Title: Climate change as a catalyst of social evolution

Authors: Jeanette B. Moss[1†] and Geoffrey M. While*[1]

Author Affiliations:

[1]School of Natural Sciences, University of Tasmania, Sandy Bay, Tasmania 7005, Australia

[†] Current Affiliation: Department of Entomology, University of Georgia, Athens, GA 30602, United States

*Correspondence

E-mail: Geoffrey.While@utas.edu.au

Phone: +61 (3) 6226 7822

ORCID ID

Jeanette B Moss: ORCID ID: 0000-0002-7207-5955

Geoffrey M While: ORCID ID: 0000-0001-8122-9322

Abstract

Anthropogenic climatic change will be a major factor shaping natural populations over the foreseeable future. The scope of this issue has spawned the integrative field of global change biology, which is chiefly concerned with identifying vulnerabilities of natural systems to climate change and integrating these into models of biodiversity loss. Meanwhile, there remains considerable latitude for investigating the multiple indirect and nuanced ways that broad-scale shifts in the abiotic environment will impact biological systems. One major unexplored category of effects is on social organisation. While climate has consistently been implicated as a major source of natural selection responsible for facilitating the evolution of complex animal societies, studies directed at testing these links on contemporary climatic time scales have thus far been limited to a select few higher-order, eusocial, taxa. Here, we present the case for how climate change, and specifically rising global temperatures, could catalyze social change at multiple stages of social evolution. We argue that these effects will manifest themselves through a range of subtle, climate-mediated pathways affecting the opportunities, nature, and context of interactions between individuals. We propose a broad conceptual framework for considering these pathways first at the individual level, and then discuss how feedbacks between bottom-up and top-down processes could mediate population-level shifts. We then implement this framework to explore the capacity for climate-mediated shifts in social evolution within three broad categories of social complexity: social group formation, social group maintenance, and social elaboration. For each category, we leverage social evolutionary theory and phylogenetic work spanning diverse systems to describe the pivotal traits that underpin transitions from each level of social complexity. In doing so, we aim to build a case for how short-term individual responses to climate could scale to impart constructive and/or destructive effects on the origins, maintenance, and diversification of animal societies.

Keywords: Temperature, behavioural plasticity, social interactions, thermal environment, contemporary evolution, social organisation, mechanisms, physiological pathways, spatiotemporal distributions, encounter rates

Introduction

Anthropogenic climate change will be a major factor shaping the trajectories of natural populations in the coming decades. Over the last 40 years alone, global warming has been linked to shifts in species' geographic distributions (Parmesan et al. 1999, Thomas and Lennon 1999, Parmesan and Yohe 2003, Tingley et al. 2009, Valladares et al. 2014) and demographic rates (Doak and Morris 2010, Lloret et al. 2012, Villellas et al. 2015), as well as shifts in traits ranging from drought tolerance (Franks et al. 2007, Hamann et al. 2018), temperature-specific development rates (Logan et al. 2003, Skelly 2004), melanization (Karell et al. 2011) and breeding phenology (Réale et al. 2003, Bearhop et al. 2005; While and Uller 2014). These processes will have profound effects on the long-term viability of species. Thus, a major objective of global change biology is to understand how variation in physiological thresholds and compensatory strategies will affect the structure of biotic communities and determine species-specific extinction vulnerabilities (Deutsch et al. 2008, Somero 2010, Arribas et al. 2012, Cahill et al. 2013, Cochrane et al. 2015).

Global-scale changes in the abiotic environment will also have a myriad of *indirect* effects on biological systems, which could operate independently or synergistically with other processes to alter ecological and evolutionary trajectories. One major avenue through which climate change may indirectly affect biological systems is by altering the opportunities, context, and nature of biotic interactions. This has been relatively well appreciated in the context of environmentally mediated shifts in interactions *between* species (Engler et al. 2013, Milazzo et al. 2013, Singer et al. 2013, Bisi et al. 2015, Werner et al. 2019). However, there is a growing realisation that altered environmental conditions will also lead to shifting interactions *within* species. Such intraspecific interactions are the fundamental building blocks of social organisation, the emergent properties of which (e.g., group size and complexity) can have major influences on evolutionary trajectories by mediating interactions between organisms and their environment (Maynard Smith and Szathmáry 1997, Krause and Ruxton 2002, Kikvidze and Callaway 2009, Kappeler 2019, Kappeler et al. 2019, Socias-Martínez and Kappeler 2019). Therefore, there is need to understand how alterations in the environment brought about by climate change could influence how individuals interact with one another and the downstream consequences of this for the ecology and evolution of social organisation.

Projecting the impacts of contemporary climate change on social trajectories necessitates an appreciation of the evolutionary relationship between climate and social organisation. Climate has consistently been implicated as a major source of natural selection responsible for facilitating the emergence, maintenance and diversification of complex animal societies. For instance, researchers have traced the diversification of eusocial hymenopteran insects along ancestral gradients in season length (Kocher et al. 2014, Groom and Rehan 2018), and cooperative breeding in birds is associated with the repeated colonization of novel and harsh environments (Jetz and Rubenstein 2011, Cornwallis et al. 2017, Lin et al. 2019). Just as past ecological conditions have been leveraged to predict convergence on complex social traits in cooperative and eusocial lineages, so too has climate begun to emerge as a major factor shaping social diversification in solitary and subsocial species. Indeed, only recently has a study on the model species, *Drosophila*, identified past climate as the foremost predictor of species variation in social interaction networks (Jezovit et al. 2020). Despite some links between sociality and past climatic conditions, there is a paucity of studies aimed at testing whether similar processes could be unfolding on ecological time scales. Indeed, the vast majority of studies that examine social behaviour through the lens of contemporary climate change are concerned with how social traits might interact with climatic stressors to alter fitness outcomes (Rézouki et al. 2016, Grew et al. 2019) or influence population persistence over the short-term (Wong 2012). Only a small number of studies have explored the consequences of climate change for the evolution of social behaviour *per se*, and those that do are largely restricted to a small sample of higher-order, eusocial taxa (Davison and Field 2016, 2018, Dew et al. 2018, Groom and Rehan 2018).

We argue that this restricted focus has overlooked a diversity of ways in which subtle changes in climate can affect social organisation across the spectrum of social complexity. In this review, we will explore the potential for rapid global climate change, and specifically rising global temperatures (projected up to 4.5°C above pre-industrial levels by 2100; Collins et al. 2013), to actuate evolutionary change at various levels of social organisation. While our focus here is on changes in global temperature, we acknowledge that other climatic variables will also be associated with anthropogenic change (e.g., precipitation, frequency of extreme weather events, pollution, habitat loss, etc.), each which is capable of catalyzing similar and/or distinct processes to those we describe. Thus, it is important to note that while specific mechanisms may differ, the broader concepts of our framework are intended to be generalizable to other environmental variables. The goal of our exploration is not to arrive at a generalized picture of which societal outcomes will result under climate change, as this would require subscribing to pre-conceived (and practically and conceptually flawed) indices of social complexity (Kappeler et al. 2019). Nor do we suggest that the particular effects we detail will occur across all biological systems and stages of social evolution, as realized outcomes will depend on how abiotic and biotic factors interact with species-specific physiologies and neural pathways. Rather, we aim to develop a framework for considering the ways in which rising temperatures might inhibit, modify, or fast-track pathways that are commonly co-opted during the evolution of complex social traits. We illustrate how climate, and particularly temperature, can mediate opportunities for selection on socially relevant traits, either through bottom-up effects – alterations in trait expression in interacting individuals – or top-down effects – alterations in temporal and spatial patterns of social interactions themselves. Throughout, we will highlight key studies that have deconstructed direct and indirect climate response pathways through which individual behavioural changes scale to effect processes of social group formation and cohesion.

Plasticity in socially relevant traits: temperature as a mediator of individual behaviour

Intrinsic pathways

All animals, including members of most asocial species, must interact socially at some stage of their life cycle. While changes at the group level can ultimately be described as top-down or bottom-up, both scenarios depend at some stage on processes that integrate cues from the biotic (e.g., social) and abiotic environment and initiate behavioural responses. Temperature is established as one of the most influential abiotic factors controlling flexible aspects of behaviour (Wood and MacDonald 1997, Angilletta and Dunham 2003) – effects that we briefly summarize in Box 1. The first major category we consider relates to mechanisms that mediate the *opportunities* for social interactions, or the probability that individuals interact simply based on their distribution over space and time (e.g., Emlen and Oring 1977; Box 1A). All animals perform best within a given range of temperatures, and most are capable of accommodating shifting thermal optima by adjusting (or limiting) when and where they are ‘active’ (e.g., outside of a nest, burrow, or other form of refuge). Thus, in the most fundamental sense, the potential for within-group interactions depends critically on the frequency, duration, and distribution of suitable thermal windows. The potentially transformative effects of temperature-mediated shifts in activity periods on the emergence and maintenance of social organisation will be explored in greater depth in the sections that follow.

