The Mother's Dilemma: Ancient maternal trade-offs explain egalitarian moral cooperation.

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Abstract:

The emergence of egalitarian moral norms is widely regarded as a crucial transition in human social evolution, yet it remains a puzzle. Existing explanatory models leave several issues unresolved and share a common reliance on male social agency and alliance-making, which predisposes them towards mechanisms based in social competition. By contrast, drawing on comparative panin socioecology, this article describes specifically female fitness incentives for collaborative counterdominance against ancestral male alpha-dominance strategies, which likely included opportunistic infanticide. In chimpanzees and bonobos, females use contingent maternal tactics to avoid male aggression, but collaborative defence is strongly moderated by habitat abundance due to effects from female feeding competition. Using game theory payoff matrices, I formalise this maternal trade-off as '*The Mother's Dilemma*'—an ecologically contingent coordination game where individually fitness-enhancing female cooperation becomes viable only when habitat abundance eliminates costs from feeding competition. This model predicts that variable ecological conditions mediated ancient in-group social cooperation across distributed sub-populations of early hominins. I develop the implications of this female-centred ecological model for hominin social evolution and argue that collaborative female counterdominance offers a more compelling explanation of egalitarian human moralities, allomaternal provisioning, and prestige-based male social competition, than existing male-centric or sexually undifferentiated alternatives.

Keywords

Human social evolution, Human morality, Egalitarian counterdominance, Female cooperation, Human self-domestication.

Introduction

Charles Darwin (1) originally theorised that human social cooperation had evolved through natural selection by providing advantages during *between-group hostility*. He reasoned that ancient cooperative groups won more intergroup conflicts, thereby enhancing their members' fitness relative to groups of uncooperative defectors (Fig.1a). However, Darwin (1) also recognised that, by contributing to group success, cooperative individuals incur fitness costs not borne by group members who contribute little or nothing; meaning cooperators should be out-competed (hence, out-reproduced) by selfish social defectors. As such, under competition between individuals *within groups*, natural selection should favour the selfish and their descendants, even though this would eventually diminish cooperation and jeopardise group success (Fig.1b).

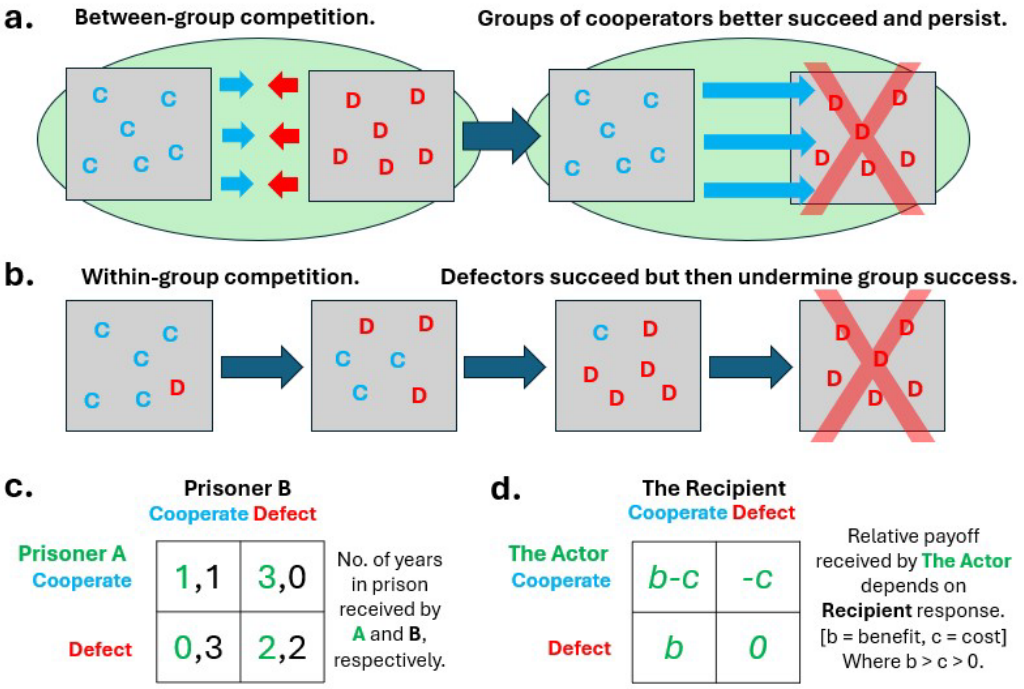

Fig. 1 The paradox of cooperation: (a) Groups of cooperators better succeed during between-group competition; (b) Adapted from (2), individual defectors are favoured under competition within groups but this reduces group success; (c) Game theory payoff matrix for 'The Prisoner's Dilemma'; (d) Abstracted Prisoner's Dilemma cost-benefit payoff structure (3).

This tension between individual and collective fitness remains the central evolutionary paradox of social cooperation, and is commonly depicted using 'The Prisoner's Dilemma' (4); a game theory scenario in which rational self-interest leads both prisoners to defect, despite mutual cooperation yielding a superior collective outcome (Fig.1c). In the abstracted evolutionary form of this model (Fig.1d) (3), cooperative actions always entail a relative cost ('*c*') to the Actor and a benefit ('*b*') to the Recipient, with the Actor's payoff depending on the Recipient's corresponding decision to cooperate or defect. Defection is the optimal default strategy for any Actor, regardless of the Recipient's response, because *b* represents a higher payoff than *b* - *c*, and *0* is greater than - *c* (3).

Despite logical individual incentives to defect, however, numerous mechanisms have been shown to promote the real-world evolution of cooperation by shifting the fitness cost-to-benefit ratio via compensating fitness advantages linked to cooperative behaviour. Five crucial examples are kin selection; direct reciprocity; indirect reciprocity; network reciprocity; and group selection (2). Each of these is known to operate in various animal taxa (5), but only humans have evolved the complex social traits and capacities needed to engage in all five (2). The fact that we do this today, however, does not explain how, or why, our less-cooperative ancient ancestors first overcame the cooperative paradox and began to distinguish themselves in this way.

