Quality, quantity, and the adaptive function of social relationships

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Abstract

Affiliative social relationships have clear links to fitness in many species, yet exactly why that is the case remains elusive. We unify theory from socio-ecology and network science to set forth testable predictions of how individuals should invest in their social relationships given the relative benefits of different social strategies across environmental contexts. We propose that relationship quality provides access to social support, which can help animals faced with local pressures such as contest competition, while relationship quantity provides access to social tolerance, which can help with global pressures such as predation. The Adaptive Relationship Framework sets the foundation for the systematic study of how social and ecological pressures drive adaptive variation in the quality and quantity of social relationships.

Social relationships: key predictors of individual fitness

Social interactions are an integral part of animal life. Rather than interacting with conspecifics at random, individuals from many species have specific partners they sleep near, travel, feed, groom, preen, huddle with and vocalise to [1]. From those repeated affiliative, or friendly, interactions emerge affiliative relationships [hereafter "**social relationships**", see Glossary; 2]. Together, those relationships result in a **social structure** that shapes how individuals experience their day-to-day environment, influencing their ability to obtain food, avoid predators, attract mates, and care for their young [1, 3]. It is therefore not surprising that social relationships are a key predictor of individual fitness, consistently emerging as having strong effects on survival and reproductive success across a variety of taxa [4-7].

This link to fitness proxies underscores that social relationships can be evolutionarily adaptive. Yet, a major question remains: Why exactly do social relationships help individuals? What do well-connected individuals obtain from their social partners that allows them to survive and reproduce to a greater extent than their less socially connected counterparts? While individual studies have begun to shed light on the potential pathways linking social relationships to fitness benefits, consolidating these

findings and identifying general trends in the adaptive function of social relationships has proven challenging [5, 8]. This difficulty stems from two interrelated issues: (1) the multitude of potential pathways linking social relationships to fitness [5, 9] and (2) the diversity of social relationships that animals form, from superficial associations to strong, long-term bonds [10, 11]. Because of this, it remains unclear which types of social relationships are adaptive in a given context, and why. A framework integrating these two issues is needed to guide systematic research and reveal broad patterns in the adaptive function of social relationships. To this end, we draw on two well-established approaches – socio-ecological theory, which provides predictions for pathways linking sociality to fitness, and network science, which provides concepts and tools to quantify social connections – to put forward the Adaptive Relationships Framework.

A socio-ecological approach to revealing the pathways linking social relationships and fitness

Socio-ecological theory provides a foundation from which to make sense of the multiple potential pathways linking social relationships to fitness. Socio-ecological theory states that social and ecological risks and resources shape **social organisation**, social structure, mating systems and care systems, the core components of social systems [1, 12]. These ideas have led to significant advances in our understanding of the evolution of social processes, including group-living, dispersal patterns and the distribution of reproduction [12, 13].

Yet, while the socio-ecological basis for variation in social organisation and mating systems has been studied extensively [3, 12], less attention has been given to social structure (i.e., the patterning of social interactions among individuals). One clear exception can be found in nonhuman primates where social relationships among females are hypothesised (with mixed empirical support to date: [13]) to be shaped by competition over food and the risk of predation and infanticide [14]. Extending the idea that socio-ecological pressures shape social structure to a broader range of taxa—capturing greater variation in both ecological conditions and social systems—could yield significant insights, as many species (whether obligatorily social or not [15, 16]) form social relationships, which are ultimately shaped by their social and ecological contexts.

Relationship quality and quantity – network science and two fundamental dimensions of social relationships

The second challenge to revealing the adaptive function of social relationships is the diversity of relationships that individuals can form. **Social network** science is particularly useful in this context, as it provides a structured way to examine the different types of relationships that exist and the benefits they may offer. One of the most influential theories in this field posits that relationships of different strengths—strong bonds and weak ties—serve inherently different functions that can only be fully understood when considered within the context of the broader social structure [17]. Strong bonds are reliable partnerships that provide critical support, while weak ties

act as bridges to the broader social network, facilitating access to resources and information. This idea that weak ties can serve an alternative but equally important function as strong bonds, also referred to as the "strength of weak ties" has been pervasive in human behavioural and network sciences. More recently it has begun to take hold in behavioural and evolutionary ecology [18, 19], with growing recognition that animal social relationships range from strong, lifelong bonds with a few partners, to weaker, more transient ties that connect individuals more widely within their social networks [10, 11, 20].

