Choosing friends in an uncertain world: information reduces relationship stability in a Bayesian learning model of cooperative partnership

Rebecca F. B. Padget^{*1, 2}, Tim W. Fawcett^{1, *}, Delphine De Moor^{1, *}, and Safi K. Darden $1, *$

¹ Centre for Research in Animal Behaviour, University of Exeter ²School of Biological Sciences, University of Bristol * Joint Senior Authors

^{*}corresponding author: rebecca.padget@bristol.ac.uk

Abstract

Social animals often form differentiated social relationships with conspecifics. Developing closer partnerships with some than others can facilitate cooperative interactions in which individuals share resources or risk. When choosing a partner, individuals face a decision: a known partner might be sub-optimal if better options are available, but switching partners can be risky if others' behaviour is uncertain. This decision likely depends on how much information individuals have about the behaviour of others in the group compared to their current partner. To investigate the effect of information on cooperative partnership, we developed a Bayesian learning model to identify when individuals should switch partner given the cooperativeness of their partner and knowledge of the population. We then extended this to simulate a population of individuals interacting and switching partners, according to the Bayesian learning model. We found that when individuals had some information about the population, they switched more often than when they did not but that once individuals had a non-zero amount of information, there was little effect of increasing information further. This suggests that populations in which individuals have (or can store) no information about others might have more stable partnerships than populations in which individuals have knowledge of others' behaviour. Our model therefore demonstrates that individuals having more information can lead to social instability that might negatively effect the maintenance of cooperation through reciprocity.

Keywords: cooperation – friendship – information – Bayesian learning – bet-hedging – social evolution

Introduction

An animal's social interactions can have important fitness consequences, particularly for animals that live in groups [\(Westneat 2012\)](#page-24-0). Animals can provide benefits to each other, for example by coordinating anti-predator behaviour [\(Seghers 1973\)](#page-23-0), sharing food [\(Carter & Wilkinson 2013\)](#page-19-0), or grooming each other [\(Cooper & Bernstein 2000\)](#page-20-0), but they can also harm each other through competition for mates [\(Andersson 1994\)](#page-19-1) or other resources [\(Birch 1957\)](#page-19-2). An individual might

therefore choose to associate with certain individuals – those who provide benefits – over others – those with whom they compete more intensely [\(Schino & Aureli 2017\)](#page-23-1).

If interactions are particularly beneficial, individuals might choose to associate with a particular partner repeatedly and behave in ways that benefit their partner in order to facilitate similarly beneficial interactions in the future. As such, 'bonds' (relationships) can form between pairs of individuals who have repeated mutually beneficial interactions (e.g. [Kings et al. 2023\)](#page-22-0). This is likely to be facilitated by kinship, but strong social relationships are not exclusive to kin [\(De Moor et al. 2020\)](#page-20-1). Relationships might strengthen over time such that individuals begin to invest in each other, incurring small temporary costs for the sake of the long-term beneficial relationship, for example by sharing food or other resources [\(Carter & Wilkinson 2013,](#page-19-0) [De Waal](#page-20-2) [1989\)](#page-20-2). We might refer to individuals who mutually invest in frequent affiliative interactions as being strongly bonded or in a 'partnership'.

Partnerships are likely to provide significant fitness benefits because individuals can use their partner to, for example, gain access to resources [\(Carter & Wilkinson 2015\)](#page-19-3), or to help defend against antagonistic interactions from others, such as aggressive conspecifics or even predators [\(Gilby et al. 2013,](#page-21-0) [Silk et al. 2009,](#page-23-2) [Croft et al. 2005\)](#page-20-3). Some partnerships can even extend to offspring care, directly facilitating increased reproductive output [\(Nguyen et al. 2009\)](#page-22-1). However, social interactions – even cooperative ones – can be costly. For example, sharing food with a partner decreases the amount of food available to the sharer, and helping to defend against threats comes with a risk of injury or even death [\(Dugatkin 1992\)](#page-21-1). The act of maintaining a partnership also comes with its own costs: for example, there could be cognitive costs to choosing specific interaction partners [\(Martin & Cushman 2015\)](#page-22-2), or opportunity costs if individuals choose (or are forced; [Schneider & Krueger 2012\)](#page-23-3) not to interact with individuals that are not their partner if their partner is not available [\(Hamilton & Taborsky 2005\)](#page-21-2). These additional costs differentiate partnerships from casual social interactions. If partnerships are costly, this suggests that there are also additional benefits that can be gained from having close affiliative associations with some but not other individuals [\(Bapna et al. 2017\)](#page-19-4).

Maintaining a partnership with any individual could (in theory) provide mutually beneficial

outcomes, but strong partnerships might differ from casual relationships in the magnitude of those benefits. Partnerships might develop between particular individuals because they have compatible behavioural phenotypes [\(Riehl & Strong 2018\)](#page-23-4), and this could be particularly important when a task requires (even rudimentary) division of labour. For example, some cooperative hunting behaviour requires close coordination of different behavioural phenotypes [\(Gazda et al.](#page-21-3) [2005\)](#page-21-3). Alternatively, animals might prefer to form partnerships with high-quality individuals [\(Bebbington & Groothuis 2023\)](#page-19-5). The traits of a high-quality individual will differ across taxa, and depend on the cooperative tasks that they perform. A high-quality individual could, for example, be one that is particularly cooperative (e.g. [Brask et al. 2019\)](#page-19-6) or well-informed (e.g. [Brent et al. 2015\)](#page-19-7). These high-quality individuals are likely to be in high demand by others in the group, meaning that relationships with these individuals might be particularly costly (because there is now competition with others, analogous with mate choice; [Fawcett & Johnstone 2003\)](#page-21-4), but could produce greater rewards.