Darwin's (1) proposed solution to the cooperative paradox in humans highlighted our 'moral sense or conscience', which he considered the greatest difference between us and all other animal species. He described '*do unto others*' as '*the foundation-stone of morality*', and yet painted reciprocity as a relatively '*low motive*' for human cooperation; emphasising our '*sentiments of glory*' and our '*love of approbation and…dread of infamy*', as far stronger promotors of altruistic social virtue (1). Using typically gendered language, Darwin (1) described how '*the praise and blame of his fellows*' could impel a man '*to sacrifice his life for the good of others*', and suggested that witnessing this behaviour would incite '*the same wish for glory in other men*'.

Darwin's (1) historic focus on natural selection through intergroup hostility is reiterated in the 'parochial altruism' hypothesis (6), which posits that human predispositions for '*in-group altruism*' coupled with '*out-group hostility*' were both selected via intergroup conflict. However, this evolutionary model is claimed to entail several questionable assumptions and simplifications (7,8). For example, it assumes '*genetically transmitted*' (6) drivers of cooperation, but ignores factors such as sexual differences, between-group mobility, and high genetic relatedness between neighbouring groups (7,8). More fundamentally though, by assuming '*hypothetical alleles*' (6) for cooperation, all gene-based models obscure the central role of shared human morality and cultural norms that Darwin (1) so heavily emphasised.

Importantly, from a 'cultural evolution' perspective (9,10), selective competition between groups needn't involve overt hostility at all, because cultural differences alone are sufficient to drive between-group fitness differentials. Diverse norms ensure diverse social behaviours, facilitating complex multi-level selective effects (10,11). Shared moral beliefs, customs, and cultural institutions form essential aspects of in-group social identities (12), facilitating social cohesion and cooperation in all human societies (13,14), regardless of any genetic differences between them (9).

As a key example, many human forager societies maintain '*assertively egalitarian*' moral norms that deter individual arrogance and social dominance, and promote equitable resource sharing among group members (15,16). Several evolutionary authors depict these widespread egalitarian human moralities as an ancient social innovation that maintained group cooperation, and thus enhanced collective survival and fitness (17–21). Knauft (17) previously theorised a 'U-shaped' trajectory of social dominance and stratification in human evolution: Starting from male alpha-hierarchies like those of our chimpanzee relatives, dominance declined over a long period under egalitarian conditions in mobile forager groups, until the resurgence of social hierarchies in sedentary Holocene societies. Notably, given this pattern, all of humanity's most distinctive socio-cognitive capacities must first have arisen during this egalitarian period. As such, explaining the emergence of egalitarian moral norms is crucial to understanding human social evolution.

Several previous hypotheses have addressed this egalitarian question, but all share a common theoretical expectation of male social agency and collaboration—this seems incongruous since males receive significant fitness benefits from high status (22–24), and dominate upper ranks in contemporary social hierarchies (25,26). Nevertheless, Boehm (27) depicted ancient egalitarianism as a 'social compact' that arose between '*adult males*' and described the first egalitarian groups as '*a moral community that coalesces around the issue of personal autonomy and equality of males*'. He argued these collaborative groups formed '*reverse dominance hierarchies*' by controlling and punishing domineering alpha male individuals, thus imposing a form of '*social selection*' that promoted complex human social cognition and cooperation (18,28–32).

Similarly, Wrangham (20,21) has argued that ancient '*beta-male*' subordinates began conspiring to execute aggressive alpha dominants; and Sarkar and Wrangham (33) infer that groups of '*subelite males*' formed 'alpha alliances' that killed individual alpha challengers. According to Wrangham (20,34,35), by selecting against '*reactive*' forms of aggression, these ancient beta-male collaborators initiated a process of '*human self-domestication*' (see also 36–39, but see 40,41), which facilitated higher-order cognition, and '*groupishness*'—a social psychology he defines as, '…*helping unrelated group members, having a social conscience,* *accepting and enforcing a moral code, conforming to group norms, sharing resources, and being concerned about fairness and reputation*' (20).

By contrast, Erdal and Whiten (19) argue collaborative moral enforcement cannot have provided the *initial* impetus for human egalitarianism, since cooperative actions reduce the relative fitness of participating individuals—i.e., collectively-based models presuppose some prior solution to the cooperative paradox. Instead, they theorise that ancient '*dominant individuals*' (implicitly, *alpha males*) gained a level of self-control and began to refrain from asserting their dominance as a fitness-enhancing strategy in increasingly '*Machiavellian*' status competition (19). In addition, contra Boehm's (18,32) 'reverse dominance', they argue that apex hierarchies persist in nominally 'egalitarian' groups, but '*counterdominance psychologies and cultures*' suppress overt domineering in favour of prestige-based social status (19)—as discussed elsewhere (42,43).

Explanations of human social evolution often draw on our close phylogenetic relationship to chimpanzees (44–48), where males are philopatric and cooperate more than females via collaborative hunting, strategic alliance-making, and coordinated intergroup hostility (49–51). For example, Wrangham (20) speculates that ancient beta-males exapted *chimpanzee-like* ancestral capacities for male bonding, collaborative violence, and vocal coordination during hunting, to enable conspiratorial killing of isolated alphas. Similarly, Erdal and Whiten describe chimpanzee alliance-making, social deception, and 'Machiavellian intelligence' as shared ancestral features that 'dominant individuals' learned to navigate. By contrast, Knauft (52) critiques explanations for altruistic human morality, culture, and language that are based on Machiavellian social competition; noting their failure to account for the '*linguistic-referential trust and social affiliation*' that underpin complex human social cooperation. Further, he notes widespread male bias in social evolutionary theory, and calls for future research to consider egalitarian counterdominance from a female fitness perspective (52).

