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Opinion

The power of caring touch: from survival to prosocial cooperation

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Cooperation is a pivotal biological phenomenon that occurs in diverse forms. In species that engage in helping, individuals vary in the time they spend together and the degree of their physical proximity, which affects the extent of physical touch between individuals. Here, we propose that touch activates a hormonal feedback loop that supports bond formation and maintenance in mating, parenting, and social contexts. Notably, extended parenting is essential for the emergence of enduring bonds and the development of the prosocial mindset that fosters forms of cooperation with delayed benefits. We incorporate these ideas into the caring-touch hypothesis (CT-H), which emphasizes the role of oxytocin-vasotocin hormones, 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 hormonal mechanisms remain rarely integrated into these theories.

Ancestrally, the hormones oxytocin (OT) and vasotocin (VT) regulated osmotic balance and metabolic stress. They subsequently evolved to support prosocial behaviours, including grooming, protection, food sharing, and bonding.

The caring-touch hypothesis emphasizes the intrinsic links between touch, OT-VT, bonding patterns, and how animals cooperate. Touch supports the development of enduring bonds and a prosocial mindset, facilitating the emergence of forms of cooperation that result in delayed benefits.

Our integrative framework provides fresh mechanistic insights into the evolution of cooperation.

The evolution of diverse forms of cooperation

Cooperation is a pivotal biological phenomenon fuelling the evolutionary transitions from multicellularity to complex societies observed in eusocial insects and in humans (*Homo sapiens*). [1]. Although **helping** (see Glossary) can also include mutualistic interactions between individuals of different species, our focus here is on helping among conspecifics that increases the fitness of the recipient(s) [2]. It is established that helping can evolve only when it 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, the proximate mechanisms of helping [2,4–6]. Notably, these studies highlight that helping occurs in diverse forms and settings [7] and that individuals vary in their association time. Thus, helping is expressed in a continuum from one-time interactions that result in immediate benefits (**transactional cooperation**) to enduring associations among partners that engage in helping, which at times result in delayed benefits (**social cooperation**) (Box 1). We focus here on mammals and birds to develop our framework in the hope that it will be expanded to cover other taxa with differing physiological pathways and neural architectures (i.e., invertebrates, fishes, amphibians, reptiles).

The importance of bonds for cooperation

Across species, **bonds** occur along a gradient from ephemeral bonds, often formed for a specific need, to enduring bonds where individuals remain together independent of the context (Box 1). Empirical studies in mammals and birds have revealed that enduring bonds are critical for the expression of social cooperation that results in delayed benefits for actors (e.g., social allogrooming, cooperative breeding, prosocial food sharing, or protecting others from predators and competitors) [8–10]. A recent theoretical model illustrated that enduring bonds can play a pivotal role in the evolution of helping [11]. This model demonstrated that repeated exchanges of helping in small groups facilitated the formation of bonds that affect partner choice and an individual's willingness to help [11] and that repeated interactions (i.e., reciprocity, [4,12]) between

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individuals reduce the risk of defection, thereby stabilizing cooperation [2,3]. However, although individuals can lose all investment if a bond partner dies, enduring bonds are highly adaptive over a lifetime [10,13]. For instance, female baboons, *Papio cynocephalus*, with stronger enduring bonds live longer and raise more offspring to independence than females with weaker bonds [14], and in bottlenose dolphins, *Tursiops aduncus*, males with stronger bonds have increased mating opportunities and therefore a higher fitness [15]. These enduring bond benefits thus raise several questions: (i) How do enduring bonds arise? (ii) Which mechanisms facilitate their formation and maintenance? (iii) What are the links between bonding patterns and the different forms of cooperation?

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Box 1. Animal association drivers, links to bonds, and cooperation

Animals can associate because of specific needs (e.g., food, predator protection) or their social lifestyle (i.e., species living in stable groups, often with relatives; Figure I). This difference influences the social features of associations and the forms of cooperation that can emerge. The first type of association is often ephemeral and therefore anonymous, and group sizes are highly variable [62]. Given the uncertainty of future interactions, individuals should only engage in transactional cooperation to avoid defection [2,5] (e.g., tit-for-tat interactions) (Figure II). By contrast, animal associations that form due to a social lifestyle are usually stable over extended periods of time, and individuals often have long-term social relationships that can result in enduring bonds. Here, individuals engage in social cooperation (e.g., cooperative breeding, prosocial food sharing [63]), which is prone to defection [2]. Individuals can limit the risk of defection via preferences for helpful partners (i.e., via enduring bonds) [11] or via punishment [2,5].

The differences in association patterns have strong links to the degree of physical touch (Figure II). Touch is a critical proximate mechanism for reinforcing bonds via the oxytocin-vasotocin (OT-VP) feedback loop (see Figure 1 in the main text), resulting in enduring bonds. In species with extended parent–offspring associations (i.e., family living [23]), individuals are born into a bond with their parent(s) [8,23], which is usually associated with an increase in proximity and touch, supporting the development of enduring bonds. Among unrelated individuals, repeated cooperative interactions can give rise to enduring bonds [11], which can be achieved by co-opting the touch-based OT-VP feedback loop [8]. Across species, individuals express a gradient in association duration and consequently touch, leading to increased bond strength and an increase in social cooperation.