Depending on the particular types of tasks that partners cooperate on, being able to reliably predict – or 'trust' – partner behaviour could lead to individuals choosing a strategy that results in the best outcome for both individuals (e.g. both cooperate) over an uncheatable strategy (e.g. defect), resulting in greater benefit to both partners over repeated interactions [\(Dijkstra &](#page-20-4) [van Assen 2017,](#page-20-4) [Cohen et al. 2001,](#page-20-5) [Milinski et al. 1990,](#page-22-3) [Crawford & Haller 1990\)](#page-20-6). For example, sticklebacks (*Gasterosteus aculeatus*) learn to trust a simulated cooperator during predator inspection [\(Milinski et al. 1990\)](#page-22-3), and zebra finches (*Taeniopygia guttata*) cooperate in an experimental iterated prisoner's dilemma but only when playing the game with a long-term partner [\(St-Pierre et al. 2009\)](#page-23-5). The ability to predict a partner's behaviour can also improve over time as individuals interact with and learn about their partner (e.g. [Milinski et al. 1990\)](#page-22-3). Learning how a partner is likely to behave could lead to greater coordination and efficiency in performing cooperative tasks [\(Riehl & Strong 2018\)](#page-23-4).

While a potential new partner might be better quality than a current partner, the outcome of an interaction with a current partner is usually more predictable. This is because individuals are likely to have less information about the others in the population than they do about their

current partner because this relies on memory of more distant past interactions and broad social sampling, which might not always be feasible [\(Rieucau & Giraldeau 2011\)](#page-23-6). There is therefore likely to be a trade-off between reliable knowledge of a current partner and uncertain knowledge of a potentially better future partner. Depending on the relative importance of predictability and quality in a partner, the information that an individual has about a current compared to a new partner will affect the decision to switch or not and thus partnership stability. If having a *predictable* partner is the primary factor for the fitness outcome of cooperation, then an individual might be better off if they maintain a stable relationship with a partner that they know better than they know others in the population. If having a *high-quality* partner is more important for the fitness outcome of cooperation, then an individual might benefit from wide sampling of the population to find the most high-quality individual to partner with, and thus less stable social relationships.

To make decisions based on the information from their current partner and what they know of the population, animals might use cognitive processes that produce outcomes similar to Bayesian updating, allowing them to integrate information about the current partner with information about the wider population [\(Trimmer et al. 2011,](#page-24-1) [McNamara et al. 2006,](#page-22-4) [Valone 2006,](#page-24-2) [Luttbeg](#page-22-5) [1996\)](#page-22-5). In Bayesian updating, an expectation (a prior) about how different individuals will behave is updated in the light of new experiences (e.g. new observations of their behaviour; [Collins et al. 2006,](#page-20-7) [McNamara et al. 2006,](#page-22-4) [Uehara et al. 2005\)](#page-24-3). We can refer to the updating of expectations through experience as learning. Interacting with a current partner allows an individual to learn about that partner's behaviour. Interacting with different partners – social sampling – allows an individual to learn about the population and how others behave. The information that individuals have about a current partner compared to the rest of the population is likely under some conditions to be important in deciding whether to switch or stay with the current partner. The ability to learn about partners has been investigated in the context of mate choice [\(Cayuela et al. 2017,](#page-19-8) [Collins et al. 2006,](#page-20-7) [Luttbeg 1996\)](#page-22-5), and demonstrated empirically in a cooperative context in sticklebacks [\(Milinski et al. 1990\)](#page-22-3). However, its role in social relationships outside of mating is less well understood theoretically.

We wanted to investigate how different levels of information about the population might affect partner-switching decisions in a population of cooperating individuals. Specifically, we wanted to identify whether having information about the population caused more or less partner switching. We developed a model in two parts to investigate how an individual should behave and then allow individuals to interact in a population following these rules.

The model

We developed a model in two parts: firstly we used a mathematical model to identify when an individual should switch partners given its current partner's probability of cooperating; we then used an agent-based simulation model to investigate emergent behaviour of a population of individuals that could switch partners. We allow individuals to learn about the cooperativeness of their partner and the population to identify how information affects partner switching and the emergent behaviour of a population.