Beyond representing strong and weak ties, we propose that these different types of relationships reflect differences in the allocation and size of **social investments**. Specifically, the diversity in social relationships essentially revolves around two key factors: how an individual allocates its social investment among potential partners and the level of investment an individual makes in each of its partners. These factors result in two fundamental dimensions of social relationships: **relationship *quantity***, an individual's number of relationships and how integrated they are in the wider social network, and **relationship *quality***, the relative strength and stability of each of their relationships (Box 1).

Box 1: What are relationship quantity and quality?

Intuitively, relationship quantity is simply the number of social relationships an individual has, and relationship quality is the strength of those relationships. But from a network perspective, it is more complex than that.

Specifically, one key feature of relationship quantity is not just that individuals have many social partners, but also the resulting indirect connections that emerge from those relationships (e.g. the partners of an individual's partners), which ultimately facilitate better integration in the overall social network [21-23]. Indeed, the "strength of weak ties" idea was proposed to encompass exactly those elements – that weak ties yield benefits because they allow individuals to be connected to individuals in the network other than their direct social partners [17].

Relationship quality is also more than just the strength of social relationships. There are other important components of relationships that define their quality, including their stability, predictability and interdependence, all of which require repeated interactions over time to develop [20, 24, 25]. In addition, it is not the absolute strength of relationships that determines their quality, but their *relative* strength (Fig. 1 & 2): quality relationships are those that are stronger, more stable, and clearly differentiated from an individual's other relationships, reflecting selective investment in a few preferred social partners [26, 27].

These considerations are particularly important when comparing relationship quantity and quality across taxa or studies. For instance, it is important to consider

whether indirect connections are included in a study's measure of quantity, and how their inclusion or exclusion might affect conclusions. Similarly, measures of quality should focus on relative strength—how much stronger certain relationships are compared to others—rather than absolute strength, in order to capture variation in social investment across studies.

The biological significance of relationship quantity and quality is supported by empirical results linking these two dimensions to fitness proxies across taxa [4-7]. For example, individuals with more connections or who are better indirectly connected to their networks live longer in some species [28-30], while individuals with strong and stable relationships live longer in others [31-33]. Comparative research across species revealed that measures of relationship quality and quantity are often only moderately, or even negatively, correlated [10, 11, 18, 34], suggesting that they represent two distinct dimensions of an individual's social network. A key question we now need to address is what selective pressures favour relationship quantity or quality.

Here, we unify the idea that social relationships vary along dimensions of quantity and quality with classic socio-ecological theory to propose testable predictions for the adaptive function of social relationships in The Adaptive Relationships Framework (Fig. 1). The goal of the framework is to move beyond linking social relationships to fitness, and toward establishing the relative benefits of investing in different social strategies across environmental contexts.

The Adaptive Relationships Framework

The Adaptive Relationships Framework outlines the broad socio-ecological pressures that animals face, identifies the **social solutions** that can help meet these pressures, and puts forward testable predictions for the **social strategies** and emergent structures that help animals gain access to these solutions (Fig. 1). Social relationships have evolved because they can help animals cope with challenges in their environments, such as avoiding predators, accessing resources, or receiving support during conflicts. Some of these social solutions are best achieved by having strong, reliable partners, while for other solutions being connected to the wider network matters more than the quality of relationships to specific partners. Animals should therefore adopt distinct social strategies: investing in strong bonds with a few key partners (prioritising relationship quality), expanding their network to include many connections (prioritising relationship quantity), or some optimal balance of both (Fig. 2).

Although for the sake of simplicity we begin by presenting the pathways from socio-ecological pressures to different social solutions, strategies and structures as distinct, it is important to bear in mind that these pathways are not mutually exclusive and exist on a continuum, with the relative benefits of investing more in relationship quality or quantity depending on the specific set of pressures faced (Fig. 2). We expand

on the discrete steps of this framework below and provide example case studies in support of these ideas.