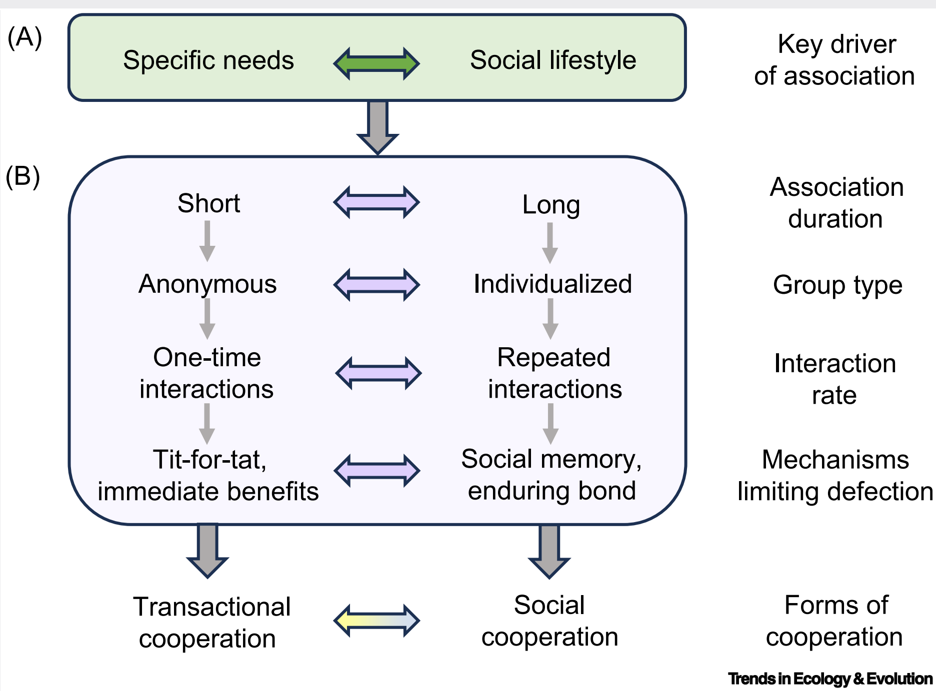

Figure I. Links between the key drivers of animal associations (A) and their effect on social features (B) and the emergent forms of cooperation.

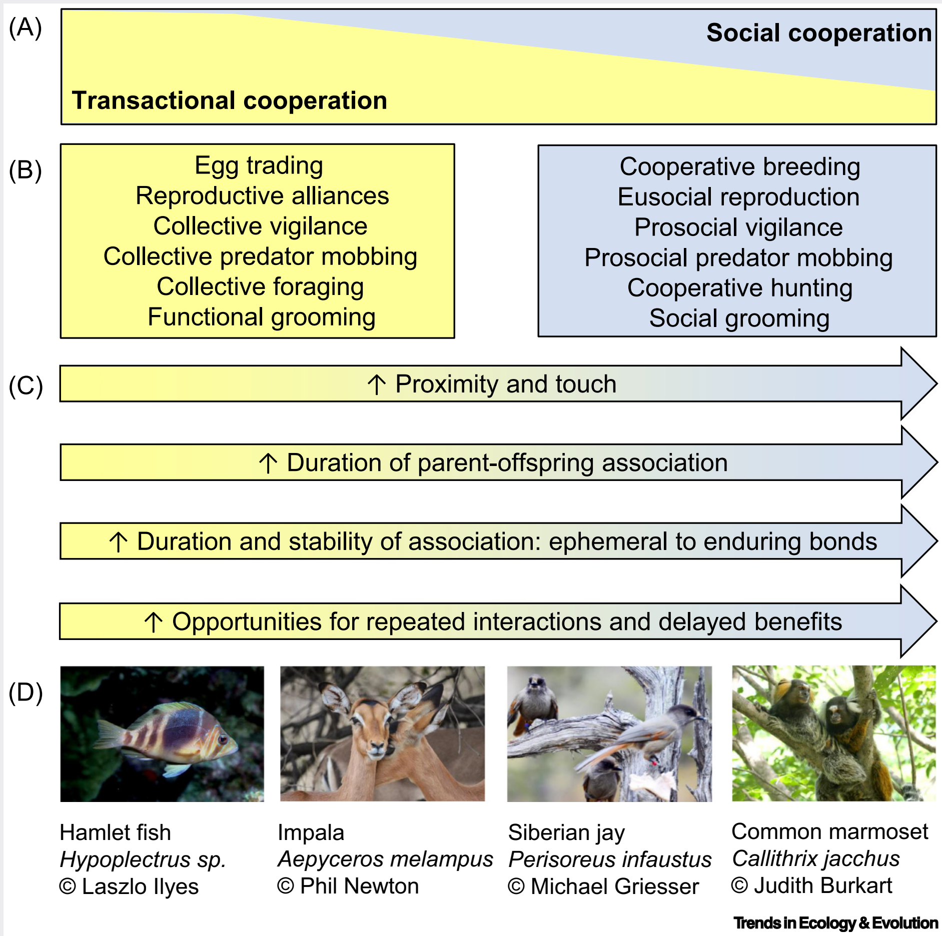

Figure II. (A) Cooperation gradient from transactional cooperation to social cooperation. (B) Examples of forms of transactional and social cooperation; some behaviours can be both transactional and social (e.g., vigilance, predator mobbing, or grooming) [64–68]. (C) Key changes along the cooperation gradient. (D) Species examples. Simultaneously hermaphroditic Hamlet fish exchange egg parcels and sperm [69]. Impalas engage in functional grooming [67]. Siberian jays cooperate during predator encounters and between-group conflicts but do not breed cooperatively [70]. Common marmosets breed cooperatively, and adults proactively offer help [71].

