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Keeping up with environmental change: The importance of sociality

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Abstract

In the current era of rapid climate change, populations are facing environments in which food availability can quickly decline or become highly unpredictable. These conditions may require a high degree of flexibility of individuals and populations to adequately respond to such changes. We propose that the evolution of such high flexibility may be facilitated in social animals that form groups and cooperate in important tasks that critically affect survival and reproduction and ultimately affect adaptive capacity. We argue that sociality is likely to be a key, yet largely overlooked factor that shapes rather than limits the potential for phenotypic plasticity. Cooperatively breeding species are most suitable for studying the influence of both the physical and the social environmental conditions on shaping the phenotypic plasticity of individuals. Cooperative breeders display variation in group size and structure, and in the extent of cooperation and competition between their members. In addition, immigrants may impose costs and/or benefits on other group members, as well as on the whole group. In cooperative breeders, we elucidate why and how group formation and interactions between group members can provide adaptive benefits to some or all individuals in the group. Observed adjustments in social behaviour may be strategic and ultimately enhance individual fitness benefits, and thus improve group and population persistence. Future studies should examine how ecology and sociality *together* shape the adjustment of animals to rapid and extreme environmental change. In addition to identifying how changes in physical and social factors impact individual behaviour, group formation and sociality, it is crucial to assess associated costs and benefits by exploring the life histories of all group members. Understanding this requires population models, as they integrate all the critical life-history phases, and different types of sociality. We are confident that future research into the ecology and social dynamics will reveal new avenues for the adaptive ability of cooperative breeders and other social species.

KEYWORDS

cooperative breeding, ecological adaptation, global change, phenotypic plasticity, social dynamics, sociality

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1 | INTRODUCTION

One of today's strongest societal concerns is the unprecedented loss of biodiversity due to altered climatic conditions, pollution and habitat loss and fragmentation (Barnosky et al., 2011; Butchart et al., 2010; Cardinale et al., 2012; Garcia et al., 2014; Hoffmann & Sgrò, 2011; Neukom et al., 2019; Ummenhofer & Meehl, 2017; Van de Pol et al., 2017). To mitigate or counter this biodiversity loss, it is important to understand how organisms are able to adapt to rapidly changing conditions (Barnosky et al., 2011; Neukom et al., 2019). If environmental changes, such as rising temperatures and changes in food availability, are fast and unpredictable, then individuals, populations and species may have no time to adequately respond to such change (Chevin & Hoffmann, 2017; Chevin et al., 2010; Sih et al., 2011; Ummenhofer & Meehl, 2017). If individuals do not adjust, or adjust too slowly, this may reduce survival or reproduction, and ultimately, lead to population and species extinction, with subsequent detrimental impacts on ecosystem functioning (Barnosky et al., 2011; Butchart et al., 2010; Garcia et al., 2014; Dustin R. Rubenstein & Lovette, 2007). Indeed, the current rate of environmental change appears to exceed the potential rate of evolutionary response of many species (Bell & Collins, 2008; Garcia et al., 2014; Hof et al., 2011; Hoffmann & Sgrò, 2011; Langenhof & Komdeur, 2018; Van de Pol et al., 2017). Given the current loss of biodiversity, it is of key importance to understand the limits to the adaptive potential of species. Unravelling these limits starts by understanding how and to what extent individuals of a species (can) respond to changing environmental condition.

Organisms may adapt to changing conditions by adjusting their morphology, physiology or behaviour (Bonamour et al., 2019; Chevin & Hoffmann, 2017; English et al., 2015; Huchard et al., 2016). This can occur via various mechanisms that act on vastly different time scales, most notably by evolutionary change (Danchin et al., 2011; Wolf et al., 1998) and phenotypic plasticity (Bollati & Baccarelli, 2010; Fusco & Minelli, 2010; Love et al., 2010; McNeeley & Lazrus, 2014; Miner et al., 2005; Nussey et al., 2005; O'Riordan & Jordan, 1999; Seebacher & Krause, 2019; Weaver et al., 2004). Adaptation through evolutionary change is relatively slow, especially in long-lived species, as it requires changes in allele frequencies that act at relatively large time scales (e.g. across generations and between populations; Danchin et al., 2011; Grindstaff et al., 2003; Wolf et al., 1998).

Organisms may also adapt to changing environmental conditions during the course of their lifetime through phenotypic plasticity, referring to the expression of variable phenotypes from a single genotype in response to environmental conditions (Bonamour et al., 2019; Chevin & Hoffmann, 2017; Miner et al., 2005). This can occur via various mechanisms, most notably by developmental plasticity (English et al., 2015; Fusco & Minelli, 2010), (epi-)genetic changes (Bollati & Baccarelli, 2010; Seebacher & Krause, 2019; Weaver et al., 2004), behavioural flexibility (Huchard et al., 2016; Love et al., 2010; Miner et al., 2005; Nussey et al., 2005) and even cultural mechanisms (McNeeley & Lazrus, 2014; O'Riordan & Jordan, 1999). Also,

in several social species, individuals could directly inherit adaptive traits from their biological parents and gain social information from each other and then programme and imprint persistent changes, for example experiences in early-life, that can have long-lasting consequences for the fitness of an individual, largely via (epi-) genetic effects (e.g. DNA methylation and histone modifications) (English et al., 2015; Seebacher & Krause, 2019). For example, in Long-Evans hooded rats (*Rattus norvegicus*) parent-offspring interactions have significant impact on epigenetic variation in offspring. Offspring reared with low levels of maternal care (i.e. pup licking, grooming and nursing) were found to have a high percentage of DNA cytosine methylation (e.g. 5'CpG dinucleotides within the transcription factor (NGFI-A) binding to the glucocorticoid receptor promoter in the hippocampus) and were more fearful and less hypothalamic-pituitary-adrenal (HPA) responses to stress as adults, compared to offspring reared with high levels of maternal care (Weaver et al., 2004). Variation in DNA methylation in the offspring also contributes to changes in adult adaptive phenotype, such as physiological alterations in response to stress in humans (Lillycrop & Burdge, 2011) and shifts in developmental outcome and behavioural status in honeybees (Kucharski et al., 2008). However, species could also have a rapidly biological response to acute environmental changes through DNA methylation modifications. For example, in the invasive sea squirt (*Ciona savignyi*), significant changes in DNA methylation frequency and epigenetic differentiation rapidly occurred at the first few hours of high environmental stressors (i.e. high-temperature exposure or low-salinity challenge). At the same time, the stressed-induced DNA methylation variation maintained shortly and quickly returned back to the control levels, namely DNA methylation resilience, which may allow to reduce the negative influence of external stimuli and increase the possibility of survival during invasions (Huang et al., 2017).

