


Exploring the causes and consequences of cooperative behaviour in wild animal populations using a social network approach

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ABSTRACT

Understanding why individuals carry out behaviours that benefit others, especially genetically unrelated others, has been a major undertaking in many fields and particularly in biology. Here, we focus on the cooperation literature from natural populations and present the benefits of a social network approach in terms of how it can help to identify and understand factors that influence the maintenance and spread of cooperation, but are not easily captured when solely considering independent dyadic interactions. We describe how various routes to cooperation can be tested within the social network framework. Applying the social network approach to data from natural populations can help to uncover the evolutionary and ecological pressures that lead to differences in cooperation and other social processes.

Key words: cooperation, social network, assortment, social structure, reciprocity, mutualism

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I. INTRODUCTION

Theorists and scientists across disciplines have struggled to understand the evolutionary origins of cooperative behaviour for decades (Hardin, 1968; Axelrod & Hamilton, 1981); if organisms are working to maximise their

own survival and reproduction, why do they cooperate with others? Why are cooperative behaviours so widespread and how can we explain the cooperation that occurs across a variety of contexts? Although we now have a broad idea of why cooperation may exist (see Section I.1), the proximate mechanisms that allow for cooperation in natural populations are

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not well understood. A wide range of behaviours among many organisms have been described as cooperative, from the release of beneficial exoproducts or exoenzymes in bacteria to the regurgitation and sharing of blood in vampire bats (Czárán & Hockstra, 2009; Wilkinson *et al.*, 2016).

There are various ways to define and operationalise cooperation which reflects the multi- and inter-disciplinary nature of research in this area. Cooperation is studied in various sub-fields of biology, anthropology, psychology, sociology, economics, and political science, and there has been much variation in the way that it is defined, even within disciplines. It seems that definitions are often chosen to fit the specific context that is being studied or the nature of the 'cooperative' behaviour that can be quantified. Here, we adopt a widely accepted biological definition of cooperation: a behaviour that confers a direct fitness benefit on the recipient while providing a fitness benefit to the actor (either indirectly, directly, or both; Sachs *et al.*, 2004).

We can further categorise cooperative behaviours by considering if the behaviour incurs a net cost to the direct fitness of the actor (in which case it is altruistic) or not (mutualistic; Fig. 1). Mutualism refers to any interaction that involves direct benefits to both parties, either through a by-product of the interaction or reciprocity (generalised, direct, or indirect; discussed further in Section I.1). As West, El Mouden &

Gardner (2011) discuss, there seems to be a general feeling among researchers that altruistic behaviours are more puzzling than those that are mutually beneficial. However, possible decreases in the relative fitness of the cooperator are what make both scenarios interesting.

(1) Forms of cooperation

Mutualistic cooperative interactions, where there is no net cost to the actor, are instances where there are benefits to both individuals because their combined efforts lead to greater benefits than if each individual had acted on its own, or not at all (Clutton-Brock, 2009; Leimar & Hammerstein, 2010). Some restrict the term 'mutualism' to inter-specific mutualism (West, Griffin & Gardner, 2007); for the purposes of this review, all mutually beneficial behaviours are considered as mutualism and are labelled as inter-specific if this is the case. Mutualism can occur in many ways: through *by-product mutualism*, where an individual benefits from the behaviours of another that would be occurring anyway (West-Eberhard, 1975; Grinnell, Packer & Pusey, 1995); *by-product or pseudo-reciprocity*, where an individual benefits from the behaviours of another that would be occurring anyway by aiding them in some way (Bygott, Bertram & Hanby, 1979; Connor, 1986); or through *coercion*, where there are

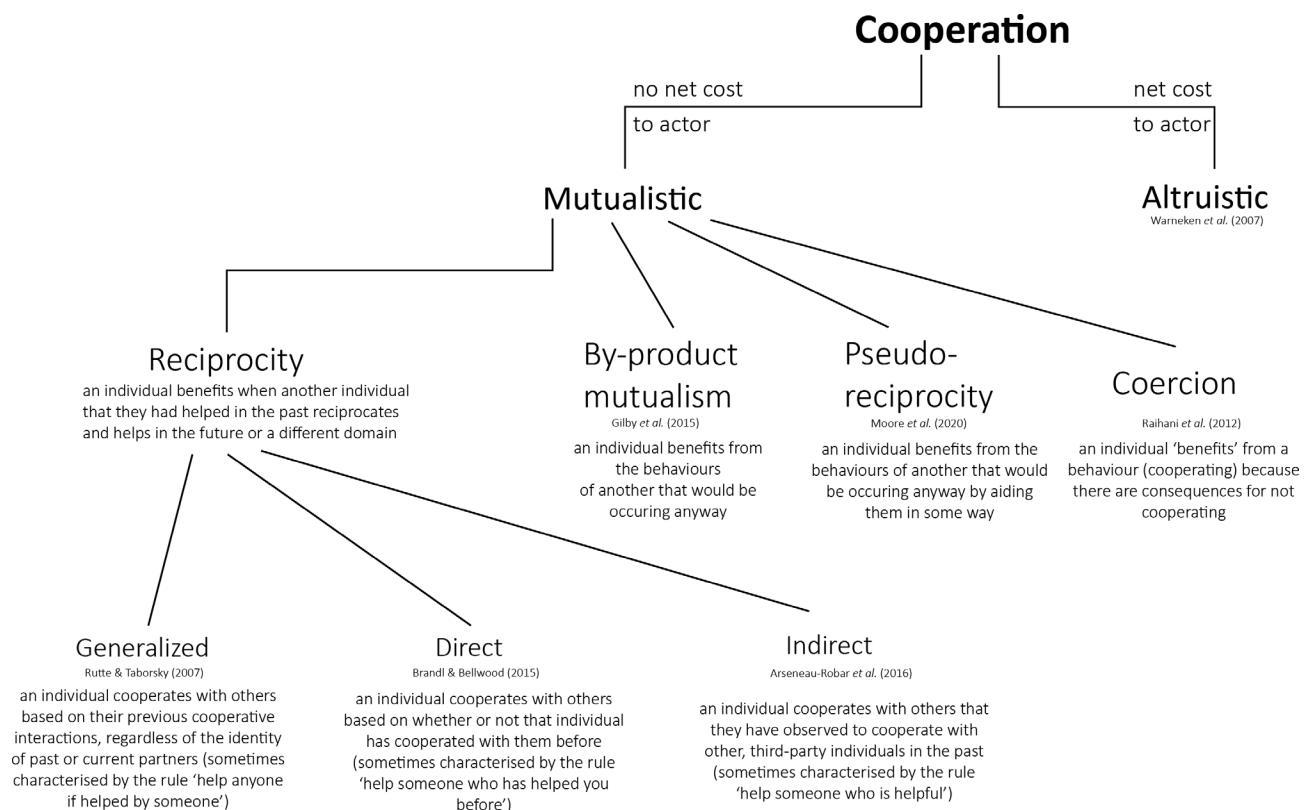


Fig 1. A simple visual representation of how different types of cooperation are related to one another, with an example and short definition of each (Rutte & Taborsky, 2007; Warneken *et al.*, 2007; Raihani, Grutter & Bshary, 2012; Brandl & Bellwood, 2015; Gilby *et al.*, 2015; Arseneau-Robar *et al.*, 2016; Moore *et al.*, 2020).

consequences for not cooperating (Kokko, Johnstone & Wright, 2002; Noë, 2006; Raihani *et al.*, 2012).

