



Cite this article: Aubier TG, Kokko H. 2022 Volatile social environments can favour investments in quality over quantity of social relationships. *Proc. R. Soc. B* **289**: 20220281. <https://doi.org/10.1098/rspb.2022.0281>

Received: 14 February 2022

Accepted: 16 March 2022

Subject Category:

Evolution

Subject Areas:

behaviour, evolution, theoretical biology

Keywords:

cooperation, social network, demography, individual-based model

Author for correspondence:

Thomas G. Aubier

e-mail: thomas.aubier@normalesup.org

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5915114>.

Volatile social environments can favour investments in quality over quantity of social relationships

Thomas G. Aubier^{1,2} and Hanna Kokko^{1,3}

¹Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

²Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA

³Konrad Lorenz Institute of Ethology, University of Veterinary Medicine, Vienna, Austria

TGA, 0000-0001-8543-5596; HK, 0000-0002-5772-4881

Cooperation does not occur in a vacuum: interactions develop over time in social groups that undergo demographic changes. Intuition suggests that stable social environments favour developing few but strong reciprocal relationships (a ‘focused’ strategy), while volatile social environments favour the opposite: more but weaker social relationships (a ‘diversifying’ strategy). We model reciprocal investments under a quality–quantity trade-off for social relationships. We find that volatility, counterintuitively, can favour a focused strategy. This result becomes explicable through applying the theory of antagonistic pleiotropy, originally developed for senescence, to social life. Diversifying strategies show superior performance later in life, but with costs paid at young ages, while the social network is slowly being built. Under volatile environments, many individuals die before reaching sufficiently old ages to reap the benefits. Social strategies that do well early in life are then favoured: a focused strategy leads individuals to form their first few social bonds quickly and to make strong use of existing bonds. Our model highlights the importance of pleiotropy and population age structure for the evolution of cooperative strategies and other social traits, and shows that it is not sufficient to reflect on the fate of survivors only, when evaluating the benefits of social strategies.

1. Introduction

The evolution of cooperation is a central theme in biology [1,2]. Past theoretical work has elucidated how cooperative traits can be advantageous over non-cooperative traits that better exploit the public good of cooperation. While inclusive fitness theory explains why cooperation among kin can evolve [3–5], reciprocity theory explains how cooperation between individuals that are not necessarily related can be enforced by reward and punishment [6–8]. In animal societies, such reciprocal cooperations can lead to the build-up of social partnerships, as shown in humans [7,9], vampire bats [10,11], some nonhuman primates [12–14], some fishes [15,16] and some birds [17,18].

A gap exists between simple evolutionary models of cooperation and the complex psychology of helping decisions in animal societies [19,20]. In particular, Connor [19] argues that thinking ‘beyond the dyad’ (i.e. not considering solely fixed pairs of individuals) is necessary if we are to understand the evolution of cooperative strategies in animal societies (as assumed when taking the ‘biological market’ perspective [21]). For animals that live in complex societies, much cooperation takes place in the context of stable social bonds that seem analogous to human friendships. Yet, very few theoretical studies have investigated the evolution of cooperative strategies within an explicit social network and have considered how the network itself evolves as a result of individual interactions [18,22–24].

A particularly intriguing question is what cooperative strategy evolves when individuals face an unavoidable trade-off between quantity and quality

of their social relationships. Cognitive limitations [25,26], and time or other resource budgets [27], create constraints such that one cannot possibly be ‘everyone’s best friend’. Differential investment in quantity versus quality of social relationships has been observed in humans [28,29], in nonhuman primates [30–32] and in other mammals such as kangaroos [33] and giraffes [34]. Carter *et al.* [11] showed that cooperative vampire bats investing in quantity of social relationships (with unrelated individuals) at the expense of relationship quality cope better with a volatile social environment; the authors named this strategy a ‘social bet-hedging strategy’, as the diversified portfolio of acquaintances protects against the worst-case outcome of none of one’s few friends remaining alive. Nonetheless, there is surprisingly little theory on the evolutionary forces shaping the cooperative strategies that ultimately determine the individuals’ social environment, which has potentially important consequences on survival [35], and which in turn may feedback into the stability of the social environment itself.

Here, we model the competition between focused strategies (our shorthand for the tendency to form few but strong relationships) and diversifying strategies (where individuals readily develop social ties with strangers but, due to the quality–quantity trade-off, these remain weaker; [11,20]) along a continuum where the readiness to invest in new social bonds varies. Perhaps counterintuitively, we show that volatility in the social environment can favour a focused, rather than a diversifying, approach. The result becomes explicable when realizing that the ultimate performance of the eventual network is not the sole criterion for its evolutionary success. The diversifying approach builds an excellent network but not instantaneously, and the focused strategy outperforms it during early life. If many individuals are relatively short-lived (due to the volatility of the social environment), it is better to sacrifice late-life performance for improved success in early life. This shows that the antagonistic pleiotropy theory of senescence [36] (see [37] for a recent review) is of relevance for the development of social strategies, not only for somatic maintenance.

2. The model

(a) Overview

We model individuals that live in groups of N individuals. Group size is kept constant by recruitment of new group members as soon as an existing member has died.

All individuals share resources and thereby participate in the dynamics of social bond forming over their entire lifetime. Reproduction is asexual for simplicity, and generations are overlapping. While all individuals use the same structural rules of Bayesian updating of social bonds (details below), they differ in their *a priori* propensity to establish contact with individuals with whom they do not have an interaction history yet. For brevity, we call such individuals ‘strangers’, though note that they live permanently in the same group.

These propensities to establish contact with strangers are genetically encoded, with two independent traits that impact an individual i ’s propensity to (i) ask resources from strangers (A_i) or (ii) to give resources to strangers (G_i). High values indicate a tendency to diversify one’s social relationship portfolio, and low values indicate a focused approach to relationships. There is both resource-independent and resource-dependent mortality, and each vacancy created by death is replaced by

a new recruit, with the parent chosen randomly from the population of living individuals. Selection on traits operates based on survival: individuals whose traits give them a reliable resource supply contribute disproportionately to future generations by virtue of them living longer. Recruits inherit their (single) parent’s trait with some mutation, allowing A_i and G_i to evolve, with the social network also changing as an emergent property of the population.

Inspired by vampire bat biology [10,11], we assume that each individual attempts to perform independent foraging at each time step, but this may fail, creating a constant supply of successful (satiated) and unsuccessful (needy) individuals who thereafter can interact socially, allowing resources to be donated to unsuccessful individuals. Note that we assume pre-existing willingness to help others (we do not give individuals the option to cheat), as our model is designed to investigate the evolution of focused versus diversified relationship tendencies, and the resultant narrow or broad social networks, rather than the origins of cooperation *per se*. For the same reason, in our main analysis, we also ignore complications brought about by kin recognition and preferential helping among kin; we thus do not track relatedness of the individuals (but see additional simulations in electronic supplementary material, figures S1 and S2).

