The power of touch: from survival to enduring, prosocial cooperation

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Abstract

Cooperation is a pivotal biological phenomenon that occurs in many forms. In species that engage in helping, individuals vary in association time and the extent of physical proximity, influencing the extent of touching between individuals. Here, we emphasize the importance of touch in the development and maintenance of parenting and mate bonds, and its link to cooperation. Touch activates a feedback loop via social hormones that supports bonds in general. Notably, extended parenting is crucial for the emergence of enduring bonds and the development of the mindset that supports investments which result in delayed benefits. We integrate these ideas in the 'caring-touch' hypothesis, highlighting the role of touch and enduring bonds in the evolution of different forms of cooperation.

Highlights

- Theories on cooperation have established the strategies, ecological settings and evolutionary pathways that support helping, but proximate mechanisms (e.g., hormones) remain poorly integrated in these frameworks.
- Although the hormone oxytocin regulates water and heat stress, it also supports maternal care and offspring bonding via touch.
- The caring-touch hypothesis emphasizes the role of the above mechanisms for the emergence of helping and highlights the strong intrinsic links between social bonding patterns, touch, and the way animals cooperate.
- Helping differs in individuals with ephemeral vs enduring bonds. Touch among enduringly bonded individuals supports the development of a caring mindset.
- Our integrative framework can provide fresh insights into the evolution of helping by uncovering the role of touch in supporting diverse forms of cooperation.

Keywords: evolution of cooperation; allo-grooming; allo-preening; friendships; social bonds; extended parental care

The evolution of cooperation and its links to social bonds

Cooperation is a pivotal biological phenomenon fuelling the evolutionary transitions from multicellularity to complex societies (e.g., colonial insects, humans) [1]. Although cooperation is sometimes defined as mutualistic interactions between individuals of different species, our focus here is on cooperation among conspecifics that increases the fitness of the recipient(s) [2]. It is well established that cooperation only emerges when helping results in direct or indirect fitness benefits for the actor [2-4]. Numerous studies have examined the strategies and the ecological conditions that favour helping, and to a lesser degree, also the proximate mechanisms of helping [2,4-6]. Notably, these studies highlight that helping occurs in diverse forms and settings, encompassing a continuum from one-time cooperative interactions that result in immediate benefits (**transactional cooperation** see glossary) to enduring associations among cooperation partners that engage in helping, which at times, results in delayed benefits (**social cooperation** see glossary), see Box 1.

Box 1

Drivers of animal associations, links to social bonds, and gradient of cooperation

Cooperation evolves only if it results in direct or indirect fitness benefits for the actor [2,3]. The context and length of time that individuals associate influences the fitness pathways, the forms of cooperation that can emerge, and the mechanisms that reduce the risk of defection. Particularly cooperation for direct fitness benefits is prone to defection [2], which individuals can limit by i) cooperating only when it results in immediate benefits, or ii) minimizing defection risk when cooperation results in delayed benefits, e.g., via preferences for helpful partners (i.e., social bonds) or punishment [2,5,7] (Fig. I). Each strategy is linked to whether animal associations form due to a specific individual need (i.e., ecology, e.g., food, protection from predators) or life-history (i.e., species life in stable groups, often with relatives).