A subset of mutualistic cooperation occurs in the case of reciprocity, where individuals that the actor had once helped in the past will reciprocate and help them in the future or in a different domain (Trivers, 1971). This is especially relevant in stable populations where individuals can track and remember the contributions of individuals over time, but reciprocity can also occur in relatively simple, unstable, and changing populations (Kern & Radford, 2018; Smith *et al.*, 2018). Cooperation through reciprocity is more likely to evolve in situations where the cost of helping is low, the benefit to the receiver is high, and/or there are frequent opportunities for helping behaviour (Taborsky, Frommen & Riehl, 2016).

Sachs *et al.* (2004) identify two mechanisms that can enable reciprocity: partner choice and partner-fidelity feedback. In partner choice, an individual (x) has the opportunity to choose who to cooperate with (y or z), based on who will provide greater fitness benefits in return. In the case of partner-fidelity feedback, when one individual (x) cooperates with (y) for an extended period of time, they become “coupled in fitness” through feedback (Sachs *et al.*, 2004, p. 137). When y benefits from x, x also benefits indirectly by having a ‘better’ cooperative partner in y. Because of this, if x does not cooperate with y, their own fitness will also decline – meaning that they are then “coupled in fitness”.

In *generalised reciprocity*, perhaps the most basic form of reciprocity, individuals are more likely to cooperate if they have had cooperative interactions in the past, regardless of the identity of past or current partners (van Doorn & Taborsky, 2011); this form of reciprocity does not require memory of the partner but only of the nature of the interaction, that is cooperation or defection (Voelkl, 2015). Cooperation can emerge and be maintained through generalised reciprocity alone if individuals are repeatedly interacting in small social groups (Pfeiffer *et al.*, 2005). Captive rats (*Rattus norvegicus*), capuchin monkeys (*Cebus apella*), and dogs (*Canis familiaris*) have been shown to engage in generalised reciprocity when tested on a cooperative task requiring the pulling of a stick or rope which presents food to their partner (Rutte & Taborsky, 2007; Leimgruber *et al.*, 2014; Gfrerer & Taborsky, 2017). In a more recent study (Darden *et al.*, 2020), a predator inspection arrangement was used to explore cooperation in Trinidadian guppies (*Poecilia reticulata*), showing that individuals would either stay with or switch their social partner on the basis of whether the partner had cooperated or defected in their most recent interaction (see Section I.3).

Direct reciprocity is one of the most widely hypothesised routes to cooperation in animals but is also a highly contested explanation (Clutton-Brock, 2009). Here, individuals are more likely to cooperate with others that have cooperated with them before. In a study of avian cooperation, Voelkl *et al.* (2015) investigated human-guided migratory V-formation flight in captive northern bald ibises (*Geronticus eremita*). Birds switched positions with the leader frequently to match the leaders’ leading time to their own. More

generally, the amount of time an individual spent as the leader was strongly positively correlated with how much that individual could benefit from being a follower. Direct reciprocity seems to require not only memory and individual recognition – the recognition and tracking of other individuals’ identities and actions to guide future interactions and behaviour – but also numerical discrimination (distinguishing between many instances of something *versus* a few instances) and the ability to account for benefits that will come in the future (Stevens & Hauser, 2004; McAuliffe & Thornton, 2015). Challenging the idea that reciprocity is cognitively complex or demanding, Brandl & Bellwood (2015) describe the ‘coordinated vigilance’ of coral reef rabbitfishes (Siganidae); one individual remains vigilant while the other forages (allowing for more efficient and thorough foraging), and pairs alternate between these two roles relatively equally. They argue that advanced social skills or complex cognition are not necessarily essential to the emergence and maintenance of direct reciprocity in animals.

Finally, the most complex form of reciprocity is *indirect reciprocity*: where individuals are more likely to cooperate with conspecifics that they have observed to cooperate with others before – this presumably requires the ability to remember and keep track of conspecifics and the interactions that they engage in. This has been discussed in terms of ‘image-scoring’, where individuals keep track of the cooperative behaviours of others and increase or decrease their scores based on cooperation or defection (Nowak & Sigmund, 1998) – a process that requires individual recognition (Tibbetts & Dale, 2007). Whether or not animals can engage in this image-scoring is a matter of great debate across many disciplines due to the proposed role of complex cognition in recognising and remembering the behaviours of conspecifics interacting among themselves (Wiley, 2013). Nevertheless, existing studies suggest that non-human animals do engage in indirect reciprocity. This has been demonstrated in: (i) birds, in the context of sentinel behaviours and experimental manipulations using the ‘dear enemy’ effect, when there is a mutual decrease in aggression among neighbours at the territory boundary that comes with increased familiarity (Akçay *et al.*, 2010; Bell *et al.*, 2010); (ii) fish, where cleaner fish engage in behaviours consistent with image-scoring and prefer more cooperative cleaners (Bshary & Grutter, 2006); and (iii) primates, in the formation of coalitions and defence of food resources (Berghänel *et al.*, 2011; Arseneau-Robar *et al.*, 2016).

Studies of human cooperation have also considered the possibility that individuals cooperate in order to increase their reputation or signal something about themselves to others (Lotem, Fishman & Stone, 2003; van Vugt & Hardy, 2010). This has been discussed in terms of ‘costly signalling’, where cooperation emerges as way to signal one’s competence or quality as a reproductive or coalition partner, or competitor (Gintis, Smith & Bowles, 2001). Several studies entertain this possibility by looking for the presence or absence of audience effects (changes in behaviour in the presence of others) on various cooperative behaviours. While

some find increases in cooperative behaviours when audiences are present (Hector, Seyfarth & Raleigh, 1989; Doutrelant & Covas, 2007), others fail to find an effect (McDonald *et al.*, 2008; Schweinfurth & Taborsky, 2016), or find the opposite (i.e. more cooperative behaviour without audience; Brügger, Kappeler-Schmalzriedt & Burkart, 2018); scepticism exists as to whether or not non-human animals adjust their behaviour in this way.

It is important to consider the possibility that these seemingly more complex routes to cooperation can also be maintained in different, less cognitively demanding ways (Carter, 2014). For example, Tognetti *et al.* (2017) suggest that cooperation may be maintained through sexual selection; if the 'cooperative phenotype' is associated with other sexually selected traits then cooperation can evolve and be maintained through its association with them. Steppe mice (*Mus spicilegus*) invest in cooperative mound building, which can be understood as a form of parental care (Tognetti *et al.*, 2017). After classifying males as more or less cooperative based on their mound building investment in the autumn, Tognetti *et al.* (2017) exposed females to one high-cooperation male and one low-cooperation male in pairs during the breeding season. Choosing a mate that makes higher investments in mound building can lead to having a larger mound which can increase the probability of offspring survival. Each pair of males had either been previously observed by the females during mound building or not. Tognetti *et al.* (2017) found that more cooperative males are preferred regardless of whether or not they were previously observed by the females, indicating that a preference for more cooperative individuals is not necessarily indicative of indirect reciprocity. It is possible that cooperative propensity is correlated with another attractive, sexually selected trait. Further research is necessary before coming to any conclusions about the skills or cognitive characteristics that are essential to these forms of cooperation and whether or not various non-human animals are capable of engaging in them.

(2) A social network approach to cooperation

Cooperative behaviours are intrinsically social, with two or more individuals interacting. Accordingly, understanding the mechanisms of cooperation requires an investigation of characteristics of social interactions at the dyadic, group, and population level. Social network analysis provides a variety of tools to look at the relationship between an individual's behaviours and the structure and characteristics of their social interactions (Croft, Darden & Wey, 2016). In some populations, cooperative behaviour and social network structure may have a complementary relationship, where the assortment and organisation of individuals allows for cooperation to spread more or less easily (Fehl, van der Post & Semmann, 2011). By systematically describing social structure at the population and individual level, social networks can help us understand how the social environment impacts individuals differently based on their position within the network. Due to the direct link between social network structure

and the maintenance and spread of cooperation, which will be explored in this review, social network analysis can be a powerful tool for empirically testing questions about cooperative behaviour that have been previously left unanswered. For example, Covas & Doutrelant (2018) stress the roles of social and sexual selection in maintaining cooperation, and point to advances in social network analysis as a promising avenue to understanding how selection pressures influence cooperation in natural populations.