Cooperative traits, A_i and G_i , jointly determine to what extent individuals focus versus diversify cooperative investments. We focus on the implications of the volatility of the social environment on the evolution of those cooperative traits. We explicitly implement four sources of volatility. First, memory of past interactions between each pair of individuals can become erased with probability p_{erase} , making the individuals strangers to each other. Second, individuals may be unsuccessful during foraging with probability p_{unsucc} . Third, successful individuals may be unavailable with probability p_{unav} not being able to give any resources. Fourth, individuals may randomly die with probability p_{die} . Increasing each of these probabilities associates with an increased volatility of the social environment, with strong social bonds being lost temporarily or permanently.

(b) Social bonds

(i) Basic properties

We model the strength of a social bond between each pair of individuals as a continuous variable (ϵ [0,1]) that changes when individuals interact with each other. We list here the properties of social bonds as we have modelled them (mathematical definitions are provided in electronic supplementary material, appendix). Social bonds are strong if individuals have helped each others reciprocally in the past (allowing us to call them ‘partners’, without however implying that the relationship excludes having outside options). Strong bonds mean that an individual that has helped another individual is predisposed to ask resources from its partner should the need arise. Conversely, an individual that has been helped by another individual will tend to return the favour. As a flip-side, an individual refusing to help another individual is less tempted to ask resources from this same individual, who, as a mirror image of the argument, will be little inclined to help.

(ii) Perspective dependence of the strength of social bonds

Each individual uses Bayesian updating to formulate its own estimate of the social bond. Individuals with different trait

values, A_i and G_i , have different estimates of the strength of the same social bond. In particular, individuals with high A_i and G_i trait values have high estimate values of the baseline strength of social bonds with strangers and are therefore more inclined to interact with them than individuals with low A_i and G_i trait values do. Hence, we define the strength of social bonds from the perspective of each individual, with $\Pi^i(i,j)$ representing the estimate by individual i of the strength of the social bond between individuals i and j , and $\Pi^j(i,j)$ representing the estimate by individual j of this same quantity (see electronic supplementary material, appendix for mathematical definitions). These estimates directly determine the cooperative behaviour of individuals (see §2c(ii) below). To describe the properties of the emerging social network, however, we act as an unbiased external observer who gives the same weight to the perspective of each actor, as detailed later.

(c) Processes

At each time step, foraging is followed by resource donations, social bond updating, mortality and reproduction.

(i) Foraging

Each time step begins with independent foraging, which ends with each individual in an unsuccessful state with probability p_{unsucc} . We assume that foraging success ($= 1 - p_{\text{unsucc}}$) is independent of each individual's previous foraging successes or previous interactions with group members.

(ii) Resource donations

If available with probability $1 - p_{\text{unav}}$, each successful individual, regardless of her trait A_i and G_i , set aside a total of R resources for donating to others (while consuming the rest of foraged resources individually; we do not model this consumption explicitly, but assume that it allows successful individuals to survive without needing help from others). This total amount R is divided into n_{give} resource 'packages' of magnitude r_{give} each (thus $R = n_{\text{give}} \times r_{\text{give}}$). Each of the n_{give} packages are set aside to be donated to a specific individual. The probability that any given individual is assigned by the focal individual to be the intended recipient is proportional to the strength of the social bond as estimated by the focal successful individual (schematized in electronic supplementary material, figure S3).

Individuals by definition do not have an interaction history with strangers. Nevertheless, the social bond with a stranger is estimated based on a prior belief (based on G_i when assigning resource packages). Depending on the value of G_i of the successful individual, the above rules therefore make it possible that one (or more) of the n_{give} packages is set aside to be donated to a particular stranger. Whether an interaction history is existing or not, a focal individual may set aside several packages (or even all n_{give} of them) in the direction of a single recipient, though this is highly unlikely in the case of strangers. Strongly targeted giving is typical for individuals who have already formed a single strong social bond with a specific partner.

Unsuccessful individuals use the social bond network analogously, from their own perspective (schematized in electronic supplementary material, figure S3). Each unsuccessful individual places, during the same time step, a total of n_{ask} requests for help, directed to specific other individuals. Analogously to the above procedure, interactions are

preferentially directed towards individuals with whom a strong social bond has been built but may be directed towards strangers based on a novel social bond estimation that depends on the focal unsuccessful individual's A_i value. Also, analogously to the successful individuals setting aside resources in a targeted fashion, unsuccessful individuals can target several or even all of their n_{ask} requests in the direction of the same individual in the network.

Note that the above decisions of setting aside resources, or placing requests for resources, are done without information on anyone else's most recent success, or on their decisions to set aside resources or to request them. This means that some of the resources set aside for donation by the successful individuals will not be matched by a request from the intended recipient (who may be successful and thus not needy, or may be unsuccessful but direct requests in some other direction). Likewise, some of the help requests are not matched by willingness to donate, either because there is nothing to donate as both the requester and the target of the request were unsuccessful or because the target of the help request did not set aside any packages for the requester. If there is a match, all matching resource packages are transferred. Note that the limited number of interaction per time step (controlled by parameters n_{give} and n_{ask}) is at the origin of a trade-off between quantity and quality of social relationships.

(iii) Social bond updating

Resource donations associate with social bond updating. We assume that the total numbers of requests and donations ($n_{i \rightarrow j}$, $n_{j \rightarrow i}$, $d_{i \rightarrow j}$ and $d_{j \rightarrow i}$ for all pairs of individuals i and j , as defined in electronic supplementary material, appendix) are updated among pairs of individuals only if (i) one individual is successful and the other is unsuccessful and (ii) if the successful individual is available and able to give resources. Individuals refine their estimates of the strengths of social bonds with individuals with whom an interaction took place or could have taken place. The total numbers of requests and donations are updated, leading to new estimate values of the strengths of social bonds, $\Pi^i(i,j)$ and $\Pi^j(i,j)$, for all individuals i and j . We also specify a parameter (identical for all individuals) F , which describes the strength of prior belief (i.e. high values of F make it more difficult to shift away from prior belief). The above rules imply that there is no social bond updating when both partners are unsuccessful. Likewise, not being able to give resources (with probability p_{unav}) does not harm relationships.

As another source of volatility of the social environment, we assume that any interaction history can be erased with probability p_{erase} leading to a state as if individuals had never interacted with each other. This differs from death in two ways: the two individuals' other social bonds are kept intact, and they can also begin rebuilding their mutual social bond. This source of volatility is by far the most unrealistic one we implement and may not be found in nature. Nonetheless, we believe it is important to implement it in our model because erasing the history of past interactions is the most parsimonious way to increase social volatility. In particular, this does not change directly age structure (contrary to a direct increase in mortality for instance).