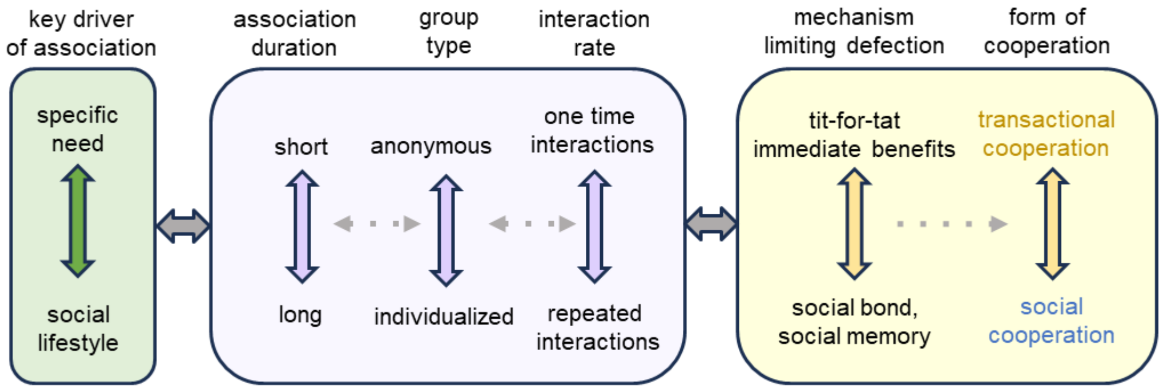


Fig I. Links between the key drivers of animal associations (green), their effect on social features (lilac), and the emergent cooperative features (yellow).

Animal associations that form due to a specific need (besides reproduction) are often ephemeral and group sizes are highly variable [8]. In these anonymous associations, individuals only cooperate for immediate fitness benefits (transactional cooperation) to avoid defection [2,5]. Alternatively, animal associations that form due to a social lifestyle are stable and individuals have often personalised relationships. E.g., in family-living species, individuals are born into a social bond with their parent(s) [9,10], and physical **touch** (see glossary) is a critical component of these bonds. Among unrelated individuals, repeated cooperative interactions may give rise to enduring bonds, which is achieved by co-opting the touch-based feedback loop (see below). Thus, individuals may also cooperate for delayed fitness benefits (e.g., social grooming, food sharing; social cooperation). Indeed, a theoretical study has shown a link between repeated cooperative interactions and bond strength, independent of kinship [7].