BOX 1: Temperature-mediated pathways of behavioural expression

A. Mechanisms Mediating the Opportunities for Interaction

Diurnal activity shifts**:** One behavioural mechanism for avoiding physiological stress imposed by thermal biology is to limit the number of active hours animals expend throughout the day. In equatorial and tropical regions, increasing air temperatures and reduced shade availability elevate risks of desiccation and heat stress, and it is projected that these factors will restrict daily activity periods in birds (Wolf 2000, Smit et al. 2016) and reptiles (Sinervo et al. 2010, Kearney 2013). Locally adapted cold-weather species could also be susceptible to activity reduction under climate change (Johansen et al. 2014, Hall and Chalfoun 2019). By contrast, higher within-season temperatures are expected to extend suitable periods for activity in many species, including high-latitude and high-elevation ectotherms (Kearney 2013) and nocturnal mammals (Stokes et al. 2001, Turbill 2008). Animals can also regulate how they experience the thermal environment by taking advantage of heterogeneity in temperature at both the micro- and macrohabitat scales. This form of behavioural thermoregulation is extremely well documented in ectotherms (insects: Ward and Seely 1996; marine invertebrates: Chapperon and Seuront 2011; fish: Matern et al. 2000; reptiles: Smith and Ballinger 2001, Sartorius et al. 2002, Goller et al. 2014) but also occurs in mammals (van Beest et al. 2012, Street et al. 2015).

Seasonal activity shifts: Climatic effects on activity are also shown to operate over broad spatio-temporal scales. For instance, trends towards warmer seasons have been implicated in earlier emergence from hibernation (Inouye et al. 2000, Sheriff et al. 2011, Gao et al. 2015), earlier arrival dates at breeding grounds (Crick et al. 1997, Gienapp et al. 2007), and earlier breeding start dates (Beebee 1995, Dunn and Winkler 1999, Both et al. 2004, Hüppop and Winkel 2006; While and Uller 2014). Advances in the start date of annual cycles could impart carry-over effects on the duration of events, setting new boundaries for the expression context-specific behaviours. For instance, a 45-year trend of advancing breeding seasons in Northern-hemisphere birds has been linked to increasingly prolonged breeding seasons (Halupka and Halupka 2017).

B. Mechanisms Mediating the Nature of Interactions

Physiological pathways**:** The thermal environment exerts considerable control over internal energetic reserves. As a result, shifts towards harsher (or more benign) temperature conditions may lead certain behaviours to be expressed less (or more) frequently. Endotherms depend on the maintenance of internal thermoregulatory machinery for their survival, and as they approach the extreme thermal limits of their biology and these processes are challenged, trade-offs are forced with other energetically taxing behaviours (Alatalo 1982, Vézina and Thomas 2000). Ectotherms, which comprise the vast majority of the word's biodiversity (Wilson 1992), present a special case as all their basic physiological functions (e.g., locomotion, growth, and reproduction) are intricately linked to the thermal environment. This is because temperature exponentially speeds up rates of metabolic reactions (Gillooly et al. 2001, Dillon et al. 2010), although careful treatment must be given to threshold effects when modelling this relationship (Gunderson and Leal 2015, 2016). In a recent review of the topic, Abram et al. (2017) broadly divided these effects into short- and long-term effects. Over the short-term (within seconds to minutes of temperature change), the speed and performance of locomotor, reproductive, and foraging behaviours (broadly, any behaviours with consequences for energy turnover; Mathot et al. 2019) will generally increase as temperatures approach a critical thermal maximum (Table 1 in Abram et al. 2017). Thermal regimes can also induce long-term changes across ontogenetic stages. For instance, the temperature-size rule in ectotherms posits that individuals reared at high temperatures will develop faster but attain smaller adult body sizes (Atkinson 1994, Angilletta and Dunham 2003, Angilletta et al. 2004). It has also been suggested that ectotherms that maintain higher body temperatures and metabolic rates throughout their lives have shorter lifespans (Valenzano et al. 2006, Scharf et al. 2015).

Neuroendocrinological pathways**:** In addition to affecting metabolic processes, the thermal environment also taps into neuroendocrinological pathways that regulate behaviour. Specifically, this pertains to pathways that have been co-opted from physiological maintenance pathways, or which are sensitive to general abiotic stressors. For instance, nonapeptides were first studied for their peripheral and evolutionarily conserved role in physiological regulation (Goodson and Thompson 2010), and yet have been co-opted to exert central control over the expression behaviours ranging from aggression (Lema 2006; Santangelo and Bass 2006) to affiliation and social bonding (Insel 1992; Carter et al. 1992) as well as gregariousness (Goodson et al. 2012a). Heat stress and fluctuating climatic conditions may also exert indirect effects on behaviour by mediating internal stress response pathways. A recent review of vertebrate stress responses to weather related stimuli found that short-term exposure to inclement weather events tends to increase circulating glucocorticoid concentrations, but prolonged exposure as to induce chronic stress may inhibit these responses (de Bruijn and Romero 2018). Indeed, acute temperature stress appears to have rapid activational effects on fish stress response pathways (Quigley and Hinch 2006, Chadwick et al. 2015), whereas chronic heat stress impairs normal responses (Quigley and Hinch 2006).

The second major category of temperature-mediated effects we consider includes any change in intrinsic state affecting the *nature* of social interactions after individuals have come together. Such complex behavioural responses (e.g., aggression, affiliation, cooperation) are controlled by a host of physiological and neurological pathways occurring within individuals (Ondrasek 2016, Seebacher and Krause 2017, Raulo and Dantzer 2018), which are in turn responsive to a range of environmental inputs, including temperature (Abram et al. 2017, Seebacher and Krause 2017, 2019; Box 1B). For instance, temperature-dependent metabolic processes could physiologically constrain and/or enhance individuals' ability to engage in energetically taxing social behaviours, including intraspecific aggression (Alatalo 1982, Vézina and Thomas 2000), fighting (Spohn and Moore 1997, Kvarnemo 1998, Biro et al. 2010, Pruitt et al. 2011, Zhao and Feng 2015) and mating (Saeki et al. 2005, Kindle et al. 2006, Jiao et al. 2009, Katsuki and Miyatake 2009, Best et al. 2012). More direct still, certain neuroendocrinological pathways such as those that regulate endogenous rhythms involved in transitions within and between socially aggregative states, are co-evolutionarily intertwined with extrinsic climatic cues (Cushing et al. 2001, Parker et al. 2001, Goodson et al. 2012b, Ondrasek 2016). Links may also be indirect; for instance, heat stress can trigger elevated levels of circulating corticosteroids (Lankford et al. 2003, Frigerio et al. 2004, Cockrem et al. 2019), which could then dampen or amplify social behaviours depending on the stage of social complexity (see Raulo and Dantzer 2018 for thorough review). In the sections that follow, we will explore how temperature-mediated shifts in the nature of interactions could catalyze socially constructive or destructive effects at successive levels of social organisation.

Extrinsic pathways

Rising temperatures will also influence individual behaviour by re-shaping the *context* for behavioural expression, or by shifting selection pressures. Such processes can upset the stabilization of social associations once they emerge. From the perspective of individuals, many benefits of group membership are determined by fundamental characteristics of social groups themselves. Indeed, opportunities to acquire information about habitat quality, enhance foraging efficiency, gain access to mates, and receive protection from predators all depend on attributes of group size, composition, and stability (Krause and Ruxton 2002). Shifting thermal environments have the potential to augment these group characteristics through a range of processes, including metabolic shifts in individual vital rates (e.g., survival, growth, and reproduction; Savage et al. 2004), differential mortality of size classes (Ohlberger 2013), impairments in fertility (Walsh et al. 2019), and changes in abundance of food resources (O'Connor et al. 2009, Dillon et al. 2010). Other major ecological determinants of group living include competition and predation (Rubenstein 1978, Chornesky 1991, Trumbo and Fiore 1994, Janson 1998, Clutton-Brock et al. 1999, Krause and Ruxton 2002), which are also subject to change with rising temperatures. Specifically, the scaled metabolic effects of temperature on community richness, abundance, and cycling can catalyze ecosystem interactions at higher trophic levels (Brown et al. 2004, Barneche et al. 2016, Ghedini et al. 2018). More broadly, increasingly hot and dry conditions under climate change will invariably alter the distributions of universal resources such as water, shelter, and retreat sites, which will dramatically alter the context for aggregation regardless of any social benefits of grouping *per se*. Irrespective of the precise causal factor, extrinsic effects on population densities have the potential to generate feedback effects on whole suites of socially relevant behaviours, as well as the frequency of social encounters themselves.

Scaling up individual responses: Social evolution on ecological time scales

In the previous section, we discussed various intrinsic and extrinsic pathways through which temperature influences patterns of individual activity or behaviour towards conspecifics. These individual responses form the foundation for patterns of group formation, structure, and cohesion, and thus their modification can have cascading effects within the social domain (Aureli and Schino 2019). To assert that these group- and population-level changes could then bring about evolutionary shifts within ecological time frames is to invoke an appreciation of the social environment as a dynamic, evolving entity, which can augment both the heritability and evolvability of traits (Pascoal et al. 2018, Rudin et al. 2019). Because social traits are, by definition, expressed during interactions with other individuals, they in turn can affect the genes expressed in interacting genotypes. Such indirect genetic effects (IGEs) can exaggerate evolutionary rates upwards or downwards (Moore et al. 1997, McGlothlin et al. 2010, Bailey et al. 2018), contributing disproportionately to patterns of long-term change and diversification. In other words, the impacts of various ecological parameters on evolutionary trajectories may be indirectly magnified if they modify the social environment experienced by individuals (Drown and Wade 2014, Bailey and Kölliker 2019). Thus, our interest is not strictly in how temperature influences individual behaviour, but in the feedbacks generated by scaled changes in the social environment (Fig 1).

