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Testing the sexual and social benefits of cooperation in animals

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Theoretical models show that sexual and social selection can stabilize cooperation. However, field tests of these mechanisms have been difficult to conduct and the results are mixed. We discuss the conceptual and practical difficulties associated with testing the role of social and sexual selection on cooperation and argue that there are alternative ways of examining these hypotheses. Specifically, approaches based on the classic theories of sexual selection and signalling and recent developments in the field of behavioural syndromes provide mechanisms to insure the reliability of cooperation. Additionally, methodological developments (social networks and micro-tracking) and long-term datasets allow measuring partner choice in a cooperation context and the resulting fitness benefits for both the co-operators and the individuals that associate with them.

**On the importance of testing the sexual and social benefits of cooperation**

Partner choice is a key aspect of evolutionary theory, and has provided convincing explanations for the evolution of puzzling traits, such as peacock tails, that bring no benefits to the survival of the bearers and even compromise it [1,2]. *Cooperation* (see Glossary) is usually presented as a puzzling trait, as it is costly to the bearer and hence individuals are expected to attempt to reap the benefits of cooperation while avoiding the costs [3]. Two main solutions to the evolutionary conundrum posed by cooperation are indirect fitness benefits, which are obtained by helping relatives [4], and direct benefits, when by cooperating individuals increase their chances of survival or reproducing [5]. For example, sentinel watching [6] or contributing to group augmentation [7] may simultaneously provide direct benefits to the actor and help the other group members. In addition, theoretical models have shown that sexual and social selection can make cooperation stable since co-operators are preferred over cheaters [8–10].
Hence, under some circumstances, individuals may rely on the action of others to obtain returns from their investment in cooperation [11]. The role of individual propensity to cooperate has been shown to play a role in social and sexual mate choice in humans [12] and there is recent evidence that cooperative investments influence partner choice also in non-human animals [5]. However, to which extent these mechanisms may influence the evolution and maintenance of cooperation in animals remains contentious.

Under social and sexual selection [13–16], co-operators gain fitness benefits as their actions increase their future chances of either receiving help or being preferentially chosen as a mate [5]. Consider for instance a cooperatively breeding group where helpers vary in their capacity to bring food to the nest, or to detect predators and warn their group mates. If helping provides honest information about these individuals’ qualities as sexual or social partners, those who help more should be more likely to be chosen [9]. Choice, in this case, is beneficial for the more cooperative individuals, who increase their chances of finding partners or being helped in the future [5,17] but, crucially, also for those who chose to associate with them, as they obtain better quality partners.

Here, we first briefly review the main factors that we feel have hindered the study of sexual and social selection in the field of cooperation. We argue that cooperative behaviour has been seen as an unreliable signal of future cooperative investment or individual quality and that the sexual and social benefits of cooperation have been considered as extremely hard to quantify or to disentangle from other factors. We then propose specific frameworks to address the problem of the reliability of helping, which are based on classical sexual selection and signalling theories, and more recent developments in the field of behavioural syndromes. Additionally, we argue that both long-term studies and recent methodological and technological developments provide robust data and new tools to test the predictions of social
and sexual selection hypotheses in a cooperation context under field conditions (these predictions are summarised in Fig. 1).

**Why have sexual and social selection been overlooked in studies of cooperation in animals?**

Four main reasons have made it difficult to conceptualise and test the role of sexual and social partner choice on cooperation in non-human animals. First, the initial formulation of the sexual selection hypothesis suggested that investing in cooperation was linked to individual quality and would thereby lead to increased ‘social prestige’ [14]. This has arguably led to some discredit among researchers working on animals, as ‘prestige’ can be seen as anthropocentric. However, while the notion of ‘prestige’ can be equivocal, the idea of cooperation as a signal is well supported in humans and some fish [18–20] and requires additional examination in non-human animals (see Box 1). Second, several authors have argued that it is unclear how information about an individual’s propensity to cooperate is obtained by others, since obtaining and using the information required was considered too cognitively demanding for most species (e.g. [21,22]). However, individuals can easily obtain information about other individuals’ investment in cooperatively tasks either through their direct interactions (e.g. [23,24]) or by eavesdropping [25] and cognitive abilities do not appear limiting [5,17,26]. For example, in a cleaner-client fish mutualism, clients avoided cleaners that they observed cheating [27] and cleaners behaved more cooperatively in the presence of an audience [20]. Third, if individuals are going to choose to associate with others based on the information they obtain from their behaviour, it is essential that the information obtained is reliable, i.e. that cheating is prevented, and that current and future cooperative behaviours are consistent or linked to the quality of those individuals as partners. If information about cooperative behaviour is detectable but not reliable it cannot be used in partner choice. Demonstrating the reliability of cooperative behaviour has been deemed a major obstacle for
testing hypotheses about the role of sexual or social selection on cooperation [22,28].