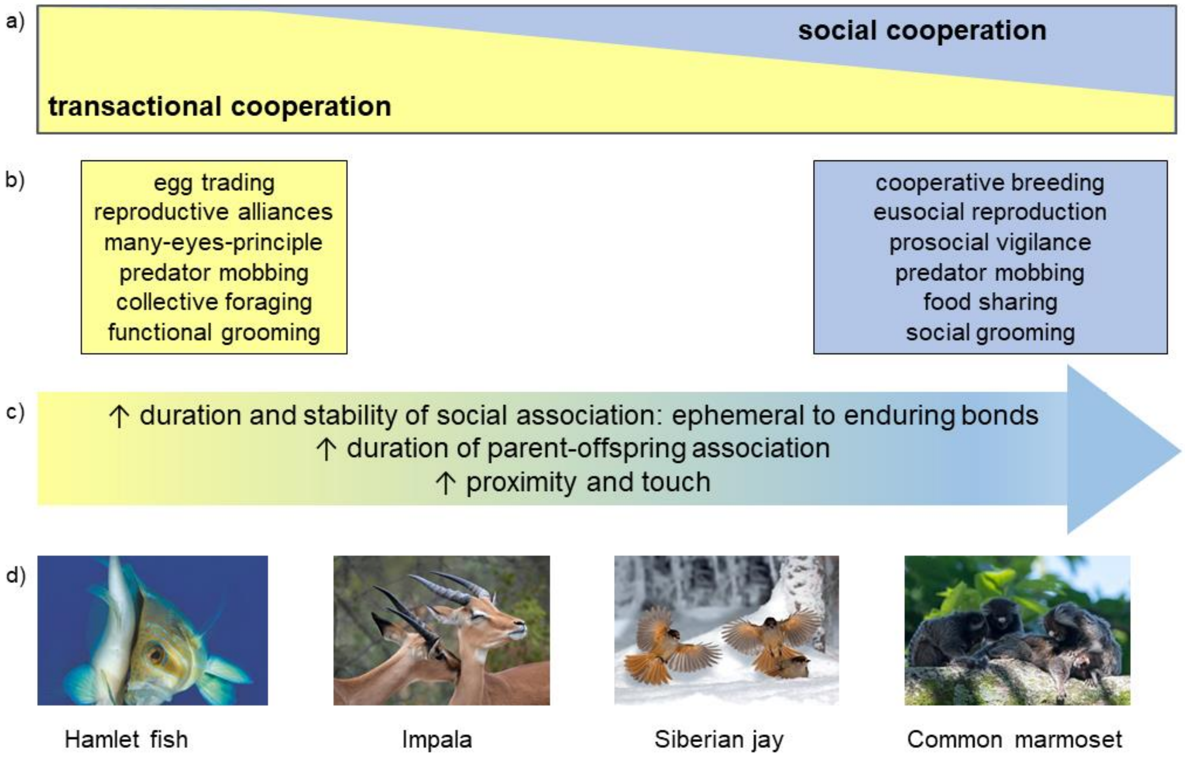


Fig II. a) Cooperation gradient from transactional cooperation, resulting in immediate benefits, to social cooperation, resulting in delayed benefits. b) Examples of expressions of transactional and social cooperation. c) Key changes along the cooperation gradient: increase in social bonding, parent-offspring associations, and physical proximity and touch. d) Species examples: Simultaneously hermaphroditic Hamlet fish exchanging egg parcels and sperm [11]. Impalas engage mostly in functional, not social, grooming [12]. Siberian jays cooperate during predator encounters and between-group conflicts, but do not breed cooperatively [13]. Common marmosets breed cooperatively and adults proactively offer help [14].

<u>**End of box 1**</u>

The importance of social bonds

Repeated interactions between individuals can reduce the risk of defection, thereby stabilizing cooperation [2,3]. A recent theoretical model showed that social bonds play a key role in the evolution of helping. Repeated exchange of help in small groups facilitates the formation of social bonds, which affect partner choice and an individual's willingness to help [7]. Across species, social bonds occur in a gradient from short-term associations often formed for a specific need, to enduring bonds where individuals remain together independent of the context (see Box 1). Primatologists label the latter as close social bonds or friendships [15,16].

Clearly, enduring bonds facilitate frequent interactions. Still, individuals engaging in enduring bonds may be at risk of defection and could lose all investment if a bond partner dies. Empirical studies in mammals and birds confirm that enduring bonds are indeed critical for the expression of social helping that does not result in immediate benefits for actors, e.g., social allo-grooming, cooperative breeding, food sharing, or protecting others from predators and competitors [10,16,17]. Over a lifetime, enduring bonds are highly adaptive [15,17]; baboon females that have stronger social bonds live longer and raise more offspring to independence [18], and bottlenose dolphin males with stronger bonds have increased fitness via a higher reproductive share [19]. The benefits of enduring bonds, thus, raise several questions: i) How do enduring bonds arise? ii) Which mechanisms facilitate their formation and maintenance? And iii) what are the links between bonding patterns and the different types of cooperation?

Social bonds drivers and link to cooperation

The fundamental importance and adaptive benefits of enduring bonds for the expression of social cooperation raises questions regarding their evolutionary facilitators. Social bonds are an integral part of reproduction and parental care [10,20,21]. Animal reproduction is mostly sexual, often requiring some form of bond between mates. In some species, mates form short-term bonds to exchange gametes, for example in many invertebrates, most fish, some mammals and lekking birds [20]. In other species, mates remain associated throughout a reproductive event, or form enduring mate bonds that can extend over multiple reproductive events [20,22]. Similarly, the extent of parent-offspring bonds varies. While most animal lineages lack parental care beyond egg laying, and accordingly lack parent-offspring interactions [20,23-25], all mammals and most birds engage in parental care beyond birth [24,26]. Consequently, parents-offspring bonds endure at least until offspring independence, but can extend well into adulthood [9].

Several observations highlight the importance of parent-offspring bonds for the evolution of enduring bonds in general (see also [27]). In many species, enduring bonds are a direct extension of parent-offspring bonds into adulthood. E.g., all 12 mammal species with enduring bonds listed in [10] have extended mother-offspring bonds but lack paternal care, suggesting that mother-offspring bonds, not mate bonds, are critical for the emergence of enduring bonds. This pattern is widespread in mammals: in most species only mothers provide parental care while quite a number of species have extended mother-offspring bonds [24]. In birds, enduring bonds remain understudied, but they have been observed in several species [28-30]. Their link to extended parent-offspring bonds, however, remains unclear.