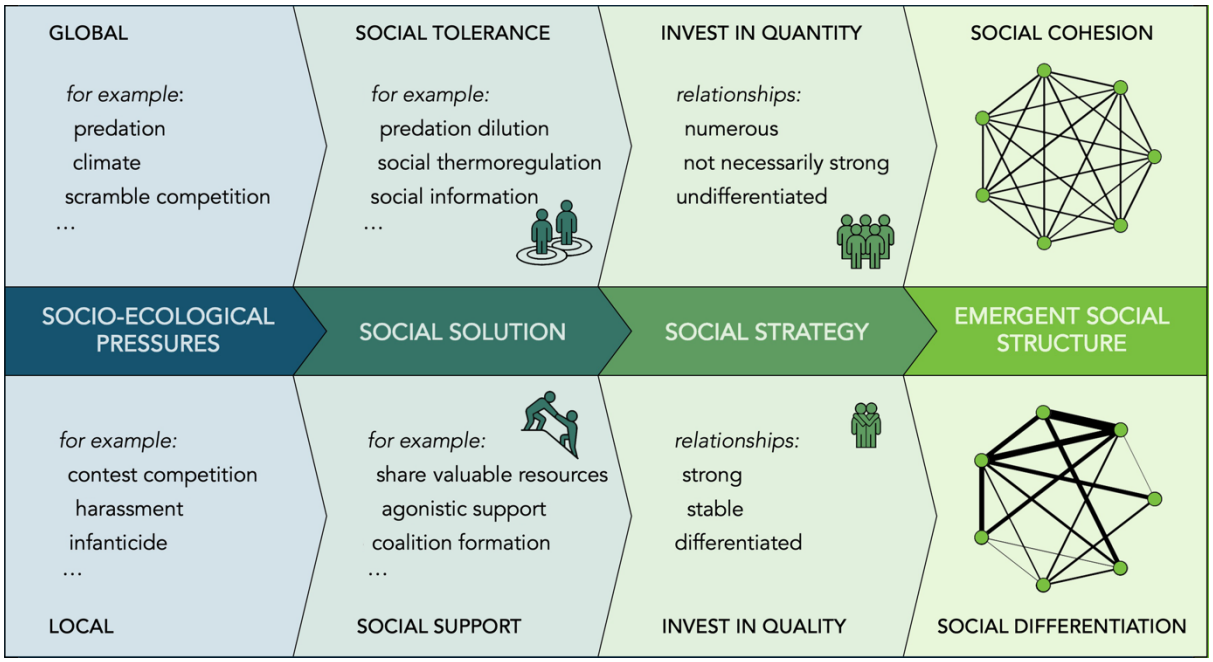

Fig. 1: **The Adaptive Relationships Framework**. We propose that socio-ecological pressures are best addressed by distinct social solutions, driving animals to adopt different social strategies and resulting in diverse social structures. Animals that experience pressures manifested at a global scale, including harsh climate and predation, can benefit from tolerance in their social environment and are predicted to invest in a social strategy characterised by its *quantity*, maximising the number of others they are connected to and resulting in cohesive and non-modular social structures. Animals that experience pressures manifested more locally, such as contest competition amongst group mates, can benefit from support from their social partners and are predicted to invest in a social strategy characterised by its *quality*, investing in a few strong and stable relationships with specific others and resulting in highly differentiated social structures. Although these pathways are presented as distinct, they exist on a continuum (Fig. 2): pressures are often not strictly local or global and animals frequently encounter multiple socio-ecological challenges at once, requiring them to balance diverse social solutions and strategies. While we focus here on the benefits of social relationships, we note that they also often come with costs, and we only expect relationships to evolve when the benefits they provide outweigh these costs.

From socio-ecological pressures to social solutions: Do you need social tolerance or social support?

Animals face a wide range of pressures in their environment, which can be broadly categorised as either global or local (Fig. 1). Forming social relationships is one way to cope with these pressures, offering adaptive benefits such as **social tolerance** and

social support. Here, we focus on these social solutions to predict how different types of pressures shape which types of social relationships may be adaptive.

Global pressures, such as climate and predation, impact entire groups or populations. That is, all individuals are exposed to the cold and are at risk of predation. These pressures can be addressed by social tolerance, which allows individuals to remain close to others and move freely within their social environment. Global pressures have long been recognised as key evolutionary forces that drive animals to group together, whether in fluid, temporary aggregations or stable social groups [1, 35]. What we propose here is that, even within these aggregations, animals who are better tolerated by others gain advantages in facing these pressures. For instance, social tolerance offers safety in numbers, mitigating the risk of predation [36]. Redshanks (*Tringa totanus*) at the margins of flocks are more likely to be targeted by sparrowhawks (*Accipiter nisus*; [37]), while vervet monkeys (*Chlorocebus pygerythrus*) that are more integrated into their social networks experience lower predation risk, benefiting from both reduced vigilance and increased foraging time [38].