Drivers of bonds and link to cooperation

The adaptive benefits of enduring bonds and their role in the expression of social cooperation raise questions regarding the factors facilitating their evolution and maintenance. Bonds are an integral part of survival, reproduction, and parental care [8,16,17]. Animal reproduction is mostly sexual, often requiring a bond between mates. In some species, mates form ephemeral bonds to exchange gametes, as in many invertebrates, most fishes, some mammals, and lekking birds [16]. In other species, mates remain associated throughout a reproductive event or form enduring mate bonds that can extend over multiple reproductive events [16,18]. Similarly, the temporal extent of parent–offspring bonds varies. While most animal lineages do not have parental care beyond the egg-laying stage and accordingly have no parent–offspring interactions [16,19–21], all mammals and most birds engage in parental care beyond birth [20,22], and thus parent–offspring bonds endure until at least offspring independence but can extend well into adulthood [23].

Glossary

Bond: association between two individuals, ranging from short-term, ephemeral bonds to enduring bonds that persist over extended periods of time. The latter does not include mate bonds *per se*; parenting bonds are special forms of enduring bonds. Primatologists differentiate among several types of bonds. Coalitions are short-term bonds of individuals formed for a specific purpose, mostly in agonistic interactions to subjugate another individual. Coalitions that are extended in time are labeled alliances. Enduring bonds, also labeled close social bonds or friendships, are enduring associations between individuals independent of the context.

Helping: a behaviour that increases the direct fitness of the recipient. Helping includes behaviours that are proactively targeted (e.g., rescuing another individual's offspring) and side-product benefits to the recipient (e.g., self-serving contributions to public goods).

Social cooperation: forms of cooperation that are restricted to bond partners and often result in delayed benefits for actors (e.g., cooperative breeding, food sharing, or social grooming) to strengthen bonds. Some forms of social cooperation also have immediate benefits (e.g., parasite removal in the case of social grooming).

Touch: two individuals physically touching each other. Touch can be aggressive (i.e., pain-causing), or sociopositive (here referred to as 'touch'). Aggressive physical interactions is linked to the establishment of a dominance hierarchy and can be counterproductive in the formation and maintenance of enduring bonds. Touch can have reproductive, sexual, or caring functions and can vary in its duration. Moreover, it activates the OT-VT–driven feedback loop illustrated in Figure 1.

Transactional cooperation: forms of cooperation that result in immediate benefits for actors (e.g., egg trading in simultaneous hermaphrodite hamlet fish, collective foraging or functional grooming to remove parasites).

Several observations indicate the importance of parent–offspring bonds for the emergence of enduring bonds in general (see also [24]). In many species, enduring bonds are a direct extension of parent–offspring bonds into adulthood. For example, all 12 mammal species with enduring bonds listed by Seyfarth and Cheney [8] have extended mother–offspring bonds and form enduring bonds with unrelated individuals. However, all these species lack extended mate bonds and paternal care, which indicates 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, and many species also have extended mother–offspring bonds [20]. In birds, biparental care is widespread [22]; enduring bonds outside the reproductive context remain understudied but have been observed in several species [25–27]. Evidently, cooperative breeding is usually associated with extended parent–offspring bonds [23], and in some cooperatively breeding species, unrelated individuals are included in the breeding units [28].

These observations suggest that parenting bonds facilitate the emergence of enduring bonds in general. Extended parenting [23] in particular requires neurobehavioural mechanisms that support enduring bonds and long-term investments. Thus, we hypothesize that extended parenting provides the neurobehavioural mechanisms for enduring bonds in general, as we detail in the next section.

The role of touch in bond formation and maintenance

Bonds often involve a high degree of **touch**, as observed in primates where grooming has a key role in establishing and maintaining bonds [8,29]. Observations in birds support this notion [30,31]. In particular, touch activates several physiological and neurological mechanisms that have intrinsic links to how recipients perceive and respond to actors. In vertebrates, touch stimulates low threshold mechanoreceptors (LTMRs) of pseudo-unipolar somatosensory neurons [32], which activate various brain regions, including the hypothalamus [33]. Here, nonapeptide hormones, including those of the oxytocin-vasotocin (OT-VT) family [34], 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]; Box 2). Hormones of the OT-VT family were subsequently co-opted to support the emergence and maintenance of social bonds in the

Box 2. Oxytocin functions: from survival to supporting enduring bonds

Hormones of the OT-VT family are part of one of the oldest physiological systems in vertebrates [34,72]. Their ancestral functions relate to survival and homeostasis [34], whereas they subsequently were co-opted to regulate prosocial behaviours that support bonding and ultimately survival. Ancestrally, physiological stressors, including water and metabolic stress [35,73], and internal drivers in females linked to reproduction, including gamete maturation [74,75], activate the production of OT-VT, which initiates several downstream physiological responses to alleviate the effects of these stressors. Notably, OT-VT downregulate the activity of other stress-related survival mechanisms, including the production of glucocorticoids (e.g., corticosterone) and endogenous opioid peptides [76]. Survival mechanisms prioritize short-term survival (e.g., pain insensitivity, mobilisation of energy reserves) over long-term fitness (e.g., immune system reactivity, reproduction) that would increase immediate survival but reduce long-term survival and fitness. Thus, hormones of the OT-VT family play a key role in defending vertebrate homeostasis from environmental physiological stressors and internal drivers, including the prolonged activation of stress-related survival mechanisms.