When taking a social network approach, various measures of social relationships and structure can be extracted which give us insights into the nature and strength of pathways and bonds among and between different individuals and groups (Farine & Whitehead, 2015). At the most basic level, social networks consist of nodes which represent single entities or components (usually an individual but can also be a group) and the edges (sometimes referred to as links or ties) or relationships (interactions or associations) among them. Edges can have different weights or directions to provide information about the nature of relations between nodes. Using this basic information, various measures of the social network can be extracted. These measures can be grouped into three levels (Wey *et al.*, 2008): individual, intermediate, and group. The individual (or local) network measures reveal information about particular, single nodes in the network while intermediate measures provide information about how edges are distributed within the network. Group (or whole) network measures account for all of the nodes and edges within the network and can give us a sense of overall social structure. Network metrics that are particularly relevant to cooperation are shown in Fig. 2.

Social network measures and positions can also be related to other social characteristics (Wilson *et al.*, 2013). For example, different levels of social connectivity may be associated with the likelihood that an individual can acquire and spread novel information or behaviours (Firth, 2020). Network positions have also been linked to stable differences in personality (Aplin *et al.*, 2013; Díaz López, 2020). More generally, individuals in more central positions may have a higher chance of entering cooperative interactions than less social individuals who may be at the periphery of the network. This can be further linked to personality differences (e.g. if bold individuals are more likely to be in central network positions). As discussed earlier, the characteristics of the entire social network can also give us an idea of how likely it is for cooperation to be maintained or spread in certain types of networks or populations (Luthi, Pestelacci & Tomassini, 2008).

The advantages of using a social network approach to understand cooperation and other emergent social properties better in animal populations have been considered by many scholars (Wey *et al.*, 2008; Sih, Hanser & McHugh, 2009; Kurvers *et al.*, 2014; Croft, Edenbrow & Darden, 2015; Farine & Whitehead, 2015; Croft *et al.*, 2016), and various empirical examples are beginning to emerge (see Section III). In particular, the social network approach is useful because it can be used to: (i) examine the relationships between properties of single individuals and

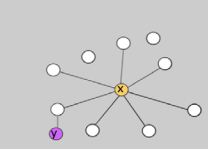
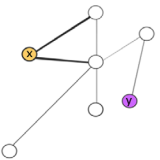
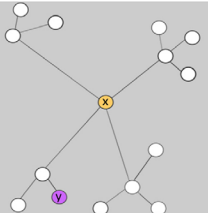
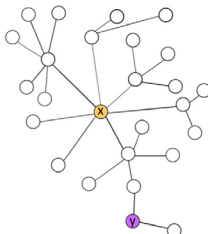
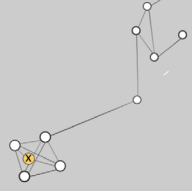
	Measure	Definition	Visualisation	Potential implications for cooperation
Direct measures: <i>measures related to the ties that a particular individual has</i>	Number of edges (node degree)	The number of edges a particular node has		Populations with a low average node degree may be more likely to cooperate (van Doorn & Taborsky, 2011)
	Strength of edges	The strength or weight of the edges a particular node has; based on the number of interactions or associations among two nodes		Individuals with stronger connections (or, in other words, higher familiarity) may be likely to cooperate with one another (Croft <i>et al.</i> , 2006)
Indirect measures: <i>measures related to the ties of all of the individuals that a particular individual is associated with</i>	Betweenness centrality	Centrality based on the extent to which a node 'bridges' the network which is calculated as the number of times a node appears on the shortest pathways between every other pair of nodes; gives an idea of how important an individual is for connecting different parts of the network		Cooperative individuals with high betweenness centrality may foster cooperation by allowing for the 'bridging' of different social clusters or groups that would not interact or cooperate in their absence (Edelman & McDonald, 2014)
Centrality measures: <i>express how structurally important an individual is on the basis of their network position in different contexts</i>	Eigenvector centrality	Centrality based on the centralities of a node's edges; high centrality can reflect a high node degree or having edges with many nodes that have a high degree		If individuals with high eigenvector centrality are cooperative, cooperation may be more likely to spread (Bird & Power, 2015)
	Clustering coefficient	Calculated by dividing the number of edges an individual has with their neighbours by the maximum amount of edges that could exist among neighbours; gives an idea of how well connected an individual's immediate network is		More clustered networks may be more likely to allow for the spread of cooperation, especially through reciprocity; this is amplified if individuals are clustered by cooperativeness (Fehl <i>et al.</i> , 2011)

Fig 2. A sample of network metrics relevant to studies of cooperation. The nodes are coloured to denote examples of high (x, yellow) or low (y, purple) values of each metric.

processes that occur at the group level, rather than considering these aspects separately (Farine & Whitehead, 2015); (ii) quantify the strength, persistence, and dynamics of social ties and individual changes in network positions; (iii) understand how network positions, measures of group connectivity, and social structure may be linked to individual or group levels of cooperative behaviour (Eguíluz *et al.*, 2005; Clutton-Brock, 2009); (iv) gain a more holistic understanding of how individuals interact and how these interactions impact the spread of cooperative behaviour in different social structures, through the identification and quantification of indirect

connections (Brent, 2015); and (v) predict, measure, or even manipulate who cooperates with whom (Croft *et al.*, 2006).

Limiting studies of cooperation to behaviour among dyads can have several limitations that can be accounted for by using the social network approach. A wide range of studies have shown that interaction with or the presence of third-party individuals can influence dyadic cooperative interactions (Connor, 2010; Earley, 2010; Aplin *et al.*, 2013; Ilany & Akçay, 2016; Newton-Fisher & Kaburu, 2017; Brügger, Willems & Burkart, 2021). By using a network approach, we can expand our understanding from dyadic interactions

to taking account of the whole social structure, therefore giving us a more complete picture of cooperation that occurs in different populations.

Examining social structure through the social network approach becomes even more pertinent when considering direct *versus* indirect genetic effects on phenotypic variation in cooperation (Dakin & Ryder, 2018). Direct effects on phenotype are based on variation among individuals in their 'intrinsic biology' while indirect effects are related to the influence of the social environment (Dingemanse & Araya-Ajoy, 2015; Dakin & Ryder, 2018, p. 1). As Kasper & Voelkl (2009) argue, while traditional research investigating social behaviour can sometimes be clouded by the complex interactions of various factors, social network analysis allows us to study the interactions themselves, alongside the behaviours that they are impacting. Furthermore, the ability to utilise social network analyses with data from natural populations allows for the study of cooperation in a more ecologically relevant manner. What is necessary now is a control for and/or explicit investigation of how complex long-term social interactions and structure influence cooperative behaviour and *vice versa*. As such, experimental approaches to manipulating, quantifying, and evaluating natural animal populations' social networks are needed to gain a better understanding of cooperation (see Section III.3).