Part 1: Individual behaviour

We imagine a scenario in which individuals in a population can form dyadic partnerships to undertake a 2-player cooperative task during which each player can either cooperate or not cooperate (meaning they 'defect' against the other player). Individuals receive different payoffs for completing the task dependent on whether one, both, or neither of the pair cooperated. The highest payoff is achieved when at least one individual in the pair cooperates. To draw our main conclusions, we report results from individuals playing a snowdrift game; payoffs are given in [Table 1.](#page-6-0) Individuals can switch to a new partner, about whom they have less information than they do about their current partner. The payoff to an individual with its current partner is given by:

$$
W_c = p_c(p_f R + (1 - p_f)T) + (1 - p_c)(p_f S + (1 - p_f)P)
$$
\n(1)

Table 1: **Payoff table for a snowdrift game.** Payoffs are those given to a focal individual (row player). In the snowdrift game, which we used to draw our main conclusions, $T > R > S > P$. Arrows indicate the highest (\uparrow) and the lowest (\downarrow) payoff; the numbers are the parameter values used in our model.

and the payoff to an individual with a new partner is given by:

$$
W_n = p_n(p_f R + (1 - p_f)T) + (1 - p_n)(p_f S + (1 - p_f)P),
$$
\n(2)

where: p_f , p_c and p_n are the probabilities of the focal, its current partner, and a new partner cooperating, respectively; and T, P, S and R are payoffs to a defector whose partner cooperates, a defector whose partner defects, a cooperator whose partner defects, and a cooperator whose partner cooperates [\(Table 2\)](#page-9-0). The payoff to an individual in their next timestep therefore depends on the probability with which they switch partners and the payoffs from staying and switching:

$$
W = p_s W_n + (1 - p_s) W_c \tag{3}
$$

where p_s is the probability that the individual switches partners.

Bayesian updating

To allow an individual to have and update its expectations about the behaviour of others based on the information that it has gathered from observing partners, we can make the assumption that an individual's expectations about the probabilities of their current or potential future partner cooperating are drawn from Beta distributions. An individual's beliefs about the probability that its current partner cooperates in the next time step can be given by:

$$
p_{c(\text{expected})} \sim B(\alpha + C_c, \beta + (I_c - C_c)),\tag{4}
$$

where C_c is the number of observations of cooperation ($C_c = p_c I_c$) and I_c is the total number of trials (or 'iterations') with the current partner. α and β are the priors. An individual's beliefs about a new partner can be given by:

$$
p_{n(\text{expected})} \sim B(\alpha + MC_p, \beta + M(I_p - C_p)),\tag{5}
$$

where C_p is the number of observations of cooperation in the population $(C_p = p_n I_p)$, I_p is the number of trials in total (i.e. with all past partners). M is a scaling factor, changing the uncertainty around an individual's population expectation. M represents how much information an individual has about the population relative to their current partner (where a value of 1 means that they have the same amount of information about both and a value of 0 means that they have no information about the population). Including this term as a free parameter allows us to make the assumption that information about past partners is less salient than information about a current partner without making any assumptions about the process of information storage or loss. These distributions represent an individual's beliefs about the probability of experiencing cooperation with either their current partner, based on prior beliefs and previous experience with that partner, or with a new partner, based on prior beliefs and previous experience in the population.

The probability p_b with which an individual believes it will experience a better payoff in the next iteration by switching partner is found by taking the difference between the expected payoff from a potential future partner and that of the current partner, and calculating the probability that a value drawn from this difference distribution is above 0:

$$
p_b = E\Big((W_n - W_c) > 0\Big). \tag{6}
$$

This represents the probability that a potential future partner is more likely to provide a higher payoff in the next iteration.

Individuals use past experience to inform their expectation of a partner, and approach a new

partner with priors based on their past experience of the population:

$$
\alpha_{\text{(updated)}} = \alpha + MC_p \tag{7}
$$

$$
\beta_{\text{(updated)}} = \beta + M(I_p - C_p) \tag{8}
$$

$$
p_{c(\text{expected})} \sim B(\alpha_{(\text{updated})} + C_c, \beta_{(\text{updated})} + (I_c - C_c)).
$$
\n(9)

We show how the probability of being better off switching (p_b) changes over time (number of iterations, I_c) as an individual interacts with and learns about a partner. Whether an individual should stay with its current partner depends on the cooperativeness of the population and in order to illustrate we show how the switching decision changes when the cooperativeness of the population is fixed at a particular value compared to when it is relative to the cooperativeness of the current partner. Manipulating cooperativeness of the population as a free parameter in this way can illustrate what an individual's best action should be given that it has some accurate (albeit uncertain) information about both its partner and the population. However, this approach cannot tell us how a population of individuals behave when following these rules.

Part 2: Emergent behaviour

Because the behaviour of a focal individual depends on the behaviour of its partner, which in turn responds to the focal's behaviour (and so on), we developed a simple agent-based simulation of the system to make predictions about how having information might affect a population of individuals who switch partners according to the above model. In this simulation, each individual had a 'true' probability that it cooperated (p_f) , and could learn the cooperativeness of its current partner (p_c) and the distribution of cooperativeness in the population (p_n) . Individuals then could decide to switch (or not) to a new partner, and were awarded a payoff in each iteration depending on whether one, both or neither partner cooperated (as in [Table 1\)](#page-6-0).