Subsequently, these hormones evolved to facilitate physical proximity and touch between individuals, thereby enhancing the establishment of enduring pair bonds. An increase in touch triggers the release of more hormones in the OT-VT family, initiating a feedback loop that strengthens the social memory and the bond between the actor and recipient (see Figure 1 in the main text). In turn, these changes increase the expression of prosocial behaviours and, as a consequence, social cooperation. Thus, the ancestral functions of OT-VT have facilitated the subsequent evolution of enduring mate and parenting bonds, which in turn have also promoted the evolution of enduring bonds in general, thereby facilitating the emergence of forms of cooperation that result in delayed benefits.

reproductive context, which likely increased survival via the reduction in stress-related metabolic responses. These hormones reduce antisocial, anxiety-like behaviours and stress reactivity, and they inhibit aggressive behaviours by acting on the amygdala and hypothalamic nuclei [37], as well as serotonergic stimulation in the limbic brain regions [36]. Simultaneously, these hormones regulate prosocial behaviours by increasing social cognition and pair bonding [38]. In combination, these behavioural changes are critical for the development of both mate bonds and parenting bonds [38,39] and are mediated via several processes: hormones of the OT-VT family directly affect visual, auditory, and olfactory inputs and interact with serotonergic systems in the nucleus accumbens in the forebrain, which in turn facilitate social learning and social recognition [40]. These mechanisms support social trust by increasing social attention and promoting behavioural synchronization [38,41]. Ultimately, this synchronization leads to an increase in social familiarity, resulting in both an increased frequency of prosocial behaviours and a decreased frequency of antisocial behaviours [40]. Thus, the neurocognitive links among touch, hormones of the OT-VT family, and prosocial behaviours create a positive feedback loop that reinforces enduring bonds (Figure 1).

We exemplify the interplay between sociality, enduring bonds, external and internal factors that activate the OT-VT feedback loop, and touch by providing comparative data on six African mole-rat species (Table 1). Increased activation of the OT-VT feedback loop is associated with increased touch, touch sensitivity, increased sociality, and the expression of social cooperation (i.e., cooperative and eusocial breeding). These changes go hand in hand with increased levels

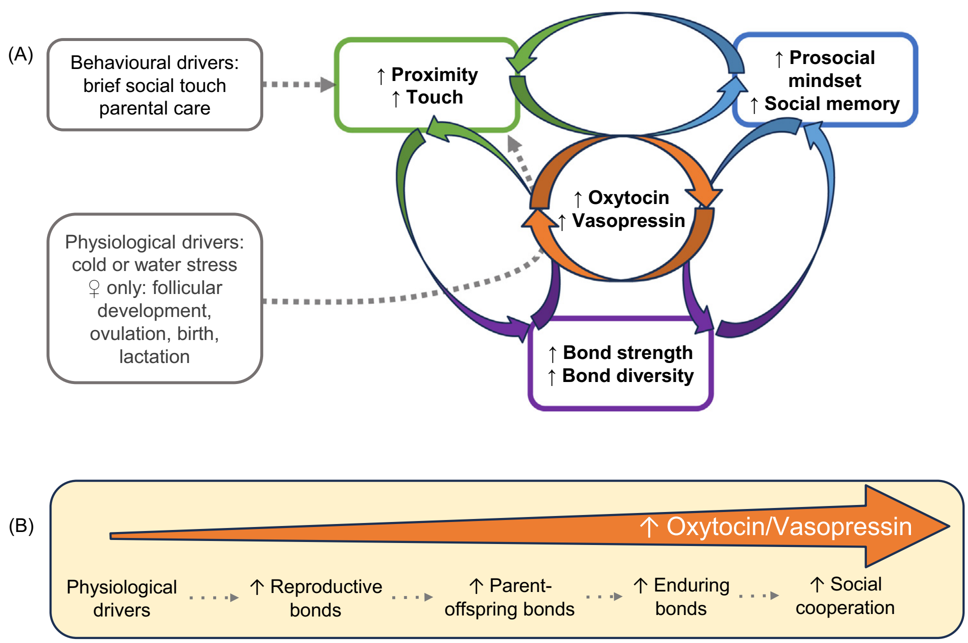

Figure 1. Key elements of the caring-touch hypothesis. (A) Touch-based oxytocin-vasotocin (OT-VT) feedback loop. Physiological and behavioural drivers (grey boxes) increase circulating levels of OT and VT, resulting in an increase in affiliative behaviours, physical proximity, and touch between actors and recipients (green box). Increased levels of OT-VT activate a prosocial mindset via increased social memory (blue box) and strengthened bonds between individuals (purple box), which in turn increase touch between actors and recipients. Notably, these mechanisms also act in the opposite direction, creating a feedback loop that increases the levels of OT-VT and the associated social and cognitive changes. (B) Hypothesized evolutionary consequences of the OT-VT feedback loop. Physiological drivers facilitate the emergence of reproductive bonds and parenting bonds, which in turn support the emergence of enduring bonds independent of kinship or reproductive interests. Enduring bonds facilitate the expression of diverse forms of social cooperation (see Box 1 in the main text).

Table 1. Interplay between the breeding system [44], external [45,46] and internal [44] oxytocin (OT) drivers, touch [45,46], the number of caregivers [47], and circulating levels of OT [48,49] in six mole-rat species[a,b].

