continue to change into the future. However, a comprehensive understanding of the form and magnitude of the effects of these environmental changes on social interactions is currently lacking. Focusing on four major forms of rapid environmental change currently occurring, we review how these changing environmental gradients are expected to have immediate effects on social interactions such as communication, agonistic behaviours, and group formation, which will thereby induce changes in social organisation including mating systems, dominance hierarchies, and collective behaviour. Our review covers intraspecific variation in social interactions across environments, including studies in both the wild and in laboratory settings, and across a range of taxa. The expected responses of social behaviour to environmental change are diverse, but we identify several general themes. First, very dry, variable, fragmented, or polluted environments are likely to destabilise existing social systems. This occurs as these conditions limit the energy available for complex social interactions and affect dissimilar phenotypes differently. Second, a given environmental change can lead to opposite responses in social behaviour, and the direction of the response often hinges on the natural history of the organism in question. Third, our review highlights the fact that changes in environmental factors are not occurring in isolation: multiple factors are changing simultaneously, which may have antagonistic or synergistic effects, and more work should be done to understand these combined effects. We close by identifying methodological and analytical techniques that might help to study the response of social interactions to changing environments, highlight consistent patterns among taxa, and predict subsequent evolutionary change. We expect that the changes in social interactions that we document here will have consequences for individuals, groups, and for the ecology and evolution of populations, and therefore warrant a central place in the study of animal populations, particularly in an era of rapid environmental change.

Key words: climate change, communication, dominance, environmental variation, habitat fragmentation, mating systems, pollution, social interactions, social network

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I. INTRODUCTION

Almost all organisms engage in social interactions with conspecifics, whether they are actively gregarious or not (Frank, 2007). These interactions can include mating, fighting, communicating, cooperating, and moving with

conspecifics. The variety of social interactions represents a key axis of biological diversity among taxa, populations, and individuals (Lott, 1991; Székely *et al.*, 2010; Rubenstein & Abbot, 2017). Social interactions are well understood to have fundamental effects on the phenotypes and fitness of individuals (Allee, 1931; Allee *et al.*, 1949) as well as the collective

behaviour of groups (Farine *et al.*, 2017; Strandburg-Peshkin *et al.*, 2017; Hunt *et al.*, 2018). Social interactions can even change the genotype–phenotype relationship by allowing genes in one individual to influence another (indirect genetic effects; Moore, Brodie & Wolf, 1997), and by allowing phenotypes of individuals to influence the fitness of others (social selection; Westneat, 2012). It is therefore clear that social interactions can be a key driving force in ecological and evolutionary processes.

An organism's behaviour, however, is rarely independent of its environment. It is well established that behaviours often show some degree of plasticity in conjunction with consistent individual differences (Dall, Houston & McNamara, 2004; Bell, Hankison & Laskowski, 2009; Dingemans *et al.*, 2010), where the expression of behaviour depends on the environmental context (Pigliucci, 2005; Stamps, 2016). Social behaviours are expected to be no different and so are likely to vary in predictable ways with changing conditions. Changes in social interactions will then have profound consequences for the evolutionary and ecological processes they play a role in. Therefore, a more comprehensive understanding of the effects of environmental variation on multiple components of social interactions is needed.

The scale of rapid environmental change currently occurring on our planet is vast. Temperatures, especially in polar regions, are increasing, as is the frequency of extreme events such as cyclones, droughts, floods, and fires. Meanwhile, habitats are being changed, fragmented, and destroyed by human activity. Light, noise, and chemical pollution are degrading terrestrial, freshwater, and marine environments, and atmospheric changes are altering the chemistry of the seas (Easterling *et al.*, 2000; Hughes, 2000). These changes, often referred to as human-induced rapid environmental change (HIREC) are expected to cause a suite of plastic and evolved responses in animals (Tuomainen & Candolin, 2010; Sih, Ferrari & Harris, 2011), which, of course, extends to social interactions. Given the ubiquity of social interactions, understanding how sociality of all forms will change in the future is an essential component of understanding the effects of rapid environmental change on biodiversity (Hughes, 2000).

Currently, we lack a large-scale overview of expected responses of social behaviours to environmental change. Previous reviews on climate change and social interactions have enhanced our knowledge on the effects of rapid environmental change by focussing on a particular aspect of environmental change, type of social interaction, or taxonomic group. For instance, Lane, Forrest & Willis (2011) considered specifically how anthropogenic disturbances can influence mating systems, Kurvers & Holker (2014) reviewed how light pollution may influence social interactions, while Banks *et al.* (2007) considered how social behaviours are influenced by habitat fragmentation. Meanwhile, Wong (2012), Moss & While (2020), and Blumstein (2012) have outlined more broadly how various abiotic stressors can influence social interactions from a more conceptual standpoint. These studies and reviews have improved our understanding of the

potential social consequences of specific human-induced environmental changes. However, there are many potential environmental variables that have not been explicitly considered, such as increases in the incidence of extreme events and the variability of weather (Bailey & van de Pol, 2016). Importantly, there have been no attempts to date to synthesise across major axes of environmental change as well as multiple taxonomic groups to gain a more holistic understanding of how social interactions, and social systems in general, are expected to change in response to rapidly changing ecosystems.

In this review, we summarise existing information about how the environmental changes anticipated in the coming decades are expected to affect social dynamics across a diversity of animal taxa. We identify general themes and suggest productive avenues for future research. We focus on four categories of expected abiotic environmental change: (i) increases in temperature (including increases in temperature and dryness, earlier springs in the northern hemisphere and reduced snow cover); (ii) increases in pollution (including light, noise, and chemical pollution); (iii) habitat fragmentation (including changes in habitat complexity and gaps between habitat patches); (iv) more variable weather (including variation in temperature and rainfall) and the increased incidence of extreme events. These categories of change are based on those identified by international reports (Meehl *et al.*, 2000; Bindoff *et al.*, 2013; Field *et al.*, 2014) as well as other reviews on the impacts of changing climates on organisms (Walther *et al.*, 2002; Tuomainen & Candolin, 2010; Hoffmann & Sgrò, 2011; Sih *et al.*, 2011; Poloczanska *et al.*, 2013). We have not considered how changes in overall population density, or changes in interspecific interactions (e.g. predation from novel species as ranges shift) might influence social interactions. We exclude these to separate the abiotic predictor variables clearly from the anticipated biotic response variables [see Blumstein, 2012 who does discuss these factors]. Furthermore, while individuals may influence each other indirectly, such as by consuming resources which others then cannot use, we do not consider these interactions here as such behaviours are not targeted directly at other individuals. We discuss specifically intraspecific variation in social behaviours in response to the four kinds of abiotic environmental changes. Focusing on intraspecific variation reduces the confounds of phylogenetic signals in the distribution of social behaviours across different environments by considering only within-species trends. We include information from four types of studies: (i) those that compare treatment groups or conduct paired studies showing within-individual responses to environmental variables in laboratory settings; (ii) studies where populations of the same species living in different conditions are compared; (iii) common garden or translocation studies where animals are moved between environments with equivalent or different conditions; and (iv) studies where a single population exposed to changing conditions over time is monitored. Each of these different kinds of studies provide valuable information about how individuals and populations respond to environmental

change. Where possible, we also note where interspecific trends might be informative for understanding intraspecific ones.

Within each broad class of environmental change, we have identified one or two main themes for how we expect social interactions to be modified. These themes differ among sections and serve to draw together existing studies and highlight areas for future work. We further partition the consequences of rapid environmental change into two levels: change in direct social interactions between individuals and change in the organisation of groups and populations (see Fig. 1 for a schematic outlining the structure). We follow this structure as Hinde (1976) described how animal societies can be examined both by looking at the behaviour of individuals, but also looking at the overall social organisation; both levels must be considered to obtain the full perspective of a social structure. At each scale, we have grouped the predicted consequences into classes of behaviours. For social interactions, we discuss consequences for inter-individual communication, social grouping and associations, and agonistic interactions. For social organisation, we explore how mating systems, dominance hierarchies, and collective behaviour will be affected by climate change. By considering multiple environmental changes and levels of predicted consequences, we can explain better how various avenues of

environmental change alter social interactions, social organisation, and scale up to influence ecological and evolutionary processes.

II. INCREASED TEMPERATURES

One of the best-established consequences of HIREC is that average temperatures and dryness are expected to increase. Increases in temperature frequently alter social interactions by altering the energetic balance of organisms. Thermal stress can limit the energy available for social behaviours, whereas increased warmth can in some cases alleviate energetic constraints, leading to a higher frequency of energetically costly social behaviours such as communication and aggression. We discuss how increasing temperature and dryness can either prevent single individuals from maintaining homeostasis thereby leading to more cooperative breeding or in other cases can prevent grouping and collective behaviour due to energetic limitations. We also discuss how increasing temperatures are likely to lift movement constraints for organisms where social behaviours, such as mate-searching behaviours, may be hampered by cold conditions. We note throughout how the specific changes can

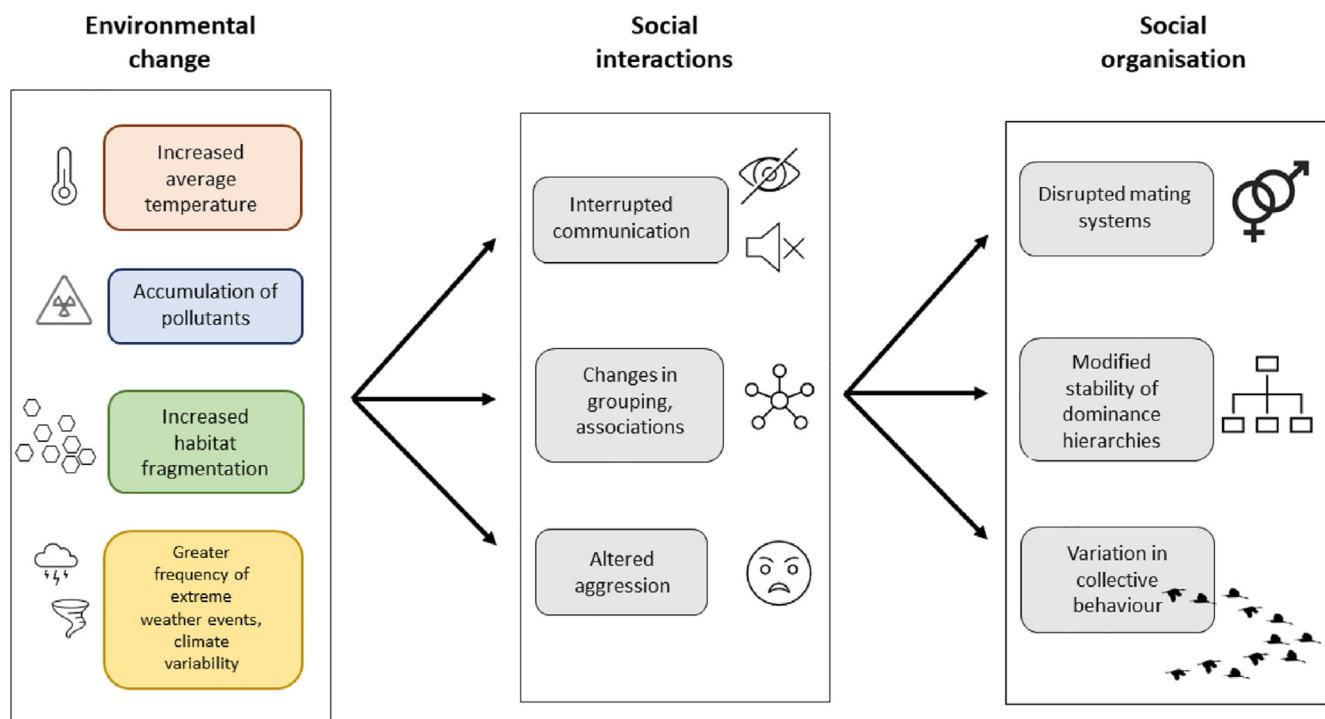


Fig 1. A schematic outlining the structure of our review. The ‘environmental change’ box describes the four main predicted environmental changes due to climate change focused on in this review. The ‘social interactions’ box describes how the environmental changes will interrupt social interactions between individuals, including the efficacy of communication between individuals, the formation of groups and associations, and the intensity of agonistic interactions. The ‘social organisation’ box represents the cascading effects of the changes in social interactions on patterns of social organisation, in terms of mating systems, dominance hierarchies, and collective behaviour.

depend on the ecology and natural history of the organism, with some general rules apparent.

(1) Social interactions

(a) Communication

Increased temperatures can in many cases relieve the physiological constraints animals are under, leading to increased rates of acoustic signals (Brenowitz, 1986). For example, tree crickets (*Oecanthus* spp.) on days of higher temperatures send acoustic signals with increased pulse rates (Symes, Rodríguez & Höbel, 2017), while ovenbirds (*Seiurus aurocapilla*) increase song output at dawn on warmer days (Foote, Nanni & Schroeder, 2017). An increase in acoustic signalling rate at higher temperatures is therefore expected in various organisms (Prestwich, 1994).

Increased temperatures can also affect visual signals which might be under energy limitations, but there is less work on this. Exactly how signal expression changes with temperature may depend on whether high temperatures facilitate expression or whether signal expression is initially energetically limited. For instance, the intensity of ultraviolet colouration in sexual signals is higher in male green lizards (*Lacerta viridis*) exposed to higher temperatures in captivity, possibly as the nanomolecules responsible for the structural colour are easier to produce at higher temperatures (Bajer *et al.*, 2012). In fireflies (*Photinus* spp. and *Luciola* spp.), flash duration and inter-flash intervals decrease as ambient temperature increases, likely as a result of faster enzymatic reactions at higher temperatures [which may be matched by a coupled change in female preference (Carlson *et al.*, 1976; Michaelidis, Demary & Lewis, 2006; Iguchi, 2010; Sharma *et al.*, 2014)]. In other cases, increased temperature and dryness may lead to food limitation, which can also affect energetically costly visual signals. For example, American redstart (*Setophaga ruticilla*) have brighter and less-red plumage in years when temperatures are high (and rainfall low) during the post-breeding moult, which is suggested to be due to lower carotenoid-rich insect prey availability in warmer and dryer conditions (Reudink *et al.*, 2015). In aquatic systems higher temperatures lead to hypoxia, which can also decrease energetically expensive behaviours such as communication. For example, captive male Siamese fighting fish (*Betta splendens*) have lower rates of opercular displays in hypoxic water compared to individuals in normoxic water as the displays interfere with water passing over the gills (Abrahams, Robb & Hare, 2005).