	Parameter Description
p_s	Probability of focal individual switching partner
p_f	Probability of focal individual cooperating
p_c	Probability of current partner cooperating
p_n	Probability of new (future) partner cooperating
p_b	Probability that a future partner is more likely to cooperate than
	the current
T	Payoff to focal individual when it does not cooperate but a partner
	does
\boldsymbol{R}	Payoff to focal individual when it does cooperate and a partner
	also cooperates
\overline{P}	Payoff to focal individual when it does not cooperate and a partner
	also does not cooperate
S	Payoff to focal individual when it does cooperate but a partner
	does not
α	Prior expectation of number of cooperation events
β	Prior expectation of number of defection events
α updated	Posterior expectation (updated prior) of number of cooperation
	events
β updated	Posterior expectation (updated prior) of number of defection
	events

Table 2: **Table of terms and their meanings.**

In each timestep, an individual observed the behaviour of its current partner (or a new one if it had just switched) and updated its beliefs about that partner and the population (p_c and p_n , starting with a uniform prior for both in the first timestep) according to [Equation 4](#page-6-1) and [Equation 5.](#page-7-0) The probability that the individual switched to a new partner was given by the probability that a future partner would be more likely to cooperate $(p_b;$ [Equation 6\)](#page-7-1). Payoffs were determined after an individual had decided whether to switch or not. There was no explicit cost to switching, but if an individual was without a partner (because it chose to switch but no others were available) then it received a payoff equal to the sucker's payoff, $S = 0.4$.

In natural scenarios, it is likely that individuals can adjust their own behaviour in response to different interaction outcomes. For example, Trinidadian guppies can adjust their behaviour based on whether they were cooperated with in a previous interaction [\(Edenbrow et al. 2017\)](#page-21-5). We therefore ran a version of the model in which individuals could adjust their cooperativeness in the future if they experienced a poor payoff from an interaction with a current partner. If

an individual's payoff was below a threshold ($\sim U(0,1)$, such that the probabiliy is inversely proportional to the payoff), it either increased or decreased its cooperativeness by adding a random small number to it ($\sim N(0, 0.1)$). Cooperativeness was bounded at zero and one such that if the adjustment resulted in a cooperativeness less than zero or greater than one, a new error value was chosen; this process repeated either until a value within the range was found, or 100 times after which if the new cooperativeness value was above one, it was assigned as one and if it was below zero, it was assigned as zero.

For both versions of the model, we varied the population information parameter, $0 \leq M < 1$, to represent individuals being more or less informed about the population (a higher value means individuals are better informed). We ran the model for 10,000 timesteps with ten individuals for twenty independent runs for each value of population information. Results shown are the population-level means taken from the final timestep of each run.

Results

Part 1: Individual behaviour

When an individual has no information about itself or the other players (i.e. in the *ex ante* stage of the game), switching and not switching are equally profitable. However, once an individual has had an opportunity to interact with a partner, they have some information about how cooperative that partner will be in future iterations. Similarly, assuming that their partner is somewhat representative of the population (as individuals do in this model), they now have some, albeit less certain, information about the cooperativeness of the population. Once an individual has some idea about the probability of their current partner (and a potential future partner) cooperating, the probability that they will get a higher payoff in the next iteration from switching than from not switching depends on these values (in the *interim* stage of the game; [Figure 1\)](#page-11-0). While an individual is still with its first partner, the means of both probability distributions (cooperation by current and future partner) are the same. This means that after 0 iterations (before animals start interacting), the probability that an individual will gain a higher payoff in the next iteration

if they switch partners is 0.5. As an individual gathers experience of its current partner (without switching), the probability of switching becomes inversely proportional to the probability that their current partner cooperates when individuals have no population information ($M = 0$). The more population information individuals have, the slower they learn about their current partner [\(Figure 1\)](#page-11-0). This means that it requires more iterations to stop being effectively indifferent to switching partners when individuals have more information.

Figure 1: **Individual behaviour: Partner switching landscape for** *fixed* **values of population cooperativeness.** How an individual's beliefs about the probability of being better off switching (p_b) change with the number of trials with that partner (I_c) and the probability of the partner cooperating (p_c) under three different conditions for population information (none, $M = 0$; weak, $M = 0.5$ and strong, $M = 1$; columns left to right) and for population mean cooperativeness $(E(p_n) = 0.25; E(p_n) = 0.5; E(p_n) = 0.75$; rows top to bottom). Focal cooperativeness is 0.5. Increasing population information increases the number of trials with the current partner needed to increase or decrease the probability of switching – in other words, the more information an individual has about the population, the more information it requires about its current partner to know if it is better off switching or not.

When we investigate how an individual should behave when faced with a partner who is more or less cooperative than the rest of the population, we find that, as expected, when an individual's partner is more cooperative than the population, it should switch less, and when an individual's partner is less cooperative than the population, it should switch more. This effect appears to be asymmetrical such that individuals are more likely to choose to switch from a less cooperative partner than they are to choose to stay with a more cooperative one [\(Figure 2\)](#page-13-0).

Part 1 of the model shows the probability with which individuals should switch partners to maximise their short-term payoff in any given timestep after I_c timesteps with the same partner. To understand how a population of individuals should behave when all following this switching rule, we ran a simple simulation.

Part 2: Emergent behaviour

When we simulated a population of individuals interacting and switching according to the probability determined by our mathematical model, we found that when individuals had information about the population $(M > 0)$, they generally switched partners more [\(Figure 3\)](#page-14-0). Most of the variation in partner switching appears to be explained by individuals going from zero to some information, with further increases in information causing only small increases in partner switching.