Species	Breeding system (colony size range[a])[44]	External and internal elements of feedback loop				Touch based elements of feedback loop[45,46]		Number of caregivers [47]		Circulating OT levels (measured) [48,49]
		External OT drivers [45,46]		Internal OT drivers [44]						
		Temperature stress	Water stress	Litters per year	Ovulation strategy	Touch sensitivity[b]	Touch frequency	Parental care	Helper sex	
Naked mole-rat *Heterocephalus glaber*	Eusocial (2–250)	High	High	2–4	Spontaneous	High	High	♀♂	♀♂	High
Damaraland mole-rat *Fukomys damarensis*	Eusocial (2–41)	High	High	1–4	Induced and spontaneous	High	High	♀♂	♀♂	NA
Ansell's mole-rat *Fukumys anselli*	Cooperative breeder (2–16)	Moderate	Low	1–3	Induced	High	Moderate	♀♂	♀♂	Moderate
Common mole-rat *Cryptomys hottentotus*	Cooperative breeder (2–20)	Moderate	Low	1–3	Induced	High	Moderate	♀♂	♀?♂?	NA
Cape mole-rat *Georychus capensis*	Solitary (1)	Low	Moderate	1–2	Induced	NA	Low	♀	–	Low
Silvery mole-rat *Heliophobius argenteocinereus*	Solitary (1)	Low	Moderate	1	Induced	Low	Low	♀	–	Na

[a]Colony size range excludes dependent offspring.

[b]Touch sensitivity is measured as the number of C-fibers (slow conducting unmyelinated nerve fibers that carry sensory information like mechanical stimuli on the skin including vibration, indentation, stretch) per Remak bundle, a structure in which C-fibers are grouped.

Blue color shadings show hypothetical effects of external and internal stressors, and the touch loop on OT release: dark blue, high OT; medium blue, intermediate OT; light blue, low OT; NA, unknown. Note that the measured circulating OT levels (purple) are concordant with hypothetical OT levels in response to drivers (blue) as predicted by the caring-touch hypothesis.

of prolactin (see [42]; not shown in Table 1), which also supports social cooperation in the reproductive context [43].

Caring touch hypothesis

CT-H posits that touch and bonding patterns play a crucial role in how animals cooperate. A key element of our hypothesis is the touch-based OT-VT feedback loop (Figure 1), providing a behavioural mechanism that allows the establishment and maintenance of enduring bonds within and outside the reproductive context.

Our hypothesis predicts that the temporal extent of bonds has a link to the forms of cooperation that can evolve. Across species, individuals express a gradient in association duration, reflecting different primary drivers (specific ecological needs versus social lifestyle; Box 1), which influences the forms of cooperation that emerge. In ephemeral associations, individuals are predicted to engage particularly in transactional cooperation based on reciprocity to minimize the risk of defection [2,12]. Extended associations provide repeated opportunities for physical proximity and touch, supporting the formation of enduring bonds. The latter often build on 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; [24]). Touch acts as a critical activator of the OT-VT feedback loop (Figure 1) by stimulating specific receptors in the skin (LTMRs) that increase key social hormones of the OT-VT family [50]. Variations or mutations in genes underlying this feedback loop have direct links to individual variation in helping. For example, chimpanzees (*Pan troglodytes*) vary in the expression of the vasopressin receptor gene (i.e., a neuromodulator part of the OT-VT family) via the allele DupB, leading to variation in their prosociality [51]. Similarly, mutation in the OT receptor genes has been associated with antisocial behaviours in humans [52].

Although the OT-VT feedback loop can explain why individuals form enduring bonds, it does not explain an individual's preference for a few partners [8]. Over time, bond partners gain knowledge of their partners' habits, leading to increased dyadic efficiency and coordination, which consequently stabilises bonds and increases the level of dyadic cooperation [8,9,13]. Empirical data support this idea: In cooperatively breeding primates, bond quality among adults predicts their investment in infant carrying and food sharing [53]. Similarly, mate bond duration is associated with parenting efficiency in birds, increasing reproductive success [31]. Indeed, it has been found that dyadic synchrony is supported by social hormones. Strongly bonded partners show synchronized fluctuations in OT [41], and experimental administration of OT can increase coordination in cooperative tasks [54,55]. Consequently, a bond partner becomes 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 [11]).

Concluding remarks and future perspectives

Previous studies have focused on the strategies, evolutionary pathways, and ecological conditions supporting the evolution of helping [2–5,7,56]. CT-H complements these frameworks by focusing on proximate mechanisms (Box 3) and specifically the fundamental role of touch that underlies the formation and reinforcement of enduring bonds, which have downstream consequences on the forms of cooperation that evolve. To understand the emergence of different forms of cooperation, it is therefore critical to consider the temporal extent of bonds among individuals that cooperate (see Outstanding questions).

Moreover, our hypothesis can provide insights into the ontogeny of cooperative interactions by assessing quantitatively (e.g., temporal distribution or intensity; sensitive periods) how touch

Box 3. Links between the caring-touch hypothesis (CT-H) and the four distinct approaches as described in [5] for the study of helping

Theoretical models (strategies)

Game-theoretical models emphasize the importance of repeated interactions (i.e., reciprocity [12,77]) and mechanisms that prevent defection [2–4] in the emergence of helping. However, empiricists frequently struggle to apply theoretical models to the helping observed in their study systems, especially as individuals often have stable bonds. Consequently, bonds play a crucial role in helping behaviours that offer delayed benefits [8]; yet, they are rarely accounted for in models (but see [11]). CT-H extends previous work by introducing a general mechanism for bond formation and maintenance. Moreover, CT-H emphasizes that bonds occur along a temporal gradient, influencing the strategies and forms of helping that can emerge (Figure II in Box 1).

Evolutionary pathways

Helping is based on direct or indirect fitness benefits [2–5], and the CT-H provides an empirical underpinning for both pathways. Bonds facilitate repeated interactions (see earlier) and thus helping via direct fitness benefits. Explanations for helping via indirect fitness emphasize a role of population viscosity [78] that leads to kin-structured populations. In natural populations, kin structure is often a direct consequence of extended parent–offspring bonds [23], providing opportunities for help that bring both indirect and direct fitness benefits.