In some species, especially humans, the subsistence strategies of species could be facilitated by cumulative cultural inheritance and adaptation that largely depends on complex cognitive and learning skills, where each individual is able to learn from others and pass this social knowledge to its descendants. Such cultural transmission (or social learning) could generate stable, but diverse, adaptive aspects of human behaviour and cultural traits, at the individual, within-group and between-societies levels (McNeeley & Lazrus, 2014; O'Riordan & Jordan, 1999). For example, in Austronesian societies of the Pacific that are not only more ambilocal (in which couples, upon marriage, live with or near either spouse's parents), but also have a "matricentric orientation," cultural traits that were most similar between mother culture and daughter culture were those related to heritable resources (such as domesticated animals), and the skills and/or material goods on the basis of animal husbandry and metalworking are derived from parents and provide the adaptive advantage of cultural transmission (Jordan et al., 2009; Mace & Jordan, 2011).

Phenotypic plasticity is often hailed as an efficient and rapid-response mechanism facilitating survival and reproduction in changing environments (Figure 1; e.g. Both et al., 2004; Chevin et al.,

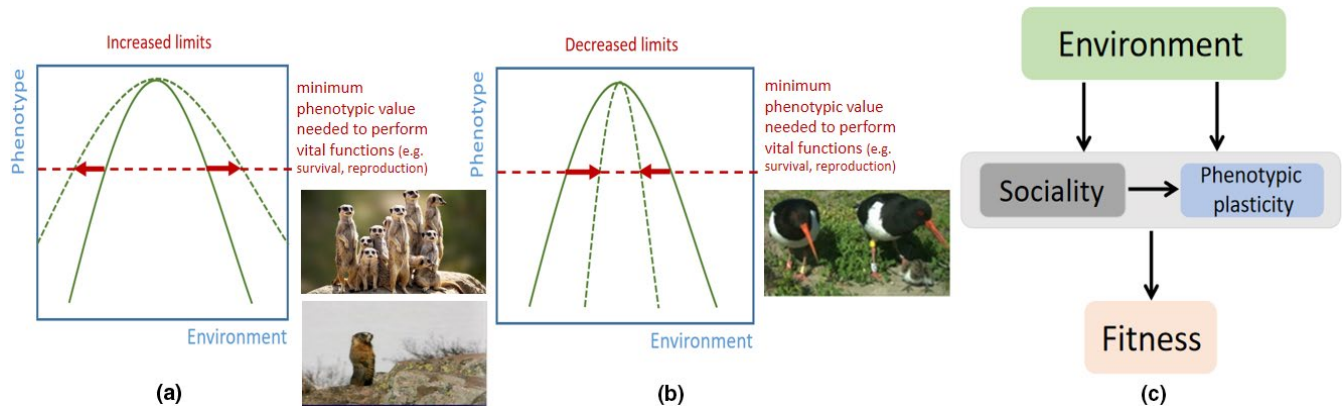


FIGURE 1 Schematic framework showing the social setting as an important factor that shapes the potential for phenotypic plasticity and thus the adaptive potential of individuals in response to changing environments (e.g. extreme and unpredictable environmental changes) in social animal species. (a and b) The increased or decreased limits of plasticity in phenotype to cope with changes in environmental conditions in social animals. Solid green line is hypothetical for non-social species, while the dashed line is for social species. (a) For example, in meerkats (*Suricata suricatta*) and yellow-bellied marmot (*Marmota flaviventris*), if group living helps individuals find food, the range of environmental conditions over which an individual is able to cope with environmental change may be widened (Blumstein et al., 2010; Paniw et al., 2019). Thus, sociality may lead to increased limits at which individuals can cope with environmental change. (b) However, in species such as the oystercatcher (*Haematopus ostralegus ostralegus*), offspring adopt the diet specialization of their parents, and under changing food landscapes, this can constrain, rather than widen, the range of conditions over which they can cope with environmental change (van de Pol et al., 2009). Thus, as our two examples illustrate, the social setting can both help and hinder the potential for plasticity in profound ways (Forsman, 2015; Ozgul et al., 2010). (c) Rapidly changing environmental conditions require a degree of flexibility through phenotypic plasticity, while sociality is likely to be a key factor that shapes rather than limits the potential for phenotypic plasticity, and thus influence organisms' fitness to adapt to environments. "Environment" indicates physical and social conditions that are variable spatially and temporally and change unpredictably at a given spatio-temporal scale (Griesser et al., 2017; Rubenstein & Lovette, 2007). "Phenotypic plasticity" indicates the degree of phenotypic plasticity in organisms, which refers to the expression of variable phenotypes from a single genotype in response to environmental conditions (e.g. Chevin & Hoffmann, 2017; Miner et al., 2005; Nunney, 2016; Pigliucci, 2005). "Sociality" indicates advanced sociality in animals, which refers to group living involving stable groups and individual relationships between group members depending on their status, state and/or relatedness (Ozgul et al., 2010; Paniw et al., 2019; Taborsky et al., 2021). "Fitness" indicates the fitness value of organisms to adapt to environments. Photos: (a) meerkat (above, Paniw et al., 2019); yellow-bellied marmot (below, Blumstein et al., 2010); (b) oystercatcher (van de Pol et al., 2009)

2010; Chevin & Hoffmann, 2017; Chevin & Lande, 2015; Leimar, 2009; Nunney, 2016; Pigliucci, 2005; Snell-Rood et al., 2018; Wolf & Weissing, 2012) as it allows individuals to change their responses within their lifetime and therefore acts at much shorter time scales than adaptation through evolutionary change. In birds, for example, the same individual may lay early in a warm year and lay late in a cold year (Both et al., 2004; Coppack & Both, 2002; Love et al., 2010; Nussey et al., 2005).