(iv) Mortality

Mortality has two components. The first, resource-independent component causes each individual, regardless of success and

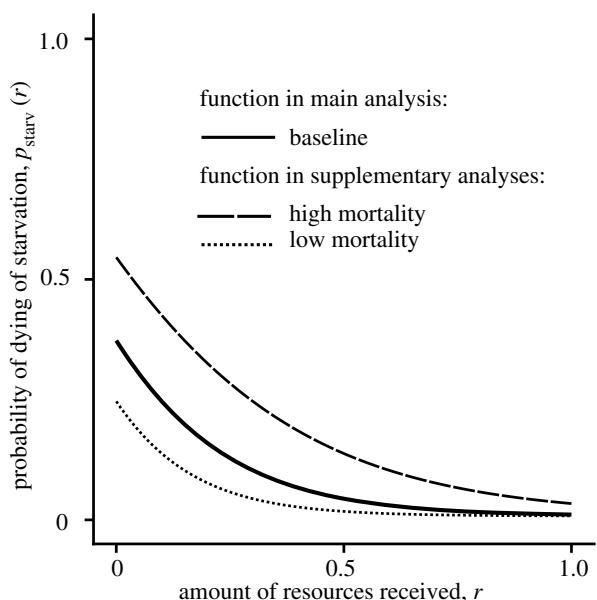


Figure 1. Probability of dying of starvation depending on the amount of resources received by the unsuccessful individual. Baseline function: $(\gamma_s, R_s) = (0.3, 0.2)$. Other functions implemented in supplementary analyses: $(\gamma_s, R_s) = (0.3, 0.15)$ (low mortality) and $(0.3, 0.3)$ (high mortality).

social interactions, to die with probability p_{die} . The second, resource-dependent component is only applied to unsuccessful individuals (thus, successful ones always have sufficient resources to survive the second step, regardless of how many resource packages they donated).

Unsuccessful individuals die of starvation during the second round of mortality with a probability that depends on the amount r of resources received during the ‘resource donation’ phase:

$$p_{\text{starv}}(r) = \frac{2\exp(-(r + \gamma_s)/R_s)}{1 + \exp(-(r + \gamma_s)/R_s)} \quad (2.1)$$

Parameters γ_s and R_s adjust the risk of death due to starvation. Functions implemented in simulations are shown in figure 1.

(v) Reproduction

Reproduction is clonal. Each vacancy, created by death, is filled with an offspring, whose mother is a randomly chosen living individual (thus selection acts via differential survival; there is no differential success among the living potential parents). The offspring traits A_i and G_i are drawn from truncated normal distributions with means equal to the corresponding parental trait value (reflecting inheritance), with standard deviation σ (reflecting mutation), and with A_i and G_i constrained to be in the interval $[0, 1]$.

In our main simulations, individuals must build their social network from scratch. By contrast, we assumed in supplementary simulations that newborn individuals initially have strong social bonds with their mother, their sisters or their mother’s partners (social inheritance). Although deviating patterns occur in special cases (that are biologically not likely scenarios, see electronic supplementary material, figure S1), as a whole our main message remains robust whether the initial network of a newborn is zero (the network has to be built from scratch) or non-zero (electronic supplementary material, figures S1 and S2).

(d) Simulation experiments

We aim at investigating how the volatility of the social environment affects the evolution of ‘social bet-hedging strategies’, i.e. strategies that diversify cooperative investments. In particular, we test whether changing volatility from low to high favours a shift from a focused to a diversifying approach to social relationships, following the intuition that focusing investments in a single most-profitable partnership is risky if partners often disappear. More precisely, we vary the values of four parameters that determine the volatility of the social environment: the probability p_{erase} of forgetting all information about past interactions with any given individual, the probability p_{die} of dying by chance (i.e. irrespective of foraging success), the probability p_{unsucc} of being unsuccessful, and the probability p_{unav} of being unavailable when successful. The intuitive prediction is confirmed if high values of these parameters lead to the evolution of high trait values A_i and G_i .

We run the model for 5 million time steps. We assume that $A_i = G_i = 0.02$ for all individuals i initially (but note that initial variation in trait values does not change qualitatively our results; electronic supplementary material, figure S4), and we consider mutations of small effect size ($\sigma = 10^{-4}$). And, unless stated otherwise, we implement a group size of $N = 500$, a baseline resource-dependent mortality function as shown in figure 1, a maximum amount of resources given by each successful individuals $R = 1$, numbers of interactions $n_{\text{give}} = n_{\text{ask}} = 100$, and the strength of the prior belief $F = 1$. A stable social environment is defined by parameters $p_{\text{erase}} = 0$, $p_{\text{die}} = 0$, $p_{\text{unav}} = 0$, and with the only source of mortality determined by cooperative relationships such that $p_{\text{unsucc}} = 0.1$. Any simulation characterized by higher values of p_{erase} , p_{die} , p_{unav} and p_{unsucc} is referred to as simulations modelling a volatile social environment. For each combination of parameters tested, we run 30 simulation replicates.

To describe simulation outputs, we assume that a partnership has been built as soon as an individual is ten times more likely to interact with this individual rather than with a stranger. The quality of partnership refers to the exact likelihood of interacting with a partner relative to that with a stranger. As noted above, we give the same weight to the perspective of each individual within a pair, and we define the quality of partnership between individuals i and j as:

$$Q(i,j) = \frac{(\prod^i(i,j)/A_i^2) + (\prod^j(i,j)/A_j^2)}{2}, \quad (2.2)$$

reflecting the degree to which individuals are more likely to interact with each other than with a stranger. Note that we get qualitatively the same result with $\prod^i(i,j)$ (resp. $\prod^j(i,j)$) relative to G_i^2 (resp. G_j^2). As noted above, we assume that a partnership has been built as soon as $Q(i,j) > 10$, with individuals being ten times more likely to interact with each other than with a stranger. This assumption is made for the purpose of describing the outcome of our simulations and does not affect the simulation. In our simulations, low traits values A_i and G_i leads to more focused cooperative investments than high traits values A_i and G_i , regardless of the definition we use to define partnership establishment (electronic supplementary material, figure S5).