Discussion

In this study, we investigated the effect of individuals having different levels of information about the population on switching between cooperative partners. From our mathematical model, we found that when individuals had more information about the population, they required more interactions with their current partner to know whether they were better off switching or not. We also found that individuals appeared to become more likely to switch from a less cooperative partner than they were to stay with a more cooperative partner. When we simulated a population of individuals interacting based on switching rules from this mathematical model, we found that

Figure 2: **Individual behaviour: Partner switching landscape for** *relative* **values of population cooperativeness.** How an individual's beliefs about the probability of being better off switching (p_b) change with the number of trials with that partner (I_c) and the probability of the partner cooperating (p_c) under three different conditions for population information (none, $M = 0$; weak, $M = 0.5$ and strong, $M = 1$; columns left to right) and for relative population cooperativeness $(p_n = 0.5p_c; p_n = p_c; p_n = 2p_c;$ rows top to bottom). When $p_n = p_c$, a focal is largely indifferent to switching when they have some information, unless their current partner is very cooperative (in which case they should switch less), or very uncooperative (in which case they should switch more). When the population is half as cooperative as an individual's current partner, an individual become less likely to switch over time and will only decide to switch from very uncooperative partners. When the population is twice as cooperative as the current partner, an individual becomes more likely to switch over time and becomes more likely to switch than not for a greater range of partner cooperativeness. The effect of relative partner cooperativeness is asymmetrical with a larger region in which switching is promoted when $p_n > p_c$ than there is a region in which staying with a partner is promoted when $p_n < p_c$.

Figure 3: **Emergent behaviour: how population information affects the number of switches without and with cooperative adjustment.** The more population information individuals have, the more they switch partners (individuals have less stable relationships). Whether or not individuals adjust their cooperativeness in response to a poor payoff does not affect this relationship.

the more population information individuals had, the more they switched partners, suggesting that uncertainty about others might constrain partner switching. These results suggest that having more information about how others in the group behave can cause individuals to switch partners more, resulting in less stable relationships.

We found that the more information individuals had about the population relative to their current partner, the more they switched partners. When an individual has no information about the population, it is indifferent to switching ($p_b \approx 0.5$) for a larger range of partner cooperativeness because it does not know whether the population is more or less cooperative than its current partner. When an individual has more information about the population, the range of partner cooperativeness values that make the focal indifferent to switching becomes smaller (the gradient in the value of p_b is steeper with respect to current partner cooperativeness; [Figure 1\)](#page-11-0) – if an individual knows how cooperative the population is, it should only be indifferent to switching when its partner is as cooperative as the population. Having information about the population therefore increases the proportion of partners that an individual would prefer to switch from but also increases the proportion of partners that a focal does *not* want to switch from. In our simulation, when an individual wants to stay with its partner, it has no control (in our model) over whether that partner stays or leaves. There is therefore an asymmetry that drives up the

number of partner switches and the number of sub-optimal partnerships that an individual experiences, resulting in partnerships being less stable than is optimal, particularly when individuals have *more* information about the population. Additionally, our mathematical model showed that when individuals have information about the population, there is a greater range of partners that an individual would prefer to switch from when their current partner is less cooperative than the population than stay with when their current partner is more cooperative than the population. This might result in there being a greater preference for switching partners than staying with a partner when individuals have information.

In [Aktipis'](#page-19-9)s 'walk-away' model [\(Aktipis 2004\)](#page-19-9), individuals are able to leave a non-cooperative partner for another about whom they have no information. This is equivalent to the scenario in our model in which individuals have no population information ($M = 0$). There is empirical evidence that Trinidadian guppies might behave according to this rule – individuals who face defection subsequently choose to interact with unfamiliar individuals rather than the familiar defectors [\(Darden et al. 2020\)](#page-20-8). Guppies in this experiment switched groups despite having no information about the new group that they were switching to. It would be interesting to extend this experiment to fish with different levels of familiarity (a proxy for information) with the groups that they can choose between in order to test the prediction from our model that information should result in greater levels of switching.

Switching itself likely forms a positive feedback loop with population information because the more an individual switches, the more information it can gather about the population, and from our model it appears that the more information an individual has, the more it will switch. It might therefore be that different strategies emerge [\(Gartland et al. 2022\)](#page-21-6), with some individuals proactively switching and sampling their social environment, and some individuals choosing not to switch (but still being switched *from*). In some animal social systems (but not modelled here), this could result in heterogeneity in the attention paid to information about others' behaviour such that proactive samplers have more information about others and non-switchers are ignorant. This might interact with cooperator/non-cooperator phenotypes dependent on the cooperative scenarios that partners might face. For example, ignorant individuals might always

choose to cooperate if the worst outcome of an interaction is when both individuals defect as bet-hedging strategy. Further modelling to investigate the effect on cooperation of diversity in the strategies of information use in a population, could allow us to predict whether we expect to observe such behavioural phenotypes as a result of selection on information use and cooperativeness.