We propose that the importance of parenting bonds for the emergence of enduring bonds in general, reflects that particularly extended parenting requires a high, long-term commitment. Abandoning offspring before their independence jeopardizes all current reproductive investment, while abandoning mates, which occurs in many species, depends on re-mating opportunities [31]. Thus, parenting necessitates mechanisms that support enduring bonds and investments that result in delayed benefits. The latter is particularly the case in species with extended parenting [9], providing the neuro-behavioural toolkit for enduring bonds, as we detail in the next section.

The role of touch in bond formation and maintenance

Social bonds usually involve a high degree of physical touch, e.g., grooming in primates [10,32]. In particular socio-positive touch activates several physiological and neurological mechanisms that have intrinsic links to how recipients perceive and respond to donors. In vertebrates, touch stimulates low threshold mechanoreceptors (LTMRs) of pseudo-unipolar somatosensory neurons, which activate various brain regions, including the hypothalamus [33]. Here, nonapeptide hormones, including oxytocin (OT) and arginine vasopressin or vasotocin (VT), are produced and secreted into the bloodstream by the posterior pituitary gland (see [34] for review). The ancestral function of these hormones is the regulation of physiological processes associated with survival (i.e., metabolism and osmoregulation [35,36]).

Subsequently evolved neuromodulator functions of OT and VT are linked to reproduction and social interactions. OT and VT reduce antisocial, anxiety-like behaviours and stress reactivity, and inhibit aggressive behaviours by acting on the amygdala and hypothalamic nuclei, as well as serotonergic stimulation in limbic brain regions [36]. Simultaneously, these hormones regulate prosocial behaviours by increasing social cognition and pair bonding [37]. In combination, these behavioural changes are critical for both the development of mate bonds and parenting bonds [37,38] and are mediated via several processes: OT and VT directly affect visual, auditory, and olfactory inputs, and interact with serotonergic systems in the nucleus accumbens, that in turn facilitate social learning and social recognition [39]. These mechanisms support social trust by increasing social attention and promoting behavioural synchronization [37,40]. Ultimately, this leads to an increase in social familiarity, resulting in both an increased frequency of prosocial behaviours and a decreased frequency of antisocial behaviours [39]. Thus, the neuro-cognitive links among socio-positive touch, OT and VT and prosocial behaviours create a positive feedback loop, reinforcing social bonds (Fig. 1). We exemplify the interplay between sociality, social bonds, external and internal factors that activate the OT feedback loop and touch in six mole-rat species (Table1). This table illustrates that an increased activation of the OT feedback loop is associated with increased touch, touch sensitivity, increased sociality and the expression of social cooperation (i.e., cooperative breeding and eusocial breeding).