(3) Assortment by cooperation

Identifying the social network structure of a population is also crucial for understanding how cooperation spreads and is maintained in that population because of the importance of assortment (Fletcher & Doebeli, 2009; Croft *et al.*, 2015). One route to assortment by cooperation results from spatial population structure (non-random spatial distribution) where individuals with similar phenotypic or behavioural traits are clustered in space, and this spatial structure drives social structure (Nowak, Tarnita & Antal, 2010). When individuals are neighbours in physical space, it is more likely that they will interact with one another. Furthermore, similar phenotypes may have similar space-use preferences, making spatial assortment even more likely (Schirmer *et al.*, 2019). It is also possible for populations to have a similarly non-random social distribution. Individuals of the same phenotype may be more likely to interact with one another and have stronger bonds regardless of their physical distance (Farine, 2014; Firth & Sheldon, 2016), for example if their phenotype governs the type of social interaction they are likely to engage in. This clustering of cooperators can allow for cooperation without assortment in spatial structure (Antal *et al.*, 2009). More generally, individuals have been found to assort by phenotype with regard to age, sex, dominance rank, and even personality (Carter *et al.*, 2015; Johnson *et al.*, 2017; Perryman *et al.*, 2019).

When there is assortment based on cooperation, cooperative individuals are more likely to interact with other cooperators, allowing them to obtain higher fitness benefits than those that do not cooperate in the same network (Nowak

et al., 2010; Brask *et al.*, 2019). In other words, cooperation can be selected for when there are non-random associations between individuals of similar phenotypes (Pepper & Smuts, 2002; Rankin & Taborsky, 2009). The characteristics of social networks therefore have an inevitable influence on how cooperation can spread or be maintained in that population (Bergmüller, Schurch & Hamilton, 2010).

Initial studies have suggested that there may be a correlation between measures of cooperation (e.g. propensity to cooperate, number of cooperative partners, etc.) and other phenotypic traits (Croft *et al.*, 2009). If this is the case, assortment based on other phenotypic traits may also lead to assortment based on cooperation (Croft *et al.*, 2015). However, some studies have shown that cooperative propensity is not repeatable over time and can vary based on an individual's internal (Wright, Maklakov & Khazin, 2001; Young, Carlson & Clutton-Brock, 2005; Scheid & Noë, 2010; Madden & Clutton-Brock, 2011) and external (Komdeur, 2006; Nichols *et al.*, 2012) environment. On the other hand, others report stable qualitative and quantitative individual differences in cooperative behaviour (reviewed by Bergmüller *et al.*, 2010; English, Nakagawa & Clutton-Brock, 2010; Le Vin *et al.*, 2011; Sanderson *et al.*, 2015; Wismer *et al.*, 2014). Further work is needed to gain a better understanding of the 'cooperative phenotype' and what explains the stability of this trait within individuals. As Bergmüller *et al.*, 2010 discuss, one of the main challenges of studying the cooperative phenotype is trying to tease apart variation due to social interactions and social structure as well as other non-social factors; social network analysis can be used to control for social relationships (by including whole networks in models, or by extracting metrics like strength or degree) when assessing overall cooperative propensity.

In the absence of a spatial or social distribution, conditional cooperation can also lead to assortment by cooperation in social networks. When there are repeated interactions between individuals, an individual's current behaviour and who they choose to interact with may be based on the previous behaviour of their social partners. Contingent responding is also possible through more basic movement rules or heuristics like the 'walk away' rule, which simply entails moving away from an individual in physical space once they defect once (Aktipis, 2004; Darden *et al.*, 2020). Network 'rewiring', or the ability of individuals to terminate or change social ties, is an important aspect of the maintenance of cooperation (Rand, Arbesman & Christakis, 2011). Cooperation is more likely to evolve in social systems where the random creation of social ties is low (Akçay, 2018), and it is important to keep in mind that rewiring can occur passively – due to turnover and general demographic and fission–fusion processes (Shizuka & Johnson, 2020). These factors can all be accounted for when using social network analysis to look at network structure and composition over time.

The utility of a social network approach for understanding how cooperation can be maintained in natural populations is clearly illustrated by a study of cooperation in the Hadza,

a human hunter–gatherer population (Apicella *et al.*, 2012). By asking individuals about who they would live with in the next camp and who they would donate honey to, Apicella *et al.* (2012) created two networks (“campmate” and “gift”) to look at how Hadza social network structure compares to a random one. All individuals were more likely to choose others who had chosen them (without being aware of this) in both networks even when controlling for genetic relatedness, suggesting that reciprocity may maintain cooperation among both kin and non-kin. Furthermore, social ties were more likely among individuals with similar physical characteristics (age, height, mass, body fat, and handgrip strength) and among individuals with similar cooperative tendencies. More specifically, there are clusters of cooperators – with more between- than within-camp variation in cooperative behaviour (Apicella *et al.*, 2012, p. 499). As individuals who donate more did not have higher measures of in- or out-degree, it is unlikely that all individuals in this population are consistently preferring cooperators. It seems that cooperators prefer to interact with cooperators. The authors emphasise the idea that cooperation is impacted by social network structures; they suggest that cooperation and the behaviours that underpin social structure may have evolved together.

Reviewing the causes and consequences of assortment by cooperation in social networks, Croft *et al.* (2015) stated that understanding the mechanisms that allow for “assortment among cooperators” is the “key” to understanding cooperation among non-kin. Accordingly, herein we examine the utility of applying social network approaches to empirical data from natural populations for uncovering the mechanisms that allow for the maintenance and spread of cooperation.

II. EXISTING WORK

(1) Existing work on cooperation in natural populations

It is possible that different combinations of multiple factors are influencing the presence or persistence of cooperation in different animal populations (Krützen *et al.*, 2003). Existing studies of cooperation among non-kin in non-human animals are detailed in Table 1, which demonstrates the wide range of behaviours that have been studied as cooperation. There is no standardised way to test cooperation in natural populations, nor is it always clear that tests actually measure cooperation. For example, a string-pulling task has often been used with captive populations to look at individual differences in cooperative propensity/ability. This usually consists of some form of an apparatus where food is on a shelf behind a mesh. The shelf is connected to a string on each side. If only one side of the string is pulled, the shelf is either pulled into a position where the food is still out of reach, or the string comes out of its nook and the shelf can no longer be pulled. However, if both individuals pull the string, the

food is moved within reach. However, whether this is a test of cooperation or coordination is unclear and it seems that individuals can solve the task without necessarily understanding or engaging in the cooperative component, as individuals can continue to solve the task even when visual access to the other participating individual is blocked (Tassin De Montaigu *et al.*, 2019). Understanding cooperation is challenging, as cooperative behaviours in different populations may be maintained by different mechanisms and similar populations may maintain the same type of cooperation in different ways.

It is important to keep in mind that the studies in Table 1 explicitly set out to examine cooperation; many studies with a different focus, but which fit under the various definitions of cooperation in Section (1) may be missing. For example, studies that consider various aspects of social tolerance, food-sharing, signalling/alarm-calling and other behaviours that are generally accepted as prosocial (defined as unsolicited acts of help or assistance to others) can give us insights into the way cooperation spreads or is maintained in natural populations (Brown, Brown & Shaffer, 1991; Jaeggi, Burkart & Van Schaik, 2010; Jaeggi & Gurven, 2013; Bonadonna *et al.*, 2020). There may be other systems which are well suited for the study of cooperation that have not previously been directly framed in this context.

Finally, there is some inherent overlap in cooperation and social interaction/association; many of the behaviours described as cooperation in the studies listed in Table 1 can also be used in the construction of social networks. This is especially apparent for the primate literature where grooming associations can be used to construct social networks and describe social structure, but grooming can also be understood as a form of cooperation in itself (Cheney *et al.*, 2010; Kawazoe & Sosa, 2019; Wooddell, Kaburu & Dettmer, 2019). Moving forward, it is important to ensure that, if we are studying cooperation with a social network approach, the measure of spatio-temporal co-occurrence that is used to ascertain social structure does not overlap with the behaviour that has been defined as cooperative in that population.