Individuals are less likely to have access to information about others when they are in large, dynamic groups. This is because it is more cognitively challenging to maintain information about larger numbers of individuals [\(Suzuki & Akiyama 2005\)](#page-24-4), and individuals in dynamic social groups are likely to behave less similarly than those in stable groups because they don't have the opportunity to conform to each other's behaviour [\(Munson et al. 2021\)](#page-22-6). We might therefore counter-intuitively predict from our model that individuals in larger dynamic groups might have more stable cooperative partnerships than those in small, stable groups. Vampire bats and Trinidadian guppies (amongst others) are able to maintain close affiliative relationships with others despite living in large and dynamic fission-fusion societies [\(Kerth et al. 2011,](#page-22-7) [Croft et al. 2009,](#page-20-9) [2005\)](#page-20-3). This could be because their uncertainty about the behaviour of others in the population means that it would not be beneficial to risk trying to find a new partner. As we show in this model, this does not require there to be an explicit cost to partner switching, though it is likely that there are additional costs to switching in real systems (e.g. increased need for vigilance; [Ridley et al. 2008\)](#page-23-7). Additional costs to partner switching could explain evidence that contradicts our model from baboons, in which females have more stable partnerships in smaller, more stable groups in which individuals are likely to have more information about the others in the group [\(Silk et al. 2012\)](#page-23-8): if the costs of being without a partner are too great, then even informed individuals might choose not to switch. Alternatively, the inherent instability of dynamic groups might preclude individuals from exerting their own preference in partnership decisions, resulting in more switching in larger, dynamic groups in nature.

Species that form cooperative partnerships are also often those that rely on social information for important fitness benefits (for example finding foraging locations and predator avoidance; e.g. [Page & Bernal 2020,](#page-22-8) [Magurran & Higham 1988\)](#page-22-9). We would therefore expect social infor-

mation as well as private information to play a role in cooperative partnership decisions. This would mean that individuals can conduct 'social sampling' without actually interacting with others, but by observing their interactions with others, and others' reactions to them. The most complex versions of this type of reputational monitoring are likely cognitively demanding, but awareness of others' relationships has been demonstrated in a variety of species (e.g. bonnet macaques (*Macaca radiata*) [Silk 1999;](#page-23-9) baboons (*Papio cynocephalus ursinus*) [Engh et al. 2005\)](#page-21-7). The ability to gain information without risking switching to a potentially worse new partner (or losing partnership altogether) could allow individuals to avoid the potential costs of switching partners. This might mean that species who rely on social information, particularly for decisions about their relationships, might be able to switch partners more often without potential costs. However, if individuals use social information to this extent, then they might not have such need for direct social sampling and we might therefore expect more stable relationships despite high levels of information. Further theoretical work to understand the social and ecological scenarios under which we might expect such third-party monitoring to evolve and how this might impact decision-making around cooperative partnership could complement future empirical work to identify if there are differences in the attention that animals pay to others as well as their partner and their consequent interactions.

Our model assumes that individuals in a population use cognitive processes that are analogous to Bayesian updating – that is integrating prior information with current observations to determine what action to take. There is evidence that animals from insects to primates can employ such updating [\(Valone 2006\)](#page-24-2), but there are other ways in which animals could learn that might be less costly and almost as effective, for example via affective/emotional state [\(Higginson](#page-21-8) [et al. 2018\)](#page-21-8). It would be interesting for future theoretical work to identify the conditions under which Bayesian updating compared to other learning mechanisms might be favoured under natural selection (e.g. [Higginson et al. 2018\)](#page-21-8) in the context of cooperative partnership decisions, which can often have major fitness implications over an individual's life.

18

Conclusions

In this study, we modelled how individuals might decide to switch from or stay with a current partner for different levels of information about the behaviour of others in their population. We found that the more information individuals had about the population, the more they switched partner, suggesting that uncertainty about the behaviour of others might partially drive the decision to remain in a cooperative partnership with a known individual. More broadly, our results suggest that animals' access to information about both past and potential new partners should be taken into account when investigating how they form and invest in their affiliative social relationships. This could be particularly important in cooperative species, for which there could be particularly strong fitness consequences from partnerships.

Acknowledgements

We are grateful to Sam Ellis and Mark Dyble for providing comments on an earlier version of this manuscript. R.F.B.P would like to acknowledge funding from the UKRI Natural Environment Research Council DTP (NE/S007504/1). D.D.M. acknowledges funding from a European Research Council Consolidator grant (FriendOrigins - 864461) awarded to Lauren J. N. Brent.

Author contributions

R.F.B.P: conceptualisation, funding acquisition, investigation, methodology, project administration, writing—original draft, writing—review and editing. T.W.F.: funding acquisition, methodology, supervision, writing—review and editing; S.K.D.: funding acquisition, methodology, project administration, resources, supervision, writing—review and editing. D.D.M.: conceptualisation, methodology, supervision, writing—review and editing.

References

Aktipis, C. A. (2004), 'Know when to walk away: Contingent movement and the evolution of cooperation', *Journal of Theoretical Biology* **231**(2), 249–260.

Andersson, M. (1994), *Sexual selection*, Princeton University Press.

- Bapna, R., Qiu, L. & Rice, S. (2017), 'Repeated interactions versus social ties', *MIS Quarterly* **41**(3), 841–A10.
- Bebbington, K. & Groothuis, T. G. (2023), 'Partner retention as a mechanism to reduce sexual conflict over care in a seabird', *Animal Behaviour* **197**, 15–26.