Chemical signals are likely to be altered in warmer environments as many parts of the chemosensory system, from initial biosynthesis to detection, are sensitive to changes in temperature (Groot & Zizzari, 2019). For example, Chinese pond turtles (*Geoclemys reevesii*) lose the ability to discriminate between pairs of similar molecules when experimentally exposed to high temperatures, probably due to an increase in the fluidity of cell membranes in the turtle olfactory epithelia (Hanada, Kashiwayanagi & Kurihara, 1994), while male

Orchesella cincta springtails produce spermatophores that are less attractive to females when exposed to artificially high temperatures compared to control males, suggesting they are not producing the correct sexual signals [Zizzari & Ellers, 2011; see Groot & Zizzari, 2019 for a review on the impact of warming on chemical signalling]. Further, while not strictly speaking a case of energetic limitation, chemical signalling can be altered by increased temperatures as the process of degradation occurs faster at high temperatures. For example, in the ant *Tapinoma nigerrimum*, workers distinguish less between marked and unmarked routes in laboratory tests at higher temperatures, suggesting that chemical signals evaporate and degrade faster with increasing temperature (Van Oudenhove *et al.*, 2011). In a mountain lizard, *Iberolacerta monticola*, laboratory studies show that male chemical signals incubated at higher temperatures attracted less interest from other males (Iglesias-Carrasco *et al.*, 2018), and male *Iberolacerta cyreni* scent marks were less attractive to conspecific females (Martin & López, 2013), suggesting that they degrade faster. However, no effect of temperature on the effectiveness of scent marks was found in two other lizard species (*Podarcis muralis* and *Iberolacerta bonalli*; Iglesias-Carrasco *et al.*, 2018). Therefore, despite some evidence that chemical signals are negatively affected by temperature changes, there are not many empirical examples to provide conclusive evidence, and more work is needed (Boullis *et al.*, 2016; Henneken & Jones, 2017). In particular, animals that use chemical communication over long distances, where the chemical may be exposed to the environment for longer, may be the most affected, and so the most worthy of study (Boullis *et al.*, 2016).

(b) Social grouping and associations

For small organisms that group to maintain homeostasis, warming temperatures can relieve energetic constraints and therefore lead to reduced grouping. For example, observational studies indicate that small-bodied birds such as common bushtits (*Psultriparus minimus*), goldcrest (*Regulus regulus*), willow tits (*Parus montanus*), and house sparrows (*Passer domesticus*) form larger huddles on colder days (Smith, 1972; Hogstad, 1984, 1988; Griesser *et al.*, 2011), while small social lizards such as desert night lizards (*Xantusia vigilis*) also reduce cold stress by forming groups on cold winter days (Rabosky *et al.*, 2012). Forming groups reduces individuals' exposed surface area-to-volume ratio, reducing heat loss. Such organisms should group less as mean temperatures increase. Meanwhile, although warming temperatures may reduce metabolic constraints among species inhabiting cold climates, they impose no such costs to those living in warmer climates. For example, changes in grouping as temperatures change is not found among birds such as plain parakeets (*Brotogeris tirica*) and maroon-bellied parakeets (*Pyrrhura frontalis*) in Brazil (Pizo, Simao & Galetti, 1997), or for various parrot species in the Peruvian Amazon (Gilardi & Munn, 1998). As such, increases in temperature may not affect organisms

in temperate climates, although here increases in dryness may be a factor (see below).

Dry conditions brought on by increased temperatures pose challenges to homeostatic systems beyond energy balance. For example, dry conditions can lead to increased grouping to prevent desiccation in animals limited by water loss. This should be particularly true in small animals, where greater surface area-to-volume ratios result in greater water loss. For instance, hermit crabs (*Clibanarius symmetricus*) can reduce desiccation risk by clustering together more at low tides, when conditions are dryer, than at high tides (Peres, Ferreira & Leite, 2018). In social spiders (*Stegodyphus dumicola*) and woodlice (*Porcellio scaber*), experiments show that individuals enjoy reduced water loss in larger groups (Broly *et al.*, 2014; Vanthournout *et al.*, 2016), suggesting that larger groups will survive better than smaller groups in dry conditions (Bilde *et al.*, 2007). This is even true in small vertebrates such as chimney swifts (*Chaetura pelagica*), which roost closer together on warmer nights (Farquhar, Morin & Nocera, 2018).

Increased temperatures and dryness can also impose energetic constraints by affecting the availability of resources and thereby influencing grouping. In species of desert rodents such as Mongolian gerbils (*Meriones unguiculatus*), Indian gerbils (*Tatera indica*), African striped mice (*Rhabdomys pumilio*), and great gerbils (*Rhombomys opimus*), social grouping, and in some cases communal breeding, are more common when conditions are benign, and smaller groups and solitary living are more common when conditions are hot and dry (Xia *et al.*, 1982; Idris & Prakash, 1985; Agren *et al.*, 1989; Randall, 1994; Schradin & Pillay, 2004; Randall *et al.*, 2005). For these species it is thought that increased solitary living in dryer conditions is to avoid resource competition when within a group. Likewise, Grant's gazelles (*Nanger granti*) maintain weaker associations with members of their wider group in dryer years, probably due to a reduction in plant productivity (Williams, Worsley-Tonks & Ezenwa, 2017). Therefore, the effect of warmer conditions on social grouping will differ between organisms limited by the cold or water loss, and those limited by access to resources. Water-limited animals should group more as temperatures increase, while resource- and cold-limited animals should group less.

(c) Agonistic interactions

Increased temperatures are well established to lead to increased aggression in many aquatic organisms, although the mechanism for the increase in aggression is not always clear. It could be due to the lifting of metabolic constraints on energetically costly behaviour, due to increases in metabolic rates that result in organisms operating outside their optimal thermal window, or due to neurons operating outside of their thermal range, producing maladaptive behaviour (Huey *et al.*, 2012; Harshaw, Blumberg & Alberts, 2017). For example, both dominant and subordinate Amazonian dwarf cichlids (*Apistogramma agassizii*) increase

how often they bite at higher temperatures compared to dominant fish in control conditions (Kochhann, Campos & Val, 2015), while another cichlid, *Julidochromis ornatus*, also exhibits more mirror-elicited aggression in experimental high-temperature groups compared to control groups (Kua *et al.*, 2020). Captive juvenile lemon damselfish (*Pomacentrus moluccensis*) exhibit short-term increases in their aggression as temperatures increase (Biro, Beckmann & Stamps, 2010; Warren *et al.*, 2016), although this effect is not seen in juvenile Ambon damselfish (*Pomacentrus amboinensis*; Warren *et al.*, 2016). We discuss the consequences of increased aggression for changes in patterns of within-group dynamics in Section II.2b.

On the other hand, increases in temperature will also mean less dissolved oxygen in water. This can reduce energetically expensive behaviours such as physical aggression, as seen in laboratory trials involving shore crabs (*Carcinus maenas*; Sneddon, Taylor & Huntingford, 1999), dominant Amazonian dwarf cichlids (Kochhann *et al.*, 2015), and in experimental groups of three-spined sticklebacks (*Gasterosteus aculeatus*; Sneddon & Yerbury, 2004). The fact that increased temperature increases aggression while increased hypoxia decreases aggression raises the question of what will happen when both occur (we discuss 'multiple stressors' further in Section VI.1). Kochhann *et al.* (2015) studied independent effects of increased temperature and hypoxia and found that both influenced aggression. Further studies with full-factorial designs would be valuable for identifying the interactive effects of temperature and hypoxia.

In terrestrial species, unlike for aquatic species, we do not have a clear mechanism for why increased temperatures should affect aggression. Aggression might increase either due to the removal of energetic constraints or it may represent a pathology due to neuronal dysfunction (Anderson *et al.*, 2000). This lack of a clear mechanism linking temperature and aggression may in part explain the mixed results from previous work. For example, individual *Formica xerophila* ants show lower aggression at ambient temperatures compared to artificially cooled temperatures, whereas a congener, *Formica integroides*, shows no such change (Tanner, 2009). Female leopard geckos (*Eublepharis macularius*) incubated at higher temperatures showed increased aggression compared to females raised at lower temperatures, but these findings are complicated by the fact that temperature also influences sex determination in this species (Flores, Tousignant & Crews, 1994). The effect of temperature on aggression in territorial animals can be context dependent, which further complicates matters. Experimentally manipulating the temperature for groups of cockroaches (*Nauphoeta cinerea*), caused an increase in aggression from low-ranked individuals but an decrease in aggression from higher-ranked individuals (Spohn & Moore, 1997). Meanwhile, captive sand field crickets (*Gryllus firmus*) show shorter and less aggressive fights in response to warmer experimental temperatures, but only in the morning (Nguyen & Stahlschmidt, 2019). These diverse results in ectotherms clearly highlight that more work is needed on the physiological underpinnings of

aggression in ectotherms and how they should be affected by increases in temperature.

Perhaps surprisingly, we found few studies exploring the effect of temperature on aggressive behaviour in mammals. This is an important gap in our knowledge as we might expect temperature to influence aggression differently in endotherms compared to ectotherms. In an exception, Greenberg (1972) found aggression was highest at intermediate temperatures in captive house mice (*Mus musculus*). This relative lack of work on mammals is surprising given the association between higher temperature and increased aggression in humans (Anderson, 1987; Anderson *et al.*, 2000). Clearly, for all taxa we need to understand better how temperature affects the mechanisms underpinning changes in aggression to allow us to make the best predictions.

(2) Social organisation

(a) Mating systems

Warmer temperatures and dryer conditions can be expected to influence mating systems by changing the relative benefits of cooperative living compared to solitary living. If warmer conditions make environments harsher for singletons, increased temperatures should increase the degree of cooperative breeding. For example, in degus (*Octodon degus*), in dry years the number of offspring produced per individual increases as group size increases, which does not occur in wetter conditions (Ebensperger *et al.*, 2014). Similarly, a population of common mole-rats (*Cryptomys hottentotus*) in an arid environment show greater rates of cooperative breeding than one in a more optimal habitat, as individuals avoid migrating alone and opt to remain in the natal nest (Spinks, Jarvis & Bennett, 2000). Groups of burying beetles (*Nicrophorus nepalensis*) are also more successful than pairs at low elevations, which are warmer, compared to intermediate elevations, where pairs are more successful (Sun *et al.*, 2014; Liu *et al.*, 2020). Warmer temperatures can also increase the incidence of communal breeding by extending the length of reproductive seasons in some facultatively eusocial species. This extension means there is more time to produce overlapping generations. A cline in sociality in this manner has been observed in a species of sweat bee (*Halictus rubicundus*), where solitary living is positively correlated with the number of days with snow on the ground (Soucy & Danforth, 2002), causing the bees to live alone at high altitudes but socially at low altitudes [Eickwort *et al.*, 1996; see also Hirata & Higashi, 2008 and Davison & Field, 2018].

On the other hand, when low temperatures limit the success of single individuals breeding, we expect rising temperatures to relieve reproductive constraints and therefore reduce rates of cooperative breeding. For example, in allodapine bees of the genus *Exoneura*, the incidence of co-founding among queens increases with cold stress (Schwarz, Bull & Hogendoorn, 1998). Co-founding allows colonies to form in conditions where single individuals cannot maintain

homeostasis (Schwarz *et al.*, 1998). This explains why a trend in sociality, from less eusocial to more eusocial, occurs in *Exoneura* bees in the Swiss alps from low to high altitudes (Kocher *et al.*, 2014). Likewise, among populations of the facultatively social spider *Anelosimus studiosus*, cold stress delays the development of offspring and risks killing off singleton mothers before their spiderlings reach a critical developmental point of independence (Jones *et al.*, 2007; Riechert & Jones, 2008). As with *Exoneura* bees, northern populations of *Anelosimus studiosus* have evolved coalitions of allomothers in colder regions that care for orphaned offspring, should any mother die prematurely (Furey, 1998). Some species, such as long-tailed tits (*Aegithalos caudatus*), are prevented from breeding alone by cold temperatures that enforce a short breeding season (Hatchwell *et al.*, 2013). Warmer temperatures and longer breeding seasons should therefore reduce the incidence of cooperative breeding in these and similar species, while increasing the rate of social breeding in species for which hot and dry conditions are too harsh for single individuals (for a review of this topic in arthropods, see Purcell, 2011).

Lin *et al.* (2019) suggested that animals may breed cooperatively to overcome problems of collective action (such as surviving harsh or fluctuating conditions) or to gain benefits from resource defence. Further, ecological conditions are predicted to influence these two different pathways differently. Harsher conditions are predicted to lead to an increase in cooperative breeding if animals are exploiting the benefits of collective action, while harsher conditions are predicted to reduce cooperative breeding for animals who breed in groups to defend resources (Lin *et al.*, 2019). Given rising temperatures can make conditions harsher in already dry environments, but more benign in cold environments, predictions for how rising temperatures will impact cooperative breeding must account for both the current environmental conditions and the reasons the animals are cooperative in the first place.

Increases in temperature can also alter the characteristics of mating systems by altering male mate-searching behaviours (Martin, Petelle & Blumstein, 2014). For example, in eastern chipmunks (*Tamias striatus*) and alpine marmots (*Marmota marmota*) earlier springs have been suggested to lead to increases in extra-pair paternity or multiple-sire litters, by reducing the movement constraints imposed by snow cover [Bergeron *et al.*, 2011; Bichet *et al.*, 2016; although Bichet *et al.*, 2016 also found greater snow cover increases rates of extra-pair paternity]. Furthermore, in sand lizards (*Lacerta agilis*), warmer years are associated with a higher level of multiple paternity as males have an increased opportunity to search for and copulate with females in those years (Olsson *et al.*, 2011). If snow, ice, or simply cooler temperatures limit the movement of animals, then a general effect of warmer weather is likely to be an increase in movement and concurrent effects on mating systems and other aspects of social organisation in taxa previously limited by these movement barriers.