As behavioural changes reverberate through the social environment, the nature of social interactions impose feedback effects. In social systems, individuals can be considered as a network of interconnected nodes, whose interactions have consequences for the collective behaviour of that system. Indirect genetic effects are most likely to accelerate evolution when positive feedbacks between trait values occur, such that interacting individuals become more similar to each other (McGlothlin et al. 2010). Interactive effects of increasing network densities can also amplify these feedbacks by increasing effects on other group members (Montiglio et al. 2018). This is demonstrated in examples such as the rapid evolution of aggression (Wilson et al. 2009), but also in instances of cooperation dominating social network nodes (Santos and Pacheco 2005, Du et al. 2009). In each of these scenarios, interactions among individuals are assumed to eventually culminate in stable equilibria, where phenotypes do not change dramatically over time. However, there are also biologically relavent scenarios in which iterative interactions among individuals can cause phenotypes within individuals to become more extreme, leading ultimately to the destablilization of systems (Trubenová et al. 2015).

In the following section, we discuss how sustained climatic warming, through its effects on short-term interactions between individuals, may induce changes at the level of the social group. It is important to note that the origin of social traits is not equivalent to the maintenance and subsequent evolution of those traits, and that the relative importance of behavioural pre-adaptations tends to degrade with evolutionary stabilization at some level of social organisation. This is because previously labile traits subject to directional selection for many generations may undergo genetic accommodation – a process by which genetic variants underlying adaptive behaviours become fixed in the population and are no longer responsive to external stimuli. To account for this variation, we begin by sorting stages of social organisation into three broad categories: the origins, maintenance, and diversification of societies. We provide an overview of important pre-adaptations that underlie each evolutionary transition, separating out routes to societal formation that occur via selection for (primarily) egalitarian versus fraternal associations. While these routes can overlap substantially in nature, our objective is to examine distinctions that exist owing to specific rules of group membership and the role of inclusive fitness. Once established, we present in-depth discussions relating pivotal social traits within each category to contemporary climatic processes, leveraging intrinsic and extrinsic mechanisms outlined in our conceptual framework (Fig 1). Taken together, the following sections will explore how short-term individual responses to temperature could have constructive and/or destructive impacts on social cohesion at multiple stages of organisation.

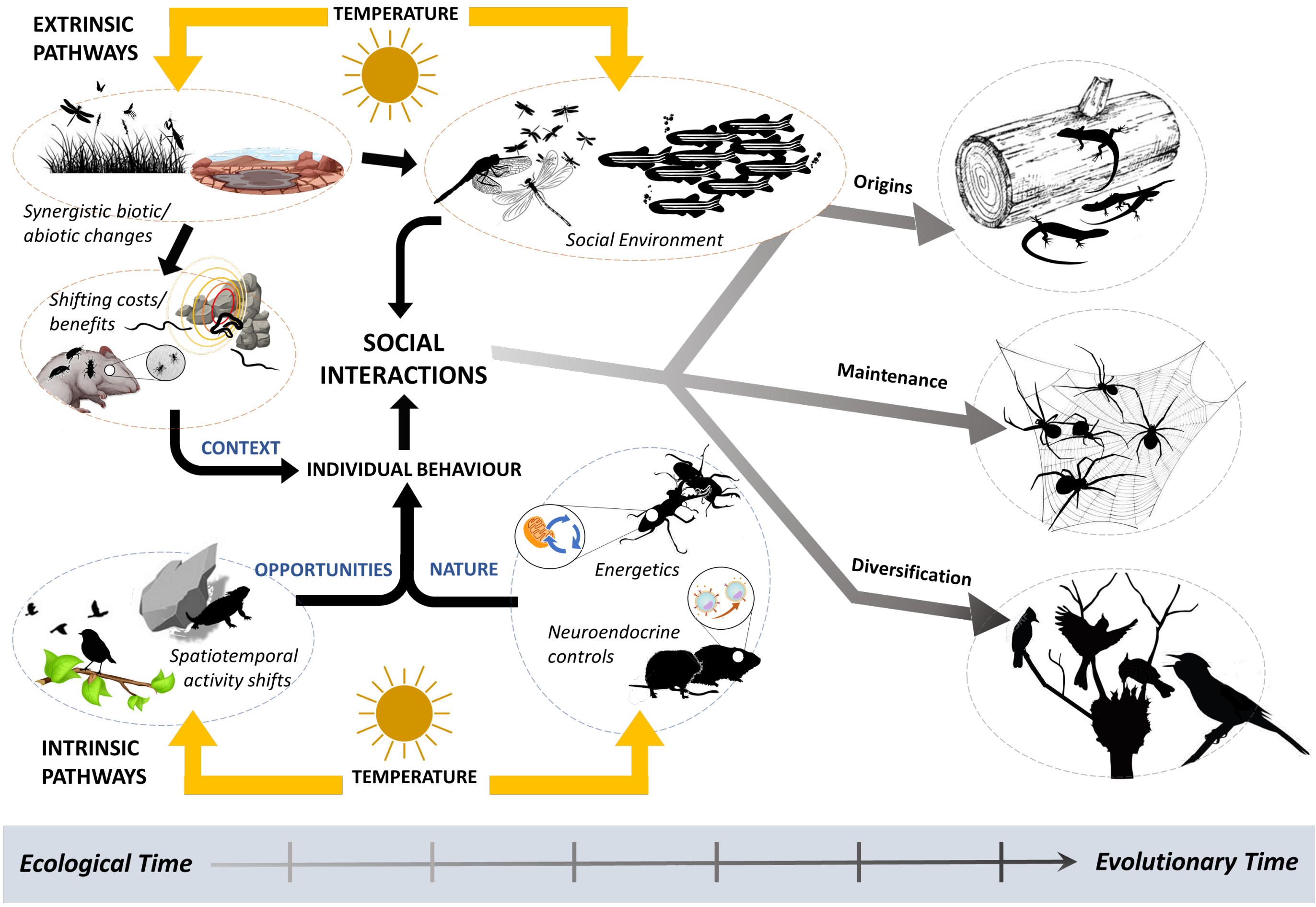

Figure 1: Conceptual framework illustrating various pathways through which subtle, temperature-mediated shifts in social interactions could scale to affect social evolutionary processes. On ecological timescales, individual behaviours may be molded by combinations of intrinsic (bottom-up) and extrinsic (top-down) temperature-dependent mechanisms. Behavioural responses at the individual level in turn shape the opportunities, nature, and context of interactions between individuals, which are subject to feedbacks from the broader social environment. Environmentally mediated shifts in the dynamics of social interactions, sustained over evolutionary timescales, ultimately have the potential to redirect the evolutionary trajectories underlying the origins, maintenance, and diversification of social systems.

Table 1: Sample of examples from the literature illustrating various ways in which subtle shifts in temperature have been shown to alter the opportunities, nature, or context for fundamental behaviours underlying evolutionary transitions in social organisation.

Trait Measured	Species	Social System	Type	Effect of Temperature	Description of Effect	Reference
Tolerance and extended associations						
mutual attraction to communal dens; aggregation	prairie rattlesnake, *Crotalus viridis*	solitary, but hibernate communally	egalitarian	-	Snakes converge on exposed rock outcroppings that facilitate optimal thermoregulation	Duvall et al. 1985
rates of interaction; proportion of time devoted to aggression	dragonfly, *Pachydiplax longipennis*	territorial and agonistic; congregate at feeding perches	egalitarian	+	Higher operative temperatures and solar radiation positively correlated with interaction rates and proportion of time devoted to aggression at feeding perches	Baird and May 2003
territorial vocalizations	Carolina wren, *Thryothorus ludovicianus*	socially monogamous and territorial	egalitarian	+	birds increased time budget on territorial vocalizations (and decreased time budget on foraging) at warmer temperatures and with food supplementation	Strain and Mume 1988
overtly aggressive interactions	sand goby, *Pomatoschistus minutus*	polygamous and territorial	egalitarian	+	Males initiate more aggressive interactions with conspecifics at higher temperatures	Kvarnemo et al. 1998
juvenile dispersal probability	common lizard, *Lacerta vivipara*	socially dispersed and territorial, no parental care	fraternal	-	overall reduction in juvenile dispersal probability correlated with 16 years of temperature rise, reflecting a negative effect of prenatal temperature rise and a positive effect of postnatal temperature rise	Massot et al. 2008
dispersal rate	house sparrow, *Passer domesticus*	highly sedentary, socially monogamous with biparental care	fraternal	+/0	rates of dispersal from low quality islands were higher at higher temperatures, but dispersal rates from high quality islands were unchanged	Pärn et al. 2011
Group structure and stability						
antipredator schooling behaviour	guppy, *Poecilia reticulata*	forms schools with stable partner associations	egalitarian	+	Nearest neighbour distances and elected group sizes increased in warmer waters	Weetman et al. 1999