Birch, L. C. (1957), 'The meanings of competition', *The American Naturalist* **91**(856), 5–18.

- Brask, J. B., Croft, D. P., Edenbrow, M., James, R., Bleakley, B. H., Ramnarine, I. W., Heathcote, R. J., Tyler, C. R., Hamilton, P. B., Dabelsteen, T. et al. (2019), 'Evolution of non-kin cooperation: Social assortment by cooperative phenotype in guppies', *Royal Society Open Science* **6**(1), 181493.
- Brent, L. J., Franks, D. W., Foster, E. A., Balcomb, K. C., Cant, M. A. & Croft, D. P. (2015), 'Ecological knowledge, leadership, and the evolution of menopause in killer whales', *Current Biology* **25**(6), 746–750.
- Carter, G. G. & Wilkinson, G. S. (2013), 'Food sharing in vampire bats: Reciprocal help predicts donations more than relatedness or harassment', *Proceedings of the Royal Society B* **280**(1753), 20122573.
- Carter, G. G. & Wilkinson, G. S. (2015), 'Social benefits of non-kin food sharing by female vampire bats', *Proceedings of the Royal Society B* **282**(1819), 20152524.
- Cayuela, H., Lengagne, T., Joly, P. & Léna, J.-P. (2017), 'Females trade off the uncertainty of breeding resource suitability with male quality during mate choice in an anuran', *Animal Behaviour* **123**, 179–185.
- Cohen, M. D., Riolo, R. L. & Axelrod, R. (2001), 'The role of social structure in the maintenance of cooperative regimes', *Rationality and Society* **13**(1), 5–32.
- Collins, E. J., McNamara, J. M. & Ramsey, D. M. (2006), 'Learning rules for optimal selection in a varying environment: Mate choice revisited', *Behavioral Ecology* **17**(5), 799–809.
- Cooper, M. A. & Bernstein, I. S. (2000), 'Social grooming in Assamese macaques (*Macaca assamensis*)', *American Journal of Primatology* **50**(1), 77–85.
- Crawford, V. P. & Haller, H. (1990), 'Learning how to cooperate: Optimal play in repeated coordination games', *Econometrica: Journal of the Econometric Society* **58**(3), 571–595.
- Croft, D., James, R., Thomas, P., Hathaway, C., Mawdsley, D., Laland, K. & Krause, J. (2005), 'Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*)', *Behavioral Ecology and Sociobiology* **59**, 644–650.
- Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J. & James, R. (2009), 'Behavioural trait assortment in a social network: Patterns and implications', *Behavioral Ecology and Sociobiology* **63**, 1495–1503.
- Darden, S. K., James, R., Cave, J. M., Brask, J. B. & Croft, D. P. (2020), 'Trinidadian guppies use a social heuristic that can support cooperation among non-kin', *Proceedings of the Royal Society B* **287**(1934), 20200487.
- De Moor, D., Roos, C., Ostner, J. & Schülke, O. (2020), 'Bonds of bros and brothers: Kinship and social bonding in postdispersal male macaques', *Molecular Ecology* **29**(17), 3346–3360.
- De Waal, F. B. (1989), 'Food sharing and reciprocal obligations among chimpanzees', *Journal of Human Evolution* **18**(5), 433–459.
- Dijkstra, J. & van Assen, M. A. (2017), 'Explaining cooperation in the finitely repeated simultaneous and sequential prisoner's dilemma game under incomplete and complete information', *The Journal of Mathematical Sociology* **41**(1), 1–25.
- Dugatkin, L. A. (1992), 'Tendency to inspect predators predicts mortality risk in the guppy (*Poecilia reticulata*)', *Behavioral Ecology* **3**(2), 124–127.
- Edenbrow, M., Bleakley, B. H., Darden, S. K., Tyler, C. R., Ramnarine, I. W. & Croft, D. P. (2017), 'The evolution of cooperation: Interacting phenotypes among social partners', *The American Naturalist* **189**(6), 630–643.
- Engh, A. L., Siebert, E. R., Greenberg, D. A. & Holekamp, K. E. (2005), 'Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships', *Animal behaviour* **69**(1), 209–217.
- Fawcett, T. W. & Johnstone, R. A. (2003), 'Mate choice in the face of costly competition', *Behavioral Ecology* **14**(6), 771–779.
- Gartland, L. A., Firth, J. A., Laskowski, K. L., Jeanson, R. & Ioannou, C. C. (2022), 'Sociability as a personality trait in animals: methods, causes and consequences', *Biological Reviews* **97**(2), 802–816.
- Gazda, S. K., Connor, R. C., Edgar, R. K. & Cox, F. (2005), 'A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatu*s) off Cedar Key, Florida', *Proceedings of the Royal Society B* **272**(1559), 135–140.
- Gilby, I. C., Brent, L. J., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J. & Pusey, A. E. (2013), 'Fitness benefits of coalitionary aggression in male chimpanzees', *Behavioral Ecology and Sociobiology* **67**, 373–381.
- Hamilton, I. M. & Taborsky, M. (2005), 'Unrelated helpers will not fully compensate for costs imposed on breeders when they pay to stay', *Proceedings of the Royal Society B* **272**(1561), 445– 454.