However, we disagree reliability represents an insurmountable problem and propose below three frameworks to test whether cooperative behaviours are reliable. Fourth, quantifying social choice and disentangling the different types of benefits and confounding factors associated with sociality and cooperation has been considered exceedingly difficult, particularly in kin groups which are formed primarily by delayed dispersal of young. However, below we suggest specific approaches exist to tackle these difficulties.

**Moving forward: solutions to the problem of the reliability of cooperation**

*Cooperation as a signal: condition-dependence and audience effects*

A crucial prediction of signalling theory [29], which has been overlooked in previous studies investigating the reliability of cooperation, is the link between condition and cooperation. Condition-dependence is one of the pillars of signalling and sexual selection theories, which considers that signals are reliable because they are costly, and costs reveal the concealed quality of an individual (e.g. quality as parents or their “good genes” [30,31]) because only good-quality individuals can invest in costly signals and remain viable afterwards [30,31]. The costs of helping are widely accepted because in order to cooperate individuals need to forgo other activities such as foraging or reproducing [32]. However the physiological or energetic costs of cooperating have only been demonstrated in a few species [33–35]. The recent developments of oxidative stress markers [36] and the understanding of telomere dynamics [37] allow to quantify physiological costs and offer meaningful ways of measuring the cost of helping in the context of animal sociality [34,35,38]. Recent technological developments that allow tracking individual body mass of small species [39] provide an additional way of quantifying short-term costs. Finally, formal tests of the condition-dependence hypothesis require experimental work to assess whether the cost of helping is less important for good quality individuals than bad quality ones (as done in the field of sexual selection[40–42]). While
studies conducted on cooperative species have shown that individual satiation or physiological condition [35] affect investment in cooperative behaviours (e.g.[24]), experimentally manipulating helping effort or condition are needed to compare how individuals in different body condition or physiological state are able to maintain their cooperative activity when challenged.

Another approach to further examine whether cooperation is a signal is to investigate audience effects, since displaying a signal is predicted to be positively affected by the presence and identity of receivers [20,27,43]. In humans, recent studies showed that men are more cooperative in the presence of women [44,45]. In animals, many studies investigated this prediction but the evidence is mixed. We review the several studies conducted on cooperatively breeding birds in Box 1. Most studies on birds found no audience effects on cooperative behaviour. However, most of these studies assumed that synchronicity at the nest was a good surrogate for an audience effect, but the complex dynamics of group movements may lead to synchronisation (or lack thereof) for other reasons besides signalling (e.g. predator avoidance or foraging). In fish, where most studies were either conducted in captivity or well-defined areas (where both observer and subjects had access to the same information), there is convincing evidence of audience effects (e.g. cleaner-client interactions [20] and cooperation as a honest signal of individual contribution in ‘pay-to-stay’ cichlids [46,47]). Thus additional tests of audience should be experimental rather than correlative or conducted under controlled, spatially confined conditions as in these fish examples.

Cooperation as a reliable feature because it is a repeatable behaviour

If cooperation is a repeatable behaviour and presents consistent differences among individuals and across contexts it can be seen as a “personality trait” [48,49], and thus can be used as a reliable cue by other individuals in partner choice. Research over the past ten years has shown that consistent inter-individual differences are widespread in animals and are stable because
they relate to physiological and life-history traits, forming a pace-of-life syndrome [48]. Animal “personalities” are predicted to have consequences for social evolution [9,50] and mate choice [51]. If individuals typically behave in similar ways in related situations (for example, by consistently being more aggressive and less cooperative), this is predicted to promote a consistent behavioural response from the other individuals in the group [52,53] (see also review in [5]). Thus, if cooperative investment is consistent among individuals, in spite of variation in context or conditions, cooperative individuals can be trusted and chosen as partners that will continue to cooperate in the future [8–10,52].

Several recent empirical studies have found intra-individual consistency (repeatability) in cooperative effort [54,55]. Cooperation can be expressed in many forms, including tending for the young, finding food, watching for predators or defending territories, and studies of mongooses and cichlid fishes have shown that some individuals invest more in specific tasks [56,57]. Hence, propensity to cooperate in certain way appears to be an individual characteristic and could be used in partner choice. More studies are needed to have a broader understanding of whether these results represent a general pattern for other cooperative vertebrates, but also to investigate longer term intra- and inter-individual variation in cooperative behaviours, as well correlations with other behavioural traits.