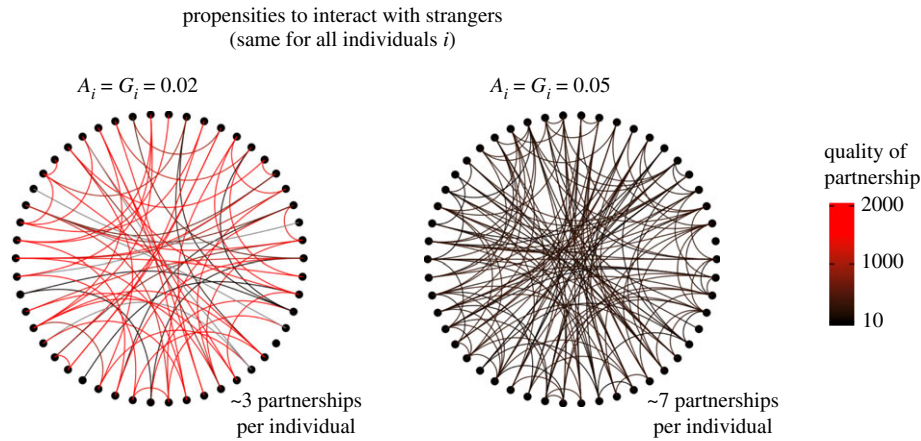


Figure 2. Examples of emerging social networks depending on the socializing behaviours of individuals under a stable social environment (see examples under volatile social environment in electronic supplementary material, figure S6). Each link represents a partnership between individuals. The colour of the link represents the quality of the partnership—i.e. $Q(i,j)$ for all pairs of individuals i and j . We assume that a partnership has been built as soon as an individual is 10 times more likely to interact with this individual rather than with a stranger ($Q(i,j) > 10$). Here, $N = 50$. (Online version in colour.)

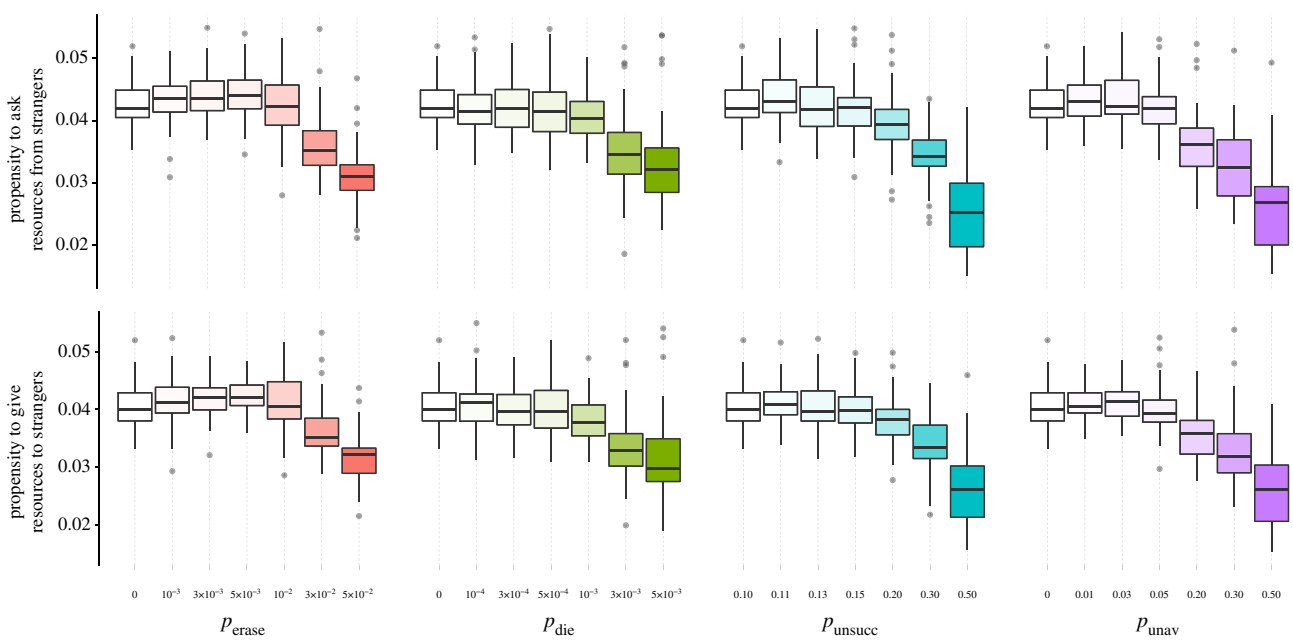


Figure 3. Trait values, A_i and G_i , at evolutionary equilibrium reached after 5 million time steps. High propensities to interact with strangers (high A_i and high G_i) are indicative of a social bet-hedging strategy. For high values of p_{erase} , p_{dier} , p_{unsucc} and p_{unavr} the social environment is volatile. Under these conditions, the evolutionary equilibrium is characterized by cooperative strategies focusing on the quality of each partnership rather than on the quantity of partnerships (low A_i and low G_i , i.e. the opposite of social bet-hedging). (Online version in colour.)

3. Results

(a) Evolutionary outcome under stable versus volatile social environments

In accordance with the definition of a ‘social bet-hedging strategy’, individuals with higher propensities to interact with strangers (high A_i and high G_i) ultimately diversify cooperative investments across more partners while building weaker social bonds with each partner (see examples of emerging social network in figure 2 and electronic supplementary material, figures S5 and S6).

Contrary to what we expected, a volatile social environment does not favour such diversifying cooperative strategy. Regardless of the type of volatility ($p_{erase} > 0$, $p_{dier} > 0$, $p_{unsucc} > 0.1$ and $p_{unavr} > 0$), higher volatility selects for lower, not higher, values of A_i and G_i (figure 3). In other words, the tendency to diversify cooperative

investments is the lowest in the most volatile environments. Our findings (figure 3) are not anomalous special cases; we find similar evolutionary outcomes when we change the group size (but note that in a very large group, individuals have to focus investment on few individuals to build partnerships, leading to low trait values A_i and G_i), the strength of prior expectations, the maximum number of donations and requests per time step, the extent of resource-dependent mortality and the shape of the resource-dependent mortality function (electronic supplementary material, figures S7–S11).

We performed additional simulations where newborn individuals have a strong social bond with their mother, their sisters or their mother’s partners (electronic supplementary material, figures S1 and S2) and do not build their social network from scratch. In most cases, volatile social environments keep favouring more focused cooperative strategy than do more stable social environment (at the exception of increased p_{erase} , which is the most unrealistic form of volatile

social environments, as detailed in electronic supplementary material, figure S1). Interestingly, we show that a focused cooperative strategy translate into a higher proportion of partnership between relative versus unrelative individuals when partnership between kins occurs but into a lower proportion of partnership between relative versus unrelative individuals when social inheritance takes place (electronic supplementary material, figure S2).

(b) Demographic feedback under a volatile social environment

It is clearly necessary to explain why a volatile social environment leads to the evolution of a strategy focusing cooperative investment on few partners. We illustrate this with an example, where we trace the life of a single mutant individual i with deviating traits A_i , G_i when all other population members j have trait values $A_j=0.035$ and $G_j=0.035$. For the mutant i , we consider traits values $A_i, G_i \in \{0.02, 0.035, 0.05\}$. We then assess the characteristics of the social relationships and the survivorship of this mutant as it ages. Age is defined based on time steps at unsuccessful state; note that this quantification of age is strongly correlated with the true age of the individual based on all time steps (electronic supplementary material, figure S12).