To this point, unlike in chimpanzees, *immigrant female* bonobos collaborate far more than patrilocal males—primarily to suppress male social aggression and dominance (53–55). This female behaviour maintains relatively egalitarian intersexual relations among bonobos (55) when compared to male-dominated chimpanzees; where males engage in sexual coercion and *occasional infanticide* (56–58). Crucially, species differences in panin female collaboration appear strongly moderated by habitat abundance (59–61), and chimpanzee females cooperate against male aggression more often when food resources are sufficient to reduce feeding competition (62–65). Given our close phylogenetic relationship, these panin behaviours offer a plausible *a priori* basis to infer similar female fitness incentives and capacities for cooperative counterdominance in our shared hominid-ape ancestors and early ape-like hominins.

With these observations in mind, this article proposes that ancestral females faced a fundamental reproductive trade-off—here termed '*The Mother's Dilemma*'—between the fitness benefits of cooperative defence against male infanticide, on the one hand, and the costs of nutritional competition due to proximate foraging, on the other. Using game-theoretic payoff matrices derived from comparative panin socioecology, I show that this trade-off produces a payoff structure distinct from the standard Prisoner's Dilemma since habitat abundance determines whether cooperation or defection is the optimum female strategy. I then develop the human implications of this model for the emergence of egalitarian moral norms, cooperative breeding, and prestige-based social competition; and argue that collaborative female counterdominance provides a more parsimonious and compelling ancestral catalyst for egalitarian moralities and groupishness than existing male-centric models.

Female counterdominance in panins

In both panin species, dominant alpha males father high proportions of the infants born during their reign, which drives strong male intrasexual selection via aggressive competition for high social status (66–68). In chimpanzees, this dominance-based male reproductive strategy extends to sexual coercion of females and occasional infanticide (56–58). However, in bonobos, females regularly collaborate to deter male aggression and social dominance (53–55)—with female coalitionary agonism targeting males 85% of the time (55). This female behaviour maintains distinctive bonobo social and sexual interactions, and is claimed to have driven a form of wild '*self-domestication*' in this species (69).

Based on regular adult male deference to juveniles, Walker and Hare (70) theorise that female bonobo collaboration against male aggression is motivated by shared maternal '*offspring defence*' psychologies that evolved to counter ancestral infanticide threats. This inference seems further supported by observations of lethal collaborative female violence in response to male threats towards infants (71,72); stronger social affiliation between bonobo mothers with young (73); and uniquely 'protective' female social behaviour around birthing bonobo mothers (74,75). By comparison, wild female chimpanzees employ primarily solo strategies to avoid male violence, including birth seclusion (58); multiple-mating (76); acquiescence to male sexual coercion (56); and avoiding aspiring males during social instability, when infanticide threats are relatively elevated (57).

Chimpanzees show sexually differentiated fitness incentives to commit infanticide: For males, infanticide eliminates offspring fathered by rival dominants, and accelerates the mother's return to fertile cycling and sexual receptivity (77,78). By contrast, females primarily target infants of newly immigrant females—especially under nutritional scarcity—suggesting a basis in maternal feeding competition (77,79). Due to regular gestation and lactation, female panins require more nutrition than males (80), but typical chimpanzee habitats provide less reliable food resources than those of bonobos (59–61). Thus, to avoid competition, wild female chimpanzees forage in relative isolation, making bonobo-like social collaboration less common. Despite this, captive chimpanzees do show third-party '*moral*' concern in response to infanticidal attacks (81), and wild females occasionally collaborate to deter aggressive males (62). Crucially, this female collaboration occurs more often in provisioned chimpanzee populations—at zoos and wild feeding sites—where feeding competition is artificially reduced (62–64).

In both panin species, therefore, specifically female fitness incentives seem to support shared maternal '*offspring defence*' psychologies (70), and aversions to destabilising male social aggression more generally (57,63,70). In turn, these maternal predispositions promote collaborative suppression of male aggression whenever socially affiliated allies are present. However, foraging proximity, social affiliation, and defensive collaboration are all strongly moderated by maternal feeding competition, thus are ultimately determined by relative habitat abundance (Fig. 2).

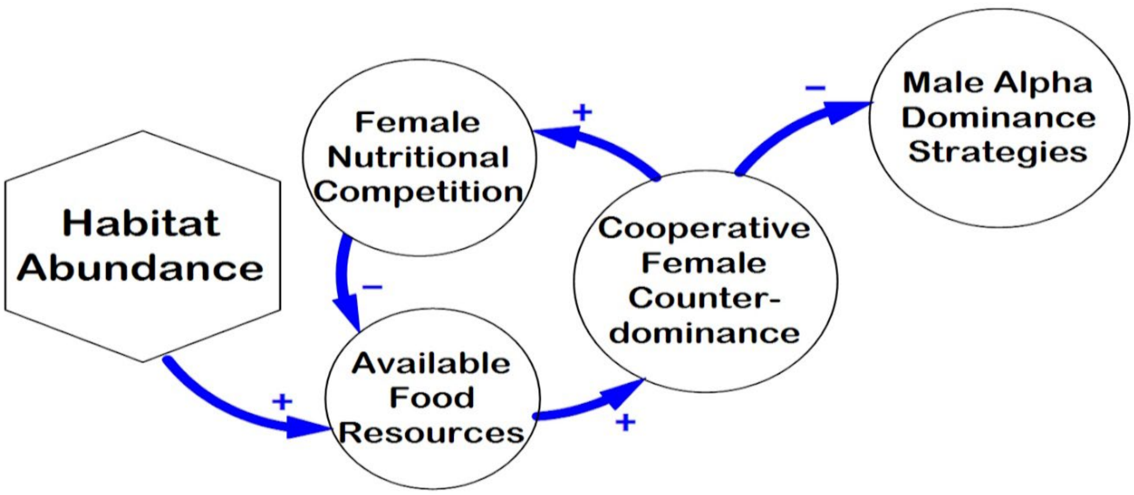

Fig. 2: A causal influence diagram showing panin female collaboration to deter aggressive alpha male dominance strategies as moderated by habitat abundance. Arrows indicate the direction of influence between variables. Positive and negative polarities represent an increase or decrease (respectively) in the target variable in response to *an increase* in the origin variable, but noted polarity acts as reversed if the origin *decreases*. For example, increased 'habitat abundance' also increases 'available food resources', but *decreased* abundance would have a reducing effect.