Social tolerance can also offer advantages in scramble competition, an indirect form of competition where individuals aim to exploit resources before others [39]. In such contexts, tolerance from social partners can allow individuals to feed together on non-defendable resources with minimal conflict. Female plains zebras (*Equus burchelli*) and eastern grey kangaroos (*Macropus giganteus*), for example, co-feed peacefully in groups due to high social tolerance [40, 41]. Additionally, social tolerance can enhance foraging efficiency by reducing vigilance and facilitating the sharing of social information about resource availability and opportunities to detect or exploit food [42]. For instance, small passerine birds (family *Paridae*) who are more central in their social networks are more likely to locate and exploit novel foraging patches than less central individuals [43].

Tolerance can also help animals cope with climatic conditions through social thermoregulation [44]. Walrus (*Odobenus rosmarus*) calves and females tend to position themselves in the most central parts of the herd, where they benefit from greater protection against both the cold and predators [45]. Barbary macaques (*Macaca sylvanus*) form larger huddles during cold winters, which increases their chances of survival [30]. Similarly, rhesus macaques (*Macaca mulatta*) cope more effectively with extreme heat by tolerating each other in shaded areas (Box 2).

Local pressures, on the other hand, arise at the level of individual interactions within the social system and affect individuals differently. Those pressures, such as contests over monopolisable resources, harassment and exposure to socially transmitted pathogens, are key costs of the presence of others. Rather than having many partners that are mere associates, local pressures are better met by having socially supportive partners that can help individuals navigate conflicts and compete with others.

Social support can play a crucial role in contest competition, for example, where individuals directly compete for valuable, defendable resources like clumped food, mates, or territories [39]. In such contexts, receiving social support in the form of

alliances or coalitions can greatly improve an individual's chances of securing valuable resources [46]. For example, male bottlenose dolphins (*Tursiops aduncus*) form stable, long-term alliances to defend females from rivals (Box 2), and grey wolves (*Canis lupus*) share meat with their social partners [47].

Social support not only directly facilitates resource acquisition but can also help individuals achieve and maintain higher dominance rank, which can further improve their priority of access to resources [48]. Common ravens (*Corvus corax*) selectively support their social partners in conflicts, increasing both their own and their partners' positions in the dominance hierarchy [49]. Additionally, social support in agonistic encounters can mitigate the costs associated with competition. In rhesus macaques, for example, social support reduces the risk of potentially fatal injuries during conflicts [50].

Social support can also offer protection against threats like harassment, infanticide, and conflicts with rival groups. Female feral horses (*Equus caballus*) experience less harassment from males when they receive social support from other females [51], and female African lions (*Panthera leo*) form coalitions to defend their cubs against infanticide by intruding males [52]. In banded mongooses (*Mungos mungo*), entire groups collectively engage in risky intergroup conflicts over food and mates [53]. Similarly, in chimpanzees (*Pan troglodytes verus*), close social partners support each other in intergroup conflicts, risking serious injury or even death to do so [54].

Finally, social support can take the form of engaging in caregiving behaviours, such as grooming social partners to remove parasites or providing food to sick partners [55]. For instance, mandrills (*Mandrillus sphinx*), banded mongooses and vampire bats (*Desmodus rotundus*) will continue to groom their closest social partners, even when they are infected [56-58]. In grey wolves, the cost of infection can be mitigated by the presence of social partners, likely because sick individuals still get to eat even when they are unable to contribute much to the hunt [59].

From social solutions to social strategies: Should you invest in relationship quality or quantity?

To gain access to social tolerance or social support individuals need to adopt distinct social strategies (Fig. 2). For social tolerance, mutual benefits typically arise from the mere presence of others [60]. Individuals therefore do not need close or even differentiated relationships with specific others, but rather benefit from spreading their social investment across a broader network of tolerant partners. For example, female yellow-bellied marmots (*Marmota flaviventer*) with a greater number of social partners delay their flight response to predators [61], and have decreased summer mortality, which is primarily caused by predation [62]. Male killer whales (*Orcinus orca*) with a greater number of social partners have higher survival rates during food-scarce years [28], likely due to their ability to access social information about where to find salmon [63].