Rapidly changing environmental conditions (Garcia et al., 2014; Hoffmann & Sgrò, 2011; National Academies of Sciences & Engineering, 2016; Neukom et al., 2019; Paniw et al., 2019; Ummenhofer & Meehl, 2017) and associated unprecedented challenges require a degree of adaptation that may be unattainable through phenotypic plasticity (Figure 1; Arnold et al., 2019; Barnosky et al., 2011; Fox et al., 2019; Ghalambor et al., 2007; Hof et al., 2011; Huey et al., 2003; Merilä & Hendry, 2014; Van de Pol et al., 2017; Vasseur et al., 2014). For example, when food resources become scarce, individuals may not get enough energy and will starve or die due to predation as a consequence of reduced investment in antipredator behaviours (Martínez-Abraín et al., 2012; Pope & Jha, 2018; Weimerskirch, 2007). However, an energetic threshold

(e.g. body mass) is needed for an individual to survive and reproduce, and thus sets limits to how well phenotypic plasticity can cope with environmental change (Merilä & Hendry, 2014; Moczek, 2010; Ozgul et al., 2010). Understanding how physical and social environments determine the limits of phenotypic plasticity and its impact on adaptation allows us to assess whether species will be able to cope with global change. Here, we argue that in addition to the aforementioned mechanisms, sociality is very important for enabling animals to inhabit environments they else are not able to live in. That is because sociality, and especially advanced sociality, is likely to be a key, yet largely overlooked factor that shapes rather than limits the potential for phenotypic plasticity. Sociality refers to association among conspecifics, whereas advanced sociality refers to group living involving individual relationships between group members depending on their status, state and/or relatedness (Ozgul et al., 2010; Paniw et al., 2019; Taborsky et al., 2021). As such, social interactions may modify how organisms are able to respond to changing environmental conditions.

Most species live in a social environment and engage in dynamic and diverse behavioural interactions with conspecifics, ranging from conflict to cooperation (Dugatkin, 1997; Kingma et al., 2014;

Komdeur & Ekman, 2010; Mitani et al., 2012; Rubenstein & Abbot, 2017; Wilson, 1975). For example, food competition may result in reduced energy reserves (body mass) for some group members, and under changing food availability, this can constrain, rather than widen, the range of conditions over which they can cope with environmental change (Charmantier et al., 2008; Studds & Marra, 2011). However, this can also be adaptive if individuals winning the competition gain more energy reserves for reproduction compared with losers, and if the increased fitness of the individuals winning the competition compensates for the loss of fitness from the losers (Clutton-Brock & Huchard, 2013; Koenig, 2002). A reduction in energy reserves necessary for reproduction of some group members may not matter too much from a fitness point of view, because many individuals in social species never reproduce, and their fitness contribution is small (Anderson & McShea, 2001; Reeve & Keller, 2001). Such individuals may benefit in other aspects, such as being allowed to stay in groups with low risk of predation (Liss et al., 2020; Lukas & Clutton-Brock, 2012). Moreover, if group living helps individuals find food and expand their territory, the range of environmental conditions over which an individual is able to cope with environmental change may be widened (Botero et al., 2015; Pigot et al., 2016; Sun et al., 2014). The social setting can both help and hinder the potential for plasticity in profound ways, and sociality may lead to increased or decreased limits at which individuals can cope with environmental change (Figure 1a,b; Forsman, 2015; Ozgul et al., 2010). Thus, social animals might expand the restricted range of adaptation that can be attained by individuals through phenotypic plasticity by forming groups and cooperating (Figure 1c). There is still a major gap in our knowledge on whether individuals respond to environmental change by forming groups and interacting with each other. Moreover, it is unknown whether and how these responses ultimately result in an increased or decreased ability to adapt successfully to uncertainty and unprecedented changes in their environments.

The aims of our paper are fourfold. First, we want to elucidate the combined role of the physical and social environmental conditions shaping individual phenotypic plasticity. This has to our knowledge been little explored. Second, we want to demonstrate that cooperative breeders are suitable species for studying the influence of both the physical and social environmental conditions on shaping the phenotypic plasticity of individuals. Third, we want to explore why and how group formation and social interactions in groups may facilitate individuals to maintain a favourable physiological state and reproductive success, and a resilient population in a rapidly changing environment. Fourth, we want to address the reasons for our limited knowledge of the mechanisms and functions of group formation with respect to enabling populations to become more resilient to rapidly changing environments. We will explicitly focus on behaviour as this is the level at which organisms interact most directly with their physical and social environments. We will argue that sociality, and especially advanced sociality, modulates and extends the degree of phenotypic plasticity, which will be a key factor contributing to the potential of individuals and populations to adapt to rapidly changing environments.

2 | ROLE OF BOTH THE PHYSICAL ENVIRONMENT SHAPING PHENOTYPIC PLASTICITY AND SOCIAL ENVIRONMENT SHAPING PHENOTYPIC PLASTICITY

Both the physical and social environments in which individuals live can act as key factors and together shape individual plasticity (Bonamour et al., 2019; Chevin & Hoffmann, 2017; Fusco & Minelli, 2010), including morphological/developmental, physiological and behavioural plasticity and even life-history traits (Antunes & Taborsky, 2020; English et al., 2015; Fischer et al., 2017; Huchard et al., 2016; Maruska & Fernald, 2010). In animals, growth strategies adopted by individuals are one of the classic examples of understanding how individuals plastically adapt to environmental changes. Changes in the social environment affect food intake and subsequent growth rate and body mass in several vertebrates, including fish (e.g. clownfish (*Amphiprion percula*), Buston, 2003; Reed et al., 2019; Lake Tanganyika cichlid (*Neolamprologus pulcher*), Heg et al., 2004a; reef fish (*Paragobiodon xanthosomus*), Wong et al., 2008) and mammals (e.g. banded mongooses (*Mungos mungo*), Cant et al., 2013; Johnstone & Cant, 1999; African wild dogs (*Lycaon pictus*), Creel & Creel, 2002; North American red squirrels (*Tamiasciurus hudsonicus*), Dantzer et al., 2013; meerkats (*Suricata suricatta*), Dubuc & Clutton-Brock, 2019; Huchard et al., 2016; olive baboons (*Papio anubis*), Sapolsky, 1991, 2005). When subordinates are larger than or similar in size to dominants, they may be perceived by dominants as competitors for breeding. Restrictive growth may be a counter-adaptation by which subordinates remain smaller and thus non-threatening to dominants in order not to be harassed or evicted by dominants (Heg et al., 2004b; Johnstone & Cant, 1999; Sapolsky, 2005; Wong et al., 2008). Such strategic growth adjustment of subordinates may be due to either subordinate self-restraint or suppression of growth by dominants, for instance in the cooperatively breeding Lake Tanganyika cichlid (Heg et al., 2004b; Wong et al., 2008).