interattraction	brown trout, *Salmo trutta*	gregarious as fry in gravel; solitary and territorial as adults	egalitarian	-	high temperatures lead to greater inter-individual distances and early dispersal from gravel aggregations	Colchen et al. 2017
huddling with unfamiliar conspecifics	meadow voles, *Microtus pennsylvanicus*	form seasonal same-sex aggregations for thermoregulation	egalitarian	-	under high temperatures, females huddle less with unfamiliar individuals of the same sex	Ondrasek et al. 2015
stability of dominance hierarchy	cichlid, *Apistogramma agassizii*	forms dominance hierarchies	egalitarian	-	dominance hierarchies are destabilized at higher temperatures by increased aggression by dominant and subordinant group members	Kochhann et al. 2015
rate of extra-pair paternity	snow bunting, *Plectrophenax nivalis*	socially monogamous, flocking	fraternal	+	warmer weather during the breeding season increases energy budget for extra-pair forays	Hoset et al. 2014
rate of extra-pair paternity	Reed bunting (*Emberiza schoeniclus*)	socially monogamous	fraternal	-	lower minimum temperatures during peak fertile period associated with higher proportions of extra-pair paternity	Bouwman and Komdeur, 2006
Cooperation and division of labour						
cooperation	burying beetle, *Nicrophorus nepalensis*	subsocial with parental care	egalitarian	+	high temperatures lead to heightened interspecific competition on carcass resources (blowfly larvae), which subsequently facilitates transition from conflict to cooperation among beetles on the same carcass	Chen et al. 2018
biparental care	Kenitsh plover, *Charadrius alexandrines*	monogamous with biparental care	fraternal	+	higher temperatures are associated with more equal division of parental care labor/increased paternal care relative to maternal care	Al Rashidi et al. 2010, 2011

cooperative brood care	pied babbler, *Turboides bicolor*	cooperative breeders	fraternal	+/-	high temperatures promote increased investment in offspring provisioning by subordinate group members, but reduced investment by dominant group members	Wiley and Ridley 2016
cooperative brood care	superb fairy wren, *Malurus cyaneus*	cooperative breeders	fraternal	+	in hot and dry seasons, females with helpers increase egg investment relative to those without helpers	Langmore et al. 2016

1 The origins of social living: Bringing individuals together

A fundamental first step in the emergence of social organisation is that individuals come together. This can occur either via nonrandom associations between unrelated individuals, in the case of egalitarian societies, or via extended associations between closely related individuals, in the case of fraternal societies. In many ways, this is the hardest step to overcome because most animals are solitary, and rather than compete for limited resources, they derive their greatest fitness benefits from avoiding conspecifics. Despite this, conspecific attraction has been observed in many 'asocial' species, implying that the benefits of occupying high-quality habitat often outweigh the costs of sharing that habitat with conspecifics (Stamps 1988). Virtually every definition of group living, however, acknowledges that for a true 'social group' to emerge from a territorial cluster requires that individual members maintain a degree of spatial proximity over time (Wilson 2000). These initial social associations are mediated fundamentally by local environmental factors, such as resource availability and weather fluctuations, which can prolong or curtail the tenure of associations either by encouraging individuals to remain concentrated in a localized area or by discouraging their departure (due to unfavorable conditions elsewhere). A complementary step in the transition from solitary to group living is tolerance of conspecifics. It is therefore important to understand which factors determine the setting of optimal or evolutionarily stable acceptance thresholds. This is true for both egalitarian and fraternal routes to group living. In both cases, the abiotic environment serves as a chief mediator not only of the rates at which individuals interact with 'desirable' versus 'undesirable' conspecifics (Reeve 1989), but also of the ability of individuals to perceive this distinction and modulate responses accordingly.

a) The origins of egalitarian societies

In the broadest sense, climate change will usher in cascades of changes in ecological context that could constrain or incentivize individuals to aggregate. Across taxonomic groups, precipitation and temperature each impose independent and interactive effects on the local availability of food resources owing to scaled effects on primary production (O'Connor et al. 2009, Dillon et al. 2010) and higher-order trophic cycling (Brown et al. 2004, Barneche et al. 2016, Ghedini et al. 2018). Both factors are predicted to change across spatial and temporal scales under projected climate models. Importantly, any reduction or redistribution of resource availability as a result of climate change could alter the extent to which initial associations between individuals emerge and, ultimately, set the stage for the elaboration of social traits. For instance, many overwintering animals congregate in communal dens or shelters for the express purpose of thermoregulation (e.g., reptiles: White and Lasiewski 1971, Graves and Duvall 1995, Shah et al. 2003, Davis Rabosky et al. 2012; mammals: Arnold 1993, Ondrasek et al. 2015, Groó et al. 2018). As mean temperatures rise, reduced exposure to extreme cold is projected to dramatically reduce this adaptive context for aggregation (Davis Rabosky et al. 2012). While links between seasonal aggregation and extrinsic cues are widely inferred, studies in rodents may soon reveal direct, mechanistic links between temperature and neuroendocrinological pathways involved in social bond formation (Ondrasek 2016). For example, binding pattern variation in oxytocin receptors – a nonapeptide that influences affiliation behaviour – has been shown to correspond with photoperiodic variation (Parker et al. 2001, Beery and Zucker 2010), and recent experiments in meadow voles (Ondrasek et al. 2015) and house mice (Groó et al. 2018) – two territorial species that form aggregations facultatively in winter – implicate temperature as a direct extrinsic mediator of time spent huddling with unfamiliar conspecifics. If validated, such mechanisms would support an intimate link between thermal environment and the evolution of complex, affiliative behaviours. Climatically induced changes in the onset and duration of suitable local conditions for aggregation could also operate via shifting seasonalities. Many excellent examples of this pattern have emerged from studies of bird migration, in which facultatively migratory species have responded to fluxes in migration season weather conditions with increased rates of residency (Meller et al. 2016), shifts in flock compositions (Mckinnon et al. 2019), and even with microevolutionary reductions in migratory activity (Pulido and Berthold 2010). Changes in migratory behaviour as a result of climate change could have significant implications for suites of social parameters related to the emergence of long-term aggregations.

In addition to meeting initial ecological requirements for aggregation, there are several mechanistic pathways through which climate change could modulate the frequency of tolerance-threshold crossing events in territorial animals. The first is through top-down effects on realized densities and rates of encounter between conspecifics. These effects may manifest as immediate, short-term changes in the number of individuals that are active in an area (Alford and Cohen 1996, Sinervo et al. 2010, Ord and Tonia Hsieh 2011, Andrew et al. 2013, Sperry et al. 2013, Gunderson and Leal 2016; Box 1A). For instance, dragonflies that congregate at feeding perches exhibit higher rates of interaction and devote a greater proportion of flight time to aggression at higher operative temperatures (Baird and May 2003). However, longer-term changes in density resulting from metabolically or synergistically induced changes in population vital rates could also facilitate microevolutionary shifts in tolerance thresholds. Models demonstrate that while saturated environments initially select for more aggressive strategies in territorial species (Kokko et al. 2006), increasing levels of intraspecific competition eventually trigger a shift from aggression to social tolerance and group territoriality (Port et al. 2011, 2017; but see Knell 2009). This reasoning is also supported empirically, with animals conditioned to living at high densities often exhibiting reduced levels of territorial aggression (Kavanagh and Olney 2006, Dantzer et al. 2012, Mayer et al. 2019) and increased gregariousness (Eggleston and Lipcius 1992, Hensor et al. 2005) compared with low-density counterparts. Through synergistic processes discussed previously (Extrinsic pathways), the thermal environment could behave as an abiotic mediator of this density threshold effect. As local densities increase, the number of potentially interacting conspecifics at any one time would also increase, which could exacerbate or dampen levels of conspecific aggression depending on the initial competitive state of a population. Conversely, a decline in local densities would mean that interactions with conspecifics may be both less likely to occur or more easily avoided, which could reinforce social intolerance.

The emergence of social tolerance in a population could also be influenced by bottom-up effects of the thermal environment on individual reactivity in social interactions. These effects may manifest primarily via release of (or constraint on) energy available for aggressive interactions and displays, and/or extended periods devoted to vigilance and defense (Box 1B). For instance, warmer temperatures have been associated with increased expenditure on aggressive and defensive behaviours in territory holding birds (Strain and Mumme 1988) and fish (Ratnasabapathi et al. 1992). However, as discussed previously (Box 1B), such dynamics are likely to exhibit threshold effects as individuals approach the upper limits of their thermal and energetic physiology. Indeed, in tropical *Anolis* lizards, rates of territorial signal production exhibit a concave relationship with ambient temperature, consistent with a physiological constraint hypothesis (Ord and Stamps 2017). In this way, shifts in the energetics underlying interactions have the potential to alter the extent to which individuals tolerate conspecifics, and thus the extent of social cohesion during the very early stages of social evolution.