Given their close evolutionary relationship to humans, these documented panin female behaviours permit an *a priori* inference of similar female fitness incentives and collaborative capacities in our ancient, shared ancestor and in ape-like basal hominins. As such, early hominin females are predicted to have faced a similar strategic trade-off between the benefits of social cooperation to avoid male infanticide, on the one hand, and the costs of nutritional competition from proximate female foraging, on the other. Here, I describe this ancestral female trade-off as '*The Mother's Dilemma*'.

The Mother's Dilemma

Imagine two panin-like ancestral hominid-ape females, both with newborn infants. Their common fitness objectives are to optimise nutrition for themselves and their offspring, and to protect those infants from danger, including potential infanticide due to the dominance-based fitness strategies of males within their social group. One isolated female is unlikely to successfully defend her offspring against an infanticidal dominant male, but two or more cooperating females can. This defensive cooperation is more likely between socially affiliated females, but affiliation requires proximate foraging, which can reduce maternal fitness via nutritional competition and promotes female agonism under extreme scarcity.

The fitness costs and benefits implied by these inferred ancestral conditions can be modelled in the form of a game-theoretic payoff matrix (Fig. 3). Here, the benefit (b) of cooperation is an increase in relative female fitness gained by preventing male infanticide. The corresponding fitness cost (c) is the potential loss of maternal and infant nutrition due to feeding competition. Importantly, it is assumed here that the costs of feeding competition exceed the benefit of preventing male infanticide; thus $c > b > 0$; unlike in the standard Prisoner's Dilemma, where $b > c$ (Fig. 1d). This is justified by the observation that wild chimpanzee females tend to forgo the benefit of cooperative infant defence, prioritising the avoidance of costs from nutritional competition instead. By contrast, in wild bonobos (and provisioned chimpanzees), where higher food abundance negates female feeding competition, females will cooperate far more readily.

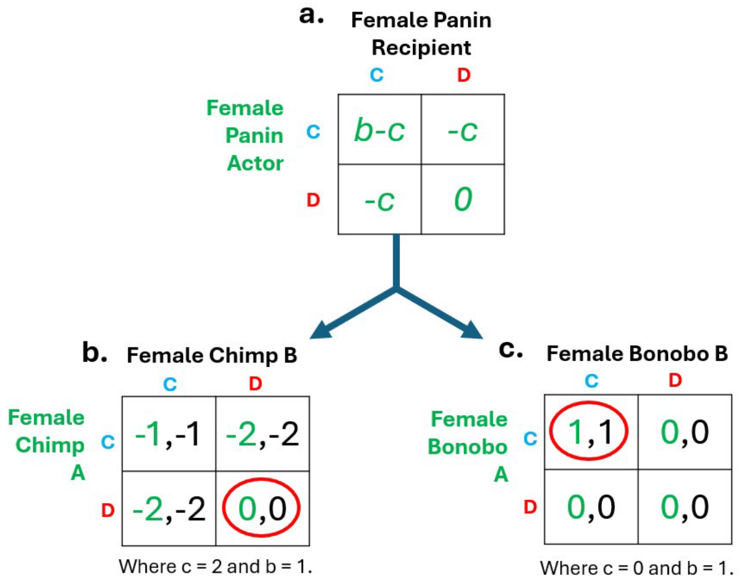

Fig. 3: Payoff matrices showing relative fitness received by 'A' and 'B' respectively. Panels b. and c. are calculated from a. using different costs (*c*) and benefits (*b*) for chimpanzees and bonobos, as shown. The cost of cooperation is zero for bonobos due to elevated habitat abundance, which negates female feeding competition. Ellipses indicate optimum female fitness payoffs in each species.

This cost-to-benefit ratio ($c > b$) represents a fundamental departure from the standard Prisoner's Dilemma where cooperation yields a positive net payoff ($b - c > 0$) but is dominated by defection—i.e., individually rational decisions lead to collectively suboptimal outcomes. In the Mother's Dilemma, by contrast, cooperation yields a mutually negative payoff under default conditions; making it not merely suboptimal, but actively fitness-reducing. Cooperation is incentivised only when habitat abundance reduces c towards zero. Thus, the Mother's Dilemma describes a contingent payoff structure in which ecological conditions, rather than strategic preferences alone, determine whether cooperation is viable.

In Fig. 3a, where both females choose to cooperate, their payoffs will be the benefit minus the cost of cooperation. Where both defect, they receive zero relative benefit or cost since they remain subject to male infanticide but can avoid nutritional competition by foraging in relative isolation. For the two asymmetric conditions, where one female cooperates and the other defects, there is no benefit to either since cooperative defence requires at least two participating females, so defection by either one negates this potential benefit (Fig. 3a). In addition, however, both still incur the cost of feeding competition (- c) because the presence of even one cooperator implies foraging proximity, regardless of whether both cooperate when needed. As such, the asymmetric condition yields the worst possible payoff for both parties.