On the contrary, individuals may increase growth rate to increase their reproductive outcome and/or attain a dominant position in the group (Henry et al., 2007; Hodge et al., 2008; Young & Bennett, 2010). Interestingly, individuals living in groups can adjust their growth rate in response to the body mass of their closest competitors irrespective of variation in food availability to the group (Huchard et al., 2016). For example, clownfish show competitive growth in the laboratory, growing faster when paired with a size-matched reproductive rival (Reed et al., 2019). Remarkably, the elevated growth rates of clownfish in competitive treatments were achieved despite the fish receiving no extra food. By remaining small, individuals run a lower risk of being attacked, but by becoming large, an individual becomes more competitive for fights, with both strategies preventing eviction from the group. In the cooperatively breeding meerkat, where dominants and subordinates live and reproduce in groups and subordinates cooperatively contribute to costly parental activities, subordinates and dominants adjust their growth rate to the size of their closest competitor to avoid the threat of being displaced or expelled from the group (subordinates) and

to maintain dominance in the group (dominants). Subordinates of both sexes raise their own growth rate and food intake in response to increases in growth compared with same-sex rivals in order to avoid the threat of being displaced. Moreover, when subordinates have obtained dominant status, they show a secondary period of increased growth if the difference between their own weight and that of the heaviest subordinate of the same sex in the group is small (Huchard et al., 2016). As such, growth rate could be a factor that determines whether groups remain stable and cooperative breeding occurs. These various examples also suggest that more competition among individuals (which may be induced by an environment changing rapidly from food-rich to food-poor) may lead to either an increase or decrease in individual growth rate and body mass, which may both be a strategic decision to be allowed to remain in the group (Gonzalez et al., 2013; Tobias & Pigot, 2019).

It should be noted that physical and social environments do not change in tandem and should be considered separately when investigating their impact on phenotypic plasticity. For instance, group size and not food availability influence female extra-pair paternity in a natural population of cooperatively breeding Seychelles warblers (*Acrocephalus sechellensis*). Females in larger groups have a higher likelihood of extra-pair paternity which may prevent inbreeding and increase offspring survival (Pant et al., 2019). In the Asian burying beetle (*Nicrophorus nepalensis*), climate (temperature) mediates the degree of competition (both inter- and intra-specific), whereas these independently and jointly influence sociality via different grouping benefits. In particular, in areas with high temperatures where interspecific competition for resources is intense, but intra-specific competition for resources is low, individuals form groups to enhance resource defence ability and receive increased fitness benefits in reproduction for individual group members. In contrast, in areas with low temperatures where interspecific competition for resources is relatively low, but intra-specific competition for resources is high, individuals receive less fitness benefits by forming groups compared with individuals breeding as pairs because of high reproductive competition among group members (Liu et al., 2020; Sun et al., 2014). In the cooperatively breeding pied babbler (*Turdoides bicolor*), hot and dry conditions lead to reduced juvenile growth, higher offspring mortality and higher mass loss in adults. The presence of more helpers in a group does not buffer these negative impacts against these extreme conditions, and even population persistence (Bourne et al., 2020; Wiley & Ridley, 2016). Although substantial progress has been made about the contribution of the various proposed ecological and social factors underlying phenotypic plasticity, a general rule on how physical and social environments interact to expand phenotypic plasticity allowing adaptation in rapidly changing environments has not yet emerged.

3 | COOPERATIVE BREEDERS AS MODEL SPECIES

The species that are most suitable for studying the influence of both the physical and social environmental conditions on shaping

the phenotypic plasticity of individuals are cooperative breeders, in which, compared to animals that live in other types of social structures (such as flocks), advanced sociality features more prominently, with stable groups and individualized relationship between group members depending on their status, state and/or relatedness (Figures 1 and 2; Table 1; Cameron et al., 2009; Frère et al., 2010; Koenig & Dickinson, 2004; Taborsky et al., 2021). Cooperative breeders display variation in group size and structure and in the extent of cooperation and competition between their members. In addition, immigrants may impose costs and/or benefits on other group members, as well as on the whole group. The evolution of cooperative breeding is generally considered a two-step process in which the formation of groups precedes the possibility of cooperation (see section 4). Cooperative breeding occurs when more than two conspecific individuals of either sex live and reproduce together to rear a single brood or litter. In such systems, some individuals of either or both sexes may or may not forgo independent breeding, join a group by remaining in their natal group or dispersing to other groups and help others (e.g. providing alloparental care) in the group (Brown, 1987; Clutton-Brock, 2016; Cockburn, 1998; Komdeur et al., 2017; Taborsky et al., 2021). Most cooperative breeding is facultative, in which individuals live either in pairs or in groups, being associated with physical and social conditions (Koenig & Dickinson, 2004; Komdeur et al., 2017). Cooperative breeding occurs in a wide range of lineages (Figure 2; Table 1; Clutton-Brock, 2016; Cockburn, 1998; Komdeur et al., 2017; Solomon & French, 1997; Taborsky et al., 2021), such as insects (Bluher et al., 2020; Chen et al., 2020; Eggert & Sakaluk, 2000; Korb & Schmidinger, 2004; Peer & Taborsky, 2007), fish (Taborsky, 1994), birds (Cockburn, 1998; Griesser et al., 2017) and mammals (Archie et al., 2014; Cant et al., 2016; Lukas & Clutton-Brock, 2017; McFarland et al., 2017), including humans (Kramer, 2010).

Breeding groups normally consist of a dominant pair and one or more sexually mature male and/or female subordinates. Subordinates may or may not help the dominant pair to raise offspring by aiding in food provisioning, protecting them against predators and defending an area with resources against competitors (Table 1). There is considerable variation to what extent subordinates help (Cockburn, 1998; Heinsohn & Legge, 1999; Koenig & Dickinson, 2004; Wong & Balshine, 2011). Cooperative breeding has received substantial attention in evolutionary biology, with a focus on understanding how helping behaviour and cooperative breeding can provide adaptive benefits to all individuals involved in the group. The presence of helper subordinates can increase the group's reproductive output. However, the presence of subordinates can also enhance competition between group members, reducing reproductive success of the dominant breeders (Brouwer et al., 2005; Brown, 1987; Clutton-Brock, 2016; Clutton-Brock & Sheldon, 2010; Cockburn, 1998; Emlen, 1991; Fitzpatrick & Bowman, 2016; Hammers et al., 2019, 2021; Hatchwell, 1999; Koenig & Dickinson, 2004, 2016; Koenig et al., 2019; McFarland et al., 2017; Mumme et al., 1989; Roulin et al., 2012; Schülke et al., 2010; Taborsky, 1994; West et al., 2007).