Box 2

The evolution of oxytocin functions: from regulating survival to social bonds

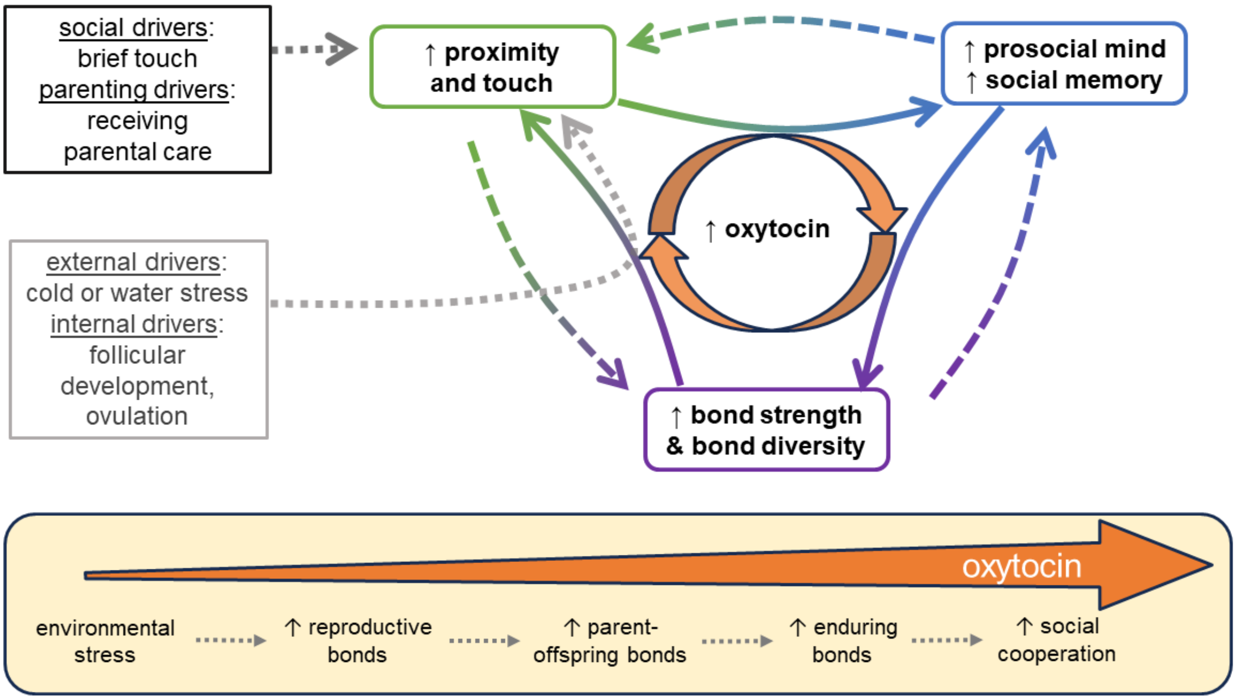
The OT-VT complex is one of the oldest physiological systems in vertebrates [34,41]. Its ancestral functions relate to survival and homeostasis [34], while it subsequently was co-opted to regulate prosocial behaviours that support bonding. Ancestrally, physiological stressors, including water and temperature stress, [35,42] and internal drivers in females, linked to reproduction, including gamete maturation [43,44]) activate the production of OT-VT, initiating several downstream physiological responses to alleviate the effects of these stressors. Notably, the OT-VT complex down-regulates the activity of other stress-related survival mechanisms, including the production of glucocorticoids (e.g., corticosterone) and endogenous opioid peptides [45]. Survival mechanisms prioritize short-term survival (e.g., pain insensitivity, mobilisation of energy reserves) over long-term fitness (e.g., immune system strength, reproduction) that would reduce immediate survival. Thus, the OT-VT complex played a key role in defending vertebrate homeostasis from environmental physiological drivers and internal drivers, including the prolonged activation of stress-related survival mechanisms.

These neuromodulators facilitate close proximity and touch between individuals, thereby enhancing the establishment of enduring pair bonds. An increase in socio-positive touch triggers the release of more OT-VT, initiating a feedback loop that strengthens the social memory and the social bond between the actor and recipient (Figure 1). Consequently, these changes increase the expression of prosocial behaviours, including cooperation. Thus, the ancestral functions of OT-VT have facilitated the subsequent evolution of enduring mate and parenting bonds, which in turn, have also facilitated the evolution of enduring bonds in general.

End of Box 2

Figure 1.

Key elements of the caring-touch hypothesis. Multiple drivers including touch, parental care, physiological stress and in females, reproductive processes increase OT and VT in individuals, resulting in an increase in affiliative behaviours, physical proximity and touch between actors and recipients. Moreover, OT and VT activate a prosocial mindset via increased social memory and strengthening the bond between individuals, which in turn increases touch between actors and recipients. This positive feedback loop strengthens social bonds. Critically, individuals can co-opt these mechanisms to form enduring social bonds via touch, independent of kinship or reproductive interests. Enduring social bonds facilitate the expression of forms of social cooperation where actors do not gain immediate fitness benefits.