- Higginson, A. D., Fawcett, T. W., Houston, A. I. & McNamara, J. M. (2018), 'Trust your gut: Using physiological states as a source of information is almost as effective as optimal Bayesian learning', *Proceedings of the Royal Society B* **285**(1871), 20172411.
- Kerth, G., Perony, N. & Schweitzer, F. (2011), 'Bats are able to maintain long-term social relationships despite the high fission–fusion dynamics of their groups', *Proceedings of the Royal Society B* **278**(1719), 2761–2767.
- Kings, M., Arbon, J. J., McIvor, G. E., Whitaker, M., Radford, A. N., Lerner, J. & Thornton, A. (2023), 'Wild jackdaws can selectively adjust their social associations while preserving valuable long-term relationships', *Nature Communications* **14**(1), 5103.
- Luttbeg, B. (1996), 'A comparative Bayes tactic for mate assessment and choice', *Behavioral Ecology* **7**(4), 451–460.
- Magurran, A. E. & Higham, A. (1988), 'Information transfer across fish shoals under predator threat', *Ethology* **78**(2), 153–158.
- Martin, J. W. & Cushman, F. (2015), 'To punish or to leave: Distinct cognitive processes underlie partner control and partner choice behaviors', *PLOS ONE* **10**(4), e0125193.
- McNamara, J. M., Green, R. F. & Olsson, O. (2006), 'Bayes' theorem and its applications in animal behaviour', *Oikos* **112**(2), 243–251.
- Milinski, M., Kü lling, D. & Kettler, R. (1990), 'Tit for tat: Sticklebacks (Gasterosteus aculeatus) 'trusting' a cooperating partner', *Behavioral Ecology* **1**(1), 7–11.
- Munson, A., Michelangeli, M. & Sih, A. (2021), 'Stable social groups foster conformity and among-group differences', *Animal Behaviour* **174**, 197–206.
- Nguyen, N., Van Horn, R. C., Alberts, S. C. & Altmann, J. (2009), '"Friendships" between new mothers and adult males: Adaptive benefits and determinants in wild baboons (*Papio cynocephalus*)', *Behavioral Ecology and Sociobiology* **63**, 1331–1344.
- Page, R. A. & Bernal, X. E. (2020), 'The challenge of detecting prey: Private and social information use in predatory bats', *Functional Ecology* **34**(2), 344–363.
- Ridley, A. R., Raihani, N. J. & Nelson-Flower, M. J. (2008), 'The cost of being alone: the fate of floaters in a population of cooperatively breeding pied babblers *Turdoides bicolor*', *Journal of Avian Biology* **39**(4), 389–392.
- Riehl, C. & Strong, M. J. (2018), 'Stable social relationships between unrelated females increase individual fitness in a cooperative bird', *Proceedings of the Royal Society B* **285**(1876), 20180130.
- Rieucau, G. & Giraldeau, L.-A. (2011), 'Exploring the costs and benefits of social information use: An appraisal of current experimental evidence', *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**(1567), 949–957.
- Schino, G. & Aureli, F. (2017), 'Reciprocity in group-living animals: Partner control versus partner choice', *Biological Reviews* **92**(2), 665–672.
- Schneider, G. & Krueger, K. (2012), 'Third-party interventions keep social partners from exchanging affiliative interactions with others', *Animal Behaviour* **83**(2), 377–387.
- Seghers, B. H. (1973), Analysis of geographic variation in the antipredator adaptations of the guppy : *Poecilia reticulata*, PhD thesis, University of British Columbia.
- Silk, J. B. (1999), 'Male bonnet macaques use information about third-party rank relationships to recruit allies', *Animal Behaviour* **58**(1), 45–51.
- Silk, J. B., Alberts, S. C., Altmann, J., Cheney, D. L. & Seyfarth, R. M. (2012), 'Stability of partner choice among female baboons', *Animal Behaviour* **83**(6), 1511–1518.
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. (2009), 'The benefits of social capital: Close social bonds among female baboons enhance offspring survival', *Proceedings of the Royal Society B* **276**(1670), 3099–3104.
- St-Pierre, A., Larose, K. & Dubois, F. (2009), 'Long-term social bonds promote cooperation in the iterated prisoner's dilemma', *Proceedings of the Royal Society B* **276**(1676), 4223–4228.
- Suzuki, S. & Akiyama, E. (2005), 'Reputation and the evolution of cooperation in sizable groups', *Proceedings of the Royal Society B* **272**(1570), 1373–1377.
- Trimmer, P. C., Houston, A. I., Marshall, J. A., Mendl, M. T., Paul, E. S. & McNamara, J. M. (2011), 'Decision-making under uncertainty: Biases and Bayesians', *Animal Cognition* **14**, 465–476.
- Uehara, T., Yokomizo, H. & Iwasa, Y. (2005), 'Mate-choice copying as Bayesian decision making', *The American Naturalist* **165**(3), 403–410.
- Valone, T. J. (2006), 'Are animals capable of Bayesian updating? An empirical review', *Oikos* **112**(2), 252–259.
- Westneat, D. F. (2012), 'Evolution in response to social selection: the importance of interactive effects of traits on fitness', *Evolution* **66**(3), 890–895.