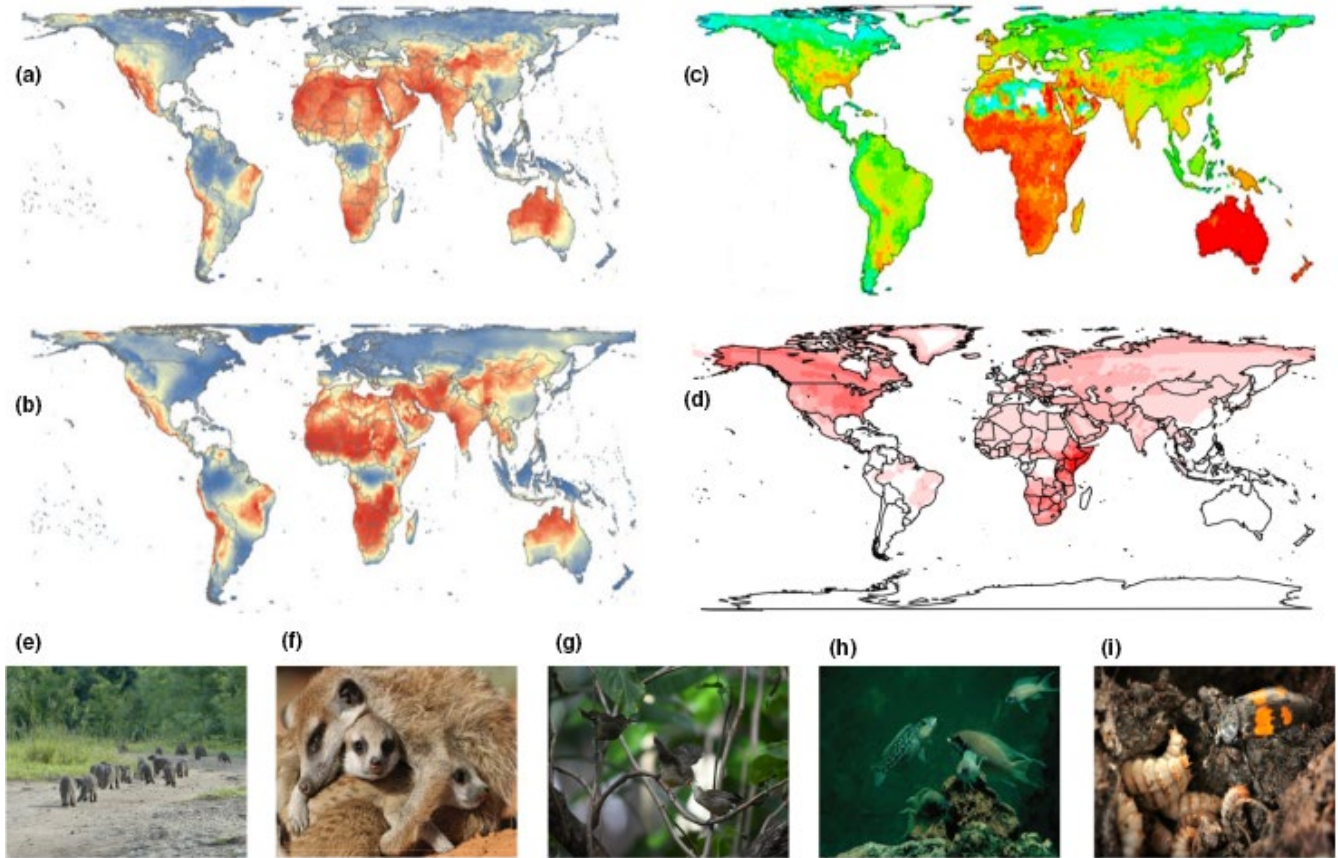


FIGURE 2 Global patterns of climatic variation and unpredictability and biogeographic distribution of cooperative breeding species in birds and mammals. Precipitation variation among (a) and within (b) years (Jetz & Rubenstein, 2011). Colours range from most variable (dark red) to least variable (dark blue). (c) Proportional richness of all cooperative breeders in birds. Colours indicate lower (sky blue) and upper values (dark red) for proportional richness. (d) Global distribution of cooperatively breeding mammals (Lukas & Clutton-Brock, 2017). Cooperatively breeding mammals are rare (white), and not more than seven species in one area (red). (e–i) Five animal species used for studies on the evolution of cooperative breeding: (e) banded mongoose. A group of banded mongooses on a forage trip. Reproduced with permission from F. Thompson; (f) meerkat (*Suricata suricatta*). Subordinates babysit the offspring of dominant pairs. Reproduced with permission from A. Russell; (g) Seychelles warblers (*Acrocephalus sechellensis*). Offspring from the dominant breeding pairs are sometimes fed by subordinate helpers. Reproduced with permission from C.S. Davis; (h) Lake Tanganyika cichlid (*Neolamprologus pulcher*). A group of individuals jointly defending their territory against predation. Reproduced with permission from M. Taborsky; (i) European burying beetle (*Nicrophorus vespilloides*). A female burying beetle remains on the carcass with her larvae. Reproduced with permission from S.A. Kingma and L. Ma

4 | EVOLUTION OF COOPERATIVE BREEDING

The evolution of cooperative breeding is generally considered a two-step process in which the formation of groups precedes the possibility of cooperation (Cockburn, 1998; Emlen, 1982, 1995; Hatchwell, 1999; Jennions & Macdonald, 1994; Ligon & Burt, 2004). In the first step, an individual must decide not to breed independently and instead join a breeding pair or an existing group as subordinate. Individuals can only be expected to delay dispersal and join others if the fitness benefits received exceed those when not in a group.

4.1 | Ecological constraints

The “ecological constraints” hypothesis argues that adverse ecological or demographic conditions, such as shortage of suitable

unoccupied breeding vacancies (habitat saturation) or mates, combined with the high costs associated with finding these, that arise in temporally fluctuating environments may lead to constraints on dispersal or independent breeding and result in increased fitness (such as increased survival or reproductive benefits, including indirect and future benefits) of individuals that join groups as subordinates (Creel & Creel, 2002; Ellis et al., 2017; Emlen, 1982; Koenig & Dickinson, 2016; McFarland et al., 2017; Schülke et al., 2010; Selander, 1964). The “ecological constraints” hypothesis has received considerable experimental support (Table 1; Hannon et al., 1985; Hatchwell & Komdeur, 2000; Heg et al., 2004b; Koenig & Dickinson, 2004, 2016; Komdeur, 1992; Ligon et al., 1991; Pruett-Jones & Lewis, 1990; Taborsky et al., 2021; Walters et al., 1992). Although this hypothesis may explain why individuals delay independent breeding, it does not necessarily provide an explanation for why subordinate individuals should stay in their group rather than move somewhere else and search for a breeding position. In some species, subordinates

TABLE 1 Examples of species with highly variable social parameters (group living/cooperatively breeding species) associated with degree of change in environmental conditions (high versus low)