(b) Dominance hierarchies

Warming temperatures can have consequences for the social structure of groups in terms of how their dominance hierarchies are organised. Temperature changes can indirectly affect hierarchy structures and rank if warming temperatures cause changes in patterns of aggressive and affiliative interactions and communication networks. For example, high temperatures disrupted dominance hierarchies in experimental groups of the Amazonian dwarf cichlid as both dominant and subordinate individuals increased their aggression levels (Kochhann *et al.*, 2015). While warming temperatures can cause changes in dominance hierarchy structure at the group level, they can also cause differences in individual outcomes within groups: even when all members of a population are experiencing the same temperature increase, warmer temperatures may affect individuals differently. For example, Spohn & Moore *et al.* (1997) observed rank-dependent effects of temperature on aggression in an experimental population of cockroaches (*Nauphoeta cinerea*). Compared to control groups, dominant individuals decreased aggressive behaviours and increased submissive behaviours, whereas subordinate individuals demonstrated the opposite effects. The effect of these contrasting changes destabilised the dominance hierarchy within an aggregation (Spohn & Moore, 1997). Warmer temperatures may also allow physiologically inferior individuals to signal at higher rates (see Section II.1*a*), which would further increase conflict as the signals would no longer be an honest indicator of resource-holding potential.

The evidence above therefore implies that we expect dominance hierarchies to be less stable as temperatures increase, at least temporarily. Less-predictable dominance structures or ranks may prove costly to phenotypes typically associated with a high social rank, who benefit most from stable dominance hierarchies. For species where all members of a group benefit from clearly delineated social ranks (Kaufmann, 1983), overall reproductive success would be expected to decrease, potentially reducing the viability of populations. However, in species where some individuals suffer but others benefit from changes in dominance hierarchies (West Eberhard, 1975), the population-level effects on reproductive output might not be negative.

(c) Collective behaviour

Given the extensive influence of temperature on both aggregative and aggressive behaviours, it is no surprise that increasing temperature can impact the collective dynamics of social groups. While we saw in Section II.1*b* that hotter temperatures can lead to larger aggregations in species at risk of water loss, evidence further suggests those aggregations would be less active at hotter temperatures. Higher daily temperatures decrease the distance a yellow baboon (*Papio cynocephalus*) troop moves in a day (although higher annual temperatures increase the overall amount of yellow baboon troop movement; Johnson *et al.*, 2015). Baboons may compensate for negative temperature effects on daily movement

by traversing wooded habitats more slowly and open habitats more quickly during high temperatures (Stelzner, 1988). Red harvester ants (*Pogonomyrmex barbatus*) make fewer foraging trips at hotter temperatures (Pinter-Wollman, Gordon & Holmes, 2012), while gypsy ants (*Aphaenogaster senilis*) decrease the overall amount of collective foraging in high temperatures (Cerdá *et al.*, 2009). Species such as ants that use chemical communication to mediate collective behaviour may be particularly affected, given that increased temperatures can decrease trail following as trail pheromones decay faster at hotter temperatures (observed in *Tapinoma nigerrimum*; Van Oudenhove *et al.*, 2011).

Energetic limitations imposed by hypoxia due to increased temperatures can reduce shoaling behaviour (Domenici, Steffensen & Marras, 2017). Both Atlantic herring (*Clupea harengus*; Domenici *et al.*, 2002) and goldfish (*Carassius auratus*; Israeli, 1996) space themselves further apart in their shoals under experimentally induced hypoxia, likely to maintain better access to oxygen. Gant danio (*Devario aequipinnatus*) swimming in a water tunnel form less cohesive shoals and are less active at higher temperatures (Bartolini, Butail & Porfiri, 2015), which may be a result of hypoxia or a direct response to temperature. Captive guppies (*Poecilia reticulata*) also show less shoaling behaviour when assayed in warmer water as long as there is no threat of predation, but increased shoaling behaviour in the presence of the threat of a confined cichlid (Weetman, Atkinson & Chubb, 1999). This latter result suggests a trade-off between accessing oxygen and avoiding predation in warm temperatures, which could have important fitness consequences. While fish shoals may be able to adjust their inter-fish spacing plastically as temperatures increase, maintaining a degree of shoal cohesion, there could be an upper limit to this plasticity. Further, greater distances between fish could negatively impact some group functions such as collective predator avoidance.

(3) Summary

Changes in social interactions in response to warming will depend both on the reason that the species in question engages in those social interactions and on how high temperatures interact with homeostatic systems either to increase or decrease energetic costs. Where increases in temperature make conditions more benign (e.g. for organisms limited by maintaining body heat), warming may relieve constraints on the ability to survive or breed alone, leading to reduced group formation or cooperative breeding. By contrast, where increases in temperature create harsher conditions for survival or reproduction (e.g. for organisms limited by water loss), warming may increase the tendency to form groups or breed together. Additionally, if warmer conditions are associated with longer reproductive seasons, warming may promote cooperative breeding by allowing for the production of a helper caste. Extending the length of reproductive seasons could also increase the prevalence of polygyny as males have more time to search for mates. Meanwhile, aggression levels can increase or decrease due to higher temperatures,

perhaps because of physiological changes, but the mechanisms are unclear. As a result of these changes in aggression, dominance hierarchies especially are likely to become less stable. Future studies need to manipulate temperatures (simultaneously with oxygen levels for aquatic species), identify the physiological pathways that then lead to increased or decreased aggression, and measure how dominance hierarchies form and are maintained. By following this whole pathway through we can achieve a better understanding of the impact of increased temperatures on animal populations. Increases in temperature are also expected to influence the production of costly signals used in communication and increase the evaporation rates of chemicals placed in the environment, potentially reducing the efficacy of this kind of communication. By contrast, some acoustic and visual signals may be easier to produce in warmer environments and therefore increase in prevalence. Identifying how increased temperatures can make some signals more costly and some easier to produce is a key next step.

III. EXPOSURE TO POLLUTANTS

As human influence expands around the globe, animal populations are increasingly exposed to pollutants. We use the term ‘pollutant’ to encompass exposure to chemical contaminants, increases in dissolved CO₂ and increased eutrophication in aquatic systems, and anthropogenic changes to noise and light levels. As the planet becomes increasingly urbanised, studying the role of pollutants in all realms of behaviour, including social behaviour, is key (Montiglio & Royauté, 2014; Candolin & Wong, 2019). In this section we discuss how various forms of pollution including artificial lighting (Rich & Longcore, 2006), acoustic noise pollution (Slabbekoorn & Ripmeester, 2008; Slabbekoorn *et al.*, 2010) and chemical compounds (Zala & Penn, 2004; Lüring & Scheffer, 2007) can disrupt communication, the formation of groups, and antagonistic behaviour through two primary pathways: by altering the medium through which signals are transmitted and received and by directly altering physiology. We discuss how disrupting communication and physiology can have substantial downstream consequences for the ability to group, act collectively, and engage in normal mating interactions.

(1) Social interactions

(a) Communication

Pollutants can have far-reaching effects on communication and recognition, influencing the physiology underpinning signal emission and reception, and altering the medium of transmission [either simultaneously or independently; for previous reviews see Scott & Sloman, 2004; Clotfelter, Bell & Levering, 2004 and Zala & Penn, 2004]. Artificially high light levels for example increase the conspicuousness of visual signals (Kurvers & Holker, 2014) meaning that visually

signalling species are expected to signal at higher rates. This may be to outcompete artificial lights (suggested for fireflies, *Aquaticus ficta*; Owens, Meyer-Rochow & Yang, 2018), or to take advantage of well-lit nights to display visual signals most effectively (suggested for eagle owls, *Bubo bubo*; Penteriani *et al.*, 2010). Increased ambient light levels at night could also commonly disrupt the timing of signals through, for example, the disruption of circadian rhythms (Swaddle *et al.*, 2015). Both observational and experimental data have shown that diurnal songbirds begin singing their morning chorus during the night if disturbed by artificial light (Miller, 2006; Borgström *et al.*, 2010; Da Silva, Valcu & Kempenaers, 2016). Artificial light can also indirectly affect signalling activity by creating environments with a higher risk of predation, which might drive a decrease in signalling rates. Green frogs (*Rana clamitans*) for instance reduce calling behaviour when experimentally exposed to artificial night lighting (Baker & Richardson, 2006), as increased visibility increases predation risk. The impacts of artificial light on signalling in terrestrial species therefore depend on whether animals are able to take advantage of, or can outcompete, the pollution (in which case they may signal earlier, more often, or more strongly) or if they cannot, in which case they may reduce signalling.

In aquatic ecosystems, on the other hand, various forms of pollution (e.g. agricultural runoff, deforestation) are likely consistently to reduce light levels in water, impeding visual communication. Both experimental alterations of ambient light and comparisons of populations under varying conditions of eutrophication and turbidity have clearly shown that changes in light levels impede visual communication in a variety of fish species including cichlids (*Nyererei* spp., *Neochromis* spp.; Seehausen, Van Alphen & Witte, 1997), three-spined stickleback (Candolin, Salesto & Evers, 2007; Wong, Candolin & Lindström, 2007), sand gobies (*Pomatoschistus minutus*; Järvenpää & Lindström, 2004), and broadnosed pipefish (*Syngnathus typhle*; Sundin, Berglund & Rosenqvist, 2010). Light pollution is therefore expected consistently to impede visual communication in water, perhaps selecting for alternative modes of communication. For instance, animals might switch to multi-modal signalling in response to blockades in the main lines of communication (Partan, 2017). Multi-modal signalling is likely driven by variability in the signalling environment that renders some signal types temporarily unreliable (Bro-Jørgensen, 2010; Stafstrom & Hebets, 2013). Determining whether all animals can switch signalling mode, or if certain groups cannot, would be useful.

Acoustic pollution can influence communication systems by cluttering signalling channels and reducing signal efficacy (Forrest, 1994; McMullen, Schmidt & Kunc, 2014). In response, animals may change both when they signal and the structure of their signals [reviewed in Luther & Gentry, 2013 and Schmidt & Balakrishnan, 2015]. In the presence of anthropogenic noise, birds [nightingales, *Luscinia megarhynchos* (Brumm & Todt, 2002); white-crowned sparrows, *Zonotrichia leucophrys* (Luther & Baptista, 2010); blackbirds, *Turdus merula* (Nemeth *et al.*, 2013)], some mammals

[common marmosets, *Callithrix jacchus* (Brumm *et al.*, 2004); Indo-Pacific bottlenose dolphins, *Tursiops aduncus* (Morisaka *et al.*, 2005; Hotchkin, Parks & Weiss, 2015)], insects (Shieh *et al.*, 2012), and frogs (southern brown tree frogs, *Litoria ewingii*, and common eastern froglets, *Crinia signifera*; Parris, Velik-Lord & North, 2009) adjust the amplitude or the frequency of their vocalisations to increase the signal-to-noise ratio and avoid anthropogenic masking. Similar to light pollution, anthropogenic noise has also been shown to influence the timing of audible signals. Experiments have shown that birds sing earlier in noisy environments (spotless starlings, *Sturnus unicolor*, and house sparrows; Arroyo-Solis *et al.*, 2013) while observations from across multiple populations have also provided evidence that birds increase nocturnal singing (European robins, *Erithacus rubecula*; Fuller, Warren & Gaston, 2007) to avoid overlap with daytime noise. In other cases, experimental playbacks have shown that organisms decrease their calling rate when anthropogenic noise is high [painted chorus frog, *Microhyla bulleri*, black-striped frog, *Hylarana nigrovittata*, banded bull frog, *Kaloula pulchra* (Sun & Narins, 2005); European tree frog, *Hyla arborea* (Lengagne, 2008)]. Pollution of the acoustic environment therefore will likely select for a shift in the timing and structure of audible signals, or a reduction in their use.

As with light pollution, the influence of anthropogenic noise on social interactions is not limited to terrestrial environments. Because sound waves attenuate more slowly under water, the effects of noise pollution are in fact likely to be even more acute in aquatic environments. The increases in underwater noise from ship traffic, tourism, and commercial and military activities in the last century particularly are thought to limit marine mammal communication (Nowacek *et al.*, 2007; Tyack, 2008). For instance, low-frequency calls necessary for long-distance underwater communication are likely to be masked by anthropogenic noise (Nowacek *et al.*, 2007; Tyack, 2008). Many cetaceans modify their signals in response to these disturbances. Both belugas (*Delphinapterus leucas*; Lesage *et al.*, 1999) and right whales (*Eubalaena* spp.; Parks, Clark & Tyack, 2007) alter the frequency of their calls in response to low-frequency vessel noise on short (within-lifetime) timescales, suggesting that behavioural plasticity can play an important role in compensating for these anthropogenic changes. Additionally, both killer whales (*Orcinus orca*; Foote, Osborne & Hoelzel, 2004) and humpback whales (*Megaptera novaeangliae*; Miller *et al.*, 2000) show plastic responses by increasing the duration of their songs in response to experimentally induced and observed changes in acoustic pollution. Unlike the more mixed messages for light pollution, noise pollution would therefore appear consistently to hamper the effectiveness of sound communication.

For animals that communicate using pheromones, chemical pollutants have substantial potential to lead to physiological disruptions that can affect both the transfer and reception of olfactory cues. Evidence of pheromone disruption in organisms experimentally treated with chemical pollutants has been found in a variety of taxa including various

insects [*Trichogramma brassicae* (Delpuech *et al.*, 1998); *Spodoptera litura* (Wei, Huang & Du, 2004); *Ostrinia furnacalis* (Zhou, Du & Huang, 2005)], amphibians such as eastern newts [*Notophthalmus viridescens* (Park, Hempleman & Propper, 2001; Park & Propper, 2002)] and fish such as Atlantic salmon (*Salmo salar*; Moore & Waring, 1996, 2001). The social behaviours of aquatic organisms specifically may be further impaired in the future as increased concentrations of atmospheric carbon dioxide disrupt the medium of information transfer by increasing the acidity of water, causing chemical signals like alarm cues to degrade more rapidly and reducing their effectiveness [observed in pumpkinseed, *Lepomis gibbosus* (Leduc *et al.*, 2003); reviewed in Briffa, de la Haye & Munday, 2012].

Chemical contaminants such as heavy metals and polychlorinated biphenyls can directly affect the production of signals such as bird song. Comparisons of populations across a contamination gradient has revealed that chemicals can reduce song repertoires, lower song output (Gorissen *et al.*, 2005), and alter song structure (DeLeon *et al.*, 2013). Such changes could result from effects of pollutants on brain development in areas associated with song production (Iwaniuk *et al.*, 2006), from negative effects of toxicants on learning (Strickler-Shaw & Taylor, 1991) or from developmental stress early in life (Nowicki, Peters & Podos, 1998). Disruption to both endocrine and information-sensing systems may have many knock-on effects for social interactions (discussed throughout the rest of Section III; see also Lürling & Scheffer, 2007).