Where payoff matrices are calculated to reflect the behavioural strategies of wild female chimpanzees (Fig. 3b), solo maternal feeding and infant protection strategies are assigned a base fitness value of *0*. The cost of nutritional constraint due to closer female foraging is a penalty of *2* (thus, *–2*), and the benefit of cooperatively avoiding male infanticide is *1* (*+1*); i.e., $c > b > 0$—note that these values are ordinal, chosen to reflect the observed behavioural ranking, rather than precise fitness estimates. As a result, however, if both cooperate, they receive a payoff of *-1*, if one cooperates and one defects the result is *-2*, whereas both defect yields *0*. In effect, wild chimpanzee females can optimise their fitness via isolated foraging and solo infanticide avoidance strategies. By contrast, due to higher bonobo habitat abundance, the fitness costs of proximate female foraging, affiliation, and defensive cooperation are effectively zero (Fig. 3c). Thus, wild bonobos (*and* provisioned chimpanzees) are incentivised to engage in collaborative defence against aggressive males.

Counterdominance and cooperative breeding

In their extensive review of human socio-political evolution, Gintis et al. (82) cite Hrdy's (83,84) '*cooperative breeding*' theory (see also 85–88) as a maternal fitness strategy that significantly enhanced human prosociality. However, they also claim that cooperative breeding maximised prosociality in humans due to a *preexisting* egalitarian moral order that arose due to the combination of human 'scavenging and hunting', 'control of fire', and 'the practice of cooking', which necessitated '*sophisticated norms for sharing meat*' (82). In contrast, cooperative breeding theorists posit that allomaternal care was already established among Pleistocene Australopiths (83,84,87), and Burkart et al. (87) recently proposed a '*cooperative breeding first*' model of hominin social evolution, arguing that alloparental contributions were an essential precondition to enhanced human cooperativeness, and heightened socio-cognitive skills, including language. Given their potential relevance, it seems pertinent to consider these two key human social traits—'*egalitarianism*' and '*cooperative breeding*'—together; both in relation to each other, and to the collaborative female counterdominance implied by the Mother's Dilemma.

In brief, according to Hrdy (83,84), and other authors (e.g., 85–88), hominin evolutionary trends towards costlier, larger-brained, slower-growing infants, shorter birth intervals, and several other distinctive human socio-cognitive traits, all result from natural selection under ‘*allomaternal provisioning*’—i.e., infant nutrition provided by individuals other than the mother. According to this theory, the presence of variable alloparental investment selected for infant traits that could elicit attention and care from surrounding adults; including neoteny, attentive eye-contact, smiling, babbling, and facial imitation (84). Although of primary benefit in infancy, these traits also enhanced adult sociability and cooperation, thus further benefiting individual survival and fitness in an increasingly cooperative hominin social niche (84–88).

Notably, however, Hrdy (84) repeatedly theorises that possessive maternal infant guarding—common in most primates—was *the principal* ancestral barrier to the evolution of hominin allomaternal care from our non-cooperatively-breeding ancestors. This maternal wariness is especially adaptive in chimpanzees, where both dominant males, and competing females, are known to commit infanticide (57,79,89). If similar threats maintained maternal possessiveness in our ancient, shared ancestor, then infanticide threats would have been a major upstream obstacle to maternal tolerance, and thus to hominin allomaternal care. To this crucial point, however, if high habitat abundance facilitated ancestral female affiliation and counterdominance, as is proposed here, then both male and female infanticide would logically have been diminished.

In bonobos, defensive female collaboration extends to ‘*protective*’ social behaviours around birthing mothers (74,75)—with attending females known to engage in ‘encouraging gestures’ and even *permitted holding* of partially expelled infants (74). This reflects a level of maternal tolerance that is extremely rare in other primates, including in chimpanzees, and suggests significant relaxation of ancestral maternal anxiety and possessiveness. Protective female birth attendance may be a relatively natural extension of collaborative ‘offspring defence’ (70), but since collaboration is more likely between affiliated females, mechanisms that enhance affiliation should also be positively selected, and stronger affiliative relationships would logically also elevate maternal trust.

As an example, female bonobo same-sex genital rubbing, which diffuses social tension and cements affiliative bonds, has been shown to elevate oxytocin production (90). Oxytocin is a widely conserved promoter of mammalian maternal–infant bonding; however, in many species, this central role is extended to support other social relationships, including friendships, pair-bonds, *and allomaternal care* (91,92). Thus, if female oxytocin was similarly elevated (via sexual interaction, or any other social stimulus) in our early ancestor because it promoted fitness-enhancing female affiliation and cooperative infant defence, this same selective impetus might eventually also predispose *allomaternal infant defenders* towards occasional *allomaternal provisioning*. Once this was available, selection for infant traits that elicit allomaternal care would enhance such predispositions, thus promoting full-blown hominin cooperative breeding.

Importantly, this proposed pathway to cooperative breeding contrasts with Hrdy's (83,84) emphasis on kin selection theory as a solution to ancestral maternal anxiety and possessiveness. Against this, however, cooperative bonobo females are typically unrelated immigrants living in male-philopatric groups (93); thus, kinship seems unnecessary for bonobo-like female affiliation, collaborative defence, and social birthing to have evolved in our shared hominid ancestor, and in ape-like early hominins. Hrdy (83,84) also speculates that allomaternal provisioning would be most strongly selected in environments where food resources were scarce, but acknowledges that hungry allomothers would be less willing to incur feeding costs (83). Notably, The Mother's Dilemma incorporates this specific ecological tension to explain variable collaborative offspring defence in female panins (Fig 2), which might plausibly extend to cooperative infant care. In effect, rather than contradicting the cooperative breeding model, this explanation of hominin counterdominance directly addresses two important conceptual issues raised by Hrdy (83,84).

Towards a coherent theory

Compared to hominin cooperative breeding, egalitarian counterdominance is associated with a different range of evolutionary changes and timelines. Boehm (30,32) suggests collective egalitarianism arose with the appearance of 'culturally modern' humans at approximately 45Ka. By contrast, Wrangham (20,21) places the transition at 300Ka, coinciding with the speciation of *Homo sapiens*, while Cieri et al. (36) highlight reductions in skeletal robusticity (also in *H. sapiens*) between 200–80Ka. Interestingly, each of these proposed time periods implies the existence of male alpha-dominance hierarchies, and *pre-moral* social behaviours, throughout nearly all of hominin evolution; as well as the absence of 'groupish' moral concerns and behaviour in all non-sapiens *Homo*.