In contrast, social support involves partners taking significant risks for one another, such as providing active support in conflicts at the risk of personal injury, sharing valuable resources that could be kept for themselves, or increasing personal disease exposure by engaging with sick individuals. Such high-risk behaviours require stronger incentives to motivate individuals to incur these costs [64]. Here, strong and stable relationships are essential because they create fitness interdependence between social partners [24, 65]. As individuals invest in their relationship, they gradually build consistency and predictability, or 'mutual trust' [24, 66]. This reduces the risk of defection and increases the likelihood that support will be reciprocated in the future [24, 65]. For example, vampire bats will regurgitate blood to feed hungry roost-mates, but only perform this high-cost behaviour towards social partners with whom they have developed strong enough relationships [67]. Over time, social partners' fates become increasingly interconnected, motivating ongoing support [25]. For instance, female hyenas (*Crocuta crocuta*) and male Assamese macaques (*Macaca assamensis*) form coalitions with their closest allies to challenge higher-ranking individuals, increasing their own dominance rank and ultimately enhancing their reproductive success [27, 68-70]. Without continuous mutual support, both partners would lose their social status and the associated benefits.

We therefore predict that global socio-ecological pressures select for individuals who prioritise investing in relationship quantity, whereas in contexts of localised socio-ecological pressures, individuals are expected to invest in relationship quality. In the absence of constraints on realising these social strategies [71], and provided the benefits of doing so outweigh the costs, we would therefore expect individuals to form many social connections, regardless of their strength, when facing global pressures, and a few strong, stable social bonds with preferred partners when facing local pressures.

From social strategies to social structure: The emergence of cohesive or differentiated networks.

Selective pressures acting at the level of the individual scale up to impact social structure at the group or population level [2, 21, 72]. Socio-ecological pressures that select for social tolerance through relationship quantity will give rise to **cohesive**, non-modular social networks. In those networks, most individuals are connected to each other through relationships that are relatively similar between all pairs. For example, rock hyraxes (*Procavia capensis*), which are vulnerable to predation and rely on social information to navigate their fragmented habitat, have higher survival rates when living in cohesive networks with weakly differentiated relationships [73].

Conversely, pressures that select for social support through the formation of high-quality relationships will result in networks that are less cohesive, more **differentiated** and modular. In these networks, some pairs have strong connections, while others may only be weakly or indirectly connected, if at all. For example, female chacma baboons (*Papio hamadryas ursinus*), which form long-term cooperative alliances to maintain rank and access resources, have highly differentiated networks [74]. In those

networks, individuals focus most of their social time on a few strong relationships, and it is the strength and stability of those relationships that link to longevity [32].

These social structures are not just emergent properties of pairwise relationships, but also have their own benefits. For example, higher network cohesion facilitates more effective collective action [75, 76] and faster spread of information [77], while greater network differentiation and modularity slow the transmission of socially transmitted pathogens [78].

Box 2: Case Studies Illustrating the Adaptive Relationships Framework

Comprehensive tests of the Adaptive Relationships Framework require evidence across all its steps, along with the fitness consequences of the social strategy or structure in question. Although rare, evidence from some systems span most steps of the framework.

Figure I. Male bottlenose dolphin alliance partners (*Tursiops truncatus*)

Male bottlenose dolphins (*Tursiops truncatus*, Figure I) in Shark Bay, Western Australia, compete for access to females – this represents a localized pressure [79]. In line with the Adaptive Relationships Framework, male bottlenose dolphins form strong, long-term bonds with a few partners, with whom they herd females [80], ultimately increasing their reproductive success [81]. Across bottlenose dolphin populations, male alliances are more common at higher densities, further supporting the idea that quality relationships are beneficial in contexts where contest competition occurs [79, 82].

Figure II. Masai giraffes (*Girafa camelopardalis*)

Female Masai giraffes (*Girafa camelopardalis*, Figure II) need to locate food on the dry Tarangire savannah, Northern Tanzania – this represents a global pressure [83]. In line with the Adaptive Relationships Framework female giraffes who associate with a greater number of other females experience higher survival [29]. Relationship quantity likely allows for shared habitat use or access to information about food availability, although there is no direct evidence for this yet.

Quantifiable changes in socio-ecological pressures provide natural experiments to test the Adaptive Relationships Framework. For example, female rhesus macaques (*Macaca mulatta*) on Cayo Santiago, an island off the coast of Puerto Rico, typically rely on strong social bonds to navigate contest competition over resources, with relationship quality predicting lower injury risk and higher survival [10, 50]. However, a major hurricane drastically altered their environment, increasing the need for access to shade. In response to this newly important global pressure, and as would be predicted by the Adaptive Relationships Framework, monkeys expanded their networks to have a larger number of weaker ties, and relationship quantity became relatively more important in predicting survival [84].