(b) Social grouping and associations

By inhibiting signals between individuals, pollutants can disrupt or alter group cohesion. Grouping and mating interactions rely on sensing the presence and behaviour of other individuals, and on generating highly species-specific and context-specific responses. It is no surprise then that pollutants can disrupt these kinds of interactions. For example, ubiquitous contaminants like 4-nonylphenol can affect social recognition and thereby disrupt social organisation in banded killifish (*Fundulus diaphanus*) (Weis & Weis, 1974; Ososkov & Weis, 1996; Webber & Haines, 2003; Ward *et al.*, 2008). Killifish orient away from instead to towards conspecifics dosed with 4-nonylphenol, likely because the contaminant induces some physiological change in the animal's chemical profile, thereby obscuring the chemical signature of the fish (Ward *et al.*, 2008).

Disruption of the medium for communication can also affect social decision-making and group formation. Under experimentally induced turbid conditions, three-spined sticklebacks show reduced preference for larger shoals, which could result from visual limitations in the ability to assess group size or quality (Fischer & Frommen, 2013). While the ability to choose the optimal group might be limited by eutrophication or turbidity, by contrast, increased light at night is expected to facilitate information sharing among group members and thus increase group cohesion and

coordination (Kurvers & Holker, 2014). In walleye pollocks (*Theragra chalcogramma*), for example, experimentally increased light levels caused neighbour distances to decrease, promoting schooling (Ryer & Olla, 1998). Although perhaps counterintuitive, noise pollution can similarly promote grouping for species that rely heavily on vocal communication for group cohesion and survival (Owens, Stec & O'Hatnick, 2012). For example, Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) increased their rate of social interactions and decreased the distance to their nearest neighbour when experimentally exposed to elevated traffic noise (Owens *et al.*, 2012). Such a response is likely to optimise information transfer and communication among flockmates in the face of perceived predation threat.

In addition to inhibiting communication, pollutants commonly have direct effects on organism physiology that can affect social grouping. For instance, benzodiazepine, a common class of psychotherapeutic drug used to treat anxiety is known to alter behaviour by binding to gamma-aminobutyric acid receptors. European perch (*Perca fluviatilis*) exposed to this contaminant in the laboratory have been shown to be less gregarious (Brodin *et al.*, 2013). Across freshwater fish such as goldfish, mummichog (*Fundulus heteroclitus*), golden shiner (*Notemigonus crysoleucas*), and banded killifish it is often observed that experimental exposure to chemical contaminants such as dichlorodiphenyltrichloroethane or mercury reduce group cohesion (Weis & Weis, 1974; Ososkov & Weis, 1996; Webber & Haines, 2003; Ward *et al.*, 2008). However, some contaminants can increase shoaling. For instance, Arabian killifish (*Aphanius dispar*) cluster more closely in response to predator cues when exposed to fluoxetine (Barry, 2013) and Atlantic silversides (*Menidia menidia*) show increased school cohesion when exposed to copper (Koltes, 1985). To make better predictions, we therefore clearly need to understand why some contaminants increase shoaling and some decrease it.

(c) Agonistic interactions

Pollutants can affect aggressive interactions between individuals by altering the medium through which individuals sense each other. For instance, in terrestrial environments brighter conditions caused by light pollution might make aggressive signals more visible and therefore lead to increased rates of agonism. Socially foraging flocks of birds and groups of mammals, for example, show increased aggression in the day relative to at night (Beauchamp, 2007). Changes in ambient light levels due to artificial lighting or pollution that increases turbidity in aquatic environments can also lead to changes in aggression. Nile tilapia (*Oreochromis niloticus*) and the cichlid acará tanga (*Geophagus proximus*), for example, show higher rates of aggression under experimental conditions of lower light intensity. This may be because turbid conditions increase the ability of fish to hide from predators, allowing fish to engage in riskier behaviours such as agonism (Carvalho, Ha & Gonçalves-de-Freitas, 2012). Some additional experimental studies support this trend, demonstrating

greater aggressive behaviour in Japanese amberjack (*Seriola quinqueradiata*) and white seabream (*Diplodus sargus*) at intermediate light levels (Sakakura & Tsukamoto, 1997; Castro & Caballero, 2004), but other experimental studies have found lower levels of aggression under lower light intensity [Atlantic salmon (Valdimarsson & Metcalfe, 2001); and African sharp-tooth catfish, *Clarias gariepinus* (Almazán-Rueda, Schrama & Verreth, 2004)]. Changes in aggression in response to light conditions may depend on the species' natural history, for example species that originate from habitats with high predation risk may reduce interactions under intense light conditions to minimise risk.

Chemical contaminants can also directly impact the expression of aggressive behaviour, although whether this is due to difficulties sensing other individuals, or due to some interference with physiological systems linked to aggression is not always investigated. Three-spined sticklebacks, for example, become less aggressive when exposed to ethinyl oestradiol (Bell, 2001, 2004) and exposure to metals such as cadmium and copper, or other noxious stimuli like acid, in rainbow trout (*Oncorhynchus mykiss*) reduces the number of agonistic encounters and increases the likelihood of an individual adopting a subordinate role (Sloman *et al.*, 2003a, 2003b; Campbell, Handy & Sims, 2005; Ashley *et al.*, 2009). Similar decreases in aggression among individuals living in environments polluted with heavy metals are seen in an ant (*Formica acquilonia*), in which individuals from a colony near a copper smelter were less aggressive towards foreign intruders than individuals from another colony in an unpolluted area (Sorvari & Eeva, 2010). By contrast, metal pollution either increases (Janssens *et al.*, 2003) or has no effect on aggression in great tits when assessed across a naturally occurring pollution gradient (Grunst *et al.*, 2018). Furthermore, exposure to other pollutants such as insecticides, herbicides, and fertilisers increases aggression in various species of fish (reviewed in Scott & Sloman, 2004) and in mice (*Peromyscus maniculatus* and *Mus musculus*; Jaeger, Carlson & Porter, 1999). In captive rodents, exposure to chemicals during development can increase aggression [*Mus musculus* (Vom Saal *et al.*, 1995); *Rattus norvegicus* (Farabollini *et al.*, 2002)] or decrease it [*Mus musculus* (Eroschenko *et al.*, 2002; Palanza *et al.*, 2002)]. The key take-home message here is that chemical pollutants are likely to alter aggressive behaviour, but the direction of the change likely depends on the specific chemical or other species-specific factors that have yet to be elucidated.

(2) Social organisation

(a) Mating systems

Chemical pollutants can induce physiological changes that can impact mating interactions through various mechanisms, such as feminisation of males, masculinisation of females, changes in sexual traits, impairment of mate-finding behaviour, courtship and willingness to copulate [reviewed in Olsén, 2011, Blocker & Ophir, 2013 and Candolin &

Wong, 2019]. By comparing experimentally treated groups with controls, changes in sexual behaviours, and in some cases reduced mating success, due to chemical pollutants has been observed in diverse taxa such as ringed turtle doves (*Streptopelia risoria*; Haegele & Hudson, 1973, 1977), starlings (*Sturnus vulgaris*; Grue & Shipley, 1981), guppies (Bayley, Nielsen & Baatrup, 1999; Baatrup & Junge, 2001), palmate newts (*Triturus helveticus*; Secondi *et al.*, 2009), Norway rats (*Rattus norvegicus*; Mably *et al.*, 1992), the amphipods *Gammarus pulex* (Pascoe *et al.*, 1994; Blockwell, Maund & Pascoe, 1998) and *Corophium volutator* (Krång, 2007), and the moth *Helicoverpa armigera* (Eliyahu, Applebaum & Rafaeli, 2003). Not surprisingly, changes to sexually selected behaviours are likely to have deleterious demographic consequences by influencing the quantity or quality of offspring produced. Kidd *et al.* (2007) experimentally added a synthetic oestrogen to an entire lake, and observed that impaired gonadal development and feminisation of male fathead minnows (*Pimephales promelas*) led to the near extinction of the population. However, weakened sexual selection could also lead to increases in the amount of genetic variation in a population and therefore improve the possibility of adaptation to novel environments (Wong & Candolin, 2015).

Pollutants can also disrupt the perception and visibility of signals and thus the ability to locate, recognise, or assess mates. Experimentally induced noise pollution hinders mate inspection and recognition in an African cichlid (*Astatotilapia burtoni*; Butler & Maruska, 2020), common gobies (*Pomatoschistus microps*; Blom *et al.*, 2019), and zebra finches (*Taeniopygia guttata*; Swaddle & Page, 2007), and can cause sufficient stress to alter a visual signal (throat sac colouration) in tree frogs (*Hyla arborea*; Troïanowski *et al.*, 2017). Additionally, light pollution has been shown to lower the mating success of *Photinus pyralis* in a manipulative field study (Firebaugh & Haynes, 2019). This is because *Photinus pyralis* (as well as another firefly *Photuris versicolor*) are lured to artificial light at night, where they are less likely to emit the bioluminescent flashing used for courtship (Firebaugh & Haynes, 2016, 2019). Similarly, turbidity due to eutrophication can affect the perception of colour signals, impeding mate assessment, as observed in fish species such as cichlids (Seehausen *et al.*, 1997; Maan, Seehausen & Van Alphen, 2010), three-spined sticklebacks (Candolin *et al.*, 2007; Wong *et al.*, 2007), sand gobies (Järvenpää & Lindström, 2004) and pipefish (*Syngnathus typhle*; Sundin *et al.*, 2010) under both experimental and naturally occurring conditions. Signals that are altered by pollution may be perceived by receivers as less threatening to rival males or less attractive to females (Patricelli & Blickley, 2006; Luther & Baptista, 2010), which likely has important implications for sexual selection. Traits that have historically been associated with mating success may therefore no longer be reliable in many systems. For example, predation risk associated with artificial lighting is known to alter the mate choice of female Túngara frogs (*Physalaemus pustulosus*), as females discriminate more between mates under darker conditions (Rand *et al.*, 1997). More complex, attractive calls may therefore not have a selective

advantage under illuminated conditions when females are likely to choose closer, simpler calls to avoid predation (Rand *et al.*, 1997). In blue tits (*Cyanistes caeruleus*), males located closer to streetlights were demonstrated to obtain greater extra-pair paternity due to starting their dawn song earlier. Since earlier singing is meant to be a signal of male quality, artificial lighting may lead to unreliable quality-indicator traits (Borgström *et al.*, 2010). Changes such as these could have myriad consequences, from shifting selection onto different traits to changing mating systems to reduce the role of courtship and the choice of mates by the choosy sex.

The impediment of signals can also remove a mechanism of reproductive isolation in species that rely on those cues. Such a loss would then lead to hybridisation and therefore the loss of biodiversity [Rhymer & Simberloff, 1996; observed for cichlids in more turbid areas of Lake Victoria (Seehausen *et al.*, 1997)]. Similarly, maladaptive mating behaviours caused by exposure to pollutants can lead to heterospecific mating and thus hybridisation. For example, in the sheephead swordtail (*Xiphophorus birchmanni*) females no longer prefer conspecific chemical cues when experimentally subjected to water polluted with sewage effluent and agricultural runoff, which then leads to interspecific matings and hybridisation (Fisher, Wong & Rosenthal, 2006). Therefore, we generally find that mating systems are consistently disrupted by exposure to pollutants. If disrupted courting and mating interactions do reduce population viability due to reduced reproductive success in general (van Geffen *et al.*, 2015; Blom *et al.*, 2019), the disruption of mating systems by pollution could represent a very serious threat to animal populations. However, hybridisation can also potentially lead to new species, or adaptive introgression that results in a net benefit to one or both parental species (Hamilton & Miller, 2016).

(b) Dominance hierarchies

Competitive behaviour is influenced both by the ability to perceive and process information about potential opponents and oneself (Hobson, 2020) and by having the coordination and energy stores to perform effectively in social encounters. Pollutants can affect physiology in a variety of ways including the disruption of sensory systems, endocrinology, metabolism and ion regulation that are central to both these abilities and thus can affect the formation and/or stability of dominance hierarchies (Sloman, 2007). For instance, Sopinka, Marentette & Balshine (2010) found that round gobies (*Neogobius melanostomus*) from contaminated lakes performed more assessment displays when interacting with a novel conspecific and were worse at establishing dominance hierarchies than fish from cleaner lakes. This suggests that the gobies had a reduced ability to recognise the relative threat or resource-holding potential of rivals. On the other hand, rainbow trout experimentally exposed to cadmium form stable hierarchies faster than controls, potentially due to cadmium build-up in the olfactory rosette which results in a reduced ability to respond to pheromonal cues and reduced levels of aggression

as a result (Sloman *et al.*, 2003b). Rainbow trout fed a copper-contaminated diet also showed reduced competitive ability (Campbell *et al.*, 2005), possibly due to an increased metabolic cost of locomotion during copper exposure (Campbell, Handy & Sims, 2002). While the formation of dominance hierarchies might be susceptible to pollutants, there is some suggestion that hierarchies, once formed, are more resilient. For example, in rainbow trout where dominance relationships were already established, exposure to metals such as copper, cadmium and lead showed no effects on social status or hierarchy structure (Sloman *et al.*, 2003b, 2005).

Individuals of different ranks can have different physiologies. Therefore, individuals of a certain social status might be more susceptible to toxicants than others (Sloman, 2007). For example, in willow tits dominant individuals were found to have significantly higher levels of cadmium, which might result from higher levels of activity or food intake (Hogstad & Pedersen, 2007). Therefore, pollutants may target a specific part of the hierarchical spectrum, which would have considerable consequences for the stability of dominance hierarchies that are so far unexplored. The broad implications of these effects for group or population stability remain to be assessed. However, evidence that disruption to the social stability of groups such as shoals of fish or flocks of birds can reduce collective foraging efficiency (observed in zebra finches; Maldonado-Chaparro *et al.*, 2018) suggests that the consequences are likely to be substantial and warrant further investigation (see Section II.2c).

(c) Collective behaviour

Pollutants, as we have seen, can affect communication and social recognition, thereby disrupting grouping behaviours. This can lead to downstream consequences for collective action and social coordination, which are often central to enabling group-living individuals to avoid predators, exchange information and locate resources. Vocalisations for example help to coordinate cooperative behaviours like foraging in animals such as killer whales (Miller *et al.*, 2000). Alterations in these signals in response to acoustic pollution may therefore have substantial effects on the efficacy of this collective behaviour and the survival of the pod as a result. Experimentally induced turbid conditions are demonstrated to impede social cohesion and shoaling behaviour due to visual constraints in three-spined sticklebacks (Chamberlain & Ioannou, 2019) and guppies (Borner *et al.*, 2015; Kimbell & Morrell, 2015). Meanwhile, in animals such as Atlantic salmon (Riley *et al.*, 2012) and various species of birds (Van Doren *et al.*, 2017) artificial lighting can impede social synchrony during migration. However, increasing light levels could also positively affect collective decision-making because it facilitates the sharing of visual information among group members (seen in walleye pollock; Ryer & Olla, 1998). Therefore, while pollution typically disrupts collective behaviour by disrupting the medium through which animals communicate, there may be exceptions where artificial light

makes conditions better. Further, if animals have one mode of communication impaired, they could use multimodal signals (Partan, 2017) to buffer social systems and prevent the collective behaviours that rely on them from breaking down.