In a separate discussion, however, based on canine size and sexual dimorphism decline in *Ardipithecus ramidus*, Suwa et al. (94,95) infer dramatically earlier reductions in male social aggression and dominance competition, nearer to our divergence from panins, circa 5-9 Ma. Relatively similar early changes have been theorised elsewhere (96–99). Suwa et al. (94,95) attribute these transitions to cryptic hominin ovulation, which, they suggest, enhanced female mate choice capacity, thus promoting male provisioning and pair-bonding. Like these authors, the present paper infers that early decline in male dominance competition explains signature changes in hominin canines. However, rather than pair-bonding, I propose collaborative female counterdominance—as empirically documented among our living panin relatives—as the ancestral driver of this process.

Three broadly overlapping phases of hominin social evolution can be inferred from this discussion: The first involved selective effects from collaborative female offspring defence in our shared ancestor with panins, and in ape-like basal hominins. The second saw increasingly reliable allomaternal provisioning among later hominins, including *Australopithecus* and early *Homo*. The third and final phase involved the emergence of prestige-based status competition, sexual divisions of labour, complex cultural and communicative capacities, and 'groupish' social moralities in relatively recent *Homo*. Each of these phases implies associated phenotypic changes, including (in corresponding order): (1) decline in basal hominin canine size and sexual dimorphism (94,95); (2) increased neoteny, slower infant development, accelerated birth rates, and initial brain size increase (83–88); and (3) further brain expansion and declines in masculine robusticity associated with a cooperative life strategy, and increasing '*self-domestication*' in recent *Homo sapiens* (20,36,38,39,100–102).

To illustrate the first two phases described above, Fig. 4 presents two expanded causal influence diagrams, with additional variables predicted to affect the overall fitness of ancestral females. Fig. 4a depicts our ancient shared panin–hominin ancestor and ape-like early hominins based on inferences drawn from living panins. As in Fig 2, higher habitat abundance elevates collaborative female counterdominance, suppressing male alpha-dominance strategies and reducing infanticide deaths. In addition, higher food availability increases maternal nutrition, providing somatic resources that are divided between having more infants ('birth rate') and nurturing current offspring. Based on panin life history, early maternal somatic investment would have been primarily directed to existing offspring, ensuring rapid growth and independence, but with a relatively slow birth rate (84).

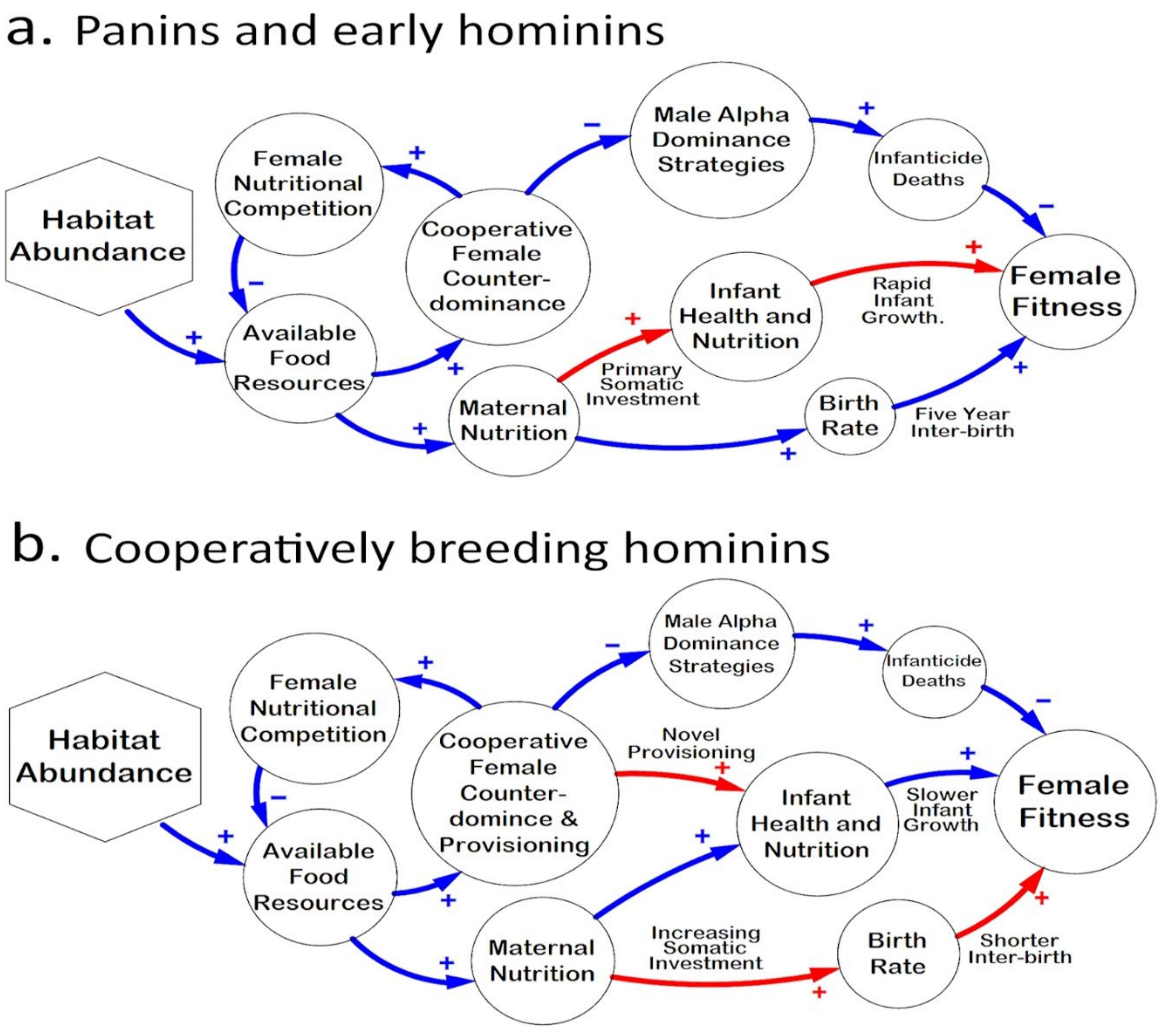

Fig 4: Two expanded causal influence diagrams, showing: (a) additional variables theorised to affect overall female fitness in our shared ancestor with panins, and in early hominins; (b) proposed novel contributions to infant health and nutrition from cooperative female affiliates. Note: interpretation of arrow direction and polarity is explained at Fig.2.