Species	Biological features of helping behaviour	Environmental conditions (physical/social factors)	Degree of sociality when environmental conditions change from high to low conditions	References
<i>Mammals</i>				
Meerkat (<i>Suricata suricatta</i>)	Joint group defence; shared brood care	Climate (e.g. rainfall); habitat quality (e.g. food availability)	Low	Dubuc and Clutton-Brock (2019); Groenewoud and Clutton-Brock (2020); Huchard et al. (2016); Lukas and Clutton-Brock (2014); Rauber and Manser (2017)
Banded mongoose (<i>Mungos mungo</i>)	Offspring babysitting, for example escort	Predation risk Food availability Group composition (e.g. age, sex)	High High High	Cant et al. (2013); Johnstone and Cant (1999); Marshall et al. (2016); Nichols et al. (2012)
<i>Birds</i>				
Seychelles warbler (<i>Acrocephalus sechellensis</i>)	Nest building and guarding, offspring provisioning	Habitat quality Predation risk	High High	Brouwer et al. (2006); Eikenaar et al. (2009); Hammers et al. (2021); Kingma et al. (2016); Komdeur (1992, 1994); Pant et al. (2019); Richardson et al. (2001, 2003)
Acorn woodpecker (<i>Melanerpes formicivorus</i>)	Territory defence; predator detection; food provisioning	Territory quality (e.g. food supplies)	High	Koenig et al. (2011, 2019); Koenig and Walters (2015)
Superb fairy-wren (<i>Malurus cyaneus</i>)	Territory defence; food provisioning	Climate (e.g. temperature, rainfall); food abundance Population composition (e.g. age); nest predation	High High	Cockburn et al. (2008); Colombelli-Négrel and Kleindorfer (2009); Langmore et al. (2016); Russell et al. (2007); van de Pol et al. (2012)
<i>Fish</i>				
Lake Tanganyika cichlid (<i>Neolamprologus pulcher</i>)	Shelter and territory defence; brood care	Territory quality Predation risk Habitat (e.g. saturation) Predation risk	Low High High High	Bergmüller et al. (2005); Groenewoud et al. (2016); Heg et al. (2004b); Heg et al. (2004a) Branconi et al. (2020); Buston (2004); Buston and Elith (2011)
<i>Insects</i>				
burying beetles (<i>Nicrophorus</i> spp.)	Joint defence of resource (i.e. carcasses); larvae provisioning	Food availability Inter-specific competition	High High	Eggert and Müller (1992); Komdeur et al. (2013); Liu et al. (2020); Scott (1998); Sun et al. (2014); Wilson and Fudge (1984)
<i>Polistes</i> paper wasp	Nest founding; foraging; offspring rearing	Climate (e.g. temperature); food availability Predation risk	High High	Field and Leadbeater (2016); Grinsted and Field (2018); Sheehan et al. (2015); Sheehan and Tibbetts (2011); Tibbetts et al. (2019)

Notes: Environmental conditions include physical factors (e.g. climate, habitat and territory quality, predation) and social factors (e.g. group structure and composition) that are associated with the degree of sociality extending the degree of phenotypic plasticity in animals. "The degree of sociality under changing environments" indicates the influence of the spatio-temporal variation of environmental conditions on the degree of sociality (i.e. high or low degree) in group living/cooperatively breeding species. "Environmental conditions change from high to low conditions" indicate the degrees of spatio-temporal variation (i.e. high versus low variation, fast versus slow variation) of environmental conditions.

remain in groups and delay independent breeding even in the absence of constraints on independent breeding (e.g. Bergmüller et al., 2005; Kokko & Ekman, 2002; Komdeur, 1992; Komdeur et al., 1995; Macedo & Bianchi, 1997; Wong, 2010).

4.2 | Benefits of philopatry

By building upon the “ecological constraints” hypothesis, the “benefits of philopatry” hypothesis was proposed (Stacey & Ligon, 1987, 1991), stating that sexually mature individuals should forego dispersal and become group members on high-quality territories because the benefits they gain there, such as survival and reproductive benefits (including indirect benefits from helping raise relatives) exceed the benefits of dispersal in order to breed independently on available lower quality territories. This may apply particularly when there is considerable and consistent spatial variation in the quality of environmental conditions (Table 1; Arnold & Owens, 1998; Covas & Griesser, 2007; Ekman et al., 2004; Hatchwell & Komdeur, 2000). The benefits of philopatry hypothesis also have received considerable support (Baglione et al., 2006; Cockburn, 1998; Griesser & Ekman, 2004; Kingma et al., 2016). The quality of “home” influences offspring philopatry and helping behaviour, and the cohesion of the family. The quality of home can be expressed in terms of availability of food resources, predation risk and also in terms of thermoregulatory benefits. Experimental manipulations of food levels showed that offspring that were given additional food in their birth territory were more likely to delay dispersal and become helpers (e.g. carrion crows (*Corvus corone*), Baglione et al., 2006; Seychelles warblers, Kingma et al., 2016; western bluebird (*Sialia mexicana*), Dickinson & McGowan, 2005; burying beetles (*Nicrophorus* spp.), Eggert & Müller, 1992; Liu et al., 2020; Richardson & Smiseth, 2020; Scott, 1998; Trumbo, 1992; Wilson & Fudge, 1984; banded mongooses, Marshall et al., 2016; Nichols et al., 2012), and thus promote group formation. In the grey mouse lemur (*Microcebus murinus*), where female offspring forgo dispersal and form long-term groups with their mothers, both mothers and daughters have enhanced survival compared with mothers and daughters living solitary, which could be due to thermoregulatory benefits from space sharing during the cold-dry season (Lutermann et al., 2006). In Lake Tanganyika cichlids, there is experimental support, showing that predation risk has a significant influence on the size and social structure of groups. Increased predation pressure suppresses subordinate dispersal from their home territory, resulting in larger groups (Heg et al., 2004b). Predation significantly decreases the survival probability of group members, especially small subordinates because these are less able to deter predators than larger individuals (Heg et al., 2004b). High predation risk leads to the formation of groups containing many large and few small group members (Groenewoud et al., 2016; Hill & Lee, 2006). However, it is unknown whether high predation risk increases the body size of group members to be able to deter predators. On the contrary, low predation risk leads to groups containing many

small and few large group members (Clutton-Brock et al., 2001; Groenewoud et al., 2016; Hill & Lee, 2006).

These examples show that a change in the physical environment in the broad sense (which includes not only changes in availability of food resources and temperature, but also changes in the biotic environment (predators)) has an effect on delayed dispersal, the size and social structure of groups group. An individual may adjust its phenotype in order to avoid reproductive conflict and being evicted from the group. In most cooperative breeding species, despite being capable of doing so, subordinates often do not reproduce with dominants and may temporarily suppress own growth and reproduction to avoid aggression and eviction (Heg et al., 2004a). Alternatively, subordinates may benefit by waiting for future reproduction, for example to improve survival and potentially inherit territories (Kingma, 2017; Kokko et al., 2001; Riehl, 2013). In some species, subordinates may share reproduction with the breeders (e.g. Komdeur et al., 2017; Lukas & Clutton-Brock, 2012, 2017; Riehl, 2013; Taborsky et al., 2021; Trubenová & Hager, 2012), which may increase reproductive output of the group and incentivize subordinates to stay and help in the group (Bergmüller & Taborsky, 2005; Clutton-Brock, 1998; Reeve et al., 1998; Zöttl et al., 2013).