(2) Existing modelling of cooperation

Early work modelling cooperation revealed several insights about the way cooperation may spread in structured populations. As reviewed by Croft *et al.* (2015), cooperation is more likely to spread in networks where assortment by cooperation is higher; this is especially the case when networks are dynamic and heterogeneous with low connectivity. Previous modelling studies have shown that social structure can give rise to properties like resilience to loss (Lusseau, 2003) or a decrease in social contagion (Jordan *et al.*, 2013), which can have important consequences for cooperation. When Luthi *et al.* (2008) simulated three games in three types of social networks they found that cooperators were more likely to be in positions that maximised their links to other cooperators – a property which encourages the spread of cooperation.

Table 1. Studies examining non-kin cooperation in natural non-human populations

	Study	Species	Sample size	Cooperative act
Bird	Godard (1993)	Hooded warbler (<i>Wilsonia citrina</i>)	12	Mutual restraint in aggression
	McDonald & Potts (1994)	Long-tailed manakin (<i>Chiroxiphia linearis</i>)	33 pairs of males	Courtship
	Krams & Krama (2002)	Chaffinch (<i>Fringilla coelebs</i>)	76	Interspecific mobbing of predators
	Krams, Krama & Igaune (2006b); Krams <i>et al.</i> (2008)	Pied flycatcher (<i>Ficedula hypoleuca</i>)	34 pairs of nest boxes, 44 'nest box triplets'	Mobbing of predators
	Krams, Krama & Igaune (2006a)	Great tit (<i>Parus major</i>)	24	Alarm calling to warn others of predator
	Akçay <i>et al.</i> (2009)	Song sparrow (<i>Melospiza melodia</i>)	12	Mutual restraint in aggression
	Akçay <i>et al.</i> (2010)	Song sparrow (<i>Melospiza melodia</i>)	10	Mutual restraint in aggression
	Bell <i>et al.</i> (2010)	Southern pied babbler (<i>Turdoides bicolor</i>)	21	Vigilance behaviour
	Krams <i>et al.</i> (2010)	Pied flycatcher (<i>Ficedula hypoleuca</i>)	28 pairs of nest boxes	Mobbing of predators
	Riehl (2011)	Greater ani (<i>Crotophaga major</i>)	35 two-pair groups and 22 three-pair groups	Cooperative nesting (several pairs lay eggs in a single nest; communal care of the clutch)
Fish	Grabowska-Zhang, Sheldon & Hinde (2012)	Great tit (<i>Parus major</i>)	24 pairs of nest boxes	Mobbing of predators
	Krama <i>et al.</i> (2012)	Pied flycatcher (<i>Ficedula hypoleuca</i>)	50 pairs of nest boxes	Mobbing of predators
	Johnstone <i>et al.</i> (2014)	Great tit (<i>Parus major</i>)	21 pairs of parents	Parental care
	Voelkl <i>et al.</i> (2015)	Northern bald ibis (<i>Geronticus eremita</i>)	14	Turn-taking in V-formation flight
	Ryder <i>et al.</i> (2020)	Wire-tailed manakin (<i>Pipra flicauda</i>)	210 males	Courtship
	Bshary & Schäffer (2002)	Bluestreak cleaner wrasse (<i>Labroides dimidiatus</i>)	43	Host choice
	Bshary & Grutter (2006)	Bluestreak cleaner wrasse (<i>Labroides dimidiatus</i>)	28	Cleaner choice
	Adam (2010)	Bluestreak cleaner wrasse (<i>Labroides dimidiatus</i>)	24	Host choice
	Railhani <i>et al.</i> (2012)	Bluestreak cleaner wrasse (<i>Labroides dimidiatus</i>)	45 pairs	Cleaning behaviour
	Brandl & Bellwood (2015)	Coral reef rabbitfish (Siganidae)	59 pairs, 24 solitary individuals	Vigilance behaviour
Mammal	Darden <i>et al.</i> (2020)	Trinidadian guppy (<i>Poecilia reticulata</i>)	136 females	Predator inspection
	Grinnell <i>et al.</i> (1995)	Lion (<i>Panthera leo</i>)	36	Mobbing of predators
	Murrant, Bowman & Wilson (2014)	Southern flying squirrel (<i>Glaucomys volans</i>)	72	Social foraging
	Wilkinson <i>et al.</i> (2016)	Greater spear-nosed bat (<i>Phyllostomus hastatus</i>)	144	Infant care
	Kern & Radford (2018)	Wild dwarf mongooses (<i>Helogale parvula</i>)	12 groups (4–9 individuals each; mean = 7)	Vigilance behaviour, grooming
	Moore <i>et al.</i> (2020)	Bottlenose dolphin (<i>Tursiops truncatus</i>)	59	Courtship
	Packer (1977)	Olive baboon (<i>Papio anubis</i>)	18	Coalition formation
	Seyfarth & Cheney (1984)	Vervet monkey (<i>Ceropithecus aethiops</i>)	9	Agonistics support in conflict
	Whitehead (1987)	Mantled howling monkey (<i>Alouatta palliata</i>)	20	Intergroup avoidance
	Muroyama (1991)	Japanese macaque (<i>Macaca fuscata</i>)	7	Grooming
Mammal (Primate)	Manson <i>et al.</i> (2004)	White-face capuchin (<i>Cebus capucinus</i>) and bonnet macaque (<i>Macaca radiata</i>)	36	Grooming
		Chimpanzee (<i>Pan troglodytes</i>)	41	Grooming

(Continues)

Table 1. (Cont.)

Study	Species	Sample size	Cooperative act
Langergraber, Mitani & Vigilant (2007)			Associations, grooming, proximity maintenance, coalition formation, meat sharing, and joint participation in territorial boundary patrols
Cheney <i>et al.</i> (2010)	Baboon (<i>Papio hamadryas ursinus</i>)	57 dyads	Grooming, responses to calls for help
Fruteau <i>et al.</i> (2011)	Sooty mangabey (<i>Cercocebus atys</i>) and vervet monkey (<i>Chlorocebus aethiops</i>)	46	Grooming
Newton-Fisher & Lee (2011)	Chimpanzee (<i>Pan troglodytes</i>)	12 (66 possible dyads)	Grooming
Dubuc <i>et al.</i> (2012)	Rhesus macaque (<i>Macaca mulatta</i>)	43 pairs	Co-feeding
Arseneau-Robar <i>et al.</i> (2016)	Wild vervet monkey (<i>Chlorocebus aethiops pygerythrus</i>)	34	Vigilance behaviour
Moscovice <i>et al.</i> (2017)	Bonobo (<i>Pan paniscus</i>)	78 dyads	Party association, proximity, grooming, GG-rubbing, and aggression
Haney & Fewell (2018)	California harvester ant (<i>Pogonomyrmex californicus</i>)	18 colonies	Reproductive investment
Invertebrate			

A large number of modelling studies have explored the consequences and coevolution of aspects of social structure for/with the emergence, spread, and maintenance of cooperation. These studies consider a wide range of factors, including: whether networks are static or dynamic (Jordan *et al.*, 2013; Rand *et al.*, 2014; Li *et al.*, 2020), whether the structure is hierarchical or not (Eguíluz *et al.*, 2005), the number of neighbours or ties individuals have (Fletcher & Doebeli, 2009; Allen *et al.*, 2017), the modularity, clustering, and assortment of the network (Riolo, Cohen & Axelrod, 2001; Antal *et al.*, 2009; Marcoux & Lusseau, 2013), the way in which ties are created in the network (Akçay, 2018), and many others. Further studies investigate how these aspects may interact with other characteristics of cooperation in the population, including: the cost of cooperating (Ohtsuki *et al.*, 2006), mechanisms for group coordination (Angus & Newton, 2020), mechanisms that maintain cooperation (e.g. generalised reciprocity: Voelkl, 2015), etc.