For comparison, Fig. 4b depicts the hypothesised pathway to cooperative breeding via collaborative female offspring defence, in which affiliated females begin provisioning group infants. With additional provisioning, infants could be weaned earlier, allowing mothers to conceive again sooner (85,87). In addition, with demands from existing offspring partially alleviated, prior stabilising selection would be reduced, allowing genes associated with shorter interbirth intervals to spread. Selection for rapid infant growth and feeding independence would similarly be relaxed—in fact, slower childhood development might be advantageous if extended infancy allowed longer access to allomaternal provisioning.

Importantly, the Mother's Dilemma predicts sexually differentiated pathways to egalitarian social cooperation in hominins. Ancestral females initiated collaborative counterdominance and allomaternal provisioning due to direct female fitness benefits conferred by these behaviours. However, competing ancestral males lacked these incentives, thus were not subject to the same selective pressures. In fact, ancestral links between male fitness and high-status, as inferred from male panins (66–68), would predispose early hominin males to aggressive social dominance strategies.

Like our panin relatives, contemporary high status men—but not women—gain higher reproductive fitness (22–24,43,103). However, recent humans tend to engage in 'prestige-based' status competition, as opposed to aggressive ancestral dominance (42,43), often via costly contributions to social groups; e.g., providing food or other valued resources (104–106), and participating in intergroup competition and conflict (107). In accord with theorised evolutionary transitions to prestige-based competition (42), experimental findings suggest that spikes in circulating testosterone heighten human 'moral sensitivity'; implying competitive androgenic effects that are *social-context dependent*, as opposed to invariably aggression- or dominance-promoting (108–111).

As a potential influence in transitions to prestige-based status competition, ancient female *counterdominance* would logically elevate the relative fitness of alternative male mating strategies. For example, males in both panin species show capacity for affiliative mating behaviours; including grooming, hand-holding, emotional support, and occasional provisioning (112–114). Since females more often initiate sexual activity with affiliative panin males (112,114, but see 56), where ancestral dominance was effectively suppressed, affiliative male behaviours would be both socially encouraged *and reproductively advantaged*.

Given reliable fitness advantages from affiliative male behaviours, intrasexual selection would enhance male affiliative capacities, and male competition for reproductive opportunity would increasingly reflect these *socially acceptable* strategies. From panin-like friendships and occasional food transfers, therefore, male social participation might come to include more-or-less reliable support for mating partners, offspring, and other members of culturally specified in-groups (Fig. 5); including conspicuously 'costly' contributions, as seen in many contemporary societies (104–106). In effect, inferring ancient female collaborative counterdominance does not preclude positive male social participation. Rather, it predicts a distinctly male evolutionary pathway to 'groupish' human social cooperation and moral policing, via fitness-enhancing competition for prestige-based social status.

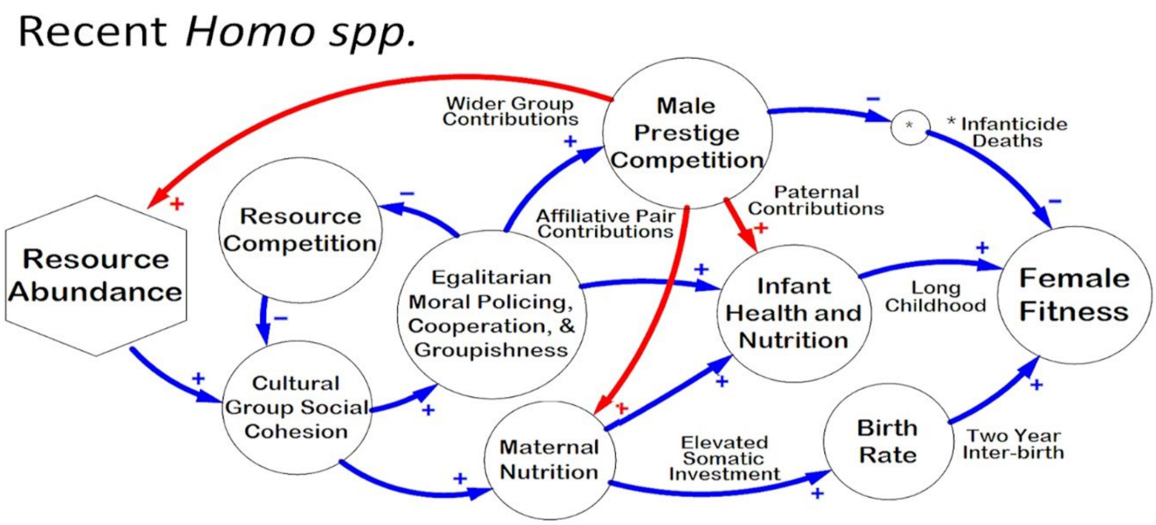

Fig. 5 Factors affecting female fitness in recent human species, showing the additional complexity of male prestige competition via contributions to female partners, offspring, and the wider group. Resource abundance is no longer an external variable—since it may be mediated by prestigious social contributions—and it now directly enhances 'cultural group social cohesion', which mediates egalitarian moralities, cooperation, and 'groupish' behaviour. Elevated resource competition reduces social cohesion, which undermines these beneficial social goods. Infant health and nutrition are supported by significant allomaternal contributions; thus, birth rates are accelerated and childhood is maximally extended. Note: interpretation of arrow direction and polarity is explained at Fig.2.