While direct masking effects of noise pollution are common, noise can also impact the ability to process sensory input through 'cross-modal' effects, where the processing of non-auditory stimuli can still be disrupted by stress or distraction induced by anthropogenic noise. Dwarf mongooses (*Helogale parvula*) for instance, are slower to detect predator scent cues and show reduced vigilance behaviours when exposed to playbacks of traffic noise (Morris-Drake, Kern & Radford, 2016). In both juvenile seabass (*Dicentrarchus labrax*), and bluefin tuna (*Thunnus thynnus*), where coordination of movement is primarily modulated by visual sensory input, playbacks of acoustic noise pollution give less-cohesive and less-coordinated shoals (Sarà *et al.*, 2007; Herbert-Read *et al.*, 2017).

Chemical pollutants can directly induce neurological or physiological changes that affect collective behaviours. For instance, in an example already mentioned above, banded killifish individuals orient away from conspecifics contaminated with 4-nonylphenol, a ubiquitous contaminant commonly found in detergents. This has significant consequences for social organisation and shoaling behaviour, a critical strategy for locating food and defending against predators, and therefore may reduce fitness (Ward *et al.*, 2008). Likewise, European starlings exposed to a polychlorinated biphenol during development delay moulting and do not orient in the correct direction for migration (Flahr *et al.*, 2015). Further, honey bee (*Apis mellifera*) colonies show reduced collective activity and foraging success when experimentally exposed to commonly used pesticides such as neonicotinoids and imidacloprid (Bortolotti *et al.*, 2003; Colin *et al.*, 2004; Henry *et al.*, 2012). Alongside exposure to chemical pollutants, rising CO₂ levels in the air will lead to higher levels dissolved in water. Experimentally increased CO₂ concentrations have been shown to interfere with an important neurotransmitter in sand smelt (*Atherina presbyter*) larvae, disrupting shoaling behaviour (Lopes *et al.*, 2016). As for mating systems, research suggests that collective behaviour is most commonly impaired due to the presence of pollutants.

(3) Summary

As we have seen, pollution of various forms disturbs the media through which animals communicate, resulting in changes in the production, transmission, and reception of signals. Further, certain chemicals can directly induce physiological changes that alter mate searching, courtship, and copulation behaviours. These changes can alter mate choice and so might relax selection on certain traits or result in hybridisation if individuals cannot differentiate between conspecifics and heterospecifics. The risk of typical sociosexual interactions being disrupted is therefore high, and as such we expect animals to make use of multimodal signalling.

Studies assessing the extent to which multimodal signalling is an effective tool at overcoming the communication challenges imposed by pollution would be valuable. If animals cannot switch modes of communication, and sexual interactions are strongly disrupted, we would expect lower recruitment rates and so declines in population sizes and the loss of biodiversity. The inability to communicate effectively due to pollutants is also likely to hamper the collective behaviour of groups, reducing the ability of organisms to congregate or act together effectively. For organisms that rely on collective action for protection from predators or foraging success, such disruptions to social organisation could have significant fitness implications. The effects of pollutants on levels of aggression are less easy to predict. In some cases, agonistic interactions may decrease while in others they may increase. However, both changes in agonistic interactions as well as limited recognition of contest partners are expected to disrupt existing dominance hierarchies or prevent new ones from forming. More research is needed to help to understand if there are consistent patterns to how different contaminants affect agonistic interactions and the ways in which the natural history of the affected species might moderate these effects. Additionally, a better understanding of how the effects of pollutants on individual-level interactions cascade through effects on social structure to alter ecological and evolutionary processes is essential.

IV. HABITAT FRAGMENTATION

An important component of ongoing environmental change is habitat fragmentation. Habitats can be fragmented in two major ways: large habitat areas are split into multiple smaller patches, resulting in reduced total habitat area and larger inter-patch distances; or habitats may have their structure modified, thereby compromising their functionality and complexity. Both of these forms of habitat fragmentation can influence social interactions by altering how signals travel through them, and by limiting movement. We discuss how reduced patch size and constrained movement can isolate individuals and groups from others and force the same number of individuals into smaller space, all of which can have diverse and severe consequences for the rates of affiliative and agonistic interactions, the types of breeding systems that emerge and the ability of organisms to move or act collectively. For a previous review on how habitat fragmentation disrupts social systems through changes in resource availability, interspecific interactions and mating interactions, see Banks *et al.* (2007).

(1) Social interactions

(a) Communication

Habitat fragmentation can affect communication through changes in the spacing of individuals or the density of territories. In territorial species, reduced density may result in

fewer neighbours with which to interact, which may shift communication patterns. We can expect these effects to be amplified for species, like many songbirds, whose dialects rely on cultural transmission and local populations. Species with relatively stable song dialects and high site fidelity are likely to be most impacted by habitat removal and fragmentation (Laiolo & Tella, 2005; Laiolo, 2010). For example, acoustic analysis of Dupont's larks' (*Chersophilus duponti*), comparing songs in fragmented and unfragmented groups, found that individuals reduced song matching in fragmented habitats (Laiolo & Tella, 2005). Further, Dupont's larks also demonstrated lower song repertoires and greater differentiation both within and among populations in patchier landscapes compared to more intact landscapes, suggesting they are cut off from hearing more distant neighbours (Laiolo & Tella, 2006). Likely for the same reason, male chipping sparrows (*Spizella passerina*), eastern kingbirds (*Tyrannus tyrannus*), and brownish-flanked bush warbler (*Cettia fortipes*) sing more intensively at dawn when they have more neighbours (Liu, 2004; Dolan *et al.*, 2007; Xia *et al.*, 2014). A reduced connectivity of metapopulations due to habitat fragmentation and the severing of lines of communication can contribute to population extinction (Laiolo *et al.*, 2008). To compensate for this, receivers in fragmented habitats may need to visit distantly spaced signallers sequentially in order to collect the same amount of information (Otter & Ratcliffe, 2005; Bircher & Naguib, 2020). In this case the energetic costs of assessment for receivers might be higher in fragmented landscapes, which may have further implications.

Many forms of communication are influenced by the structure of the environment, and the acoustic signals that animals emit are typically well matched to the specific amount of reverberation from habitat features in the environment to facilitate efficient transmission (Wiley & Richards, 1978; Forrest, 1994; Padgham, 2003). The modification of habitat structure changes the medium through which acoustic signals travel and will therefore alter their reliability and structure. Environmental changes, such as the removal or destruction of specific elements of a habitat, can therefore impact animal interactions in relatively subtle ways. At the scale of forests, selective tree removal, in contrast to clear cutting, modifies environments and environmental complexity rather than creating patches or increasing the distances between patches. Therefore, the alteration of habitat structure can influence both the structure of acoustic signals as well as the reliability of acoustic communication (reviewed in Rabin & Greene, 2002). For example, the songs of Hawai'i 'amakihi birds (*Chlorodrepanis virens*) in less-complex habitats have more energy at higher frequencies than songs in closed habitats (Pang-Ching *et al.*, 2018). Observational comparisons of black-capped chickadees found that birds in disturbed habitats have reduced signal reliability and can likely hear fewer other males compared to chickadees living in high-quality old-growth habitat (Hansen *et al.*, 2005). By contrast, the destruction of habitats or reduction in their complexity may enable the transmission of acoustic signals, either within

or between patches. Recent work on alarm signalling in communication networks suggests that alarm signals transmit further across gaps than through continuous forest and thus habitat fragmentation may facilitate information transfer (Mathers-Winn, 2019). Other research has demonstrated how changes in vegetation density due to deer browsing reduces the degradation of simulated animal signals, perhaps improving sound transmission (Boycott, Gao & Gall, 2019). Habitat fragmentation is therefore mostly likely to disrupt or at least alter typical patterns of communication, although habitats with sparser vegetation may allow audible communication to travel further.

(b) Social grouping and associations

Habitat fragmentation typically results in decreasing patch size, which can alter interaction rates among individuals within a population, especially if individuals are directed into smaller areas, and the ability to move among patches is constrained. Fire outbreaks in grassland reduce grass cover and so create patches of suitable habitat, causing red-backed fairywrens (*Malurus melanocephalus*) to move to the remaining areas with relatively high cover (Lantz & Karubian, 2017). As individuals are funnelled into fewer areas, interactions occur more frequently, leading to increased overall social connectivity and stronger associations between individuals (Lantz & Karubian, 2017). A similar pattern occurs in sleepy lizards (*Tiliqua rugosa*), which interact more often and therefore have a more stable social structure in experimental trials with additional barriers as they are funnelled into smaller areas to interact (Leu *et al.*, 2016). By contrast, laboratory groups of three-spined sticklebacks form smaller social groups in structured environments compared to more open environments, perhaps as they cannot coordinate the movement of many individuals when there are barriers present (Webster *et al.*, 2013). Meanwhile, in guppies, habitat complexity does not directly alter overall patterns of social interactions (Edenbrow *et al.*, 2011) and in European minnows (*Phoxinus phoxinus*), the preference for particular social partners is unaffected by habitat complexity (Orpwood *et al.*, 2008). Evidence therefore suggests that more solitary organisms may be forced into higher interaction rates due to habitat fragmentation, while group-living species may be unable to maintain large group sizes in small patches, but evidence in animals beyond fishes is needed (see also Section IV.2c).

(c) Agonistic interactions

Limited movement and decreased patch sizes due to habitat fragmentation can alter rates of aggression among individuals within a group. In densely packed habitat patches, we may observe higher rates of aggression for two reasons. First, habitat fragmentation may reduce the availability of refuges, preventing subordinates from avoiding dominant individuals who may try to monopolise resources (Syme, 1974).

Lattanzio & Miles (2014), for example, showed that patchiness of habitats due to fire results in more frequent aggressive interactions between previously less-aggressive male tree lizards (*Urosaurus ornatus*), as remaining patches are typically dominated by larger and more aggressive males. Second, aggression might increase due to increased encounter rates between individuals within a patch. This is seen in sleepy lizards, who encounter each other more often in more complex habitats, resulting in higher levels of aggression (Leu *et al.*, 2016). Similarly, ringed-tailed lemurs (*Lemur catta*) living at different densities show increased agonism in smaller, more crowded, patches (Gabriel, Gould & Cook, 2018). These effects are not just limited to intra-group interactions. Polydomous wood ants (*Formica aquilonia*) exhibit more inter-colony aggression following habitat loss (Sorvari & Hakkarainen, 2004). Meanwhile, reduced water levels in freshwater systems are a likely consequence of climate change due to increased drought, and this can have a similar effect as decreased patch size in terrestrial habitats. In an experimental study in brown trout (*Salmo trutta*), Sloman *et al.* (2001) found an increase in competitive interactions due to reduced water levels, ultimately resulting in a breakdown of their social hierarchy. Likewise, Flood & Wong (2017) found that decreasing the water depth in tanks of eastern mosquitofish (*Gambusia holbrooki*) led to increased levels of conflict and agonistic interactions. Habitat fragmentation would therefore appear to lead consistently to increases in aggressive interactions. However, we note that higher densities may only be short term before populations decline due to habitat loss. An increase in aggression may represent a short-term response to habitat fragmentation, not a long-term one.

(2) Social organisation

(a) Mating systems

When habitats are fragmented and patches of habitat removed, movement in the form of breeding dispersal may also be limited. Receptive females who can no longer leave their current area may cluster in the remaining habitat patches, allowing resource defence polygyny to emerge (Lane *et al.*, 2011). For example, laboratory populations of male water striders (*Aquarius remigis*) exhibit continuous variation in their level of mate search and harassment behaviour when habitat patches are large (Eldakar *et al.*, 2009b; Montiglio *et al.*, 2016; Sih *et al.*, 2017). However, in smaller habitat patches, such as when streams have lower water levels and pools are isolated by rocks or riffles, males can defend access to females, leading to divergent mating tactics. More aggressive males in captive populations attempt to guard females while they forage on the water surface, while other males attempt to copulate with females when both share refuges (Eldakar *et al.*, 2009a, 2010; Sih *et al.*, 2017). Therefore, habitat fragmentation and the connectivity between patches determines the mating system and so the traits favoured by sexual selection (Rowe *et al.*, 1994; Weigensberg & Fairbairn, 1994; Sih, Lauer & Krupa, 2002). Similarly,

comparison of natural populations of mountain brushtail possums (*Trichosurus cunninghami*) exhibit a monogamous mating system in unfragmented habitat, and a polygynous system in more fragmented habitats (Martin & Martin, 2007).

Habitat fragmentation is typically associated with increased costs of dispersal. In species with sex-biased dispersal, habitat fragmentation can alter the operational sex ratio through increased mortality of the dispersing sex [Dale, 2001; seen in the agile antechinus, *Antechinus agilis* (Banks *et al.*, 2005)]. Depending on the resulting frequencies of each sex, this could influence which sex is choosy, which sex competes for access to the other, and the relative mating rates of males and females. Limitations to dispersal may also decrease the availability of mates, the rate of extra-pair copulations and/or multiple mating, and increase the rate of inbreeding (Dale, 2001; Banks *et al.*, 2007). For instance, tracking movements made by male hooded warblers (*Wilsonia citrina*) showed that they do not fly more than 500 m across open fields, indicating that highly fragmented habitats will prevent them from engaging in extra-pair copulations (Norris & Stutchbury, 2001). However, in both Cunningham's spiny-tailed skink (*Egernia cunninghami*) and the reticulated velvet gecko (*Hesperoedura reticulata*) genetic analyses revealed there was not a higher rate of inbreeding in fragmented habitats (Stow & Sunnucks, 2004; Lange *et al.*, 2013), which could be due either to inbreeding avoidance within patches, or to higher rates of movement between patches. As such, mating behaviour may adjust plastically to habitat fragmentation to maintain some aspects of mating systems intact.