In the past (last) decades, both the ecological constraints and the benefits of philopatry hypotheses have been shown to play important roles in group formation and cooperative breeding (Clutton-Brock, 2016; Ekman et al., 2004; Emlen, 1982; Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2016; Taborsky et al., 2021). It has been shown in many study systems that either in temporal or spatial varying environmental condition subordinate individuals achieve higher fitness by remaining on high-quality territories in groups than dispersing to lower quality territories (Table 1; Brouwer et al., 2006; Hatchwell & Komdeur, 2000; Heg et al., 2004a; Koenig & Dickinson, 2016; Komdeur, 1993; Ligon & Burt, 2004; Taborsky et al., 2021). In line with the two traditional hypotheses, several empirical studies have shown that group formation and cooperative breeding are beneficial in areas of relatively high quality (such as food availability or low predation) and predictably stable environmental conditions (Baglione et al., 2006; Dickinson & McGowan, 2005; Kingma et al., 2016; Komdeur, 1992; Liu et al., 2020; Marshall et al., 2016; Nichols et al., 2012; Scott, 1998; Wilson & Fudge, 1984). It has been recognized that the evolution of delayed dispersal, and thus the evolution of sociality and cooperative breeding, can best be explained by both hypotheses in concert (Figures 1 and 2; Table 1; Dickinson et al., 2014; Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2016; Koenig et al., 1992; McFarland et al., 2017; Silk et al., 2010; Stanton & Mann, 2012; Walters et al., 1992). Based on the combined predictions of both hypotheses, it has been highlighted that it is crucial to determine how factors, such as environmental and social factors, determine the costs and benefits of each option: staying and/or helping versus dispersing to breed independently (Covas & Griesser, 2007; Ekman et al., 2004; Hatchwell, 2010; Koenig et al., 1992; Walters et al., 1992). However, very few studies have investigated the simultaneous influence of both temporal variation and spatial

variation in environmental living conditions on dispersal behaviour, group formation and cooperation.

5 | NEW PERSPECTIVES: THE ROLE OF SOCIALITY SHAPING ADAPTIVE POTENTIAL IN COOPERATIVELY BREEDING SPECIES

Cooperative breeders seem disproportionately to occur more often in regions that historically, were productive, but turned variable (Cockburn & Russell, 2011; Griesser et al., 2017). However, in the last decade, comparative studies on mammals, birds and insects across the world revealed a higher prevalence of grouping and cooperative breeding in geographical regions with extreme variability and unpredictability of climatic conditions (Figures 1 and 2; Table 1; Botero et al., 2015; Cornwallis et al., 2017; Jetz & Rubenstein, 2011; Kennedy et al., 2018; Koenig & Dickinson, 2016; Liu et al., 2020; Lukas & Clutton-Brock, 2017; Rubenstein, 2011; Rubenstein & Lovette, 2007; Sheehan et al., 2015; Shen et al., 2012, 2017; Zhang et al., 2017). For example, cooperative breeding species have a high abundance in Southern Africa, America and Australia, with subtropical climates and savanna habitats, suggesting that ecological constraints favour the evolution of helping behaviour (Arnold & Owens, 1998; Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2004; Rubenstein & Lovette, 2007). Climate variability refers to the degree to which all the climate variables remain inconstant spatially and temporally. For example, climate variability in some regions is extremely high, with extreme droughts/wet or with extreme hot/cold condition (Rubenstein & Lovette, 2007). Climatic variability can be highly unpredictable, as among- and within-year variation in temperature and rainfall does not always follow the same pattern across space and time, but shows sudden changes (Griesser et al., 2017; Jetz & Rubenstein, 2011). Such extreme climatic conditions and changes therein may result in environments with unprecedented low and unpredictable food availability.

It has already been proposed that cooperative breeding may be an adaptation that allows species to cope with degrading environmental conditions (Cockburn & Russell, 2011; Griesser et al., 2017). This adaptive pattern reflects a higher ability of cooperative breeders to occupy these harsh habitats compared with noncooperative breeders, because helpers could buffer high reproductive failure in harsh environments (Cockburn & Russell, 2011; Griesser et al., 2017; Rubenstein, 2011). However, living in harsh environments may be necessary but not sufficient to drive the evolution of cooperative breeding. Recently, some comparative studies by contrasting cooperative and noncooperative breeding species have proposed that family living (i.e. offspring remain with their parents beyond nutritional independence) is a pivotal stepping stone in the evolution of cooperative breeding (Cockburn & Russell, 2011; Cornwallis et al., 2017; Drobniak et al., 2015; Griesser et al., 2017), where families are formed at first, and second, retained offspring can help in subsequent breeding attempts or engage in redirected helping at the nest. Specifically, the formation of family living is linked with more

productive and seasonal environments, and helping at the nest can help individuals deal with variable and unpredictable environmental conditions.

By forming, or joining groups, in which subordinates assist dominant breeders with resource defence and offspring care, the presence of subordinate members may increase the reproductive output of the breeders and reduce variation in reproductive output compared with breeding as separate pairs (Koenig et al., 2019; Komdeur et al., 2017; McFarland et al., 2017; Schülke et al., 2010). For example, a comparative analysis of 45 species of African starlings shows that cooperative breeding is highly adaptive in temporally and spatially unpredictable environments, such as in semiarid savanna habitats and rainfall, because it allows both reproduction during benign conditions and sustained breeding in harsh conditions (Rubenstein, 2007; Rubenstein & Lovette, 2007). Specifically, in a long-term field study of cooperatively breeding superb starlings (*Lamprolornis superbus*), the reproductive success is temporally and spatially variable in relation to changes in the environment and territory quality, and variation in reproductive success is reduced when the birds cooperate (i.e. increased group size) (Rubenstein, 2011). The reduced variance in reproductive output achieved by the formation of groups and cooperative breeding may be especially useful when living in regions with long-lasting, low-quality conditions or regions with unpredictable environmental conditions, and may buffer a decline in reproductive output caused by poor environmental conditions. However, other comparative studies have reported no or even a reversed association between cooperative breeding to changes in climate (Gonzalez et al., 2013; Tobias & Pigot, 2019). For example, in hornbills (*Bucerotidae*) the occurrence of cooperative breeding (i.e. species with cooperative reproduction) is negatively associated with the degree of both inter-annual climatic variability and intra-annual climatic variability, which demonstrates that hornbills may be less susceptible to climate changes, perhaps because of their dietary niche or increased body mass that reduce the negative influence of environmental variability (Gonzalez et al., 2013).