Individuals with high A_i and G_i values ultimately have many partnerships of poor quality (first and second rows in figure 4). Nonetheless, at early age, these individuals have fewer partnerships than individuals focusing on few partnerships (with low A_i and G_i values). Focusing on few partnerships speeds up social bonding and increases the exploitation of the benefits associated with the existing partnerships, ultimately increasing survival at early age (third and fourth rows in figure 4). Although the focused approach carries some risk, they are smaller than the reduction in early performance if attempting to diversify when one's own network is still in the first stages of being built. This occurs even if newborn individuals do not need to build their social network from scratch; exploiting the benefits associated with the pre-existing social bonds (e.g. with the mother; electronic supplementary material, figure S13) at the expense of diversifying cooperative investments increases survival at early age.

In other words, focusing on few partnerships appears necessary at early age, whereas building many partnerships proves beneficial at older ages once the many partnerships have been built.

Under a volatile social environment (when $p_{\text{die}} = 5 \times 10^{-3}$ in figure 4; but this is also true for high p_{erase} , p_{unsucc} and p_{unav} as shown in electronic supplementary material, figures S14–S16), diversifying cooperative investment benefits old but not young individuals (old individuals with high A_i and G_i trait values have a higher survivorship than old individuals with low A_i and G_i trait; last row in figure 4). In that sense, the premises on the benefits associated with a 'social bet-hedging strategy' hold: in volatile social environments such diversifying cooperative strategy proves beneficial late in life because it reduces the temporal variance in cooperative returns caused by unpredictable changes in partner availability [11]. Nevertheless, the evolution of such a cooperative strategy does not depend only on the performance of individuals belonging to a certain age group. Here, a key question is how much of one's life one will spend being 'young' versus 'old'. As a whole, the selection gradient changes as the age distribution changes (electronic supplementary material, figure S17).

Overall, high mortality increases the proportion of young individuals relative to old individuals. As a result, under a volatile social environment, fewer individuals reach old ages where they can reap the benefits of diversifying cooperative investment. The details differ between settings: a volatile social environment may associate with high mortality directly (high p_{die}), indirectly (high p_{erase} and high p_{unav}) or both directly and indirectly (high p_{unsucc} ; via resource-dependent mortality and via a lower pool of helpers). Regardless of the specific route to short lives, volatility means that relatively few individuals reach sufficiently old age to reap the benefits of a diversified approach to network building. Instead, speeding up the socializing process and exploiting existing partnerships at an early age matters the most (see percentage in last row of figure 4), even if this proves deleterious later in life (should the individual still be alive, which is relatively unlikely under high volatility). This explains why a 'focused' rather than diversifying approach to cooperative investment is beneficial under a volatile social environment.

4. Discussion

Our model shows the fragility of the intuitive prediction that stable social environments should favour individuals that develop few but strong relationships, while volatile social environments favour those whose social networks end up 'broad but shallow'. Our model shows that the premises on the benefits associated with a diversifying cooperative strategy hold: 'broad and shallow' social networks can prove beneficial because they reduce the temporal variance in cooperative returns caused by unpredictable changes in partner availability (as argued by [11]). Nevertheless, our model also highlights that the evolution of cooperative strategies does not depend solely on the performance of the social networks once they are built. When accounting for the costs associated with the build-up of such social networks, selection can lead to the precise opposite outcome: volatility selects for focused network building.

The reason is clear once reciprocity theory is linked to theories of senescence, specifically antagonistic pleiotropy that hypothesizes that alleles that enhance fitness early in life but are detrimental later can be favoured because selection is stronger early in life than late in life [36,37]. Diversifying cooperative investments can be beneficial late in life (once the individual has built its social network), but this is preceded by a substantial cost early in life while the network has to be built. Since the probability to reach a sufficiently old age is low in volatile environments, the negative effect early in life predominates, and the successful strategy is one that focuses cooperative investments on few partners. Focusing allows individuals to build strong partnerships more quickly while also exploiting existing social bonds (including those with relatives, and inherited ones). It is notable that a strategy that focuses reciprocal interactions on few individuals is able to spread in a population, even though it clearly has the potential to lead to a disastrous loss of all 'friends' for some individuals. Our model accounts for this cost, and simply shows that the beneficial effects of a focused strategy are on average better than those of a diversifying one.

Pleiotropic effects are also discussed in the field of social behaviour, where it has been suggested as a mechanism stabilizing cooperation in slime moulds and bacteria [38] (but