Figure III. Rhesus macaques (*Macaca mulatta*) sharing a patch of shade

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It's more complicated, of course

We have thus far presented a framework that is a simplified version of reality—where groups or populations face a single socio-ecological pressure, need the corresponding social solution, which in turn determines the social strategy that individuals adopt and the resulting structure of their society. In reality, populations face multiple pressures simultaneously [13], and within these populations, individuals may experience different pressures or encounter the same pressures to varying degrees based on factors such as their age, sex, and reproductive status [18]. Moreover, socio-ecological pressures can be dynamic, shifting in predictable or unpredictable ways over time [85, 86].

Social solutions also exist on a continuum, reflecting the gradients of socio-ecological pressures to which they respond (Fig. 2). For example, while there are clear cases of scramble feeding competition– where relationship quantity provides social information and tolerance around non-defendable food patches [28, 41, 87] – and clear examples of contest competition – such as prey carcasses that can be defended by high-quality social partners who support each other [88, 89]– there are also food resources that are partly but not wholly defendable. In these cases, we expect selective tolerance of a few close partners – a midway point between quantity and quality [90, 91]. Similarly, dealing with predation ranges from predator dilution, which requires only social tolerance, to strategies that require more active social support to mob and repel predators [92, 93]. It is also important to note that social relationships are not universally adaptive, nor do they provide the only solutions available for coping with environmental challenges.

The social strategies outlined in this framework are not entirely distinct, and social relationships often provide access to both social tolerance and support to some extent. By investing in quality relationships individuals still maintain a network of partners

that tolerate them [10, 94], and while focusing on the quantity of relationships might initially result in a large number of weak connections, these can serve as the pool from which strong relationships may be built [95, 96]. Networks too aren't simply cohesive or differentiated, but instead most networks carry signatures of both cohesion and differentiation [97]. Finally, social relationships do not only bring benefits—they also come with costs. For instance, having many social partners can increase the risk of disease, make individuals more visible to predators, or reduce the share of food and other resources available [1, 98]. Similarly, forming strong bonds and supporting close partners can be risky and may limit opportunities to invest in other relationships [11]. Animals therefore need to carefully balance the costs and benefits of different social strategies, with the constellation and magnitude of the socio-ecological pressures faced determining whether they form social relationships, and tipping the balance between individuals prioritising quality or quantity (Fig. 2).