Increased costs of dispersal due to habitat fragmentation can also promote delayed dispersal and the helping of reproductive relatives. This mechanism for promoting cooperative breeding is known as the 'ecological constraints hypothesis' (Emlen, 1982). This hypothesis is generally supported in both observational and experimental studies within facultatively cooperatively breeding birds [see Hatchwell & Komdeur, 2000 for a review]. For instance, an experimental study on the Seychelles warbler (*Acrocephalus sechellensis*) found that juveniles have higher reproductive success when staying and helping at the natal nest than when dispersing to low-quality patches (Komdeur, 1992). Habitat fragmentation may also reduce the number of available groups in a local 'market' that helpers can join, which is predicted to increase the amount of help a helper is required to give in order to be allowed to stay at a nest (Grinsted & Field, 2017). Habitat fragmentation therefore frequently alters mating systems, by limiting individuals' options for dispersal, available territories, and by increasing the defensibility of mates.

(b) Dominance hierarchies

Restricted movement imposed by habitat fragmentation often results in repeated interactions among conspecifics, which can increase the stability of dominance hierarchies. The establishment of dominance hierarchies depends on repeated interactions in a competitive context. Iterative

interactions allow individuals to recognise their group mates, remember the outcomes of past fights (Pagel & Dawkins, 1997; Hobson & DeDeo, 2015; Seyfarth & Cheney, 2015), adaptively partition social roles (Bergmüller & Taborsky, 2010), and potentially queue for status (Kokko & Johnstone, 1999). As discussed previously, individuals in fragmented habitats may often essentially be forced to remain in their groups, and higher densities within groups will likely lead to more repeated interactions, especially if the individuals are of similar rank (e.g. in brown trout; Kaspersson, Höjesjö & Pedersen, 2010). The forced group stability that fragmented habitats can impose can then result in more structured and stable hierarchies. Stability in group membership often leads to denser dominance networks, better resolved dyadic relationships, and more linear hierarchies (McDonald & Shizuka, 2012). Further, limited dispersal may reduce within-group aggression and instead promote tolerance, if costs of conflict are moderate or high, if levels of within-group relatedness increase, and/or if cooperative breeding increases in prevalence (discussed in Section IV.2a; see also Mathot & Giraldeau, 2010).

However, as noted in Section IV.1c), fragmented habitats often result in increases in aggression, and increased aggression can destabilise dominance hierarchies, at least in the short term. For example, by altering dominance scores of individuals pre- and post-manipulation, experimentally induced habitat loss was demonstrated to lead to changes in the structure of the group's dominance hierarchy in brown trout (Sloman *et al.*, 2001). If fragmented or altered habitats disrupt ranking systems or lead to an overall increase in the rate of agonistic interactions, we may see the (temporary) dissolution of dominance hierarchies in animal social systems. If however densities decrease over time due to habitat loss, then aggression levels may return to original levels or even lower. This could then allow dominance hierarchies with similar structure to those in original habitats to be re-established.

Given that both increases and decreases in competitive interactions can be expected as habitats become fragmented, how do we know which response will occur? Ims, Rolstad & Wegge (1993) suggested that individual aggressiveness may predict intraspecific variation in response to habitat loss. For example, in experimental populations of voles (*Microtus oeconomus*), aggressive females exhibit a 'fission response', wherein a single individual takes over a patch and all other individuals are excluded, resulting in an increase in aggressive interactions. However, non-aggressive females showed a 'fusion response', where multiple individuals will coexist in a single patch leading to an increase in cooperative behaviour (Ims *et al.*, 1993). Directly testing this suggestion more widely would be valuable. Similar mechanisms may also facilitate interspecific variation in responses to habitat fragmentation. In facultatively cooperative breeding species, rates of helping at the nest may increase when fragmented habitats impose high costs of dispersal, while species that compete for resources and so already engage in higher rates of agonism, may become more aggressive. Therefore, the existing traits of the organisms will doubtlessly help to shape

how their social interactions change in response to habitat fragmentation.

(c) Collective behaviour

For gregarious species, a decrease in the amount of available habitat and an increase in the distance between patches can interfere with the group's ability to stay and move together, disrupting group cohesion. For example, habitat fragmentation is believed to contribute to the development of fission–fusion dynamics in howler monkeys (*Alouatta spp.*), wherein the spatial cohesion and individual membership in a group changes over time (Arroyo-Rodríguez & Dias, 2010). Howler monkeys also exhibit populations in fragmented habitats that have a lower proportion of adult males and a greater frequency of uni-male groups (Arroyo-Rodríguez & Dias, 2010). Therefore, reductions in patch size are likely not only to cause changes in group size but also to affect social composition and group cohesion.

An increase in the distance between patches can compromise or interrupt an animal's ability both to disperse and to migrate with others. When interpatch interval increases, the costs of moving between patches also increases, as individuals may be increasing their risk of mortality, energy expenditure and predation risk (reviewed in Bonte *et al.*, 2012). Indeed, we can generally expect a decrease in the frequency of collective migration in fragmented habitats (Cote *et al.*, 2017), although this effect may depend on the composition of the group. Using a theoretical and empirical approach, Michelena *et al.* (2010) examined collective dispersal in groups of domestic sheep (*Ovis aries*) which differed in shy/bold personalities. Both mathematical models and experimental data demonstrated that habitat fragmentation was more likely to decrease the dispersal abilities of shy groups of sheep compared to groups of bold individuals (Michelena *et al.*, 2010). Increased fragmentation will require animals to travel longer distances to their migratory grounds, or they may be forced to travel longer distances without refuelling (Alerstam, Hedenström & Åkesson, 2003). Indeed, theoretical models exploring habitat patch distribution and migration predict a general decrease in migratory behaviours as habitat fragmentation increases (Guttal & Couzin, 2010), a pattern which has been observed in wild blackcaps (*Sylvia atricapilla*; Pulido & Berthold, 2010). Habitat fragmentation in the future will therefore influence how animal groups move together. Further work on how habitat fragmentation influences collective foraging or the completion of group tasks would be useful.

(3) Summary

Habitat destruction and fragmentation are well known to cause a loss of biodiversity and a reduction in the reproductive output of surviving individuals. Habitat fragmentation further risks reducing the complexity of social interactions across a variety of systems by increasing agonism and reducing successful dispersal in the short term, while animals may

have to trade off interacting with conspecifics for accessing resources in smaller patches. More frequent agonistic interactions between group mates may then lead to more robust hierarchies, although increased levels of aggression can also destabilise dominance hierarchies by changing which individuals are dominant. Identifying which of these two outcomes is more common and why is a key next step. Modification of habitat structural complexity will also alter the effectiveness of acoustic signals, although work on other kinds of signals, especially visual signals, would be welcome. Collective behaviours are often maintained through specific individual decision-making processes such as consensus decision-making and interindividual communication, which may not be functional in a fractured landscape. For facultative cooperative breeders, cooperation may increase as opportunities for breeding alone decrease. Meanwhile, smaller, defensible patches may change mating systems by making mate guarding more feasible. We note that many of the studies reviewed here were observational, with only a limited number using an experimental approach. Experimental approaches to how habitat fragmentation influence social interactions are possible, and we encourage more researchers to explore these options.

V. INCREASED VARIABILITY OF WEATHER AND EXTREME EVENTS

Extreme events such as intense storms are already thought to have become more common due to changing climates, and their frequency is likely to increase further. Meanwhile, less-extreme weather patterns are becoming more variable. Research into how the variability of weather and frequency of extreme events influence social interactions is less common compared to research into the other three environmental factors discussed in this review (see Bailey & van de Pol, 2016). This deficit is due to a variety of reasons including, but not limited to, that such conditions are hard to recreate in the laboratory, are infrequent in nature, and may primarily occur in regions further from human settlement. Nevertheless, there is some research documenting how the variability of weather and extreme events influences social interactions. An early theme is that energetic and survival costs for animals result in changes in social interactions. These changes occur either to compensate for the extreme events and avoid significant consequences, or as an unavoidable consequence of substantial disruption. We also discuss how social behaviours can differ from normal during extreme events and how post-extreme event landscapes may differ from pre-event landscapes, again causing differences in social behaviours.

(1) Social interactions

(a) Communication

Extreme and variable weather conditions are thought to impose high energetic costs on organisms (Mangan

et al., 2017). Signalling is often energetically expensive, and so can be expected to be reduced or eliminated in conditions associated with more extreme weather. A decrease in acoustic signalling with increasing wind or rainfall and at extreme temperatures is seen in some orthopterans [*Pterophylla camellifolia* (Franklin *et al.*, 2009); *Copiphora brevirostris* (Velilla *et al.*, 2020)], birds [tawny owls, *Strix aluco* (Lengagne & Slater, 2002); eastern phoebes, *Sayornis phoebe* (Bruni & Foote, 2014)], amphibians (hourglass treefrog, *Dendropsophus ebraccatus*; Schwartz & Wells, 1983), and mammals (Mueller's Bornean gibbons, *Hylobates muelleri*; Clink, Hamid Ahmad & Klinck, 2020). In the immediate aftermath of extreme events, conditions may still not be favourable for communicating. Tawny owls broadcast calls transmit significantly less far on wet nights compared to dry nights, suggesting that calls have low efficacy in challenging conditions (Lengagne & Slater, 2002). However, in some circumstances, signals may be an energetically cheaper option than other forms of interaction. Juvenile brook charr (*Salvelinus fontinalis*) in laboratory stream channels for example reduce physical aggression and increase displays to maintain their territories during artificially increased water flow (McNicol & Noakes, 1984). The shift away from physical aggression to displays is likely to preserve energy. Evidence reviewed in Section V.1c suggests that aggressive behaviours are often changed in freshwater organisms if water flow and volume increase. The change in aggressive behaviours may be due to the disruption of communication between individuals, but direct evidence of, for example, how the efficacy of chemical signals is changed by altered water flow, appears to be lacking. In summary then, while we might expect animals to signal less or not attempt to signal at all during and immediately after extreme weather events, there is not enough empirical evidence to date to make a confident prediction.

(b) Social grouping and associations

Extreme weather events can pose survival risks, especially for small animals, which promote social behaviours that aid survival or limit social behaviours by breaking up groups. For example, following a cyclone strike which reduced a population of black howler monkeys (*Alouatta pigra*) by 42%, solitary individuals were seen frequently, which is unusual, and only gradually over time were groups observed to re-form (Pavelka *et al.*, 2003; Behie & Pavelka, 2005). This reduction occurred due to reduced availability of food, increasing competition, with juveniles, who are the most socially active, suffering the highest mortality (Pavelka *et al.*, 2003; Behie & Pavelka, 2005; see also Negrín *et al.*, 2016). Howler monkeys also form smaller sub-groups following cyclone strikes to reduce within-group competition for limited resources (Schaffner *et al.*, 2012). Atlantic spotted dolphins (*Stenella frontalis*), on the other hand, show higher rates of social associations following high rates of mortality due to a cyclone (Elliser & Herzing, 2014). This increase is perhaps adequate compensation for the mortality, as most other aspects of social organisation are maintained (Elliser & Herzing, 2014). In other

cases, extreme events can lead to conflict-reducing or cooperation-promoting grouping behaviours to boost survival and reproduction. Helping at the nest is more common in Taiwan yuhinas (*Yuhina brunneiceps*) if there is heavy rainfall before the incubation period, as foraging efficiency and nest initiation are reduced in the rain (Shen *et al.*, 2012). Shen *et al.* (2012) also suggested that intragroup conflict in this species might be reduced in heavy rainfall, as reproductive success is higher in high-rainfall conditions, although conflict was not explicitly measured. Heavy rain also reduces interactions and collective foraging of colonies of red imported fire ants (*Solenopsis invicta*; Porter & Tschinkel, 1987) and communities of ground-dwelling ants in an Indian rainforest (Basu, 1997). Extreme conditions will therefore immediately disrupt animals' abilities to form groups, although in some cases they resort to greater levels of grouping to survive in the aftermath.

Increased variation in weather will also mean periods of drought or flood and periods of extreme hot or cold are experienced more often. This can create uneven distributions of resources in both space and time. Animals may respond to the challenge of obtaining enough energy in these conditions by forming and moving in groups to locate resources. Clumped resources mean that individual European shore crabs (*Carcinus maenas*) start to move as a group even when not foraging (Tanner & Jackson, 2012). Meanwhile, an experiment in free-living New Caledonian crows (*Corvus moneduloides*) showed that pulses of a clumped preferred food item encouraged within-group interactions, possibly increasing the opportunity for the exchange of information within groups, but did not affect the flow of information between different groups (St Clair *et al.*, 2015). Ilany, Booms & Holekamp (2015) found that spotted hyena (*Crocuta crocuta*) maintain more social associations in years of low rainfall, which may be a strategy to locate more unevenly distributed prey. There is some evidence therefore to support the suggestion that more variable weather will increase grouping and cooperative interactions, similar to the patterns observed above in response to extreme weather events.

Animals do not always respond to more variable environments by increasing grouping, however. Captive guppies maintain consistent social dynamics and preferences for the same social partners in the face of multiple disturbances to the physical environment, including changes in water depth, change in pool size, and translocations, which are predicted consequences of increased rainfall (Wilson *et al.*, 2015; Krause *et al.*, 2017). This may be because guppies shoal in response to predators rather than environmental conditions. It therefore seems plausible that the specific response to more variable weather will depend on whether animals tend to cooperate with members of their own group for access to food or to avoid predators, but there is not enough evidence to evaluate this hypothesis now.

(c) Agonistic interactions

Extreme weather can remove signals from the environment, impairing assessment of conspecifics and leading to increased

aggression. In particular, animals living in freshwater and riparian environments subject to storms and flooding will experience variability in water volumes and flow rates, which can affect rates of aggression through the disruption of communication (see also Section V.1a). In Nile tilapia, frequent water changes in a laboratory setting cause an increase in aggression from the subordinate fish in a dominant–subordinate pair, possibly as recognition of status is impaired through the removal of chemical cues (Gonçalves-de-Freitas *et al.*, 2008). As a result, dominant individuals may be forced to increase their levels of aggression to maintain their rank in more variable systems. Such an increase was seen by Sneddon *et al.* (2006) with three-spined stickleback exposed to laboratory conditions that simulated increased turbulence and drought. For terrestrial organisms, Shen *et al.* (2012) suggested that highly variable environments could impose costs that limit the expression of energetically costly behaviours such as high aggression levels. However, direct tests of this suggestion appear to be absent. There may also be changes to water clarity due to increased flow rates and we discussed the impact of turbidity on social interactions and social organisation in Section III. In general, changes in water flow rates and volumes can influence aggressive interactions and the relative ranking of captive freshwater fish. However, data on how levels of aggression change in other animals in more extreme and more variable environments are lacking.