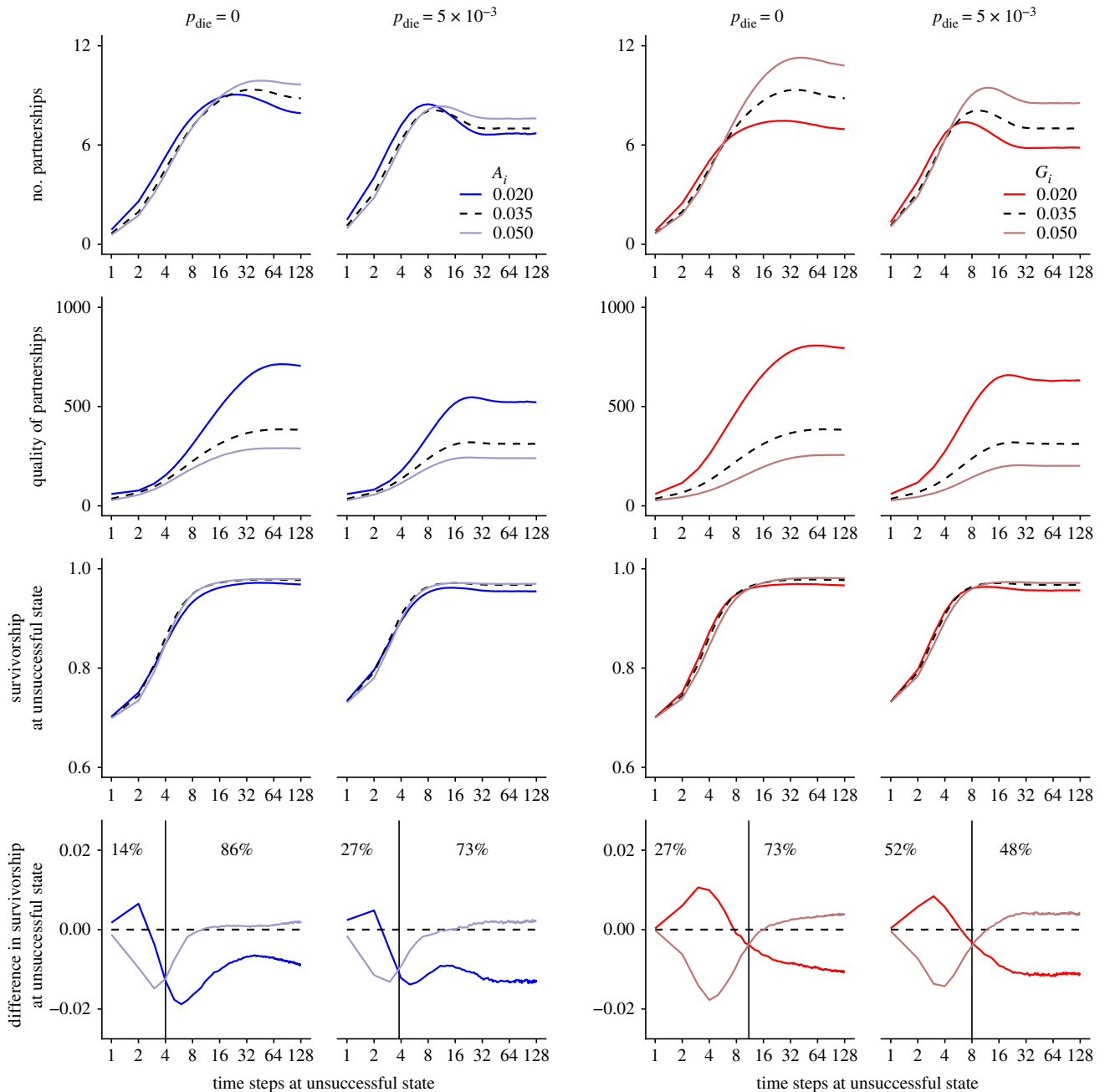


Figure 4. Characteristics of social relationships and survivorship of one individual i depending on its age and on its trait value in a population where $A_j = G_j = 0.035$ for all other individuals j either under a stable social environment or under a volatile social environment ($p_{\text{die}} = 5 \times 10^{-3}$). The mutant individual i differ either by its trait value A_i (in blue) or by its trait value G_i (in red). From top to bottom, we represent the quantity of relationships (following the criterion $Q(i,j) > 10$), the quality of relationships ($Q(i,j)$), survivorship and difference of survivorship compared with other individuals in the population. In the last row, the vertical line delimits age categories where investing in few relationships (trait value = 0.02; dark colour) is beneficial compared with investing in many relationships (trait value = 0.05; light colour) and vice versa. Percentages correspond to the proportion of individuals in each of those two age categories. (Online version in colour.)

see [39]). These cases, however, do not have the same pleiotropic structure as the one we consider. We focus on a situation where pleiotropy is clearly age-dependent, and our question is also different: we do not consider whether cheats can spread and destroy cooperation, instead we ask how reciprocal cooperation deals with the quantity-quality trade-off ‘beyond the dyad’ (as advocated by Connor [19]). It is of interest to note that the field of social behaviour is generally starting to realize that the social environment is very likely different for individuals differing in their age; Croft *et al.* [40] discuss this with respect to kinship (see also [41]). Our work shows that the social state, i.e. the position of an individual within its network of social partners and the properties of this network, can be age-dependent in a manner that

can switch selection from favouring narrowing this network down or broadening it further.

In our model, pleiotropy arises from differences in the exploitation of existing social bonds but also from differences in the speed at which social bonding takes place. What is known as ‘social bet-hedging strategy’ refers to a diversifying approach to social relationships and via the quality–quantity trade-off, we have shown it associates with slow social bonding. Cooperation typically relies on some form of assortment [42,43], which involves individual recognition and social bond formation (at least in the type of organisms that our model is inspired from). We know very little on how social bonds initially form, especially when they entail investments of time and energy. Social bonding may be characterized by a

raise in cooperative investments over time, as long as reciprocal cooperation takes place [44,45]. In our knowledge, however, the speed at which social bonding takes place has rarely been assessed (but see [45]). Our model shows that the speed at which social bonding takes place is likely to have a strong impact on the evolution of cooperative strategies because most of social bondings occur early in life.

It is interesting to reflect on the pitfalls of intuition. Intuition often involves ‘putting oneself in another organism’s shoes’—in sometimes fallible ways [46]. In the current context, intuition may be based on imagining what one should ideally have done, given the sudden death of a social partner. Clearly, having built a broad network helps to recover future fitness prospects, mitigating the current loss. Strangely, intuition does not prompt us to reflect equally much on the possibility that death might target ‘oneself’ (the focal individual). Yet volatility obviously also strikes, with some regularity, this way, and now the hope is that one did whatever one could to maximize performance until that age; death made performance at later ages unmeasurable and irrelevant. If intuition only considers actions and their benefits among those who keep avoiding death themselves, it falls victim to the well-known effects of ‘survivorship bias’.

Survivorship bias also is a tough problem for the empirical aspects of the question, as data collection on behavioural details can, logically, only be based on observations involving current survivors. While frustrating, this also helps to understand apparent discrepancies between data and our model. Losses of individuals whose networks did not help them avoid death create a process of selective disappearance within each cohort. This makes it exceedingly hard to collect unbiased data: unless one traces social bonds longitudinally and records every death, any analysis among living individuals will pay disproportionate attention to the successful subset of individuals who are presently observable by virtue of being alive—a problem which applies to a wide range of taxa (beyond bats), whenever aiming to document effects of the quantity versus quality of social relationships [11,28–34]. Whenever disappearance is selective (not random), the problem is exacerbated by the fact that situations where selection is at its strongest also produce the most severe data collection biases. To help solve this conundrum, future empirical studies paying particular attention to the longitudinal aspect of individual lives (and the age-dependent dynamics of their networks) could shed new light onto the question of well performing networks and their temporal trade-offs.

One notable study with a temporal aspect is the one by Testard *et al.* [47], where the authors showed that macaques diversified their social relationships after their population was devastated by a hurricane. We believe that the discrepancies between this result and our theoretical predictions can be explained. First, such a dramatic event is far from the level of instability we modelled, and second, the observed changes in cooperative behaviours in those macaques were an example of plasticity, not an evolutionary response to permanent volatility that would select for a different type of behaviour due to individuals routinely dying young. Testard *et al.*'s [47] study therefore highlights some limits of our modelling approach. It is a clear avenue for future work to consider plasticity, as expression of behaviours is often remarkably sensitive to environmental conditions [48].