social drivers:
brief touch
parenting drivers:
receiving
parental care
external drivers:
cold or water stress
internal drivers:
follicular
development,
ovulation
↑ proximity
and touch
↑ prosocial mind
↑ social memory
↑ oxytocin
↑ bond strength
& bond diversity
oxytocin
environmental
stress
↑ reproductive
bonds
↑ parent-
offspring bonds
↑ enduring
bonds
↑ social
cooperation

species	breeding system (colony size range) [46]	external and internal elements of feedback loop				touch based elements of feedback loop [47,48]		extend of social bonds [48]		OT measured [49,50]
		external OT drivers [51,52]		internal OT drivers [46]						
		temperature stress	water stress	litters per year	ovulation strategy	touch sensitivity*	touch frequency	parental care	helper sex	
Heterocephalus glaber	eusocial (2-250)	high	high	2-4	spontaneous	high	high	♀♂	♀♂	high
Fukomys damarensis	eusocial (2-41)	high	high	1-4	induced & spontaneous	high	high	♀♂	♀♂	NA
Fukomys spp.	cooperative breeder (2-16)	moderate	low	1-3	induced	high	moderate	♀♂	♀♂	moderate
Cryptomys hottentotus spp.	cooperative breeder (2-20)	moderate	low	1-3	induced	high	moderate	♀♂	♀?♂?	NA
Georychus capensis	solitary (1)	low	moderate	1-2	induced	NA	low	♀	-	low
Heliophobius argenteocinereus	solitary (1)	low	moderate	1	induced	low	low	♀	-	NA

Tabe 1. Interplay between the breeding system, external and internal OT drivers, touch, social bonds and OT in six mole rat species. Colony size range excludes dependent offspring. * Touch sensitivity is measured as C-fibre per Remak bundle, a structure in which C-fibres are grouped; blue colour shadings show hypothetical effects of external and internal stressors, and the touch loop on OT release: dark blue: increase, medium blue: stable, light blue: decrease; NA: unknown.

The caring-touch hypothesis

The caring-touch hypothesis integrates the above insights and highlights the strong intrinsic links among social bonding patterns, physical touch, and the way animals cooperate.

Across species, individuals express a gradient in association duration, reflecting different primary drivers (specific needs vs social lifestyle; Box 1), which may be directly affecting the forms of cooperation that emerge. In ephemeral associations, individuals engage in transactional cooperation to minimize the risk of defection. Extended associations provide repeatedly opportunities for proximity and touch, supporting the formation of enduring bonds. The latter often build upon extended parent-offspring bonds, which provide the neuro-behavioural toolkit to support the formation of enduring bonds independent of kinship or reproductive interests (see above, [27]). Touch acts as a critical primary activator of the positive feedback loop (Fig. 1), by stimulating specific receptors in the skin (LTMRs) that increase key social hormones (OT, VT; [53]), and link directly between individual variation in helping. For example, chimpanzees vary in the expression of the vasopressin receptor gene (via the allele DupB), leading to variation in prosociality [54]. Similarly, mutation in the oxytocin receptor genes have been associated with anti-social behaviours in humans [55].

Although the positive feedback loop may explain why individuals form enduring social bonds, it does not fully explain an individual's preference for few partners [10]. However, over time, bond partners gain knowledge of their partners' habits, leading to increased dyadic efficiency and coordination, which consequently may stabilise bonds and increase the level of dyadic cooperation [10,15,16]. In cooperatively breeding primates, bond quality among adults predicts infant carrying and food sharing [56]. Similarly, mate bond duration is associated with parenting efficiency in birds, increasing reproductive success [57]. Indeed, dyadic synchrony is also supported by social hormones. Strongly bonded partners show synchronized fluctuations in OT [40], and experimental administration of OT may increase coordination in cooperative tasks [58,59]. Consequently, a bond partner may become a valuable resource whereby switching to new partners is costly, which further stabilizes enduring bonds, and explains the preference for few bond partners (see also [7]).

Conclusions, integrating with existing frameworks and moving forward

Theoretical studies focussed on the strategies, evolutionary pathways, and the ecological conditions supporting the evolution of helping [2-5,60]. The caring-touch hypothesis complements these frameworks by focusing on proximate mechanisms, and specifically the fundamental role of touch that underly the formation of enduring bonds, which have downstream consequences on the type of cooperation that evolve. To understand the evolution of different forms of cooperation, it is therefore critical to differentiate between helping that occurs in bonded vs unbonded dyads.