A final consideration with regards to predicting how rising temperatures will affect the evolution of social tolerance is the role of thermal environment (and climatic variables more generally) in mediating conspecific familiarity and recognition (Box 2). In territorial species, familiarity through habituation is considered to be the primary mechanism through which reduced conspecific aggression evolves (Marler 1976, Shettleworth 1998, Langen et al. 2000). This process therefore depends on factors that promote stability within the social environment. On the one hand, warmer temperatures could facilitate faster habituation by extending the temporal period suitable for activity, and thereby increasing opportunities for interaction between neighbours. Alternatively, because fluctuating seasonal temperatures have been shown to alter normal home range structures (Rivrud et al. 2010, Seki and Koganezawa 2011, Morellet et al. 2013), cues originating from incorrect boundaries might in fact lead to dishabituation responses. This phenomenon has been documented in studies that experimentally manipulate conspecific cue positions, provoking residents to resume aggressive responses towards displaced familiar neighbours (Falls 1982, McGregor 1993, Carazo et al. 2008). More directly still, abiotic factors including temperature may lead to inappropriate aggression by disrupting social recognition pathways. Acoustic communication signals are a common mechanism used to discriminate among territorial neighbours in birds (Brooks and Falls 1975, Stoddard et al. 1990, Lovell and Lein 2004), amphibians (Bee and Gerhardt 2001, Lesbarrères and Lodé 2002), and mammals (Trefry and Hik 2009, Siracusa et al. 2019), and high temperatures have been shown to alter acoustic call rate and structure (Box 2). Temperature can also disrupt chemosensory recognition pathways (Box 2). For instance, intensified conspecific aggression in normally social yellow bullhead fish reared at high temperatures parallels effects observed when olfactory senses are surgically disrupted, which suggests a possible mechanistic link between temperature and conspecific recognition (McLarney et al. 1974).

b) The origins of fraternal societies

In contrast to egalitarian societies, fraternal societies refer to cases of group formation that predominantly involve close kin. Such social associations tend to emerge in species for which life history traits and ecological conditions keep closely related individuals together (Arnold and Owens 1998, 1999, Hatchwell and Komdeur 2000). The main route via which this occurs is when parents tolerate their offspring for prolonged periods of time. Indeed, promoting increased levels of association between parents and offspring is a crucial early step in the evolution of more elaborate forms of postnatal parental care and kin-based cooperation (Wilson 1975, Clutton-Brock 1991, Queller 1994, Field and Brace 2004, Royle et al. 2012). Such elaborations become selectively favored when inclusive fitness benefits are spread to all members of the kin group (Hamilton 1964a, 1964b, Maynard Smith 1977), and once started may become evolutionarily self-reinforcing due to coevolutionary feedbacks between parents and offspring that render parental involvement necessary to offspring survival (Tallamy and Wood 1986, Royle et al. 2016).

In many ways, the conditions that promote parental tolerance of offspring are not dissimilar from those implicated previously in promoting tolerance of conspecifics. The pivotal decision of whether offspring should delay dispersal from the natal territory is mediated through a combination of ecological constraints and familiarity, with habitat saturation understood to be among the most important factors underlying the emergence of extended kin associations (Brown 1969, Emlen 1982, Arnold and Owens 1998, Hatchwell and Komdeur 2000, Kokko and Lundberg 2001). This expectation is consistent with patterns derived from natural and semi-natural systems, for which offspring retention has been shown to correlate with multiple measures corresponding to limited suitable habitat (e.g., high population densities: Halliwell et al. 2017, Mayer et al. 2017; low adult turnover: Kokko and Ekman 2002; clumped resource distributions: Botterill-James et al. 2016). Each of these factors shows tendencies to change across gradients in climate. Consistent with this, a phylogenetic review of non-cooperative passerines revealed that latitudinal clines in adult longevity (e.g. slower rates of territory turnover in tropical species) correspond to longer durations of post-fledging parental care (Russell et al. 2004). In a similar pattern, lower latitude Spanish barn swallows are found to exhibit higher rates of natal philopatry than their Danish counterparts; yet in the more temperate location of Denmark, increasingly benign climatic conditions over a 20-year period have seen significant reductions in dispersal probability (Balbontín et al. 2009). Such climatic trends in natal dispersal could be augmented by local variation in habitat quality. For instance, in a 15-year study of sparrows, increasing conspecific densities brought on by warmer spring temperatures were found not to affect natal dispersal from high quality habitat, yet were associated with higher rates of departure from sites characterized by low food availability (Pärn et al. 2011).

For ectothermic species, anticipating the ways in which climate change could alter the costs and benefits of natal dispersal introduces further nuances. This is because in ectotherms, the thermal environment not only contributes directly to habitat quality, but the optimal setting of this component can vary between individuals. Indeed, variation in juvenile dispersal tendencies in common lizards are partly explained by between-individual variation in thermal optima (Bestion et al. 2015). In cold-adapted ectotherms, overlapping generations and high incidence of viviparity also introduce unique opportunities for maternal effects to modulate offspring dispersal decisions (Halliwell et al. 2017b). Despite revealing the expected trend of higher natal dispersal in years with warmer postnatal temperatures (i.e. which promote accelerated growth and exacerbated kin competition), a 16-year study of common lizards found that rising temperatures in the prenatal period were correlated with an over 50% reduction in juvenile dispersal probabilities (Massot et al. 2008). The suggestion emerging from these patterns is that while mothers use temperature as a cue of nonlocal environmental conditions, an ability to transfer this knowledge to offspring could inhibit natal dispersal. These examples illustrate the diversity of possible pathways through which altered thermal conditions could influence offspring dispersal strategies. In systems meeting the qualifying ecological and life history criteria as to permit offspring tolerance, such effects could set the stage for prolonged parent-offspring associations. In some lineages, climate change could even alter the context for the physiological innovations (e.g. viviparity) that facilitate extended maternal effects. Dupoué et al. (2020) demonstrate this in a recent study of common lizards, which showed that an evolutionary reversion from viviparity to oviparity along an altitudinal gradient could be explained by variation in water availability (i.e., maternal-fetal conflict) during pregnancy.

Another avenue through which temperature could perturb parent-offspring associations is via the breakdown of simple cues upon which parents rely to recognize and tolerate their offspring. Parental facilitation, whereby the presence of parents in a territory is essential to offspring decisions to delay dispersal (Brown and Brown 1984), appears across a diversity of taxa (birds: Ekman and Griesser 2002, Eikenaar et al. 2007; reptiles: Langkilde et al. 2007, Davis 2012; mammals: Mayer et al. 2017). This is because offspring receive nepotistic benefits from parents that they don’t receive from other adults, or if they were to establish their own territory (e.g., relaxed resource competition via tolerance: Ekman et al. 1994, Kokko and Ekman 2002, Komdeur and Ekman 2010; protection from conspecific infanticide: O’Connor and Shine 2004;

predator alarm calling: Griesser and Ekman 2004, 2005; recruitment to foraging patches: Radford and Ridley 2006). Such prolonged associations with parents can also illicit plasticity in simple behavioural traits (e.g., activity, exploration, boldness) that provide offspring with greater access to resources independent of any direct intervention from the parents (Munch et al. 2018). However, selection for nepotistic behaviours in parents depends on their ability to correctly direct investment towards offspring, rather than non-kin. As with transitions from territorial defense to neighbour familiarity, spatial proximity is the simplest mechanism through which habituation and tolerance arises in parents of independent offspring (Lion and van Baalen 2007, Aktipis and Fernandez-Duque 2011, Botterill-James et al. 2016), and probably underlies the ultimate switch from infanticidal to caring behaviours in parents (Lion and van Baalen 2007). As rising temperatures promote enhanced mobility in both offspring and parents, shifting thermal regimes could degrade the predictability of individual locations. This then increases opportunities for parental investment to be misdirected to non-kin (Aktipis and Fernandez-Duque 2011) or for aggression to be misdirected towards offspring (e.g., as is seen to occur following prolonged parent-offspring separation: Nelson and Elwood 1997; G. While pers. comm.). Thus, reduction in the reliability of simple spatial cues could ultimately constrain the stabilization of parent-offspring associations in early evolutionary stages, thereby hindering further elaboration in systems of recognition (e.g. kin recognition) and care (see also Box 2).

BOX 2: Climate effects on communication and recognition

Communication underpins many of the interactions that facilitate social living. Factors that influence the strength and efficacy of communication should, therefore, play a fundamental role in mediating the emergence and maintenance of social behaviour. Communication across all signaling modalities is influenced strongly by the local abiotic environment, such that climate change will likely affect multiple components of animal communication from signal production, transmission and perception to behavioural response.

Visual*:* Visual communication between animals involves complex behavioural displays that often leverage features of an organism's phenotype, such as bright colouration or elaborate ornamentation. These traits are used to communicate with other individuals in several social contexts, from mate choice and competition to social dominance. The efficacy of visual displays, both in terms of the signal itself and the transmission of the signal, relies heavily on local environmental conditions, such as wind, temperature and precipitation (Bian et al. 2019). Changes in environmental conditions as a result of climate change are therefore likely to affect signal efficacy. For example, in aquatic systems, increased water turbidity as a result of global warming is likely to decrease visual signal transmission. Indeed, disruptions in visual communication as a result of changes in the transmission spectrum of lakes have been shown to result in the breakdown of pre-zygotic mating barriers and increased instances of hybridization in cichlids (Carleton et al. 2005). In terrestrial systems, changes in multiple climatic variables (e.g., temperature, wind, humidity) could alter the transmission efficacy of visual signals via subtle effects such as attenuation, diffraction, and distortion (Partan 2013, Bian et al. 2019). While there is some evidence that organisms compensate for altered signal transmission through behavioural modifications (Møller 2011, Bian et al. 2019), there are likely constraints on the extent to which this compensates for information lost from these signals.