**Cooperation as a trait indicated through other reliable traits**

A more classical but poorly studied hypothesis to explain how cooperation can be used in partner choice is that cooperation itself is not a signal or a cue but is linked to other reliable traits, in the same way as future parental care can be signalled by ornaments or displays [58]. In humans, cooperativeness has been linked to morphological facial traits [59] and in microorganisms and ants there is good evidence for ‘green beards’ (i.e. phenotypic traits which can only be produced by particular genes, causing the bearers of these genes to recognise each other and cooperate [60]). Recently, one study found that levels of cooperation in barn
owl nestlings were related to pheomelanin-based plumage [61]. Some of the key regulators of melanogenesis are thought to have pleiotropic effects that link melanin-based colouration to phenotypic traits such as aggression, stress and immunity [62]. Hence, melanin-based traits are among those that could be explored as possible ‘badges of cooperation’.

Moving forward: new and overlooked tools to measure sexual and social benefits of cooperation

Social and sexual selection are predicted to favour the evolution and maintenance of cooperation (i) if cooperative individuals are preferentially chosen as social or sexual partners and (ii) if the individuals that choose to associate with co-operators have fitness benefits arising from that choice. In humans, more cooperative individuals are perceived as more attractive [18,19] and are also preferred as non-sexual partners [12,63]. In non-human animals, some studies suggested increased mating probability of helpers [64,65] or individuals that invest more in a communal good [66] and there is evidence for social mate choice based on cooperation in fish, rats, dogs [5] and primates [67] (but see [68]). However, the majority of these social preference tests were conducted in laboratory settings using artificial tasks under artificial social conditions, making the biological significance of the results sometimes difficult to interpret [28]. Below we discuss field tests that can represent promising avenues to study social benefits arising from cooperative investments.

The importance of long-term studies on free-ranging animals

Assessing the predictions of social and sexual selection for the evolution of cooperation (Fig. 1) requires robust measures of cooperative investments as well as mating success, reproductive output and survival of the same individuals, while accounting for relatedness. Additionally, these fitness indicators should be measured for both the co-operator and the individuals that chose to associate with them, which requires long-term data from wild populations. Long-term
studies provide the knowledge about the species’ social and kin structure, which behaviours are important and key fitness indicators such as lifetime reproductive success [69]. Additionally, long-term data are needed because the links between traits and fitness are often dependent on environmental variation and hence variable in time. For example, female preferences can vary from strong in some years to absent in others, and hence shorter-term studies could miss these patterns entirely (e.g. [70]). The long-term perspective is therefore important in order to measure the strength of these effects in relation to the long-term variation [71].

Technological innovations and social network analyses: new ways of measuring social associations in relation to cooperation in the wild

Recent developments in technologies – such as Radio Frequency Identification (RFID), GPS, or image recognition – are allowing unprecedented levels of animal tracking at both a micro- and macro-scale. These technologies combined with methodological advances like social network analyses [72] are starting to provide major insights into the social dynamics, collective movement and cultural transmission in wild animals [73,74]. Similar approaches can be applied to the study of cooperation to allow robust measures of cooperative investments in animals [75] and to study possible social benefits. For example, detailed tracking, either through combined GPS technology [74] or image analyses [76], can facilitate studying individual investment in cooperative behaviours which are complex and hard to follow in the wild, such as joint mobbing or territorial defence. Individuals marked with Passive Integrated Transponders (PIT-tags) also can be used in cooperation experiments, for instance by triggering devices that give other individuals access to food (or preferred food types, or other relevant resource), thereby simulating a cooperative action. A recent study on great tits Parus major used this technology to experimentally show that individuals are willing to reduce their own access to food in order to maintain their social relationships [77].
Simultaneously, social network analyses [72] provide a way of measuring whether cooperative investments influence how animals associate. Summarizing the social connections among both related and unrelated individuals in a succinct way provides a quantitative framework for analysing patterns of interactions and social assortment [78] in relation to cooperation. In systems where groups are formed mostly through delayed dispersal it may be difficult to determine whether or not there is social partner choice, but even in such systems, behaviours like coalition dispersal, communal roosting or food sharing can take place, which involve social partner choice. Under social selection, individuals that invest more in a cooperative task are predicted to benefit through more or better social connections and received reciprocation in a similar or different task (while controlling for relatedness and dominance; see Fig 1). A good example is the recent work in the dwarf mongoose *Helogale parvula*, a cooperative breeder that lives in extended family groups where individuals that contributed more to sentinel behaviour had a better position in the grooming network [17]. Other examples are provided by vampire bats *Desmodus rotundus*, where individuals have a network of related and unrelated individuals with whom they share food based on reciprocal exchanges (Carter & Wilkinson 2013, 2015; Carter et al 2017) or guppies *Poecilia reticulata* where cooperative predator inspection is more frequently conducted with social partners [79].