Ecology and life history

The ecology and life history of a species matter for repeated interactions (and thereby for helping), which are facilitated by sedentariness and overlapping generations. In birds, these factors are associated with stable and productive environments, larger body mass, and increased longevity [23]. Together, these factors lower the parental costs of extended offspring care [79], which allows parents to provide their offspring with enhanced skills, learning opportunities, and other benefits that result in increased survival [80,81]. CT-H provides the mechanistic underpinning of these bonds and emphasizes their role in the emergence of enduring bonds in general.

The approach of social scientists

This approach is dominated by human studies, often using artificial laboratory settings [5]. Consequently, this approach remains poorly integrated with the other three approaches. CT-H has potential to foster new links between the social science approach and the other approaches: It emphasizes the fundamental role of bonds and their duration for the emergence of different forms of helping (see Box 1) and the role of touch for the formation and maintenance of bonds via the touch-based feedback loop (see Figure 1 in the main text).

Outstanding questions

What is the link between transactional cooperation, social cooperation, and the different game theoretical strategies?

How can the proposed framework be extended to triadic and multilevel social interactions?

What are the consequences for bond stability and cooperation if the OT-VT feedback loop is activated via external mechanisms (e.g., increased parasite load, predation risk, environmental stressors)?

Are the levels of social cooperation between bond partners different if the mechanism is external (ecological, social pressures that facilitate proximity) versus internal (touch)?

Can species that lack parent–offspring bonds develop enduring bonds?

How many elements of the OT-VT 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?

Could the OT-VT feedback loop also be involved in between-species cooperation? For example, bluestreak cleaner wrasse (*Labroides dimidiatus*) use tactile stimulation when interacting with hosts, especially after defecting and eating mucus instead of ectoparasites. Could this behaviour help reduce the stress response of their hosts and thus support bonds that facilitate between-species cooperation?

Does domestication exploit the OT-VT feedback loop and trigger prosocial mindsets in animals, as suggested in the case of canid domestication?

What is the interplay between mate bonds, parenting bonds, and enduring bonds? While extended parenting bonds seem essential for the development of enduring bonds, could mate bonds also play a role in fostering enduring bonds?

Could sexual behaviours facilitate the formation of enduring bonds? For example, female bonobos (*Pan paniscus*) engage in mutual genital rubbing, a sexual behaviour that activates the OT-VT feedback loop.

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 with children exposed to sensitive parenting with ample caring touch [57]. Work in rodents showed that altered expression of OT receptors is associated with the intergenerational transmission of parenting behaviour [58]. Another question arising from our hypothesis concerns the strategic use of touch. In primates, allogrooming is also associated with the formation and maintenance of strategic alliances between individuals [59], which leads to coalitional support [60]. In chimpanzees, border patrols (which can escalate to warfare) are often preceded by allogrooming, leading to an increase in OT and an associated increase in group cohesiveness and willingness to cooperate [61]. Thus, touch might also have a key function in regulating social interactions among individuals with short-term alliances, raising the question whether touch is used to manipulate other individuals to provide help. We also note that other sensory stimuli, including gaze, can support the activation of the OT-VT feedback loop [24]. To conclude, our hypothesis provides a proximally rooted hypothesis to explore the evolution of different forms of cooperation, specifically focusing on the role that bonds and touch play in this process.

How does our hypothesis link to enduring bonds among same-sex dyads?

How do age-related hormonal changes impact bonding patterns?

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Declaration of interests

The authors declare no competing interests.

References

1. Bourke, A.F.G. (2011) *Principles of Social Evolution*, Oxford University Press
2. Lehmann, L. and Keller, L. (2006) The evolution of cooperation and altruism – a general framework and a classification of models. *J. Evol. Biol.* 19, 1365–1376
3. Kay, T. *et al.* (2020) The evolution of altruism and the serial rediscovery of the role of relatedness. *Proc. Natl. Acad. Sci. U. S. A.* 117, 28894–28898
4. West, S.A. *et al.* (2007) Evolutionary explanations for cooperation. *Curr. Biol.* 17, R661–R672
5. Bshary, R. and Bergmüller, R. (2008) Distinguishing four fundamental approaches to the evolution of helping. *J. Evol. Biol.* 21, 405–420
6. Rubenstein, D.R. and Abbot, P. (2017) *Comparative Social Evolution*, Cambridge University Press
7. Taborsky, M. *et al.* (2021) *The Evolution of Social Behaviour*, Cambridge University Press
8. Seyfarth, R.M. and Cheney, D.L. (2012) The evolutionary origins of friendship. *Annu. Rev. Psychol.* 63, 153–177
9. Cords, M. and Thompson, N.A. (2017) Friendships, coalitions, and alliances. In *APA Handbook of Comparative Psychology: Basic Concepts, Methods, Neural Substrate, and Behavior* (Vol. 1), pp. 899–913, American Psychological Association
10. Silk, J.B. (2007) The adaptive value of sociality in mammalian groups. *Philos. Trans. R. Soc. B* 362, 539–559
11. Leimar, O. and Bshary, R. (2024) Social bond dynamics and the evolution of helping. *Proc. Natl. Acad. Sci. U. S. A.* 121, e2317736121
12. Trivers, R. (1971) The evolution of reciprocal altruism. *Q. Rev. Biol.* 46, 35
13. Silk, J. (2002) Using the 'F'-word in primatology. *Behaviour* 139, 421–446
14. Alberts, S.C. (2019) Social influences on survival and reproduction: insights from a long-term study of wild baboons. *J. Anim. Ecol.* 88, 47–66
15. Gerber, L. *et al.* (2022) Social integration influences fitness in allied male dolphins. *Curr. Biol.* 32, 1664–1669.e3
16. Balshine, S. (2012) Patterns of parental care in vertebrates. In *The Evolution of Parental Care* (Royle, N.J. *et al.*, eds), pp. 62–80, Oxford University Press
17. Kendrick, K.M. (2004) The neurobiology of social bonds. *J. Neuroendocrinol.* 16, 1007–1008
18. Kvarnemo, C. (2018) Why do some animals mate with one partner rather than many? A review of causes and consequences of monogamy. *Biol. Rev.* 93, 1795–1812
19. Furness, A.I. and Capellini, I. (2019) The evolution of parental care diversity in amphibians. *Nat. Commun.* 10, 4709
20. West, H.E. and Capellini, I. (2016) Male care and life history traits in mammals. *Nat. Commun.* 7, 11854
21. Halliwell, B. *et al.* (2017) Live bearing promotes the evolution of sociality in reptiles. *Nat. Commun.* 8, 2030
22. Cockburn, A. (2006) Prevalence of different modes of parental care in birds. *Proc. R. Soc. B* 273, 1375–1383
23. Griesser, M. *et al.* (2017) Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLoS Biol.* 15, e2000483