(2) Social organisation

(a) Mating systems

Environments with highly variable conditions will alter the availability and distribution of resources, which will affect mating systems that depend on ecological factors such as these (Emlen & Oring, 1977). In particular, for facultatively cooperatively breeding species, solitary breeding may be disfavoured. For instance, Sheehan *et al.* (2015) found that regions with greater temperature instability show higher rates of cooperative nesting in the social wasps *Polistes dominula* and *Polistes exclamans* (although in *Polistes fuscatus* the opposite is true; Sheehan *et al.*, 2015). Similarly, in banded mongoose (*Mungos mungo*), years of variable rainfall, which give lower female survival, cause older males to invest more in communal helping, possibly as mating opportunities are reduced (Marshall *et al.*, 2016). In fact, subordinate banded mongooses only breed in benign conditions, as dominant females suppress subordinate reproduction during resource limitation (Nichols *et al.*, 2012). These within-species relationships between climate variability and mating system are matched by studies across species that also find links between climate variability and the incidence of cooperative breeding in birds, social spiders, and Australian rodents (Jetz & Rubenstein, 2011; Guevara & Avilés, 2015; Firman *et al.*, 2020). However, Sheehan *et al.* (2015) found that among-species trends tended not to mirror within-species trends in *Polistes* wasps (see also Lin *et al.*, 2019), indicating

that we need to be careful when generalising results from these across-species results to expected trends within species.

Extreme events may impose stronger selection on one sex than another (Acker *et al.*, 2020). This sex-biased mortality could influence the adult sex ratio. In this case, mating systems would be altered depending on which sex experienced higher mortality (Widemo & Sæther, 1999; Székely, Weissing & Komdeur, 2014). Extreme events may also select against certain behavioural phenotypes, for example favouring migrants over residents (seen in European shags, *Phalacrocorax aristotelis*; Acker *et al.*, 2020). If this behavioural phenotype is relevant to aspects of a mating system, such as the ability to form monogamous pairs or engage in extra-pair copulations, of if the relative abundance of a phenotype influences whether it is favoured in sexual selection, patterns of sexual selection could well drive shifts in mating systems. Any consequences will also depend on whether selection in years or seasons without extreme events are aligned or not with selection induced by extreme events, as well as by the plasticity and heritability of the traits under selection (Acker *et al.*, 2020). Estimating such evolutionary parameters is data intensive and, given the difficulties in carrying out even small-scale studies into the effects of extreme events, may represent a challenge we cannot currently surmount. Combining data across the numerous long-term studies of birds and mammals (Clutton-Brock & Sheldon, 2010) might provide one route for us to assess the impact of extreme events on the evolution of animal populations.

(b) Dominance hierarchies

Increasingly variable conditions can disrupt dominance hierarchies as previously dominant individuals may no longer have the upper hand. For example, Sneddon *et al.* (2006) found that three-spined stickleback dominance hierarchies in the laboratory decrease in stability during both simulated increased turbulence and drought. Previously dominant individuals are only able to maintain their top rank if they respond to the changing conditions by increasing their aggression levels (Sneddon *et al.*, 2006). Likewise, increasing the flow rate in experimental tanks of brown trout (*Salmo trutta*) destabilises the group's dominance hierarchy, even though overall levels of aggression do not change (Sloman *et al.*, 2002). The change in rank order of individuals may be caused by the physical displacement of high-ranking individuals from their preferred spatial locations within the tanks or because the higher rate of water flow causes chemical cues of rank to be removed from the system (Sloman *et al.*, 2002). Both these studies suggest that it is high-ranking individuals that lose out due to more variable conditions, which would remove selection for the traits that previously predicted social dominance. However, more studies, especially in non-fishes, are necessary to confirm this initial suggestion.

(c) Collective behaviour

In the immediate aftermath of an extreme weather event, mortality and habitat disruption can fracture previously

stable groups (see Section V.1*b*) and prevent them from acting together. Black howler monkeys suffered extensive mortality and disruption to their social groups as the result of a tropical cyclone. Further, collective howling, used by this species to delineate group territory boundaries, was also uncommon following the cyclone, assumed to be due to the reduced rates of intragroup contact (Pavelka *et al.*, 2003). By contrast, extreme conditions may favour increased collective action if such behaviours allow organisms to avoid reduced survival and reproduction. Facultatively social spider (*Anelosimus studiosus*) colonies in the south-eastern USA that show higher levels of collective aggression are more likely to survive cyclone strikes than their less-aggressive counterparts (Little *et al.*, 2019). Similarly, as noted above, Taiwan yuhinas breed more cooperatively (Shen *et al.*, 2012) and various ant species (such as *Solenopsis invicta* and *Formica selysi*) make ‘ant rafts’ with their bodies, where ants attach to each other to create a single buoyant structure which can remain afloat for up to 12 days (Wheeler, 1910; Adams *et al.*, 2011; Purcell *et al.*, 2014) as a response to more intense rainfall. Without resorting to increased levels of cooperation, organisms may not be able to persist in areas that become exposed to increasingly intense storms, as the energetic costs of nest repair under extreme rainfall can prohibit the persistence of solitary individuals and even small groups from habitats where storms are common (Purcell, 2011).

Meanwhile, even if increased environmental variability does not lead to such immediate mortality and destruction as extreme weather events, it can still lead to increased collective action. Increased environmental variability is likely to cause increased patchiness of resources in time or space. If animals form groups or interact more closely within groups in response to patchy resources (Tanner & Jackson, 2012; Ilany *et al.*, 2015; St Clair *et al.*, 2015), then we would expect an increase in collective foraging as a means to access shared information about ephemeral resources. Therefore, extreme conditions such as very heavy rainfall may then either limit animals from interacting collectively or promote collective actions if they are the only route to survival. Recreating these conditions in the laboratory and testing the collective behaviour of groups of animals in a captive setting is the next logical step to testing these hypotheses.

(3) Summary

Mobility, communication, and persistence in environments when weather is unpredictable or extreme becomes more challenging. A potential solution to this problem is that organisms increase how cooperative they are, a pattern thought to explain differences among species, and so should be observable within species. Variable and extreme environments may also increase energy expenditure, which could reduce social interactions that have a net energetic cost but promote social interactions that help conserve energy. Energetic costs may be felt most strongly by the most dominant individuals, which can remove the benefits they previously enjoyed, disrupting dominance hierarchies. However, if

cooperative breeding is favoured, then dominant breeders may benefit from an increased number of helpers. Ultimately, we are limited from making strong conclusions due to the sheer lack of data. This deficiency can be addressed, given that studies of environmental variability in the laboratory are possible. Further, the typical study on extreme events in the wild lacks controls or any replication in space or time (Pruitt *et al.*, 2019), which should be addressed to increase the quality of inference we can make from such studies. If the negative impacts of extreme and variable environments on survival and reproduction are strong enough, and within- or across-generation change is not sufficient to mitigate these costs, then the extirpation of animals from populations undergoing rapid change is expected.

VI. FUTURE CONSIDERATIONS

In this review, we identified various ways in which we expect social behaviours to change due to rapidly changing environments. Below, we pick out several common themes that warrant further attention and highlight approaches that will improve our understanding of the evolutionary consequences of environmentally induced changes to social behaviour.

(1) Synthesising patterns in observed changes

The research reviewed herein shows a diverse array of behavioural responses to environmental change. We summarise some of the more general expectations for future change in Table 1 to highlight responses to HIREC that could be common, if not necessarily universal. For example, HIREC can either impose or lift energetic constraints (see Sections II and V). As such we can expect social interactions that require high energy expenditure to be directly affected, even if the direction of the effect depends on the particular behaviour. Through energetic limitations, or through modification of habitats, HIREC can also impose movement constraints (see Sections II and IV), that have various consequences for mating systems, communication networks, and the ability of animals to move and act in groups. HIREC can also directly cause pathologies or reduce survival (see Sections III and V), directly disrupting social interactions and group formation, but also possibly creating conditions where higher levels of cooperation are favoured. Additionally, by both altering the environment through which signals travel (see Sections II–V) and altering physiology (see Sections II and III) HIREC can disrupt the ability of individuals to communicate and recognise each other. Disrupting communication has downstream consequences for social structures such as dominance hierarchies and mating systems. Finally, changing environmental conditions of all kinds can influence different individuals in contrasting ways (individual by environment interactions), destabilising dominance and mating structures by changing the relative rankings of

Table 1. Summary of the diverse changes in social interactions expected in response to the four aspects of environmental change delineated in this review. For each of the four broad environmental changes, we list more narrow kinds of environmental change, the direct effects of these on organisms (often physiological but not exclusively) and their consequences for social interactions and social structure. Social consequences are based on empirical evidence where available and informed predictions where research is lacking. Changes due to increased temperature are highlighted in red, pollution in blue, habitat fragmentation in green, and extreme and more variable weather in yellow

Environmental change	Direct effect	Social consequence	References
Increased temperatures	Longer reproductive seasons	Increased rates of polyandry	Bergeron <i>et al.</i> (2011); Olsson <i>et al.</i> (2011)
		Overlapping generations allowing cooperation between parents and offspring	Soucy & Danforth (2002)
	Decreased cold stress	Reduced grouping in small animals	Lanham (2001)
	Reduced physiological limitations on signalling	Generally increased call rates, call rates may not reflect the quality of individuals	Symes <i>et al.</i> (2017)
	Evaporation of chemical signals	Reduced use of chemical signals, disruption to collective behaviour	Martín & López (2013); Iglesias-Carrasco <i>et al.</i> (2018)
Increased dryness	Difficulty in maintaining water balance	Increased grouping and reduced activity for animals in dry environments	Gordon (2013)
Increased hypoxia in water	Physiological limitations on energetic behaviours	Reduced signalling leading to poor mate discrimination	Jones & Reynolds (1999)
		Reduced aggressive interactions	Abrahams <i>et al.</i> (2005)
Chemicals in the environment	Disruption to the medium through which signals are sent and received	Reduced ability to recognise partners, altered mate choice, less stable dominance hierarchies, disrupted collective behaviour	Lürling & Scheffer (2007); Brodin <i>et al.</i> (2013)
	Various physiological changes including disrupted sensory systems and metabolism	Altered aggression levels, disrupted dominance hierarchies and collective behaviour	Sloman <i>et al.</i> (2003a); Sloman (2007); Flahr <i>et al.</i> (2015)
Light pollution	Disruption of circadian rhythms and earlier perceived daylight	Increased/earlier activity in diurnal species potentially leading to unreliable quality-indicator traits	Miller (2006); Borgström <i>et al.</i> (2010); Da Silva, Valcu & Kempenaers (2015)
	Increased risk of predation	Decreased activity and aggression, reduced interactions, altered mate choice, disrupted mating success	Rand <i>et al.</i> (1997); Carvalho <i>et al.</i> (2012)
	Enhanced visibility of visual signals	Increased information sharing, increased group cohesion and coordination	Ryer & Olla (1996); Kurvers & Holker (2014)
Increased turbidity and eutrophication	Disruption to the medium through which signals are sent and received	Reduced ability to recognise partners, impeded social cohesion, altered mate choice, breakdown of sexual selection leading to hybridisation	Seehausen <i>et al.</i> (1997); Candolin <i>et al.</i> (2007)
Auditory/noise pollution	Disruption to the sending and receiving of auditory signals	Altered signal characteristics (e.g. amplitude, frequency, and signal timing), reduced ability to recognise partners, altered mate choice	Brumm & Todt (2002); Luther & Baptista (2010)
	Cross-modal effects – non-auditory stimuli affected by stress or distraction due to noise	Impeded information use, reduced coordination and cohesion of social groups	Sarà <i>et al.</i> (2007); Morris-Drake <i>et al.</i> (2016); Herbert-Read <i>et al.</i> (2017)
Larger gaps between habitat patches	Increased costs of dispersal	Increased aggression in resource-limited species	Lattanzio & Miles (2014); Gabriel <i>et al.</i> (2018)
		Increased cooperation in facultative cooperative breeders	Hatchwell & Komdeur (2000)
	Reduced mate choice options	Increase in scramble mating systems, increased inbreeding and hybridisation	Norris & Stutchbury (2001); Banks <i>et al.</i> (2005)
	Increased ability to monopolise mates/resources	Increase in polygynous mating systems	Eldakar <i>et al.</i> (2009a); Sih <i>et al.</i> (2017)
Reduced habitat complexity	Disrupted auditory communication	Reduced ability to recognise/find conspecifics	Hansen <i>et al.</i> (2005); Van Oort <i>et al.</i> (2006)
Reduced quality of habitat	Physiological limitations on energetic behaviours	Reduced energetically costly social behaviours	Negrín <i>et al.</i> (2016)

Table 1. (Cont.)

Environmental change	Direct effect	Social consequence	References
Higher frequency of heavy rain and storms	Difficulty persisting in environment	Increased grouping and use of protective structures	Adams <i>et al.</i> (2011)
Variable water flow	Physiological limitations on energetic behaviours	Reduced aggressive interactions	McNicol & Noakes (1984)
	Removal of chemical cues	Reduced recognition and so less-stable dominance interactions	Sloman <i>et al.</i> (2002); Gonçalves-de-Freitas <i>et al.</i> (2008)
Variable resource availability	Difficulty in predicting resource locations	Increased grouping to ensure information exchange and ability to find ephemeral resources	Tanner & Jackson (2012); St Clair <i>et al.</i> (2015)

phenotypes. Social interactions typically link different processes together (such as resource intake and mating success) and as such knock-on effects and downstream consequences of changes in social interactions due to HIREC are common.

Acknowledging variation in the ecology of study organisms, like their natural history and the key limiting resources in their environment, allows us to understand apparently contradictory patterns. For example, small animals often cluster to achieve homeostasis more quickly. Such organisms may cluster in dry conditions to limit their water loss, and in cold conditions to limit their heat loss. Therefore, as cold environments become warmer, small organisms may respond by decreasing grouping as heat loss becomes less of a problem. By contrast, as warm environments become even warmer and dryer, small organisms should increase grouping as water loss becomes a greater problem. It is clear, then, that opposite trends are not in conflict once we consider the organisms' ecology. The same is true of changes in aggression or social tolerance as habitats fragment. Organisms limited by access to resources may increase aggression as space is reduced, but organisms limited by available breeding habitat are predicted to show increased social tolerance as their ability to breed alone is reduced (see also Ims *et al.*, 1993). The take-home message is that we need a firm grasp of organisms' ecology, such as the limiting factors imposed by the environment they inhabit, before we can predict how their social interactions will respond to predicted environmental change.