Social networks, however, are correlative and while it is possible that being more cooperative in some contexts leads to being more or better connected to other individuals in other contexts, it is also possible that more or better connections lead to increased cooperation. For example in humans, cooperation was favoured by the possibility of forming social networks with more cooperative individuals [80] and other studies have shown that the social environment influences the expression of cooperative tasks [81,82]. It is therefore essential to use experiments to manipulate the apparent level of cooperation and quantify subsequent network associations.
Quantifying the benefits of mating with more cooperative individuals

Under classical sexual selection theory, mating with more cooperative individuals is expected to provide direct fitness benefits if more cooperative individuals are better quality or more cooperative mates (e.g. that provide better parental care), or indirect fitness benefits if mating with more cooperative individuals yields better quality offspring or offspring that will inherit a higher propensity to cooperate.

Surprisingly, whether or not more cooperative individuals are better quality mates and produce offspring with higher fitness remains poorly known. One of the predictions of the sexual selection hypothesis is that more cooperative individuals should provide better parental care when they become breeders (Fig.1), and this translates into higher reproductive output and lifetime fitness for both the co-operator and their mates. Most existing long-term studies on cooperative breeders collect data that allow researchers to examine this hypothesis.

Whether more cooperative individuals produce offspring with higher propensity to cooperate can be estimated using quantitative genetic methods [83] that examine if the propensity to cooperate and preference for mating with more cooperative individuals are heritable, as well as whether there is a genetic correlation between the two. Heritability of cooperation has been shown in humans [84] and cooperatively breeding birds [85,86], but social and developmental factors seem equally important [87,88]. Again, many long-term studies have data allowing to investigate this. Another potentially interesting avenue will be making use of genomic tools to search for genetic regions associated with cooperation – using a candidate gene approach (e.g. [89]) or genome-wide association studies [90]. These approaches will allow to better estimate the potential indirect benefits obtained through mate choice.
Concluding remarks

Partner choice is a central aspect of evolutionary theory and can play an important role in stabilising cooperation, but the empirical tests conducted to date produced mixed results. We delineated here the predictions that arise if cooperation is under sexual or social selection and brought together theory and techniques from different fields in an attempt to address past difficulties that have hindered the testing of these predictions in the field. Specifically, we encourage different tests of the reliability of cooperative behaviours and urge researchers to conduct more studies on wild populations and to use new techniques as well as existing long-term data to obtain meaningful fitness indicators of cooperative investments (see Box 2). We also emphasise that understanding and quantifying the possible benefits obtained not only by co-operators, but also by the individuals that choose to associate with co-operators is crucial to examine these hypotheses. Finally, we argue that studies aiming to determine the benefits and costs of cooperation should ideally consider individual contributions to – and returns from – different cooperative behaviours in order to obtain a meaningful understanding of the importance of cooperation for lifetime fitness (see also outstanding questions).

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Fig 1. Key predictions that must be tested in order to determine whether cooperation can be under sexual or social selection. In black are the predictions that should be verified for both hypotheses, in green those referring to sexual selection, and in blue to social selection.
### Glossary

**Altruism**: extreme form of cooperation, when a behaviour is costly to the actor and beneficial to the recipient; cost and benefit here are defined as direct costs and benefits (hence excluding possible benefits arising from kin selection)

**Audience**: the individual(s) that intentionally or unintentionally witness an interaction between two or more individuals

**Cooperation**: a behaviour that provides a benefit to another individual. It may or not be beneficial to the actor, but has some sort of immediate or longer-term cost to the actor.

**Cooperative breeding**: When parental care is provided by a group of adults, which include the genetic parents and one or more adults.

**Cue**: a trait that provides information to a receiver but, unlike a signal, has not evolved to provide information (e.g. a mice walking over leaves makes a rustling sound that can be used by an owl to locate it, but has not evolved for that reason).

**Direct Benefits**: the component of fitness gained through behaviours that will lead to increased production of offspring. For example, choosing sexual or social mates that will provide enhanced access to resources (e.g. better parental care or predator vigilance).

**Eavesdropping**: the behaviour of intentionally observing an interaction between two individuals in order to obtain information about them.
Indirect fitness benefits: the component of fitness gained through genetic effects by either aiding the reproduction of related individuals or by transmitting ‘good’ genes to the offspring thereby increasing the fitness of the descendants.

Mutual benefit: a behaviour that is beneficial to both the actor and the recipient.

Personality: consistent, intra-individual behavioural difference across contexts and time.