Theoretical studies have suggested that reducing variance in reproductive output can contribute as much to fitness as improving the mean reproductive output (Gillespie, 1977; Lehmann & Balloux, 2007; Sæther & Engen, 2015; Tuljapurkar, 1990). Furthermore, there are a large number of population model studies that are largely based on long-term demographic and trait studies of cooperatively breeding species, showing how life-history traits and population dynamics respond to climate changes (Canale et al., 2016; Layton-Matthews et al., 2018; Ozgul et al., 2010; Paniw et al., 2019). For instance, in meerkats from the Kalahari Desert, changes in seasonal climate variation influence individual fecundity and survival and population dynamics through effects mediated by adult mass and density (Paniw et al., 2019). In particular, adult mass in the pre-breeding season is positively associated with individual fecundity in the breeding season, whereas an increase in mass and survival in a warmer nonbreeding season would decrease negative effects of reduced rainfall during the breeding season, which promotes population persistence and decreases the risk of extinction. Also, in a

population dynamics study of a group-living bird, the Siberian jay (*Perisoreus infaustus*), where climate, forestry and population density simultaneously influence seasonal life-history rates (i.e. survival and reproductive rates) and population dynamics, population growth is relatively unstable in managed forests compared with in natural forests, and climate change could accelerate the rate of population decline (Layton-Matthews et al., 2018).

Reduced variance in reproductive output by group formation and cooperation may increase adaptive ability and survival of groups and the species in a rapidly changing world. This is an exciting perspective and contrasts the traditional views of “ecological constraints” and “benefits of philopatry” on group formation and cooperative breeding. Climate change and the resulting novel conditions and unprecedented challenges may be causing a paradigm shift in our thinking of the underlying causes and consequences of group formation, cooperation and sociality. Could it be possible that social animals adjust their social behaviour and rewire their social networks in the face of change (see section 6)? The question will then be whether such social behaviour and resulting network changes succeed to buffer impacts of environment, and whether sociality promotes the capacity of populations in social species (*viz.* cooperative breeders) to adapt to rapidly changing environment. Or is it a hit-and-miss and do these social adjustments ultimately exacerbate these impacts? We need research to underpin this exiting possibility and show that adjustment in social behaviour currently happens in the natural systems of our rapidly changing world, and how it ultimately impacts the adaptive ability of individuals, groups and species.

6 | FUTURE AVENUES FOR RESEARCH

Why would individuals form groups and cooperate in environments with low and unpredictable resource availability? Accepting an individual into a group, as a new immigrant or as offspring deciding to stay in the natal territory may generate both benefits and costs for the offspring or immigrant and for the other group members (Shen et al., 2012, 2017). In times of resource scarcity, for dominants it may pay to keep some subordinates in their own group to boost up their reproductive success and survival. When groups experience low or unpredictable food availability and they consequently decline in size, it may be beneficial to dominant breeders to show increased tolerance towards immigrants and to allow subordinates to participate in reproduction (Keller & Reeve, 1994). For example, in splendid fairywrens (*Malurus splendens*, Russell et al., 2007), carrion crows (Canestrari et al., 2011) and Lake Tanganyika cichlids (Taborsky et al., 2007), mothers reduce their parental investment in eggs (e.g. produce smaller eggs) when helpers are present, which is compensated by the higher provisioning provided by helpers. This, in turn, is associated with increased breeder survival (Archie et al., 2014; Crick, 1992; Ellis et al., 2017; Hatchwell, 1999; Heinsohn, 2004; Russell et al., 2007). Furthermore, dominant females may gain from suppressing their own reproductive output and allowing immigrant subordinates to reproduce to make female subordinate helpers remain

longer in the group and help dominants raise offspring (Hammers et al., 2019), and to acquire reserve energy for themselves for future survival and breeding attempts (Hammers et al., 2021). In the Seychelles warbler, the presence of helpers enhances reproductive output and group size because the number of helpers in a territory is positively associated with the chances that offspring survive to adulthood. Seychelles warbler parents that receive help with offspring provisioning reduce their effort spent with raising their offspring (van Boheemen et al., 2019), and received help increases survival and slows down ageing for dominant warblers (Hammers et al., 2019, 2021). These observations are all benefits, but some social adjustments may induce costs to individual group members as well. Group members often compete over resources and reproduction, and individuals in large groups may suffer from enhanced predator attraction or a higher risk of disease (Brent et al., 2017; Krause & Ruxton, 2002). Additionally, larger groups are not always beneficial to adults, as individuals in larger groups had lower survival probabilities than individuals in small groups due to increased competition for food (Brouwer et al., 2006).

Future studies should examine how ecology such as food availability and sociality *together* shapes the adjustment of animals to rapid and extreme environmental change (Figure 1). First, it will be important to identify how rapid and uncertainty changes in ecological and social factors impact population dynamics, individual behaviour (e.g. dispersal behaviour) and sociality (e.g. group formation and cooperation in groups). How does variation in food availability, group size and composition together influence individual foraging and reproductive success, phenotypic flexibility and the response to stress? And how do these factors in turn affect social interactions among group members, dispersal behaviour, immigration success into groups and group formation? Second, it will be important to assess the associated costs and benefits by exploring the life histories of all group members in the long term. How do food availability and group characteristics and dynamics affect the reproductive output and survival of group members and potential immigrants? Will larger groups indeed persist longer, especially during periods with low or unpredictable food availability? Third, it will be important to investigate at the population level, the long-term effects of variation in dispersal behaviour, group size and group dynamics on demography and population viability. Probably, the most captivating challenge for future research is the clarification of multiple and multicomponent selection mechanisms that cause cooperation and measuring fitness consequences of different strategies under varying experimental conditions in natural systems. Comparing cooperatively breeding with non-cooperatively breeding species that also live in stable groups allows testing whether group living or cooperative breeding itself buffers rapidly environmental conditions. The construction of population models of social (grouping but not cooperatively breeding species) and cooperatively breeding species enables us to investigate in what way social animals are capable of adjusting to environmental change. Population models are a powerful tool to identify the critical life-history phases, and thus different types of sociality, that may suffer most from climate change, and provide the

opportunity to model the effect of changing climatic conditions on population size. We are confident that future research into these topics will reveal important causes and consequences of variation in social dynamics of this intensely studied model system.

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CONFLICTS OF INTEREST

The authors declare that they have no conflict of interests in this study.

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