Discussion

The Mother's Dilemma depicts an ecologically contingent game-theoretic model in which the relative fitness costs and benefits of ancestral female cooperation are determined by habitat abundance. In effect, unlike the standard Prisoner's Dilemma, in which cooperation is individually suboptimal but yields a positive collective payoff, the Mother's Dilemma describes an interactive social context where female cooperation is actively fitness-reducing until ecological conditions shift the prevailing payoff structure. Thus, in resource scarce ancestral contexts, where nutritional competition between early hominin females exceeded the benefits of cooperative infant defence ($c > b$), solo defection was the fitness-optimising female strategy—as observed in wild chimpanzees. However, where elevated habitat abundance negated female feeding competition, the optimal strategy shifted to cooperative counterdominance—as seen in bonobos, and provisioned chimpanzees.

Previous evolutionary debate (e.g., 115–118) often explicitly portrays our last common ancestor with panins as *either* male-dominated, aggressive, and hierarchical, like chimpanzees; *or* relatively female-dominated and peaceful, like bonobos. However, genetic evidence of past interbreeding between panin species and subspecies (119), and among divergent human lineages (120), suggests this theoretical dichotomy may be both artificial and misleading. Apparent contrasts *and similarities* between the two panin species (116), combined with substantial diversity within the four dispersed subspecies of chimpanzee (121,122), demonstrate significant behavioural flexibility across our close panin relatives when considered as a whole.

As an alternative to dualistic either/or models, therefore, our ancient ancestors might be more accurately viewed as an interbreeding metapopulation composed of subpopulations with diverse social and sexual behaviours that varied according to ecological context—as is observed in panins today (121). As such, in ancient habitats with high resource abundance, reduced competition between females would likely have facilitated collaborative female counterdominance; whereas, in harsher environments, or where interspecific competition proved nutritionally limiting, female feeding competition and aggressive male dominance would prevail. This ecologically contingent ancestral diversity is more consistent with existing human social diversity and complexity than any ancestral model based on only one, or the other, of our panin relatives.

The Mother's Dilemma hypothesis of egalitarian counterdominance generates multiple testable predictions. For example, economic comparisons and experiments should show sensitivity of female cooperation to perceived resource availability or security. Further, if female cooperation was the ancestral catalyst for human egalitarian counterdominance, then anthropological comparisons would likely show cross-cultural correlations between resource abundance, female coalitionary support, and reduced *in-group* male aggression and social dominance. In addition, paleoanthropological evidence of increased hominin social cooperation and complexity should correlate with periods or places of increased resource abundance—although causal relationships might be hard to decipher, given social cooperation can also elevate resource availability.

Inferring ecologically contingent, panin-like female counterdominance capacities and incentives in basal hominins makes many important aspects of recent human social cooperation far more succinctly explicable. As a principal example, ancient maternal psychologies that promoted collaborative defence against male dominance and aggression closely align with egalitarian moralities (17,32) and '*counterdominance*' (19) seen in recent foragers; and would logically support past transition from dominance-based competition to socially-mediated ‘prestige’ (42,43). Female ‘*offspring defence*’ psychologies (70)—as opposed to male aspiration for high status and interpersonal dominance—also present a more likely initial motivator for apparently ‘*costly*’ (123), or ‘*altruistic*’ (124), social punishment of moral transgressors. Cooperation between *unrelated immigrant females* within male-patrilocal ancestral groups may also help to explain why human altruism does not require genetic kinship, yet is higher between individuals with shared social identities. Similarly, ancestral female defence of *in-group* affiliates and infants aligns with the ‘*parochial*’ nature of human altruism (6)—whereby support is given to group members, but ‘dehumanisation’ of out-groups regularly fosters hostility, and allows suspension of due moral concern (125).

Many historic authors have lamented humanity’s supposedly innate predispositions for destructively competitive self-interest—as depicted in Hardin’s (126) theoretical ‘*Tragedy of the Commons*’. Against this, however, Darwin (1) emphasised the shared moral norms that suppress individual self-interest and sustain group cooperation as the most distinguishing feature of our evolution. The traditional egalitarian moralities that counter self-interested social dominance and promote contributions to collective welfare in contemporary forager societies are but one widespread example. Ostrom’s (127) empirical contributions to economic theory documented numerous cultural systems where collectively enforced behavioural norms moderate individual use of shared resources in ways that maintain collective benefits; despite theoretically rational individual incentives for selfish overexploitation.

The Mother’s Dilemma implies that these complex moral norms and groupish human behaviours originated from an ancient maternal trade-off that, under favourable ecological conditions, made collaborative counterdominance a fitness-optimising female strategy—laying the foundations for subsequent features of human moral psychology and social cooperation. Despite many widespread examples, however, egalitarian counterdominance and moral cooperation are not unconditionally innate. Under resource scarcity and elevated competition, or where diversified identities promote social disconnection and stratification, collective moral capacities to suppress anti-social self-interest may prove limited. This is consistent with the reemergence of stratified social hierarchies under Holocene sedentism, and continuing inequality between social groups and sub-groups in contemporary human societies.

Currently, collective aspirations for global peace and cooperation, forged in response to two devastating world wars, are threatened by the rise of increasingly autocratic state-based hierarchies. In addition, divisions of wealth, class, race, religion, ethnicity, nationality, and sex, remain faultlines for continuing social exclusion, inequality, and moral failure. As such, at this moment in our shared history, better understanding the evolution of egalitarian moral psychology, and the socioecological conditions under which it is degraded, or might be more effectively asserted, may prove both scientifically and practically consequential.

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