While there is value in examining each stressor in isolation, we also recognise that the environmental changes caused by climate change are unlikely to occur singly and instead are simultaneous ['multiple stressors' (Wong & Candolin, 2015; Orr *et al.*, 2020)]. In this review, we saw that a given type of social interaction or social organisation will be influenced by multiple aspects of changing environments. For instance, aggression in aquatic organisms might become more common as waters warm, but is predicted to decrease under hypoxia, which is also a likely consequence as environments change due to warming and pollution (Kochhann

et al., 2015). There are therefore conflicting (also known as dampening or antagonistic; Orr *et al.*, 2020) responses. In simple systems it might be possible to take observed responses of social behaviour to single stressors, assume limited interactive effects, and predict how responses to two simultaneous stressors might sum (Liess *et al.*, 2016). However, any unexpected interactive effects between the two stressors would render these predictions inaccurate (Thompson, MacLennan & Vinebrooke, 2018). The same is true of potentially synergistic (also known as amplifying; Orr *et al.*, 2020) effects. For example, aggression could increase both due to increases in temperature, and as habitats fragment and encounters with rivals increase in frequency. The overall increase in aggression could be equal to the sum of these two effects independently, but equally could be much greater or smaller. While making predictions based on known physiological and neurobiological pathways is possible (see Moss & While, 2020), ultimately we suggest full-factorial manipulative experiments are required to determine what the consequences of multiple simultaneously changing stressors are. Such concurrent effects of multiple aspects of environmental change may have larger ecological and evolutionary consequences than can be understood when examining the influence of a single axis of environmental variation alone. Therefore, additional research on the multifaceted nature of environmental change on social dynamics is imperative.

Our review has also highlighted the fact that work on how animal social behaviour responds to changing climates covers an enormous range of taxa. This breadth creates challenges for synthesising results, as comparing changes among different behaviours, among different organisms, and with different study designs, is difficult. A potential solution to facilitate comparisons across diverse taxonomic groups is to use social network analysis (Croft, James & Krause, 2008; Wey *et al.*, 2008; Krause *et al.*, 2014). Representing animal social interactions as networks facilitates the quantitative analysis of diverse, multifaceted, and dynamic interactions within a single framework (e.g. Meise, Franks &

Bro-Jørgensen, 2019). For example, several authors have quantified fish shoaling dynamics as social networks in order to assess how group cohesion changes with habitat complexity (Orpwood *et al.*, 2008; Edenbrow *et al.*, 2011; Webster *et al.*, 2013), or represented ungulate herds as networks to measure how they differ due to differences in resource availability and distribution (Rubenstein *et al.*, 2007; Sundaresan *et al.*, 2007; Williams *et al.*, 2017). Although in the former case no clear patterns emerged, in the latter case studies agree that more unevenly distributed resources promote more cohesive and well-connected networks. Social network analysis therefore represents a valuable tool which might allow us to draw out consistent patterns of change in social behaviour in response to key axes of environmental variation across a diverse range of organisms.

(2) Harnessing different study designs to understand the evolutionary consequences of environmental change

Throughout our review, it is apparent that many kinds of study have been used to explore how environmental change can influence social interactions. Laboratory studies may expose groups of adult individuals to different treatment regimens or expose the same individuals to different conditions, while observational studies in the wild may compare different populations of the same species living in different habitats or monitor a single population over time as it experiences environmental change. Further, the balance of different study types is not the same for each category of change. For example, investigations of the effects of temperature and pollution involve many laboratory studies where two (or more) experimental groups are exposed to different temperatures or chemical concentrations, and the differences in their behaviour compared. By contrast, studies of habitat fragmentation and extreme and variable weather contain far fewer experimental studies (especially for the latter) and a higher proportion of observational studies, either comparing populations exposed to the stressor to different degrees or using a longitudinal approach to determine how one population responds to environmental alterations over time. It is difficult, although not impossible, to re-create extreme or variable weather conditions in the laboratory but is comparatively straightforward to expose organisms to a range of temperatures or contaminants.

The different balance of study types has some consequences for our understanding of how social interactions respond to environmental change. For example, studies on captive animals may not observe natural behaviours and realistic responses to stressors, while the relative magnitude of experimental treatments may be larger than experienced by animals in the wild. Further, comparing populations that are separated by space or time does not allow one to assign conclusively any observed differences to local adaptive change or phenotypic plasticity. Both processes can lead to seemingly adaptive differences between one population and a population in another location under different conditions

(Stamp & Hadfield, 2020) or the same population at different time points under different environmental conditions (Boutin & Lane, 2014).

Untangling the role of plasticity and local adaptation in facilitating the ability of organisms to cope with rapid environmental change is important, and has been the subject of several in-depth reviews (Sih *et al.*, 2011; Wong & Candolin, 2015). If organisms do not or cannot show plastic responses of an adaptive nature, perhaps because the trait is highly canalised, then local extinctions become more likely unless evolutionary change is relatively rapid (e.g. Behrman *et al.*, 2018). The potential for an evolutionary response is also limited by the extent of standing genetic variation. Previous exposure to the novel environmental conditions in a species' evolutionary history might facilitate the maintenance of genetic variation that can allow for swift adaptation (Sih, 2013). However, human-induced changes such as habitat fragmentation and reductions in population size are also likely to reduce standing genetic variation and therefore limit the potential for evolutionary change (Wong & Candolin, 2015). Meanwhile, individual-level selection and adaptation can still lead to outcomes that are suboptimal at the population level (López-Sepulcre & Kokko, 2012).

While evolutionary potential is often likely to be limited, the rapidity of phenotypic plasticity can often protect organisms from experiencing immediate detrimental effects of environmental change and is therefore expected to play a vital role in helping to buffer populations from the impacts of anthropogenic influences. Most responses to anthropogenic disturbance are in fact facilitated by phenotypic plasticity rather than population-level evolutionary responses (Hendry, Farrugia & Kinnison, 2008). The predominance of plasticity is actually the general pattern for cases of phenotypic differences between populations (Stamp & Hadfield, 2020). However, it is important to recognise that plasticity will not always be sufficient, nor is it always expected to be adaptive as 'ecological traps' can lead individuals to respond inappropriately to environmental change (Wong & Candolin, 2015; Stamp & Hadfield, 2020). Plastic responses can also prevent selection from occurring, thereby limiting subsequent evolutionary change, although plasticity can also facilitate evolutionary 'rescue' by exposing hidden genetic variation or preventing drastic population declines which allows time for genetic changes to accrue (Pigliucci, 2005; Ghalambor *et al.*, 2007; Edelaar & Bolnick, 2019). In the latter case, genetic assimilation can occur, giving a genetic basis to the previously plastically expressed phenotype (Waddington, 1953, 1956). Understanding the possible mechanisms through which animal populations respond to environmental change, or are prevented from doing so, allows us to predict longer-term trends better such as extinctions or divergence from or return to ancestral forms.

Reciprocal transplant studies (or common garden experiments) are useful in determining whether differences between populations are due to local adaptation or plasticity. Despite this, there appears to be a general scarcity of such

experiments for assessing whether differences in social behaviour between populations are due to adaptive evolution of plasticity. We urge more researchers to take this approach. If translocated groups are able to adapt to their new environment, then phenotypic plasticity is driving the local change. In a rare example from our review, Davison & Field (2018) transplanted sweat bees from a northern population where they tend to be solitary, to a southern population where they tend to be eusocial. Most transplanted bees remained solitary, suggesting genetic differences and thus local adaptation is responsible for the between-population difference. Identifying that these sweat bees show limited plasticity in behaviour then allows us to predict how they will respond to environmental change (i.e. not through plastic changes in sociality, but through adaptive evolution), and therefore how we should manage populations that might decline before showing any change in behaviour. Understanding whether among-population variation in social behaviour is underpinned by plasticity or local adaptation is therefore key to going beyond just understanding how social behaviours are expected to change with rapidly changing ecosystems and moving towards identifying solutions to mitigate the consequences of these changes.

(3) Indirect genetic effects and future evolutionary trajectories

When animals engage in social interactions, an important part of their environment is the phenotypes of the individuals with whom they interact. Organisms can influence the phenotypes of those around them, for instance, either coercively (e.g. taking resources that the other would have used) or consensually (sharing of food with group mates). When the ability to affect others socially is itself heritable, then the genotype of one individual will affect the phenotype of its interacting partner(s) (Scott & Fuller, 1965; Griffing, 1967; Moore *et al.*, 1997).

Such influences are known as ‘indirect genetic effects’ (Moore *et al.*, 1997; Wolf *et al.*, 1998). The effect is ‘indirect’ as the focal individual’s phenotype is influenced by the genotype of its social interaction partner(s), whereas a ‘direct’ effect would be where the genotype of the focal individual influences its own phenotype (a ‘direct genetic effect’). Direct and indirect effects can covary, and if the covariance has a genetic basis, evolutionary trajectories can diverge greatly from situations where direct effects alone influence phenotypes (Muir, Bijma & Schinckel, 2013; Ellen *et al.*, 2014). For example, indirect genetic effects on the body mass of pen mates in Japanese quail (*Coturnix japonica*) are negatively correlated with direct genetic effects, so any change to increase direct breeding value (i.e. selection for heavier birds) leads to an increase in indirect breeding value [e.g. how strongly the birds compete for resources (Muir, 2005; Muir *et al.*, 2013)], which will *decrease* the mass of pen mates. This change in the social environment changes the mean expression of any trait influenced by competition for food. In this case, the outcome is reduced mean body mass, which

prevents a response to artificial selection. Therefore, evolutionary changes in social interactions can result in changes in other aspects of organisms’ phenotypes. Understanding how indirect genetic effects change with environments will help us to anticipate these changes.

Indirect genetic effects have two components: (i) individuals influence each other’s phenotypes; and (ii) the effect is heritable. As we have seen throughout this review, social interactions frequently change between environments, and so, as environments change, we can expect how individuals influence each other to change too. Furthermore, the heritability of traits is known to change among environments. Traits heritable in one environment may not be heritable in others (Hoffmann & Merilä, 1999; Charmantier & Garant, 2005; Wood & Brodie, 2015), and novel environments can expose genetic variation that is ‘hidden’ under typical conditions (Hermisson & Wagner, 2004; Schlichting, 2008; Paaby & Rockman, 2014). Studies of the impacts of environmental variation on measures of heritability and additive genetic variation have generally shown that favourable conditions tend to increase trait heritability, especially for traits with minimal fitness consequences (reviewed in Charmantier & Garant, 2005). We may then predict that organisms in rapidly changing and deteriorating environments will show reduced trait heritability, and potentially reduced variance in indirect genetic effects. This will, possibly dramatically, alter the evolution of populations that were previously subject to indirect genetic effects.

Indirect genetic effects have now been documented in a wide range of species, including animals (Ellen *et al.*, 2014), plants (Mutic & Wolf, 2007; Costa e Silva *et al.*, 2013), and fungi (Rode *et al.*, 2017). However, only a handful of studies have investigated how indirect genetic effects change between different environmental conditions. Piles *et al.* (2017) showed that rabbits (*Oryctolagus cuniculus*) fed restricted diets exert indirect genetic effects on pen-mates’ growth rates that covary negatively with direct genetic effects, while direct and indirect genetic effects do not covary among rabbits that have unrestricted diets. Therefore, alterations to the resource environment should affect how direct and indirect genetic effects contribute to evolutionary change. In *Drosophila melanogaster*, males exert indirect genetic effects on female movement, but this effect is weaker in environments containing ethanol compared to those without (Signor *et al.*, 2017). North American red squirrels (*Tamiasciurus hudsonicus*) influence each other’s breeding dates more strongly at high than at low population densities, and this social effect may only have a genetic component at high densities (Fisher *et al.*, 2019). This could cause very different evolutionary change depending on how population densities change in the future (Fisher *et al.*, 2019). Finally, Camerlink *et al.* (2015) found that indirect genetic effects on growth in pigs (*Sus scrofa*) were present, and did not change between groups kept with straw bedding compared to groups without bedding. Unfortunately, studies on indirect genetic effects examining the types of environmental change discussed herein, such as habitat fragmentation or changes in mean

temperature, are sorely lacking. Yet, the four studies listed above provide evidence that indirect genetic effects, and therefore the evolution of the social environment of populations, may change depending on environmental conditions. Given the ubiquity of social interactions and their importance in many facets of organisms' lives, it is imperative we achieve a greater understanding of how indirect genetic effects change with environments, particularly for the kinds of environmental change predicted in the future.

VII. CONCLUSIONS

- (1) Animals frequently show changes in their social behaviours due to changing environments. This ranges from responses that act to maintain fitness in the face of environmental change to responses that are probably pathological. We can therefore expect populations to show different patterns of social interactions in the future.
- (2) In general, we can expect a decrease, at least temporarily, in complex and costly social interactions in the future. This is due to more variable, more polluted, more fragmented, and more disturbed environments disrupting existing social structures by reducing group stability, increasing energetic demands, and jamming communication systems. We may however see an increase in interactions that facilitate energy savings or promote survival, such as social grouping in dry conditions.
- (3) The diversity of effects that we have documented does not necessarily imply that future changes are unpredictable. Changes in social behaviours are typically dependent on the ecology or natural history of the organism in question. This means that we can predict more accurately the response of a population to environmental change when we account for its ecology, such as whether the limiting factor for an organism's reproduction is access to food, space, or available mates, and so on.
- (4) A given social behaviour can be influenced by several of the environmental changes expected in the future, and not necessarily in the same direction. Therefore, overall changes may not follow simple or narrow predictions. This means that we must appreciate multiple stressors when predicting future changes in any behaviour and forthcoming work should attempt to understand the synergistic or antagonistic effects of multiple axes of environmental change.
- (5) Methodological and analytical techniques like social network analysis are promising tools to uncover consistent patterns across a range of taxa. Meanwhile, determining whether populations will show plastic or evolved responses, and using the indirect genetic effects framework, will help us to predict how

populations could evolve in response to novel environmental conditions.

- (6) Overall, we have given a general account of how animal social behaviours are predicted to change in the future as the environment changes. If changes are underpinned by plasticity, overall biodiversity or complexity may be maintained under a broad range of environmental conditions. However, genetically canalised social behaviours are likely to be comparatively more susceptible to environmental change, and less recoverable too. Along with declines in the abundance and diversity of animals, potential declines in biodiversity in the form of social interactions should be appreciated. Alterations to social interactions with changing environments should be monitored, understood, and managed.

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