Many theoretical papers have considered the mechanisms underlying the maintenance and spread of cooperation, which have been accompanied by empirical studies of individuals ‘cooperating’ in the wild with little discussion of the link between them. As Noë (2006) discusses, theoretical studies of cooperation often have one of three goals: to analyse existing, naturally occurring cooperation, to identify the proximate mechanism of cooperation, or to test game-theoretical models. Social network analysis can allow us to work towards multiple goals at once by facilitating the integration of theoretical and empirical work – an important precursor to understanding cooperation (West *et al.*, 2007).

One particularly relevant example of this is a simulation study on primate social networks. Using data from 70 different primate groups, Voelkl & Kasper (2009) created weighted graphs for each of the groups to simulate the spread of two strategies (cooperation and defection) using a death–birth update rule. 1000 simulations were run for each group and the authors looked at how long it took for either strategy to reach fixation. By calculating a ‘fixation difference’ they show that in a majority of the groups (87%), cooperation is more likely to reach fixation than it would be in a better mixed group of the same size, and conclude that social structure promotes cooperation in primate groups. By using social network analysis alongside other methods (as done by Voelkl & Kasper, 2009), it is possible to make and test predictions in a manner akin to evolutionary graph theory while additionally accounting for important details about actual social structure(s). Social network analysis is a promising approach for investigating the impact of social structure on actual cooperative behaviour in real, natural populations.

(3) Existing empirical, social network studies of animal cooperation

We identified 10 existing studies that utilise social network analysis with data from natural populations to uncover the mechanisms of cooperation. The first series of studies that

used social network analysis to investigate cooperation were conducted on guppies (Croft, Krause & James, 2004; Croft *et al.*, 2006, 2009; Brask *et al.*, 2019). In their initial study, Croft *et al.* (2004) confirmed that guppies have stable social structures with repeated pairwise associations among females, making way for cooperation through reciprocity. Guppies engage in predator-inspection behaviours where an individual will leave the group to obtain information about a predator, taking a risk to gauge the probability of future aggression (Dugatkin & Alfieri, 1991). This has been studied and characterised as a form of cooperation, as individuals often take part in inspection with a cooperative partner (Dugatkin & Wilson, 2000). In a follow-up study, Croft *et al.* (2006) again found evidence for a stable social structure with stable interactions among females. Individuals with stronger social connections were more likely to engage in predator inspection together. Furthermore, pairs of individuals that engaged in predator inspection more frequently, changed their relative position (leader, follower) more quickly, perhaps to combat the increased risk associated with the leading position to carry out inspection in a more cooperative manner (Croft *et al.*, 2006).

In a subsequent study, Croft *et al.* (2009) additionally quantified each individual's behavioural phenotype by assessing predator inspection and shoaling tendencies. They found positive assortment among individuals with similar behavioural phenotypes which they suggest is an “amplifier of selection” for cooperation in predator-inspection behaviour. Finally, in their most recent study, Brask *et al.* (2019) used a similar predator-inspection procedure to assess individual repeatability of cooperative behaviour in eight populations of guppies. After finding evidence for the existence of a “cooperative phenotype”, they used social network analysis to look at the social structure of two populations with varying levels of predation risk. They found that although both populations were not kin-structured, only the population under high predation risk (where cooperative behaviours may have higher fitness consequences) was socially assorted by cooperative phenotype. This final study highlights not only the utility of social network analysis for understanding how social structure is related to cooperation, but also how its use alongside data from natural populations can give us insights into how ecological factors may play a role in shaping social structure and/or the propensity of individuals to cooperate.

Studies that utilise social network analysis with data from natural populations to study cooperation have also been conducted with mammalian and avian species. In their study of aggression and grooming in three groups of capuchins, Crofoot *et al.* (2011) looked at responses to the playback of calls indicating that neighbouring groups were ‘intruding’ on their territory as well as creating association matrices of aggression, grooming, and proximity. In terms of social structure, they found that the aggression network was comprised of small clusters while the grooming network was one large group held together by an individual with high betweenness centrality. They also note that the number and strength of associations in the proximity network was related to the

structure of the grooming network but not the aggression network. In terms of the reciprocation of behaviours, individuals who received aggression more often were also more likely to initiate grooming of others. Finally, after analysing the networks in relation to the intrusion simulation responses, the authors argue that females who pay the lowest costs for living in the group (i.e. receive low aggression) are also most likely to participate in group defence. Although it is difficult to draw conclusions from this study about the mechanisms that allow cooperation among non-kin because genetic relatedness between individuals was not considered, this study highlights the range of measures and characteristics of social structure that can be extracted and the comparisons that can be made using social network analysis. Consideration of the ‘multi-layered’ nature of social interaction types within particular social settings and groups (Silk *et al.*, 2018; Finn *et al.*, 2019; Hasenjager, Silk & Fisher, 2021) can be useful for detailing which particular contexts of social associations may be related to cooperation.

Daura-Jorge *et al.* (2012) conducted a study with bottlenose dolphins (*Tursiops truncatus*) in the lagoon systems of southern Brazil who are said to cooperate with fishermen by driving schools of fish towards them and signalling when to throw their nets. This can be understood as a form of inter-specific pseudo-reciprocity (Simões-Lopes, Fabián & Menegheti, 1998). After classifying individuals as cooperative or non-cooperative and quantifying the association strength between them, the authors find that association values are higher among individuals of the same foraging tactic (cooperative or not). Clusters of individuals exist and the clustering coefficient for cooperative dolphins was significantly higher, suggesting that they are better connected with stronger relationships, which Daura-Jorge *et al.* (2012) suggest may promote the spread of this behaviour through social learning. Again, genetic relatedness was not accounted for in this study. Nevertheless, the authors do demonstrate that assortment by cooperation does exist in this population. The fact that individuals who cooperate with humans are also better connected to one another may point to a cooperative phenotype in this species.

Using a different approach, Madden, Nielsen & Clutton-Brock (2012) looked at the relationship between kinship and networks of social interaction (dominance interactions, grooming, foraging competition) in meerkats (*Suricata suricatta*). Although there was a correlation between kinship and dominance interaction networks, kin were not more likely to groom each other or to avoid competition for food. They claim that although meerkat social networks are highly kin-structured, cooperation is unlikely to be maintained by indirect fitness benefits alone. Their study emphasises the utility of social networks for understanding the effects of kinship *versus* other mechanisms on cooperative behaviours and the importance of considering other mechanisms facilitating cooperation among non-kin, even in populations that may be highly structured by kin.

In a study of male cooperation in long-tailed manakin (*Chiroxiphia linearis*) leks (areas where unrelated males carry

out communal breeding displays) with a slightly different focus, Edelman & McDonald (2014) demonstrate that individuals are more likely to cooperate if their partner is: close in space, an indirect connection ('friend of a friend'), or an individual that they had cooperated with before. Similarly, in an explicit attempt to quantify the indirect genetic effect of the social environment, Dakin & Ryder (2018) looked at cooperative (male–male) coalitions in a natural population of wire-tailed manakins (*Pipra filicauda*). This research found that individuals with high numbers of 'cooperative relationships' who engaged in frequent cooperation elicited similar behaviours in their partners, highlighting not only the importance of indirect effects through variation in social influence but also the further impact that assortment by cooperators can have on the spread of cooperation (through social contagion).