24. Blumenthal, S.A. and Young, L.J. (2023) The neurobiology of love and pair bonding from human and animal perspectives. *Biology* 12, 844
25. Boucherie, P.H. *et al.* (2016) Bonding beyond the pair in a monogamous bird: impact on social structure in adult rooks (*Corvus frugilegus*). *Behaviour* 153, 897–925
26. Hobson, E.A. *et al.* (2014) The socioecology of monk parakeets: insights into parrot social complexity. *Auk* 131, 756–775
27. Elie, J.E. *et al.* (2011) Same-sex pair-bonds are equivalent to male–female bonds in a life-long socially monogamous songbird. *Behav. Ecol. Sociobiol.* 65, 2197–2208
28. Riehl, C. (2013) Evolutionary routes to non-kin cooperative breeding in birds. *Proc. R. Soc. B* 280, 20132245
29. Silk, J.B. *et al.* (2006) Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behav. Ecol. Sociobiol.* 61, 183–195
30. Kenny, E. *et al.* (2017) Allopreening in birds is associated with parental cooperation over offspring care and stable pair bonds across years. *Behav. Ecol.* 28, 1142–1148
31. Griffith, S.C. (2019) Cooperation and coordination in socially monogamous birds: moving away from a focus on sexual conflict. *Front. Ecol. Evol.* 7, 455
32. Walker, S.C. *et al.* (2017) C-tactile afferents: cutaneous mediators of oxytocin release during affiliative tactile interactions? *Neuropeptides* 64, 27–38
33. Ziolkowski, L.H. *et al.* (2022) Tactile sensation in birds: physiological insights from avian mechanoreceptors. *Curr. Opin. Neurobiol.* 74, 102548
34. Theofanopoulou, C. *et al.* (2021) Universal nomenclature for oxytocin–vasotocin ligand and receptor families. *Nature* 592, 747–755
35. Natochin, Y. *et al.* (2018) New functional role of oxytocin – participation in osmoregulation. *Dokl. Biol. Sci.* 479, 60–63
36. Feldman, R. *et al.* (2016) Oxytocin pathway genes: evolutionary ancient system impacting on human affiliation, sociality, and psychopathology. *Biol. Psychiatry* 79, 174–184
37. Keller, D. *et al.* (2022) A thalamo-preoptic pathway promotes social grooming in rodents. *Curr. Biol.* 32, 4593–4606. e4598
38. Herbeck, Y.E. *et al.* (2022) Fear, love, and the origins of canid domestication: an oxytocin hypothesis. *Compr. Psychoneuroend.* 9, 100100
39. Carter, C.S. and Cushing, B.S. (2017) Proximate mechanisms regulating sociality and social monogamy, in the context of evolution. *Orig. Nat. Soc.* 99–121
40. Fineberg, S.K. and Ross, D.A. (2017) Oxytocin and the social brain. *Biol. Psychiatry* 81, e19–e21
41. Finkenwirth, C. *et al.* (2015) Strongly bonded family members in common marmosets show synchronized fluctuations in oxytocin. *Physiol. Behav.* 151, 246–251
42. Gilbert, J.D. *et al.* (2022) The elusive role of prolactin in the sociality of the naked mole-rat. *Horm. Behav.* 143, 105196
43. Potticary, A.L. and Duckworth, R.A. (2021) A neuroendocrine perspective on the origin and evolution of cooperative breeding. *Auk* 138, ukab036
44. Hart, D.W. and Bennett, N.C. (2022) Seasonality of reproduction in Bathyergidae is a function of group size: A novel hypothesis (Rodentia). *Lynx* 53, 53–64
45. Hart, D.W. *et al.* (2022) Energetics and water flux in the subterranean rodent family Bathyergidae. *Front. Ecol. Evol.* 10, 867350
46. Šumbera, R. (2019) Thermal biology of a strictly subterranean mammalian family, the African mole-rats (Bathyergidae, Rodentia) – a review. *J. Therm. Biol.* 79, 166–189
47. Faulkes, C.G. and Bennett, N.C. (2007) African mole-rats: social and ecological diversity. In *Rodent Societies: An Ecological and Evolutionary Perspective* (Wolff, J.O. and Sherman, P.W., eds), pp. 427–437, University of Chicago Press
48. Kalamatianos, T. *et al.* (2010) Telencephalic binding sites for oxytocin and social organization: a comparative study of eusocial naked mole-rats and solitary cape mole-rats. *J. Comp. Neurol.* 518, 1792–1813
49. Valesky, E.M. *et al.* (2012) Distribution of oxytocin-and vasopressin-immunoreactive neurons in the brain of the eusocial mole rat (*Fukomys anselli*). *Anat. Rec.* 295, 474–480
50. Donaldson, Z.R. and Young, L.J. (2008) Oxytocin, vasopressin, and the neurogenetics of sociality. *Science* 322, 900–904
51. Staes, N. *et al.* (2015) Chimpanzee sociability is associated with vasopressin (Avpr1a) but not oxytocin receptor gene (OXTR) variation. *Horm. Behav.* 75, 84–90