Auditory: Acoustic signals serve as the primary form of communication for a wide range of animals. The efficacy of acoustic signals depends on both the acoustic signal itself and the process of sound transmission. Both factors are likely to be altered by changes in the environment bought about by climate change. The factor that is most important in this context is temperature. Studies across a range of amphibian and invertebrate species have shown that patterns of song production are closely linked to temperature. For example, the thermal environment is known to shape key components of calls themselves (e.g., rate: Gayou 1984, Greenfield 2002; frequency: Walker 1962, Gayou 1984, Luther and Danner 2016, Conrad et al. 2017), through temperature-dependent process that regulate vocal circuits and sound producing muscles. The transmission of the call can also be tightly linked to changes in temperature and humidity, both of which mediate sound attenuation. Crucially these effects can differ both between and within species depending on call type (Torricelli et al. 1990, Connaughton et al. 2000). Similar effects of climate change on auditory communication are predicted for aquatic environments (Partan 2013). As CO_2 absorption in the water increases, so does water acidity. This alters the acoustic absorbance properties of the water – specifically, increasing the absorption of lower sound frequencies (Hester et al. 2008).

Olfactory: Olfactory communication between animals is facilitated by 'semiochemicals' – a class of organic compounds including pheromones – which are used for intraspecific communication in a wide range of organisms (Wyatt 2003). The specificity, longevity, and 'honesty' of chemical signals makes them more versatile across social contexts than any other type of signal, including species recognition, neighbour/stranger discrimination, and kin recognition (Wyatt 2003). The nature of the specific signals used in olfactory communication and their efficacy have been shown to vary in response to climatic gradients across both micro- (e.g., Heathcote et al. 2014, Sentis et al. 2015) and macro- (e.g., Martín and López 2006, Baeckens et al. 2018, Iglesias-Carrasco et al. 2018) ecological scales. This is not surprising given that many components of chemical communication are heavily environmentally dependent. At a basic level, as chemical compounds are metabolic products, the emission rate of chemical signals is likely to scale with metabolic rate (Sentis et al. 2015), which itself is temperature dependent (Box 1B). Additionally, many of the compounds that make up an organism's chemical profile are themselves dependent on particular environmental conditions to support their longevity and their efficacy. Indeed, changes in temperature have been shown to alter the composition of pheromone blends (e.g., Gibbs et al. 1998, Heathcote et al. 2014) as well as their stability in the environment (e.g., Van Oudenhove et al. 2011, Martín and López 2013). Changes in the thermal environment also affect signal perception, such that different chemical profiles are often selected depending on the thermal environment (e.g., Linn et al. 1988, Beckers and Schul 2008, Sentis et al. 2015). Such changes in perception can occur in the same or opposite direction of changes in the signal itself, which could disrupt the signal receiver match. Finally, synergistic shifts in other environmental parameters, such as wind and humidity, brought about by climate change can also alter the speed, direction, and distance of chemical dispersion.

2 The Maintenance of Social Living: Keeping individuals together.

After a group initially forms, its cohesion will largely depend on the stabilization of interactions between individuals and whether those interactions are beneficial or costly. In social groups that emerge primarily via egalitarian routes, this will be dictated by aspects of the local environment that affect the costs and benefits of association either directly (via alterations in the ecological context of those associations) or indirectly (via alterations in the composition of the social group). In social groups that emerge primarily via fraternal routes, stability will also be determined by the extent to which the environment influences key parameters underpinning within-group relatedness.

b) The maintenance of egalitarian societies

In contrast to solitary species, individuals that live in groups derive direct fitness benefits from aggregating. These may include diluted predation risk, improved vigilance, more efficient food acquisition, increased mate access, or thermal advantages (Krause and Ruxton 2002). In the simplest case, aggregations form as loose amalgamations of anonymous and largely unrelated individuals. During these early 'disordered' stages, groups form (and break) rapidly, such that individual membership may be highly transient and subject to change with sudden shifts in environmental conditions (Aviles and Guevara 2017, Javarone and Marinazzo 2017). Numerical simulation models indicate that the maximum gain achieved by being part of a group (as opposed to not) occurs when groups are homogeneous (i.e. members belong to similar age, sex, or size classes; Javarone and Marinazzo 2017). Consequently, environmental factors that reduce similarities among group members, or otherwise reduce incentives of synchronizing activities with other group members, disrupt group spatial coherency and can lead to dissolution (Conradt and Roper 2000, Javarone and Marinazzo 2017). However, as group membership stabilizes and becomes more ordered over time, simple mechanisms are less likely to result in breakage (Javarone and Marinazzo 2017). At this point, preferential attachments within a heterogeneous group structure can still be consistent with cohesion because group interconnectedness will be determined by individuals with the highest number of connections, such that cooperation dominates (Santos and Pacheco 2005, Du et al. 2009). In such structured networks, adhering to particular 'rules' of interaction can strengthen social bonds and even lead to the formation of dominance hierarchies (Aureli and Schino 2019). In these cases, unstable phenotypic fluctuations and social dissolution may be driven instead by factors that promote socially inappropriate behaviours that are both strong and reciprocal when expressed (e.g. aggressive escalations; Trubenová et al. 2015).

In the broadest sense, temperature could influence the stability of group living by altering its costs and benefits. As detailed above, aggregating can confer a number of benefits to individuals (e.g., reduced predation risk, access to resources including food, shelter, mates), but can also impose a number of significant costs (e.g., increased competition, aggression, disease risk). Therefore, any environmental factor that offsets this cost-benefit trade-off has the potential to significantly affect social stability. For example, in aggregations that emerge largely as an anti-predation strategy, shifts in the frequency of predator-prey interactions are likely to impart selective effects on behaviour. This has been nicely documented in aquatic ecosystems (Sylvester 1972, Yocom and Edsall 1974), where warmer waters are suggested to serve as environmental cues for enhanced anti-predator shoaling behaviours (Weetman et al. 1999, Pritchard et al. 2001, Beiswenger 1977). Alternatively, rising temperatures could generate selective context for group living through effects on resource availability. One projected environmental shift expected to be widespread – an increasing frequency and severity of droughts – will dramatically reduce watershed volumes. In African hippos, such dry season conditions are associated with excessive localized crowding, to which the side effect is exacerbated socially agonistic encounters and fracturing of subordinate males from core congregations (Stears et al. 2019). Thus, while the immediate outcome of resource restriction may be to bring individuals together, subsequent costs of within-group conflicts could jeopardize the benefits of membership for some individuals.

A more mechanistic pathway through which group cohesion may be enhanced or disrupted under changing thermal regimes is through temperature-mediated changes in encounter frequencies, which could perturb established relationships between group members or the opportunities to form new bonds. Where group membership is already very large, warming might enhance social network connectivity by facilitating a greater degree of movement and exchange within the group. For example, frequent roost switching in bats helps to reinforce long-term relationships among colony members (Willis and Brigham 2004, Wilkinson et al. 2019), and this behaviour is likely to increase under high temperature conditions that accelerate roost decay (Patriquin et al. 2016). Such effects could have significant implications for other components of the social system, because roost switching determines the spatial distribution of females and thus the mating opportunities of males (Wilde et al. 2018). Energetic effects of temperature also influence the dynamics of interactions between group members. While groups in a resting state are able to maintain cohesive 'interattraction' between conspecifics independent of orientation (Fletcher 2008, Michelena et al. 2008, Mougenot et al. 2012), metabolic changes in activity levels physically alter the alignment of individuals, which could disrupt the cohesion of a group in motion. Depending on how temperature interacts with factors such as group size and heterogeneity, increasing activity could enhance or disrupt synchronicity among group members. Failing to 'agree' on a departure time upon mobilization could result in group splitting or dissolution (Dostálková and Špinka 2010), where non-homogeneous groups are likely to destabilize and segregate faster than homogeneous groups due to differential compromises in activity budgets (Conradt and Roper 2000, Michelena et al. 2008). Changes in thermal environment could therefore be an important factor contributing to group splitting, as individual metabolic responses to temperature have been shown to vary based on factors such as body size (Johansen et al. 2014) and personality (Biro et al. 2010). Indeed, several studies in fish report that greater activity in warmer waters disrupts interattraction within shoals (Hurst 2007, Colchen et al. 2017, Bartolini et al. 2015).