Most recently, Ripperger *et al.* (2019) captured female vampire bats (*Desmodus rotundus*) to form an artificial group in captivity. Individuals were fasted to induce food sharing and bouts of social grooming were recorded in order to quantify social bonds and levels of cooperative behaviour over the course of 22 months. When these bats were subsequently released into the wild, indicating a drastic change in their social and physical environments, they preferentially associated with one another and levels of cooperation in captivity predicted who they would roost with in the wild. However, some strong bonds were lost in the wild and the change in environment did lead to some changes in roosting associations. The authors argue that this highlights the fact that both partner choice and partner-fidelity feedback (see Section I.1) are vital to the maintenance of cooperation. Social network studies also provide the opportunity for gaining detailed insights into the relative strength of dyadic bonds, and thus partner choice and partner fidelity, exceeding the insight available from considering information at the individual level alone. For instance, by considering the social associations across the entire social network, a study on great tit (*Parus major*) pair-bonding was able to quantify the pre-breeding strength of future breeding partner bonds in relative terms, and determine individuals' propensity to associate with their partners more often than expected simply from individual differences in general sociability (Firth *et al.*, 2018). As such, through incorporating these analytical methods and considering the wider social network structure, studies on cooperation will be able to separate out variation in individuals' general propensities to associate with others from preferences for forming specific partnerships/relationships.

For cooperation to be maintained, the probability that an individual will receive some benefit (immediately or in the future) for cooperating in the present needs to be relatively high – the existing work suggests that this is more likely to occur in social networks with a stable social structure and assortment by cooperators (Croft *et al.*, 2015). Reciprocity is most likely to be facilitating the maintenance of cooperation when interactions are heterogenous and there are high levels of social clustering (van Doorn & Taborsky, 2011); indicated by low average node degree, a high clustering coefficient, and

high modularity in the network. The probability of there being edges between individuals with similar levels of cooperative behaviour can also be used to measure the degree of assortment by cooperation. It seems that we can use social network analysis not only to observe and describe different forms of cooperation but also to comment on the relevant contributions of different mechanisms.

III. FUTURE DIRECTIONS

(1) A social network approach and experimental manipulation

A particularly effective way of studying cooperation in natural populations is through experimental manipulation, because it can be used to establish causal (rather than correlational) relationships between the social environment and the phenomena being observed (in this case, cooperation). By imposing experimental manipulations on natural populations and comparing rates of cooperation and network metrics before and after the manipulation takes place, we can directly observe the impact of social networks on cooperation and *vice versa*. Due to advances in various technologies that allow for automated monitoring of large numbers of individually identifiable animals [Radio-Frequency Identification (RFID), Global Positioning Systems (GPS), deep learning algorithms, image analyses], manipulations can be imposed and the consequences tracked in natural populations in several different ways.

One approach is to manipulate who can interact with whom to see how this alters the social structure and what consequences this may have for cooperative behaviours. For example, Firth *et al.* (2015) programmed selective feeders, which detect visits from individually RFID-tagged great tits, so that they only delivered food to different halves of the population (those whose RFID tag codes ended with either odd or even digits). Individuals from pair bonds with incongruent RFID tags (one odd, one even) continued to forage together even though they could not feed in the same locations, presumably in order to maintain their social relationships. Furthermore, members of these pairs developed a potentially cooperative 'scrounging' technique: the individual who could not access the feeder directly was more likely to approach it immediately after their partner to retrieve food before the feeder was locked (which occurred within 2 s of the initial detection). The manipulation had implications for overall social structure, with individuals becoming more likely to interact with others of the same PIT tag type (greater assortment). Here, individuals were divided randomly and some breeding pairs happened to be separated. However, manipulations can be on the basis of factors like age, sex, breeding status, or species or on measured traits that have been previously related to rates of cooperation, such as familiarity or dominance (Fraser & Bugnyar, 2012; Grabowska-Zhang *et al.*, 2012). We can also manipulate how often individuals interact or the relative pay-off that individuals

get for cooperating and assess how this impacts social structure and population levels of cooperation (measured through observation or experimentally). Some suggestions for the use of a social network approach alongside experimental manipulations and observational data collected from natural populations are detailed in Table 2.

The suggestions in this section have been more focused on mechanisms of cooperation that occur through reciprocity (although many can be applied to cases of mutualism that do not include reciprocity). To our knowledge, there are no studies which explicitly consider the relationship between social structure and mutualism (without reciprocity) in natural populations. However, Daura-Jorge *et al.*'s (2012) study on dolphin–fisherman cooperation may give us some insights. It is possible that repeated interactions among individuals with strong social bonds are necessary for the spread and possibly the emergence of mutualism through the facilitation of social learning; an individual must first observe that another individual is performing a behaviour that they can also benefit from before they can engage in any form of mutualism. It may also be possible that in cases of inter-specific mutualism, initial

mutualism may allow for the development of more complex social structures which make way for further benefits and future cooperation. For example, Kasson *et al.* (2016) argue that the initial mutualistic relationship between a clade of ambrosia beetles (*Ambrosiophilus*) and a wood-decaying fungus (*Flavodon ambrosius*) allowed for the evolution of a more complex social structure than is found in other ambrosia beetles, with an extensive overlap of generations and large communal colonies.

In their study of mixed-species flocks, Farine & Milburn (2013) suggest that individuals who join these flocks may start to forage in areas that are not necessarily their most preferred niches in order to benefit from the reduction in predation risks that comes with group foraging, which itself increases the likelihood of interspecific interaction. They argue that flocks are mutualistic, as membership in the flock comes with mutual benefit for all individuals. Further investigation through the observation and manipulation of the social structures of various interspecific groups could help us to gain a better understanding of how mutualism spreads or is maintained and how it shapes various other social processes (Ross & Fletcher, 1985).

Table 2. Examples of ways that a social network approach can be combined with experimental manipulations or observational data to understand questions related to the emergence, development and maintenance of cooperation

Examples of using experimental manipulations on natural populations in combination with a social network approach	
Manipulating which individuals can interact	<ul style="list-style-type: none"> • Can familiarity (increased rates of interaction) alone initiate or lead to increases in cooperation? • How long do individuals need to interact before they are familiar or cooperating? How does this vary with various characteristics of the focal individual?
Manipulating how often individuals can interact	<ul style="list-style-type: none"> • How often do individuals need to interact in order to become cooperative partners? • Do individuals who can no longer interact often, stop cooperating? How does this vary with various characteristics of the focal individual?
Manipulating the relative pay-off individuals receive for cooperating	<ul style="list-style-type: none"> • If one individual (x) from a pair is consistently rewarded for a cooperative behaviour but the other individual (y) is not, for how long will y continue cooperating with x? Is this mediated by the relationship between x and y and/or by their relative social positions? • Are unequal rewards in cooperative endeavours enough to break social ties? If cooperation is maintained through reciprocity, how equal does this reciprocation need to be for cooperative relationships to persist?
Examples of using observational data from natural populations in combination with a social network approach	
Creating multiple networks on the basis of different cooperative behaviours over time	<ul style="list-style-type: none"> • Does reciprocity occur across domains? • What is the timescale for the reciprocation of cooperative acts in different species? • Are individuals consistent in their cooperativeness? If an individual is highly cooperative in one domain, do they exhibit similarly high levels of cooperation in other domains? Is there a trade-off between being highly cooperative in some contexts/relationships and not others?
Identifying the consequences of network positions	<ul style="list-style-type: none"> • Are individuals in different network positions influenced in different ways by experiences of cooperation <i>versus</i> defection (and consequently react in different ways)? Does this interact with the characteristics of the individual? • Can the reciprocation for a cooperative act in one domain be the facilitation of movement to or maintenance of a more advantageous network position? In other words, do individuals who cooperate receive benefits in the social domain? • Are individuals who seem to be at a 'loss' for cooperating actually occupying more beneficial network positions as a result of their cooperative behaviour?
Testing wild-caught individuals on a cooperative task	<ul style="list-style-type: none"> • How are individuals distributed within the network in terms of their level of cooperativeness? • Is there assortment by cooperativeness? • How does the occupation of particular network positions by highly cooperative/uncooperative individuals influence population-level cooperation?