52. Smearman, E.L. *et al.* (2015) Social stress and the oxytocin receptor gene interact to predict antisocial behavior in an at-risk cohort. *Dev. Psychopathol.* 27, 309–318
53. Finkenwirth, C. and Burkart, J.M. (2018) Why help? Relationship quality, not strategic grooming predicts infant-care in group-living marmosets. *Physiol. Behav.* 193, 108–116
54. Arueti, M. *et al.* (2013) When two become one: the role of oxytocin in interpersonal coordination and cooperation. *J. Cogn. Neurosci.* 25, 1418–1427
55. Gebauer, L. *et al.* (2016) Oxytocin improves synchronisation in leader-follower interaction. *Sci. Rep.* 6, 38416
56. Kingma, S.A. *et al.* (2014) Group augmentation and the evolution of cooperation. *Trends Ecol. Evol.* 29, 476–484
57. Bos, P.A. (2017) The endocrinology of human caregiving and its intergenerational transmission. *Dev. Psychopathol.* 29, 971–999
58. Curley, J. *et al.* (2011) Social influences on neurobiology and behavior: epigenetic effects during development. *Psychoneuroendocrinology* 36, 352–371
59. Schino, G. (2007) Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behav. Ecol.* 18, 115–120
60. De Waal, F. (2007) *Chimpanzee Politics: Power and Sex among Apes*, Johns Hopkins University Press
61. Samuni, L. *et al.* (2017) Oxytocin reactivity during intergroup conflict in wild chimpanzees. *Proc. Natl. Acad. Sci. U. S. A.* 114, 268–273
62. Griesser, M. *et al.* (2011) Understanding animal group-size distributions. *PLoS One* 6, e23438
63. Kopp, K.S. *et al.* (2024) The proximate regulation of prosocial behaviour: towards a conceptual framework for comparative research. *Anim. Cogn.* 27, 5
64. Beauchamp, G. (2015) *Animal Vigilance: Monitoring Predators and Competitors*, Academic Press
65. Griesser, M. (2003) Nepotistic vigilance behavior in Siberian jay parents. *Behav. Ecol.* 14, 246–250
66. Carlson, N.V. and Griesser, M. (2022) Mobbing in animals: a thorough review and proposed future directions. *Adv. Study Behav.* 53, 1–44
67. Hart, B.L. and Hart, L.A. (1992) Reciprocal allogrooming in impala, *Aepyceros melampus*. *Anim. Behav.* 44, 1073–1083
68. Carter, G.G. and Wilkinson, G.S. (2015) Intranasal oxytocin increases social grooming and food sharing in the common vampire bat *Desmodus rotundus*. *Horm. Behav.* 75, 150–153
69. Fischer, E.A. (1988) Simultaneous hermaphroditism, tit-for-tat, and the evolutionary stability of social systems. *Ethol. Sociobiol.* 9, 119–136
70. Ekman, J. and Griesser, M. (2016) Siberian jays: delayed dispersal in absence of cooperative breeding. In *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior* (Koenig, W.D. and Dickinson, J., eds), pp. 6–18, Cambridge University Press
71. Burkart, J.M. *et al.* (2007) Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. *Proc. Natl. Acad. Sci. U. S. A.* 104, 19762–19766
72. Knobloch, H.S. and Grinevich, V. (2014) Evolution of oxytocin pathways in the brain of vertebrates. *Front. Behav. Neurosci.* 8, 31
73. Lawson, E.A. (2017) The effects of oxytocin on eating behaviour and metabolism in humans. *Nat. Rev. Endocrinol.* 13, 700–709
74. Mitchell, M. *et al.* (1981) Plasma oxytocin concentrations during the menstrual cycle. *Eur. J. Obstet. Gynecol. Reprod. Biol.* 12, 195–200
75. Windle, R. *et al.* (1997) Central oxytocin administration reduces stress-induced corticosterone release and anxiety behavior in rats. *Endocrinology* 138, 2829–2834
76. Bales, K.L. and Rogers, F.D. (2022) Interactions between the κ opioid system, corticotropin-releasing hormone and oxytocin in partner loss. *Philos. Trans. R. Soc. B* 377, 20210061
77. Axelrod, R. and Hamilton, W. (1981) The evolution of cooperation. *Science* 211, 1390–1396

78. Hamilton, W.D. (1964) Genetical evolution of social behaviour I. *J. Theor. Biol.* 7, 1–16
79. Ekman, J. *et al.* (2004) Delayed dispersal. In *Ecology and Evolution of Cooperative Breeding in Birds* (Koenig, W.D. and Dickinson, J.L., eds), Cambridge University Press
80. Griesser, M. *et al.* (2006) Reduced mortality selects for family cohesion in a social species. *Proc. R. Soc. B* 273, 1881–1886
81. Griesser, M. and Suzuki, T.N. (2017) Naïve juveniles are more likely to become breeders after witnessing predator mobbing. *Am. Nat.* 189, 58–66