Other intrinsic avenues through which temperature could influence group stability involve social decisions that create opportunity for conflicts within groups. For instance, temperature-mediated shifts in metabolic demands tend to incentivize behaviours that have consequences for energy turnover (e.g., movement, foraging, boldness; Mathot et al. 2019), which includes some more risky social behaviours (Biro and Stamps 2008, Careau et al. 2008). In a diversity of ectothermic species (e.g. fish: Kvarnemo 1998, Biro and Stamps 2010, Zhao and Feng 2015; and spiders: Pruitt et al. 2011), warmer thermal regimes are linked to increasing frequencies of overtly agonistic behaviours. Such effects are apparently further magnified among individuals with bold personalities, as boldness has been shown to covary with preferred body temperature and metabolic rate (Stapley 2006, Biro et al. 2010). In an experiment on dwarf cichlids, both dominant and subordinate individuals were observed initiating more agonistic interactions under high temperature treatments, culminating in the loss of feeding advantage held by dominant fish (Kochhann et al. 2015). Spohn & Moore (1997) observed a similar effect in cockroaches: heat stress increased the number of aggressive acts initiated by submissive males while decreasing the number in dominant males. The consequence of such breaks in group social code is the destabilization of established hierarchies, the form of which could ultimately push societies beyond their ‘social tipping point’ (Pruitt et al. 2018). Doering et al. (2018) provide one experimental demonstration of this principle in a study where heat stress was applied to colonies of social spiders (*Anelosimus studiosus*), and rapid transitions from calm to hysteretic states were reported. However, the speed and reversibility of this transition depended on the ratio of aggressive to docile personalities in the group. Hence, while temperature has repeatedly emerged as an important environmental factor influencing the nature of social interactions, it is clear that scaling these effects to the group level introduces many nuances, including how group size, composition, and the factors that underlie them shape collective behaviour under stress (Aviles 1986, Watanabe 2008, Gordon 2013). For instance, spider colonies in nature appear to become collectively less aggressive at higher elevations, perhaps because infighting and heightened metabolic rates impose greater limitations to persistence in resource- and enemy-poor environments (Lichtenstein et al. 2019).

b) The maintenance of fraternal societies

As with egalitarian societies, once relationships between (family) members emerge those associations need to be stabilized in the face of significant conflicts of interest. These pervade not only between parents and offspring, but also between mothers and fathers and between siblings. The resolution of these family conflicts permits stabilization and ultimately sets the stage for the emergence of more complex forms of social organisation. While in some circumstances conflicts within the family may be managed through similar processes as occur in egalitarian systems (i.e. as outlined above, where grouping confers benefits to non-kin), members of fraternal groups can also take advantage of benefits that are attainable exclusively through their relatedness to other group members. Hence, the stability of kin groups is not only reinforced by direct costs and benefits of aggregation, but also by the extent to which inclusive fitness benefits may be spread to all members of the group. The classic formulation of this prediction can be found in Hamilton’s rule (Hamilton 1964a, 1964b), which holds that cooperation between group members should be selected for when the product of within-group relatedness and the benefits conferred to recipients is greater than the cost to the actor, in terms of reproductive success. Therefore, for fraternal groups, any factors that influence relatedness between group members or the costs and benefits of extending associations with family members will be important for maintaining family life. Temperature can influence both these factors, and thus may induce feedbacks on the stability of kin-based social systems more broadly.

Genetic monogamy is key to the maintenance of cohesive groups centered around a dominant breeding pair. In addition to ensuring high relatedness between helpers and the siblings they raise, genetic monogamy often correlates with a high level of parental and social coordination between partners (Møller and Birkhead 1993, Ketterson and Nolan 1999, Møller and Cuervo 2000, Lukas and Clutton-Brock 2013, Matysioková and Remeš 2013) and could thus provide hormonal and cognitive pre-adaptations for the subsequent evolution of cooperative breeding (Dillard and Westneat 2016). Indeed, genetic monogamy, or at least reduced promiscuity, is implicated as the most probable ancestral state across social Hymenoptera (Hughes et al. 2008), cooperatively breeding birds (Cornwallis et al. 2010), and social mammals (Lukas and Clutton-Brock 2012). Scenarios likely to compromise genetic monogamy include any in which males can acquire matings outside the social pair bond (broadly, male and female mating behaviour). Importantly, changes in climate could mediate mating behaviour through several direct and indirect mechanisms (see García-Roa et al. 2018 for thorough review). First, alternations in climate could mediate the costs and benefits of seeking extra-pair copulations. For instance, environmentally dependent shifts in offspring need, and thereby the need for biparental investment, might dictate the probability of desertion. This argument is invoked to explain mating patterns in a cold-weather swallow, which exhibits lower rates of extra-pair paternity compared to a related species breeding at tropical latitudes (Ferretti et al. 2016). Alternatively, the thermal environment could influence the time and energy budget available for mating. In line with this prediction, experimental studies of insects have produced a wealth of data supporting a positive link between temperature and mating rates (Saeki et al. 2005, Kindle et al. 2006, Jiao et al. 2009, Katsuki and Miyatake 2009, Best et al. 2012). While complementary bodies of evidence from the wild are more limited, a few longitudinal studies implicate a role for temperature in between-season variability in mating rates. In a long-term study population of Swedish sand lizards (*Lacerta agilis*), elevated seasonal temperatures have been correlated with an increase in the degree of polygyny, number of sires per clutch, and opportunity for post-copulatory sexual selection, presumably due to higher rates of intersexual interaction (Olsson et al. 2011a, 2011b). Complementing this are several recent studies of birds and mammals, which have highlighted the effects of progressively longer breeding seasons on mating rates. In alpine marmots monitored over 22 years, increasing annual proportion of extra-pair litters have been attributed to the fact that earlier snowmelt relaxes energetic, movement, and time constraints on mating (Bichet et al. 2016). Similarly in two separate longitudinal studies of arctic-breeding passerine, the relative loss of paternity to extra-pair males was found to decrease with cold weather during the female's fertile period, probably because climatic conditions constrain the total energy budget available for extra-pair forays (Russell et al. 2005, Hoset et al. 2014). Conversely, seasonal temperature extremes can be expected to differentially constrain time and energy budgets at lower latitudes. A study out of the Netherlands, for instance, found high rates of extra-pair paternity associated with lower minimum temperatures during the peak fertile period for a passerine (Bouwman and Komdeur 2006).

Finally, temperature could influence male and female mating rates by shifting the nature and outcome of post-copulatory processes (García-Roa et al. 2018). For example, in wolf spiders, higher rates of re-mating under higher temperatures results not from mating rates per se but from greater efficiency of sperm transfer, and therefore less time spent on courtship and individual copulations (Jiao et al. 2009). Similarly, in bean beetles, longer duration of sperm transfer at low temperatures has been suggested to reduce a female's willingness to re-mate (Katsuki and Miyatake 2009). All in all, there is growing appreciation for the prediction that fluctuating ambient temperatures in future decades will influence sexual selection and sexual conflict over mating (García-Roa et al. 2018). While the consequences of variation in mating rates (e.g., genetic monogamy) for levels of within-brood conflict has not been quantified in these systems (and is not relevant in systems that do not form family groups), these examples nevertheless serve as proof of principal, which can be applied to kin-based societies. Where climatic conditions have the potential to shape patterns of paternity, such effects could substantially alter the balance between the benefits of cooperation versus conflict and ultimately, the stability of family organisation.

3 The Diversification of Social living; From cohabitation to cooperation and division of labor

Once social groups have emerged, either through egalitarian or kin-based routes, the diversification of social organisation will depend upon the extent to which environmental conditions reinforce additional social interactions between individuals. Evidence for a tight link between environmental conditions and the refinement of complex cooperative behaviours can be found across diverse systems. Phylogenetic studies point not necessarily to a causal role for climate in the origins of cooperative societies (Remeš et al. 2015, but see Firman et al. 2020), but rather to the importance of cooperative behaviours, once evolved, in coping with abiotic challenges and facilitating the colonization of harsh environments (Kocher et al. 2014, Cornwallis et al. 2017). Thus, at these higher levels of social organisation, shifting abiotic conditions may be expected to interact with ongoing social evolutionary processes more in a complementary capacity, selecting for refinement of existing behaviours rather than for evolutionary innovation *per se.*

Interestingly, emerging ecological trends appear to parallel these macroevolutionary patterns. Studies of social-living birds and mammals support the notion that exposure to stressful or unpredictable climatic conditions serve as an ecological primer for investment in cooperative behaviours (Blumstein and Armitage 1999, Canário et al. 2004, Covas et al. 2008, Guindre-Parker and Rubenstein 2018a, 2018b). Importantly, measurable improvements in performance of cooperative groups appears to be linked to the ability to flexibly adjust behaviours, such as coordination and synchronicity, when faced with adverse conditions. Field and experimental studies of plovers have revealed that division of labour within biparental pairs becomes increasingly egalitarian as exposure to extreme temperature rises during incubation, with levels of paternal investment increasing relative to maternal investment (AlRashidi et al. 2010, 2011, Vincze et al. 2017). Climatic conditions also appear to shift the dynamics of labour division within extended family groups. Cooperatively breeding fairy wrens, for instance, invest more in egg production in the presence of helpers than in their absence when faced with hot, dry breeding seasons (Langmore et al. 2016). Taken together, these studies illustrate on an ecological scale how shifts to harsher climatic conditions could positively affect the selective context for cooperation within families.