Table 3. The six advantages of long-term, individual-based studies (Clutton-Brock & Sheldon, 2010), with regard to cooperation and social structure

	General benefit	Relation to cooperation/social structure: possible questions
Analysis of age structure	“Documenting age-related changes in life history parameters” to “identify and assess age effects” on “behaviour, reproductive performance, and survival” which allows for the exploration of “ecological and evolutionary processes” while controlling for these effects (p. 563)	How does age structure impact cooperation at the population level? Does age have an impact on the likelihood of individuals adopting novel cooperative behaviours? Do certain age structures make certain social structures more likely?
Linkage between life-history stages	Can “connect events at one stage of the life history to those at another” which allows for “insights into the cause of variation in growth, breeding success, and survival” (p. 563)	How does cooperative propensity change over the lifetime? Is there a crucial period in development which determines cooperative propensity? Does occupying certain network positions early in life influence future position and overall fitness?
Quantification of social structure	To “document the kinship structure of populations and to assess the effects of social relationships on survival and breeding success” (p. 563)	Which social structures are conducive to cooperation? How does cooperation impact social structure? Is assortment by cooperators necessary for the maintenance of cooperation? Can an individual’s ties to cooperators be used to estimate their own levels of cooperation? Do manipulations to monitored social structure carry over to shape cooperation?
Derivation of lifetime fitness measures	To “measure the extent to which breeding success differs between individuals and their offspring and to assess the causes of these differences” (p. 563)	Does cooperation have net fitness benefits? Do individuals that occupy certain network positions have higher fitness?
Replication of estimates of selection	“Provide[s] opportunities for repeated measurement of the strength and direction of selection” for “exploring the effects of demographic factors such as population density or environmental variation on selection” (p. 563–564)	Does cooperative propensity covary with other traits? Do certain demographic factors or environmental conditions make the spread of cooperation more/less likely?
Linkage between generations	Can study “quantitative genetics of phenotypic traits in wild populations” (p. 563)	To what extent is cooperative propensity heritable and/or a plastic response? To what extent does social structure carry over between generations, and what are the implications for cooperation?

Currently, few studies explicitly examine mutualism within species, highlighting the need for further examination of mutually beneficial behaviours occurring among individuals in natural populations. As discussed by Farine, Garroway & Sheldon (2012) social network analysis allows for an investigation of the relationships among social interactions, social structure, and the immediate benefits that individuals obtain through various forms of mutualism to explain the relationship between mutualism and social structure (and *vice versa*). These methods can be adjusted to the circumstances and the combination of species and systems that are being studied.

(2) The utility of long-term data from natural populations

Throughout this review we emphasised the utility of social network analysis for understanding cooperation; this is also

driven by the fact that social network analysis can be used with data from natural populations which can provide us with more ecologically relevant results. In the wild, individuals are frequently able to choose their social partners (Dakin & Ryder, 2018), but these interactions and choices take place within the context of the environment they experience. This is especially important when considering how the prevalence of cooperation may impact social structure itself. Furthermore, cooperation is shaped not only by evolution but also by ecology. It is more likely that we can tease out these ecological effects when working with natural populations because it is possible, to some extent, to quantify their real social environment and the physical environment that they are in (He, Maldonado-Chaparro & Farine, 2019). By testing populations of the same species in different locations, for example, we can tease apart the variation in cooperative behaviour that is being driven by social *versus* non-social factors (Bergmüller *et al.*, 2010).

As discussed by Clutton-Brock (2002), although there may be some similarities between various cooperative populations (of the same, or different species), there are also meaningful qualitative and quantitative differences in how cooperation is maintained. Working with natural populations gives us the opportunity to identify these differences and how they may be related to social structure. Using natural populations also potentially allows for the experimental manipulation of certain factors (social or non-social) that may be related to cooperative behaviour. Finally, social network analysis can also be used in concert with detailed monitoring of individuals, for example physical measures, hormone and stress levels or with genetic analysis, simultaneously to investigate the biological basis of differences in cooperative propensity and social network structure (Samuni *et al.*, 2018). All of the advantages of using social network analysis become amplified when using natural populations over long periods of time (Clutton-Brock & Sheldon, 2010; see Table 3).

(3) A reciprocal relationship: the study of cooperation and the study of networks

Studying cooperation can also give us insights into social network structures and positions themselves. Varying levels or forms of cooperation may be associated with different social structures (Apicella *et al.*, 2012). As Voelkl & Kasper (2009) reveal with their simulations on real graphs, although some social network structures are more likely to promote the fixation of cooperative behaviour (when compared to a random, well-mixed group), others do not. Even among those groups with conducive social networks there was still a considerable amount of variation in social structure and the level of cooperation. Fehel *et al.* (2011) suggest that the co-evolution of social structure and cooperation-enhancing behaviours (i.e. breaking ties with defectors) allowed for assortment and consequently, the evolution of cooperation. Looking at the co-variation of real and/or simulated cooperation with social structure in natural populations may provide insights into how cooperation and social structure are correlated and why various animal societies are structured differently to one another.

At a more individual level, studying cooperation in relation to social network structure can help us to explain how and why the occupation of certain positions in different types of social structures by certain types of individuals might make way for or hinder the spread of cooperation (Hauser *et al.*, 2019). Studies of human social networks have already investigated how the occupation of certain positions impacts behaviour and the dynamics of social interaction in gangs (Papachristos, 2006) and businesses (Venkataramani *et al.*, 2016). For example, if individuals in highly influential network positions, such as those with many connections to many well-connected others (i.e. high eigenvector centrality), are frequent, or infrequent cooperators, what consequences does this have for the spread of cooperation in that population? Finally, different social network positions can also be associated with varying rates of survival, contracting diseases, and reproductive success (Lehmann, Majolo & McFarland, 2016;

Page *et al.*, 2017; Balasubramaniam *et al.*, 2019); do cooperation and social structure evolve together to allow more cooperative individuals to benefit from more advantageous network positions (Kern & Radford, 2018)? It seems that cooperation and social network structure have a reciprocal relationship in so far as understanding one of the two phenomena more thoroughly can enhance our understanding of the other and *vice versa*.

IV. CONCLUSIONS

- (1) It is now widely accepted that cooperation exists due to the direct and indirect fitness benefits that individuals can receive for cooperating with others. However, there are still major gaps in our understanding of how cooperation is manifested in different natural populations.
- (2) Using a social network approach can help to further understanding of the emergence, spread, and maintenance of cooperation. It appears that it is more likely that cooperation will spread when individuals are assorted by cooperative propensity in social and/or physical space (Croft *et al.*, 2015). Therefore, investigating the characteristics of social networks, which account for the interactions and relationships among individuals, is crucial to uncovering the mechanisms of cooperation.
- (3) Advances in various technologies that allow for large-scale tracking of natural populations allow for the observation and description of cooperative behaviours through a network approach. The impact of social and/or physical manipulations to the environment can also be explored, leading to a more detailed understanding of the ecological factors that impact cooperation.
- (4) Studying cooperation with a social network approach can also give us insights into how differing mechanisms or levels of cooperation may impact social structure, social dynamics, and other social processes.
- (5) The benefits of taking a social network approach to studying cooperation are amplified when working with wild, long-term populations. By quantifying real social environments, it is possible to untangle the evolutionary and ecological pressures that lead to differences in cooperation among different species or populations.

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