Plasticity could also make traits age-dependent and also perhaps dependent on the state of one's own network: cooperative behaviours could change through life. If one's social network is already broad enough, one may change its cooperative strategy and stop expanding it further. Such age-dependent and/or network state-dependent plasticity has received some empirical support in rhesus macaques, where older females engage less in the social environment compared to younger ones [49], and should therefore be investigated in future theoretical studies. Based on our predictions, a strategy focusing cooperative investment on few partners at early age and diversifying cooperative investment on many partners at old age could conceivably be optimal. However, note that a social network of an individual at any point in its life is an accumulation of an entire ‘career’ of work towards it. Even if behavioural changes are possible, it is not clear that an adjustment schedule is able to choose performance in early life such that two goals are simultaneously optimized: to have as good as possible fitness should death happen at a relatively young age, and, should early death not occur, to ‘prepare’ the individual's social network to allow best possible capitalization of the gains that follow from a switch in strategy (since any attempt to broaden the network must start from where early-age efforts ended). Since it is never clear how long an individual life will last, antagonistic pleiotropy may be unavoidable even under plastic social traits.

As a whole, our model highlights the importance of population age structure for the evolution of social traits such as cooperative behaviours. The evolution of social traits has been traditionally studied using evolutionary game theory [50] and quantitative genetics [51], without much emphasis on the implication of demography. Recent studies have started to uncover the role of spatial structure for the evolution of social traits (e.g. [52–54]), but little is known on the role of age structure (but see [41] for an age-dependent kin-selection model). We appreciate that our individual-based modelling approach comes with its limits, including the absence of analytical insights; we hope however that the predictions of our model will stimulate further theoretical and empirical investigations assessing the role of population age structure for the evolution of social traits.

Data accessibility. All code needed to reproduce the analyses are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.k6djh9w87> [55].

The data are provided in electronic supplementary material [56].

Authors' contributions. T.G.A.: conceptualization, formal analysis, investigation, methodology, software, validation, visualization, writing—original draft, writing—review and editing; H.K.: conceptualization, funding acquisition, methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. This research was supported by grants from the Swiss National Science Foundation and from the National Science Foundation.

Acknowledgements. We thank G. G. Carter for discussion and inspiration. We also thank D. R. Farine, M. Servedio, B. Lerch, K. Xu and two anonymous reviewers for comments that have helped improve our manuscript. Simulations were performed on the computing cluster of the Science Cloud platform of the University of Zurich.