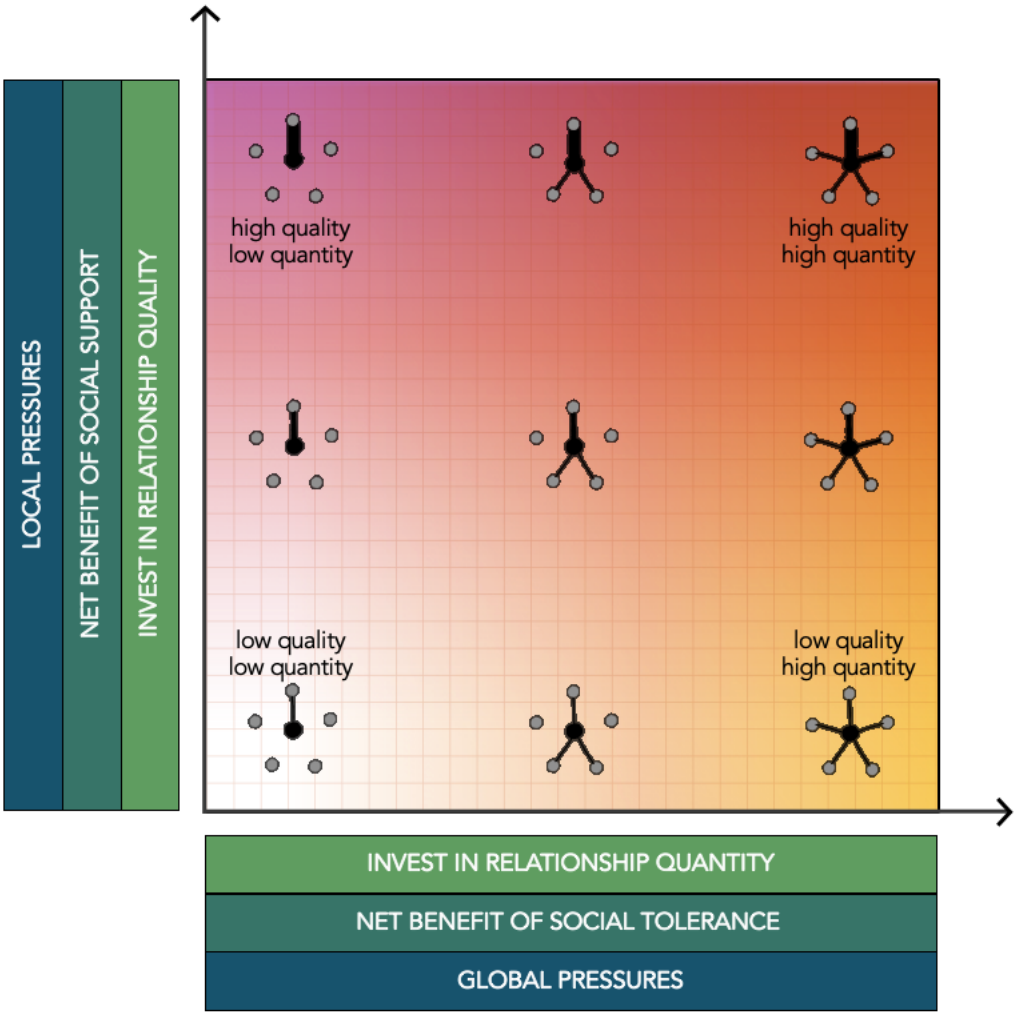

Fig. 2: Socio-ecological pressures and their corresponding social solutions and strategies exist on a continuum. Socio-ecological pressures are typically not strictly global or local but instead vary continuously from more global to more local. Consequently, the social solutions and strategies predicted by our framework (Fig. 1) also fall along a continuum. Each network in this figure represents an individual (central black node) and its potential social partners (grey nodes). The connections

represent social relationships, where thicker lines represent stronger relationships. The heat map illustrates four points: 1) as the extent to which individuals face local pressures that can be mitigated socially (y-axis) increases, the net benefit they may gain from high-cost, high-risk social support goes up and individuals should increasingly invest in relationship quality; 2) as the extent to which individuals face global pressures that can be mitigated socially (x-axis) increases, the net benefit they may gain from social tolerance goes up and individuals should increasingly invest in the quantity of their relationships; 3) when individuals face both global and local pressures that can be mitigated socially, they should invest in both the quality and quantity of their relationships accordingly (top right of figure); and 4) when individuals either do not face pressures that can be mitigated socially or when the costs of forming relationships outweigh the benefits, they are not expected to invest in either relationship quality or quantity (bottom left of figure). Note that increasing relationship quality does not simply mean that individuals strengthen all their social relationships, but rather that they increase their relative investment into their top partners (Box 1). As a result, the individual network in the top right is not simply a network with many strong relationships, but one with many relationships and a marked difference between the few strong relationships and the weaker ones.

The socio-ecological pressures and corresponding social solutions discussed here are not exhaustive, but illustrative examples meant to inspire further inquiry. For example, we have included infectious disease as a local pressure – something that comes about, in part, as a cost of socialising. But of course, disease exposure, avoidance, infection, and recovery can all intersect with social factors in myriad ways, dependent in part on the pathogen, its transmission pathways, virulence levels, and responsiveness of the immune system to it [55, 99]. The complexity of disease ecology warrants an entire framework with respect to the function of social relationships unto itself and has received only superficial treatment here.

Finally, social structure is inherently linked to social organization. In theory, an individual could form relationships with any other individual in their population. For instance, even species that spend most of their lives alone, whose social organization might be classed as solitary, can still exhibit a differentiated social structure, where they interact with some individuals in their population more than others [15, 16]. In practice, however, social organization (who individuals group with, and the size and stability of those groupings) strongly influence which social relationships are formed. The reverse is also true: grouping patterns can reflect certain individuals preferentially interacting. This interplay between social structure and organisation makes the scale at which social networks are defined—whether across an entire population or within more stable subgroups—especially important for drawing meaningful comparisons across species with different forms of social organization [71].

There are other important factors, such as kinship, life history, and demographic patterns, that we have not addressed but that interact with socio-ecological pressures to shape the required and realised functions of social relationships and structures. We refer to excellent reviews on how these factors impact social relationships [100-105].

By studying social relationships from these multiple angles, we can better disentangle the factors driving their variation, and integrating these perspectives will be essential for understanding their evolution.