Alternatively, stressful climatic shifts could lead to reductions in cooperation if there is disruption in communication, or if caregivers are forced to trade off their own body condition against that of their young. Hatchling birds incubated at high temperatures exhibit lower body condition post hatching, and as a result beg less aggressively and illicit less provisioning from their parents (Mueller et al. 2019). Variation in provisioning rates may also stem directly from parents. In cooperatively breeding pied babblers, dominant caregivers provision their offspring significantly less on hot days, while the level of provisioning by subordinate caregivers remains unchanged (Wiley and Ridley 2016). Research on sociable weavers (Leighton and Vander Meiden 2016) and mongooses (Nichols et al. 2012, Cant et al. 2014) indicates that such disproportionate division of labour during times of stress is enforced via aggressive policing of subordinant group members by dominant breeders, leading to the one-way suppression of selfish behaviour. In this way, periods of environmental stress could be expected to have destabilizing effects on cooperative groups by provoking social conflict from within. Rather, Firman et al. (2020) propose that the diversification of traits that mediate social conflict, such as body size dimorphism, could simply be an inevitable accompaniment of greater environmental selection for social living.

There is also mounting evidence that climatic factors are involved in the emergence of cooperative behaviours between non-kin. In sub-social burying beetles, the degree to which breeding pairs cooperate with other breeding pairs on a shared resource has been shown to vary across elevational gradients of resource competition. Specifically, at high-temperature, low elevation sites where parents face heightened interspecific competition for resources, larger and more cooperative groups outperform non-cooperative groups due to the enhanced resource defense capacities facilitated through collective action. In contrast, pairs have higher fitness than groups at intermediate elevations and temperatures because conflict between group members is enhanced under conditions of low interspecific densities (Sun et al. 2014, Chen et al. 2018, Liu et al. 2020). In a similar example, Barbieri et al. (2015) demonstrated that the foraging efficiency and interspecific aggression of large colonies of ants (*Prolasius advenus*) varies with ambient temperature. Specifically, higher temperatures were found to promote higher levels of collective aggression against allopatric *Monomorium antarcticum*, which could affect the persistence and co-occurrence of ant societies under climate change. Combined this evidence suggests that changes in climate can mediate both the emergence of cooperation itself as well as its refinement over ecological time scales.

Table 2: A generalizable guide to future studies on climate-mediated sociality. These will expand the number of explicit, hypothesis-based tests of the links between ecologically relevant climatic variables and specific traits underpinning the origins, maintenance, and/or diversification of animal societies. Convergent social traits are products of their ultimate (evolutionary) causes as well as proximate (including climatically sensitive) mechanisms, and each must be considered in concert to arrive at predictions for how social attributes of populations will likely be altered under climate change. The direction of climate-mediated effects also depends on population-specific projections, which may vary based on local environmental or biological parameters. To accommodate this variation, alternative predictions are listed and articulated to facilitate broad application across taxa and environments. The predictions listed below are not exhaustive, but rather highlight a subsample of possible experiments that could be implemented to test links between climate change and sociality.

Target social trait	**Ultimate mechanism (selective context) underlying trait evolution**	**Proximate (climate-mediated) mechanism underlying trait expression**	**Predicted trait response under warming trends**
Origins (egalitarian)			
aggregation	resource abundance/distribution	length of residency at a site	Projected **Δ** in local weather conditions: • More benign: no change or more aggregation, depending on conditions elsewhere • More extreme: less aggregation
	thermoregulation	communal denning/clustering	Less aggregation with milder winters
conspecific tolerance	reduced energetic expenditure under metabolic challenge	territorial aggression or display rate	Projected **Δ** in energetic reserves: • Constraint: higher tolerance/less aggression • Release: less tolerance/more aggression
	reduced energetic expenditure in repeated encounters, particularly with familiar conspecifics	encounter frequencies, or rate of habituation	Projected **Δ** in energetic reserves: • Constraint: no change or elevated social reactivity via lower encounter rates • Release: short-term elevated social reactivity, long-term subdued reactivity via habituation
Origins (fraternal)			

extended parent-offspring associations	habitat saturation	natal dispersal	Projected **Δ** in adult turnover rates: • Positive: higher rates of natal dispersal to fill vacant territories • Negative: lower rates of natal dispersal, provided abundant resources in natal site
	inclusive fitness via offspring recognition	duration of offspring retention	Projected **Δ** in mobility/spatial structure: • Positive: shortened span of offspring retention due to disrupted spatial proximity. • Negative: offspring retention unchanged
Maintenance (egalitarian)			
group membership	predator protection	individual membership decisions	Projected **Δ** in predator activity: • Positive: more individuals joining groups • Negative: no change or decrease
	resource abundance/distribution	individual membership decisions	Projected **Δ** in critical resource distribution: • More concentrated: initial increase in individuals joining groups, but with potential fracturing due to infighting • More dispersed: fewer individuals joining groups in favor of solitary strategy
cohesion among group members	enhanced grouping benefits (via synchronicity)	encounter frequencies and/or interattraction	Group structure: • Homogeneous: enhanced cohesion via greater temperature-mediated rates of interaction • Heterogeneous: group fracturing via greater temperature-mediated activity
	enhanced grouping benefits (via group 'social code')	frequency of 'socially inappropriate' agonistic behaviour	Heat stress could lead to societal dissolution via this mechanism.
Maintenance (fraternal)			
within-family conflict	inclusive fitness benefits spread to all family members	mating rates (mediating within-family relatedness)	Projected **Δ** in energetic reserves: • Constraint: family conflict unchanged • Release: increased conflict via increased rates of mating, decreased relatedness
Diversification			

cooperation	social buffer against climatic harshness, interspecific competition	division of labour, reduction in intragroup conflict	Projected **Δ** in climatic 'harshness' or uncertainty: • More benign: cooperative effort is unchanged; conflict may be greater • More extreme: greater effort divided or re-allocated among members to increase efficiency

Conclusions

Global climate change has been implicated as a major driver of ecological and evolutionary change across biological systems. However, the question of whether climate change modulates the evolution of social systems has largely been ignored. In this review, we have detailed a range of scenarios through which projected climate change could impact social systems via relatively simple, climatically sensitive, mechanisms that shape socially relevant behaviours. We argue that the subtle ecological shifts in the opportunities, nature, and context of these social interactions have the potential to fundamentally alter the processes underlying the evolution of social systems in a range of different ways. While such responses are likely to have the largest effect in systems where socially relevant traits are expressed facultatively and where social structures have yet to achieve long-term stability, they could also resonate across gradients of social complexity. We therefore argue that an underappreciated consequence of climate change is the role it plays in catalyzing a myriad of constructive and destructive effects on the emergence, maintenance and diversification of social organisation.

While existing empirical evidence can be woven into a convincing framework for predicting how the effects we outline may play out in natural systems, there are significant limitations in our current understanding. First, the current literature is deficient of empirical evidence that explicitly tests the extent to which climate does or does not social behaviour in nature. Second, our mechanistic understanding of the links between climatic variables and complex social behaviours is limited. Third, we have yet to embrace integrated approaches tackling larger questions of how such effects could scale to influence social evolution over the short- and long-term. These limitations must be addressed if we are to fully appreciate the extent to which ongoing climate change might act as a catalyst for social evolution, and what ecological consequences may accompany these changes. While the aim of this review was explicitly non-prescriptive in this respect, it has highlighted several key questions and predictions that could be targeted to begin to generate this broader understanding (Table 2). Addressing these questions will require the integration of scientific insights from diverse fields; from ongoing correlative and experimental studies examining co-variation between climate and social traits at multiple levels of biological organisation, to studies targeting the hormonal, neruo-molecular and physiological mechanisms underpinning social responses to climate, to experimental evolution. Combined, these approaches will deepen our understanding of underappreciated avenues through which climate change has the potential to alter biological systems. In addition, while our focus here was primarily on social effects likely to result in response to shifting thermal regimes, projected climate change will undoubtedly alter additional components of the local and global environment. These effects include, but are not limited to, precipitation, the frequency of extreme weather events, pollution and habitat loss. Each of these effects has the potential to alter the trajectories of social systems in similar or distinct ways to those outlined above and, in some instances, could exacerbate the effects of temperature. Thus, we propose that future research aimed at testing predictions of climate-mediated sociality via the mechanisms we have outlined in this review (Table 2) should also incorporate additional climatic and environmental factors.

As global environments rapidly change, greater depth of knowledge is crucial for informing a broader understanding of the interface between ecology and evolution. Expanding future studies to interrogate the predictions outlined in this review will contribute to this goal in two major ways. First, exploring in detail the mechanisms through which subtle shifts in climate underlie behaviours involved in intraspecific interactions will provide novel insights into the eco-evolutionary dynamics governing social evolution. Second, until now studies of the impact of rapid environmental changes on biotic systems have mainly focused on the direct effects of climate change. We argue that this approach overlooks a multitude of indirect effects and feedbacks that can both exacerbate or constrain the effects of global climate change. Indeed, many aspects of social living are susceptible to transformation under climate change, which could dampen or exacerbate current predictions of deleterious outcomes via impacts on population vital rates, and the capacity of species to buffer environmental uncertainty. By providing novel perspectives and data regarding probable effects of climate change on biological systems, we will ultimately generate a more holistic understanding of the ways in which climate change will affect populations across both ecological and evolutionary time scales.

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