1. West SA, Griffin AS, Gardner A. 2007 Evolutionary explanations for cooperation. *Curr. Biol.* **17**, R661–R672. (doi:10.1016/j.cub.2007.06.004)
2. West SA, Cooper GA, Ghoul MB, Griffin AS. 2021 Ten recent insights for our understanding of cooperation. *Nat. Ecol. Evol.* **5**, 419–430. (doi:10.1038/s41559-020-01384-x)
3. Hamilton WD. 1964 The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**, 1–16. (doi:10.1016/0022-5193(64)90038-4)
4. Bourke AFG. 2011 The validity and value of inclusive fitness theory. *Proc. R. Soc. B* **278**, 3313–3320. (doi:10.1098/rspb.2011.1465)
5. Kay T, Keller L, Lehmann L. 2020 The evolution of altruism and the serial rediscovery of the role of relatedness. *Proc. Natl Acad. Sci. USA* **117**, 28 894–28 898. (doi:10.1073/pnas.2013596117)
6. Trivers RL. 1971 The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57. (doi:10.1086/406755)
7. Axelrod R, Hamilton WD. 1981 The evolution of cooperation. *Science* **211**, 1390–1396. (doi:10.1126/science.7466396)
8. Clutton-Brock T. 2009 Cooperation between non-kin in animal societies. *Nature* **462**, 51–57. (doi:10.1038/nature08366)
9. Rand DG, Arbesman S, Christakis NA. 2011 Dynamic social networks promote cooperation in experiments with humans. *Proc. Natl Acad. Sci. USA* **108**, 9193–19 198. (doi:10.1073/pnas.1108243108)
10. Wilkinson GS. 1984 Reciprocal food sharing in the vampire bat. *Nature* **308**, 181–184. (doi:10.1038/308181a0)
11. Carter GG, Farine DR, Wilkinson GS. 2017 Social bet-hedging in vampire bats. *Biol. Lett.* **13**, 20170112. (doi:10.1098/rsbl.2017.0112)
12. Packer C. 1977 Reciprocal altruism in *Papio anubis*. *Nature* **265**, 441–443. (doi:10.1038/265441a0)
13. Lehmann J, Korstjens AH, Dunbar RIM. 2007 Group size, grooming and social cohesion in primates. *Anim. Behav.* **74**, 1617–1629. (doi:10.1016/j.anbehav.2006.10.025)
14. Schino G, Aureli F. 2008 Grooming reciprocity among female primates: a meta-analysis. *Biol. Lett.* **4**, 9–11. (doi:10.1098/rsbl.2007.0506)
15. Fischer EA. 1984 Egg trading in the chalk bass, *Serranus tortugarum*, a simultaneous hermaphrodite. *Ethology* **66**, 143–151. (doi:10.1111/j.1439-0310.1984.tb01361.x)
16. Hart MK, Kratter AW, Crowley PH. 2016 Partner fidelity and reciprocal investments in the mating system of a simultaneous hermaphrodite. *Behav. Ecol.* **27**, 1471–1479. (doi:10.1093/beheco/arw065)
17. McDonald DB. 2007 Predicting fate from early connectivity in a social network. *Proc. Natl Acad. Sci. USA* **104**, 10 910–10 914. (doi:10.1073/pnas.0701159104)
18. Dakin R, Ryder TB. 2020 Reciprocity and behavioral heterogeneity govern the stability of social networks. *Proc. Natl Acad. Sci. USA* **117**, 2993–2999. (doi:10.1073/pnas.1913284117)
19. Connor RC. 2010 Cooperation beyond the dyad: On simple models and a complex society. *Phil. Trans. R. Soc. B* **365**, 2687–2697. (doi:10.1098/rstb.2010.0150)
20. Cantor M *et al.* 2021 The importance of individual-to-society feedbacks in animal ecology and evolution. *J. Anim. Ecol.* **90**, 27–44. (doi:10.1111/1365-2656.13336)
21. Noë R, Hammerstein P. 1995 Biological markets. *Trends Ecol. Evol.* **10**, 336–339. (doi:10.1016/s0169-5347(00)89123-5)
22. Ohtsuki H, Hauert C, Lieberman E, Nowak MA. 2006 A simple rule for the evolution of cooperation on graphs and social networks. *Nature* **441**, 502–505. (doi:10.1038/nature04605)
23. Delton AW, Krasnow MM, Cosmides L, Tooby J. 2011 Evolution of direct reciprocity under uncertainty can explain human generosity in one-shot encounters. *Proc. Natl Acad. Sci. USA* **108**, 13 335–13 340. (doi:10.1073/pnas.1102131108)
24. Akçay E. 2020 Deconstructing evolutionary game theory: coevolution of social behaviors with their evolutionary setting. *Am. Nat.* **195**, 315–330. (doi:10.1086/706811)
25. Dunbar RIM. 1992 Neocortex size as a constraint on group size in primates. *J. Hum. Evol.* **22**, 469–493. (doi:10.1016/0047-2484(92)90081-J)
26. Tamarit I, Cuesta JA, Dunbar RIM, Sánchez A. 2018 Cognitive resource allocation determines the organization of personal networks. *Proc. Natl Acad. Sci. USA* **115**, 8316–8321. (doi:10.1073/pnas.1719233115)
27. Ozaktas HM. 1996 The optimal number of friends in the information age. Paper presented at the First International-Traditional Fool-Proof Research Symposium, Drexel University, Philadelphia, PA.
28. Sato Y, Zenou Y. 2015 How urbanization affect employment and social interactions. *Eur. Econ. Rev.* **75**, 131–155. (doi:10.1016/j.eurocorev.2015.01.011)
29. Vacca R. 2019 Structure in personal networks: constructing and comparing typologies. *Netw. Sci.* **8**, 142–167. (doi:10.1017/nws.2019.29)
30. Silk J, Cheney D, Seyfarth R. 1999 The structure of social relationships among female savanna baboons in Moremi reserve, Botswana. *Behaviour* **136**, 679–703. (doi:10.1163/156853999501522)
31. Ellis S, Snyder-Mackler N, Ruiz-Lambides A, Platt ML, Brent LJJ. 2019 Deconstructing sociality: the types of social connections that predict longevity in a group-living primate. *Proc. R. Soc. B* **286**, 20191991. (doi:10.1098/rspb.2019.1991)
32. Morrison RE, Eckardt W, Stoinski TS, Brent LJJ. 2020 Comparing measures of social complexity: larger mountain gorilla groups do not have a greater diversity of relationships. *Proc. R. Soc. B* **287**, 20201026. (doi:10.1098/rspb.2020.1026)
33. Menz CS, Carter AJ, Best EC, Freeman NJ, Dwyer RG, Blomberg SP, Goldizen AW. 2020 Higher sociability leads to lower reproductive success in female kangaroos. *R. Soc. Open Sci.* **7**, 200950. (doi:10.1098/rsos.200950)
34. Bond ML, Lee DE, Farine DR, Ozgum A, König B. 2021 Sociability increases survival of adult female giraffes. *Proc. R. Soc. B* **288**, 20202770. (doi:10.1098/rspb.2020.2770)
35. Snyder-Mackler N *et al.* 2020 Social determinants of health and survival in humans and other animals. *Science* **368**, eaax9553. (doi:10.1126/science.aax9553)
36. Williams GC. 1957 Pleiotropy, natural selection, and the evolution of senescence. *Evolution* **11**, 398–411. (doi:10.2307/2406060)
37. Flatt T, Partridge L. 2018 Horizons in the evolution of aging. *BMC Biol.* **16**, 93. (doi:10.1186/s12915-018-0562-z)
38. Foster KR, Shaulsky G, Strassmann JE, Queller DC, Thompson CRL. 2004 Pleiotropy as a mechanism to stabilize cooperation. *Nature* **431**, 693–696. (doi:10.1038/nature02894)
39. Dos Santos M, Ghoul M, West SA. 2018 Pleiotropy, cooperation, and the social evolution of genetic architecture. *PLoS Biol.* **16**, e2006671. (doi:10.1371/journal.pbio.2006671)
40. Croft DP, Weiss MN, Nielsen MLK, Grimes C, Cant MA, Ellis S, Franks DW, Johnstone RA. 2021 Kinship dynamics: patterns and consequences of changes in local relatedness. *Proc. R. Soc. B* **288**, 20211129. (doi:10.1098/rspb.2021.1129)
41. Rodrigues AMM. 2018 Demography, life history and the evolution of age-dependent social behaviour. *J. Evol. Biol.* **31**, 1340–1353. (doi:10.1111/jeb.13308)
42. Fletcher JA, Doebeli M. 2009 A simple and general explanation for the evolution of altruism. *Proc. R. Soc. B* **276**, 13–19. (doi:10.1098/rspb.2008.0829)
43. Garcia T, Doucier G, De Monte S. 2015 The evolution of adhesiveness as a social adaptation. *Life* **4**, e08595. (doi:10.7554/eLife.08595)
44. Roberts G, Sherratt TN. 1998 Development of cooperative relationships through increasing investment. *Nature* **394**, 175–179. (doi:10.1038/28160)
45. Carter GG, Farine DR, Crisp RJ, Vrtiljek JK, Ripperger SP, Page RA. 2020 Development of new food-sharing relationships in vampire bats. *Curr. Biol.* **30**, 1275–1279. (doi:10.1016/j.cub.2020.01.055)
46. Kokko H. 2017 Give one species the task to come up with a theory that spans them all: what good can come out of that? *Proc. R. Soc. B* **284**, 20171652. (doi:10.1098/rspb.2017.1652)
47. Testard C *et al.* 2021 Rhesus macaques build new social connections after a natural disaster. *Curr. Biol.* **31**, 2299–2309. (doi:10.1016/j.cub.2021.03.029)
48. Snell-Rood EC. 2013 An overview of the evolutionary causes and consequences of behavioural plasticity. *Anim. Behav.* **85**, 1004–1011. (doi:10.1016/j.anbehav.2012.12.031)
49. Brent LJJ, Ruiz-Lambides A, Platt ML. 2017 Family network size and survival across the lifespan of

- female macaques. *Proc. R. Soc. B* **284**, 20170515. (10.1098/rspb.2017.0515)
50. McNamara JM, Leimar O. 2020 *Game theory in biology*. Oxford, UK: Oxford University Press.
51. McGlothlin JW, Akçay E, Brodie III ED, Moore AJ, Van Cleve J. 2021 A synthesis of game theory and quantitative genetic models of social evolution. *bioRxiv*. (doi:10.1101/2021.03.27.437341)
52. Débarre F, Hauert C, Doebeli M. 2014 Social evolution in structured populations. *Nat. Commun.* **5**, 3409. (doi:10.1038/ncomms4409)
53. Peña J, Wu B, Traulsen A. 2016 Ordering structured populations in multiplayer cooperation games. *J. R. Soc. Interface* **13**, 20150881. (doi:10.1098/rsif.2015.0881)
54. Su Q, Li A, Wang L, Eugene Stanley H. 2019 Spatial reciprocity in the evolution of cooperation. *Proc. R. Soc. B* **286**, 20190041. (doi:10.1098/rspb.2019.0041)
55. Aubier TG, Kokko H. 2022 Data from: Volatile social environments can favour investments in quality over quantity of social relationships. Dryad Digital Repository. (doi:10.5061/dryad.k6djh9w87)
56. Aubier TG, Kokko H. 2022 Volatile social environments can favour investments in quality over quantity of social relationships. Figshare.