Box 3: Testing the Adaptive Relationships Framework

The Adaptive Relationships Framework can be tested through observational studies of wild animals in their natural environments and experimental approaches in controlled settings, with each approach offering complementary insights [106]. Observational studies provide ecological relevance by examining social behaviour within the complexity of naturally occurring social and ecological pressures (Box 2). While there is much to learn from long-term study systems with extensive observational data and well-characterised social structures, it will be important to expand research to less well-studied taxa. Broadening research to cover more habitat types and the full spectrum of social organisation—spanning species that are solitary, form fluid associations, and live in stable social groups—will contribute to a more complete understanding of the evolution of social relationships across ecological and social contexts.

Comparisons across populations experiencing different socio-ecological pressures, or across years in which pressures vary within the same population, offer a powerful way to test the Adaptive Relationships Framework. While comparative research on social relationships has been hindered by challenges in compiling, standardising and analysing cross-species data [107], these issues are increasingly being addressed by methodological advancements and collaborative efforts to build comparative social databases [71, 108-110]. These initiatives are bound to yield insights into the ecological and evolutionary drivers of social relationships.

Emerging technologies will also be important for broadening the scope of studies on social relationships, enabling researchers to collect social data at larger scales and in challenging contexts. Tools such as drones, automated individual recognition, and tracking devices like GPS collars and accelerometers are increasingly making it possible to construct social networks in systems where traditional observational methods are difficult to execute (e.g., for animals that are nocturnal, aquatic, or live in remote locations) [111]. Environmental pressures can also be quantified using novel technologies—for example, remote sensing can be used to monitor temperature and track food availability, while camera traps can be used to estimate predator density [111].

Finally, experimental studies conducted in controlled settings offer a valuable counterpart to observational research. They allow for the systematic manipulation of specific socio-ecological pressures to test if such changes influence social relationships. For example, playbacks of predator vocalisations, experimental manipulations of food availability, or the removal of social partners could be used to test how individuals adjust their social relationships under heightened predation risk, varying resource conditions, or changes in group composition. These experiments

complement observational studies by enabling researchers to isolate and test the causal effects of specific pressures on social strategies [106].

Concluding remarks and future perspectives

Social relationships appear to have adaptive value across a wide range of taxa, but exactly why that is the case remains unclear. To fill this gap, we propose the Adaptive Relationships Framework, unifying classic socio-ecological theory with fundamental ideas from network science about different types of social relationships and their functions. Testing this framework will require systematic studies across taxa and environments (Box 3). These studies should not only quantify the fitness benefits of social relationships, but also compare the relative importance of relationship quality and quantity, and test why each dimension of sociality is adaptive by linking it to the social solutions those relationships provide. This approach will clarify two fundamental questions: (1) which types of social relationships are adaptive in a given socio-ecological context, and (2) which pathways link social relationships to fitness (see Outstanding Questions). With the Adaptive Relationships Framework, we provide predictions that are broad enough both conceptually and operationally to be tested across a variety of taxa (Box 3; [112]). Fully realising its potential will require expanding research beyond well-studied systems, measuring social relationships in ways that lend themselves to comparative approaches, and investigating the generative processes that underlie social relationships and networks (see Outstanding questions). Ultimately, this will generate broad insights into the factors that shape social relationships and societies across the animal world and will reveal the reasons why social relationships evolved.

Glossary

Relationship quality: The strength and stability of an individual's relationships relative to their other relationships. An individual who prioritises relationship quality invests in strong, enduring relationships with a few partners.

Relationship quantity: The number of relationships an individual has and how well it is integrated into its wider social network. An individual who prioritises relationship quantity spreads its social investment across many partners.

Social cohesion: The extent to which all individuals in a network are connected, regardless of the strength of their relationships. A cohesive network is one where most individuals are connected to each other.

Social differentiation: The extent to which the strength of relationships in a network varies. A differentiated network is one where some relationships are very strong, while others are weak or non-existent.

Social investment: The total amount of time and energy individuals devote to developing and maintaining their social relationships.

Social network: A representation and quantification of the social structure of a social unit.

Social organisation: The size and composition of a social unit, including the sex, age and kinship relationships of its members.

Social relationship: The nature and patterning of repeated interactions between two individuals. In this paper, we refer specifically to affiliative social relationships, which emerge from repeated positive interactions.

Social structure: The nature and patterning of social relationships among members of a social unit. In this paper, we refer specifically to the social structure of affiliative social relationships.

Social tolerance: Being allowed to remain in close proximity of social partners without receiving aggression, leading to higher social integration. Granting social tolerance involves little cost or risk and is often mutually beneficial.

Social support: Receiving active help, resource sharing, or care from social partners, which can offer protection in risky situations and access to valuable resources. Providing social support comes at high cost and risk and requires mutual trust between partners.

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