Moreover, our hypothesis may provide insight into the ontogeny of cooperative interactions, by assessing quantitatively (e.g., temporal distribution or intensity; sensitive periods) how touch influences the establishment of bonds. In humans, patterns of touch experienced during ontogeny have a strong impact on an individual's adult parenting style, whereby touch-deprived children exhibit a low-touch parenting style compared to children exposed to sensitive parenting with ample caring touch [61]. Another question arising from our hypothesis concerns the strategic use of touch. In primates, allo-grooming is also associated with the formation and maintenance of strategic alliances between individuals [62], which leads to coalitional support [63]. In chimpanzees, border patrols (that may escalate to warfare) are often preceded by allo-grooming, leading to an increase in OT and an associated increase in group cohesiveness and willingness to cooperate [64]. Thus, touch may also have a key function in regulating social interactions amongst individuals with short-term alliances, raising the question of whether touch can be used to manipulate other individuals to provide help. Thus, our hypothesis provides a proximal mechanism to explore the evolution of different forms of cooperation, specifically focusing on the role that bonds play in this process.

Outstanding questions

- What is the interplay between touch, and relative pay-offs in public goods versus private goods cooperation [5]?
- How do we extend the proposed framework to triadic and multi-level social interactions?
- How does an individual transition ontogenetically from a receiving offspring to a giving adult?
- Can the feedback loop be activated via external mechanisms (e.g., increased parasite load, predation risk, environmental stressors), and what are the consequences for bond stability and cooperation?
- Are the levels of social cooperation between bond partners different if the mechanism is external (ecological, social pressures that facilitate proximity) vs internal (touch)?
- Can species that lack parent-offspring bonds develop enduring bonds?
- How many elements of the feedback loop need to be present so that animals engage in social cooperation?
- Do all vertebrates have this feedback loop, or does it differ between lineages (e.g. in fish birds, mammals)? E.g., most fish do not engage in parental care but still some are touch sensitive (see below).
- Could the same feedback loop be involved in between-species cooperation? E.g., cleaner fish use tactile stimulation when interacting with hosts, especially after defecting and eating mucous instead of ectoparasites [65].
- Does domestication exploit this feedback loop and trigger cooperative mindsets in animals, as suggested in case of canid domestication [37]?
- What is the interplay between mate bonds, parenting bonds and enduring bonds? Although extended parenting bonds seems to be critical for the emergence of enduring bonds, also mate bonds could in some cases be a stepping stone.
- Could sexual behaviours facilitate the formation of enduring bonds? E.g., female bonobos engage in mutual genital rubbing, a sexual behaviour, that activate the feedback loop [66].

- How does our hypothesis link to social bonds among same-sex dyads [67]?

Glossary

Bond: association between two individuals, ranging from short-term bonds to enduring bonds that persist over extended time periods; the latter do not include reproductive bonds (i.e., mate bonds [57]); parenting bond are special forms of enduring bonds. The bonds have also been labelled friendships [15].

Touch: two individuals physically touching each other. Touch can be aggressive (i.e., pain-causing), or socio-positive (referred to as touch in our paper). Aggressive touch, is linked to the establishment of a dominance hierarchy and is usually counter-productive in the formation of enduring bonds and continued maintenance of social bonds [68,69]. Socio-positive touch can have a reproductive, sexual or caring functions, and can vary in its duration [70]. This type of touch activates the oxytocin driven feedback loop illustrated in Figure 1.

Transactional cooperation: forms of cooperation that results in immediate benefits for actors, e.g., egg trading in simultaneous hermaphrodite hamlet fish [11], collective foraging [71] or functional grooming to remove parasites [12].

Social cooperation: forms of cooperation that results in delayed benefits for actors, e.g., cooperative breeding [72], food sharing [73], or social grooming to strengthen bonds [32].

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