Social selection: Selection arising from increased association success (in order to form groups, coalitions or long-term relationships). This may be due to the benefits obtained by associating with social partners that exhibit certain traits, or to competitive advantages of these individuals in access to resources.

Sexual selection: Selection arising from increased mating success due to preferential choice for sexual mates exhibiting certain traits or behaviours (intersexual selection), or competitive advantage of certain individuals that provides them access to more mates (intrasexual selection)

Signal: a trait that has evolved to transmit information and provides fitness benefits to the emitter

Social network: quantitative description of the patterns of associations or interactions (edges) among individuals (nodes)

BOX 1. SIGNALLING IN COOPERATIVELY BREEDING BIRDS

Although cooperative breeding in birds usually takes place in family groups, in ca. 45% of species unrelated individuals also help [64]. Among the hypotheses put forward to explain the possible benefits obtained by non-related helpers, two more contentious
ones propose that helpers use cooperation as a signal. Under the ‘Pay to Stay’ hypothesis individuals help to have access to the group’s communal resources [46], whereas under the ‘social prestige’ hypothesis helping is used to signal individual quality in a partner choice context [14].

Initial tests of helping as a signal looked for evidence of cheating, expecting false feeding to be a way of maximising benefits while reducing the costs of helping. Instead, false feeding appeared to be linked to nestling satiation (e.g. [91,92]). However, while signalling theory predicts that cheating can occur, it also predicts that signals need to be reliable in order to be used in partner choice. Therefore, it is the mechanisms ensuring the reliability of the signal that need to be examined. (see main text).

Other studies investigated the showiness of helping behaviour by looking for audience effects [93], mostly by investigating whether feeding events were synchronised with the arrival of the putative receivers of the signal, usually the breeders (e.g. [94,95]). However, these results are difficult to interpret because synchronisation may occur for other reasons, such as predator-avoidance [96] or group foraging strategies [97] and the identity of the putative receiver may differ depending on whether co-operators look for social or sexual benefits. Also synchronisation at the nest is probably not necessary to transmit information on helping. While sometimes individuals are spread out across large areas, any individuals wanting to obtain information about the behaviour of others may do so, both visually and acoustically, from a nearby location, but may not be seen by a human observer focusing on the nest. Additionally, the target of any ‘cooperative displays’ could be outside of the breeding group [98].

Finally, since the hypothesis of helping as a signal predicts competition for helping [14], studies have looked for aggressive interactions around helping, which were seldom observed [94,95]. However, in stable social groups, competition and conflicts are
expected to be resolved through dominance hierarchies and not by continuous costly aggression [99]. Under this view, instead of competing aggressively for helping, more dominants individuals would be predicted to help more than subordinates.

**Box 2 • On the importance of determining which mechanisms are involved**

Here we propose three approaches to solve the problem of the reliability of cooperation; cooperation may be a i) condition-dependent signal, ii) a cue (i.e. a personality trait), or iii) a behaviour signalled by other traits (‘badge of cooperation’; see text). From an evolutionary perspective determining the mechanism involved is important because while all three mechanisms predict that cooperative individuals have more chances to be chosen as a partner, the target of selection, and thus the effects of this choice on the evolution of cooperation, drastically differs. Under the signalling hypothesis, individuals cooperate in part to transmit information about their quality and the evolution of cooperative behaviours is directly influenced by sexual or social selection. By contrast, if cooperation is signalled through other specific morphological traits such as colour, individuals do not cooperate to be chosen as a partner and the target of sexual or social selection will not be the cooperative investment but the signal associated with it. Finally, if cooperation is part of a behavioural syndrome, it is a personality trait (cue), and it is the whole behavioural syndrome that would be selected and not simply the tendency to cooperate.
WHAT IS PREDICTED IF COOPERATION IS A TRAIT UNDER SEXUAL AND/OR SOCIAL SELECTION?

Cooperation must be variable, seen and trusted, i.e. **reliable**. Three possible mechanisms:

- 1. Cooperation is a signal: condition dependence and audience effects
- 2. Cooperation is a cue: part of a behavioural syndrome or a ‘personality trait’
- 3. Cooperation is a trait indicated through other reliable traits (e.g. colouration or morphology)

Direct benefits of cooperating (arising through partner choice):

- Increased probability of being chosen
  - as a breeding partner
  - as a social partner

Benefits of choosing to **mate** or to **associate** with cooperative individuals

- Increased fitness for
  - the choosing individual (obtaining a more cooperative partner)
  - for the offspring (better parental care and/or inheriting greater propensity to cooperate)

Cooperation must bring benefits to the co-operators and those choosing to associate with them