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Cite this article: Smith JE, Natterson-Horowitz B, Mueller MM, Alfaro ME. 2023 Mechanisms of equality and inequality in mammalian societies. *Phil. Trans. R. Soc. B* **378**: 20220307.
<https://doi.org/10.1098/rstb.2022.0307>

Received: 20 February 2023
Accepted: 9 May 2023

One contribution of 20 to a theme issue
'Evolutionary ecology of inequality'.

Subject Areas:

behaviour, evolution

Keywords:

cooperation, coalition formation, dominance, food sharing, hierarchy, inequity aversion

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.6662596>.

Mechanisms of equality and inequality in mammalian societies

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The extent of (in)equality is highly diverse across species of social mammals, but we have a poor understanding of the factors that produce or inhibit equitable social organizations. Here, we adopt a comparative evolutionary perspective to test whether the evolution of social dominance hierarchies, a measure of social inequality in animals, exhibits phylogenetic conservatism and whether interspecific variation in these traits can be explained by sex, age or captivity. We find that hierarchy steepness and directional consistency evolve rapidly without any apparent constraint from evolutionary history. Given this extraordinary variability, we next consider multiple factors that have evolved to mitigate social inequality. Social networks, coalitionary support and knowledge transfer advantage to privilege some individuals over others. Nutritional access and prenatal stressors can impact the development of offspring, generating health disparities with intergenerational consequences. Intergenerational transfer of material resources (e.g. stone tools, food stashes, territories) advantage those who receive. Nonetheless, many of the same social species that experience unequal access to food (survival) and mates (reproduction) engage in levelling mechanisms such as food sharing, adoption, revolutionary coalitions, forgiveness and inequity aversion. Taken together, mammals rely upon a suite of mechanisms of (in)equality to balance the costs and benefits of group living.

This article is part of the theme issue 'Evolutionary ecology of inequality'.

1. Introduction

Wealth inequality is widespread, globally influencing patterns of health [1], reproduction [2] and lifespan [3] for humans. Unequal access to material resources accumulated in the environment, embodied differences (e.g. size, strength or knowledge) and social connections [4,5] exerts a powerful influence on the health [6] and opportunities [7] of individuals. The unequal distributions of wealth can shape divergent destinies [8,9], contributing to the economic concept of intergenerational wealth mobility [10–12], and even alter the evolutionary trajectories across human societies [13]. This imbalance [13,14] is featured in small-scale agricultural [5], pastoral [5] and large-scale modern [15] societies. Humans regularly challenge these sources of inequality through food sharing, peacekeeping, inequity aversion and forgiveness. Inequality also characterizes many animal societies from mole rats [16], hyaenas [17] and mongooses [18] to chimpanzees [19] across the tree of life [20–22], but the evolutionary forces shaping inequality across species have received far less attention.

The notion of natural systems as intrinsically unfair is widespread in western culture—Tennyson's widely quoted lines from *In Memoriam* [23] which paint a natural world filled with 'evil dreams' (p. 34), 'at

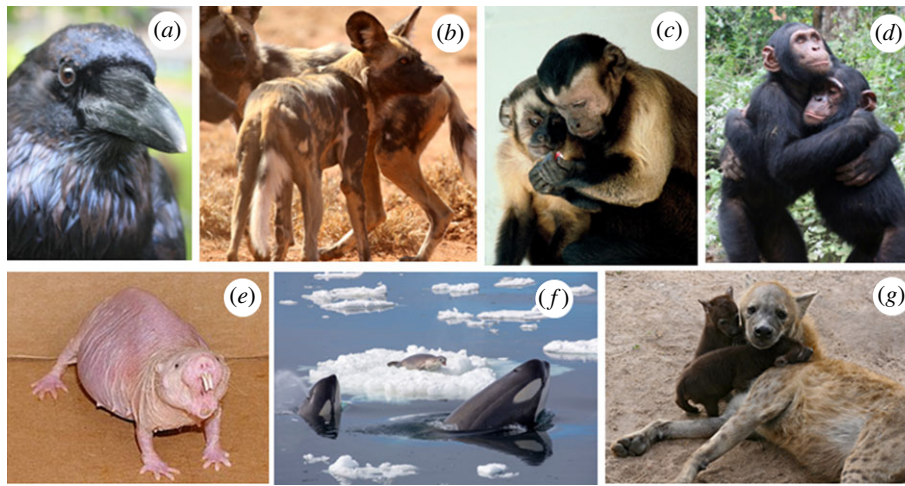


Figure 1. Mechanisms of equality and inequality in animals. Among the many examples in nature: (a) ravens co-feed with non-kin, are averse to inequity and reconcile after fights, (b) African wild dogs share food even with adults and adopt young born to others, (c) capuchins share food and are averse to inequity, (d) chimpanzees inherit tool sites and forgive each other after fights, (e) naked mole rat queens dominate reproduction within their unequal societies, (f) killer whales share food and knowledge, and (g) spotted hyaenas inherit social status and land within family lineages. Photographs reproduced via Creative Commons Licence or permission: (a) Stephan Dickson, (c) Frans de Waal, (d) (copyright: the Jane Goodall Institute)/by Fernando Turmo, (f) Callan Carpenter and (g) Bernard Dupont.

strife' (p. 34) with God, and 'red in tooth and claw' (p. 36) offer but one example. This view contributes to the notion that 'nearly all societies are structured by some type of dominance hierarchy' [24, p. 2]. By contrast to these popular treatments of social organizations, social structures vary from egalitarian to those with strict dominance hierarchies [25,26]. At present, we have a poor understanding of the controls governing the evolution of fairness in animal societies. Comparative evolutionary approaches offer the potential both to characterize the extant diversity in social systems across the tree of life and reveal new insights into the evolutionary origins and underlying mechanisms promoting equality and inequality in animals [20,21,27].

2. (In)equality in mammalian societies

Inequality refers to the phenotypic variation shaped by social structures—reinforced within or across generations—that privileges some individuals over others. It is not simply phenotypic differences among individuals in resource access, well-being, survival and reproduction but rather inequality refers to differences imposed on individuals or classes of individuals by structural features of a social system. There are multiple axes of inequality that reflect social structures ranging from egalitarian to hierarchical. These in turn influence key phenomena from resource distributions to collective decision-making. Our emphasis here is on social processes pertaining to influence in a *resource* hierarchy (e.g. dominance rank; [28–30]) rather than in a decision-making (e.g. leadership; [31,32]) hierarchy. Specifically, we focus on systematic, socially driven inequality in wealth and the effects this has on differential power (social influence or control over conspecifics), well-being (health, stress, mortality, etc.), reproduction and ultimately fitness [33]. We define wealth as attributes or possessions that contribute to well-being or fitness, including material (e.g. food, territory), relational (e.g. social networks) and embodied (e.g. knowledge, skill) forms [5,20,21].

Here, we quantitatively test whether one measure of inequality (dominance) in animal societies is evolutionarily

constrained, discuss evidence for developmental and social factors contributing to more or less equal societies and review mechanisms that have evolved to counter inequality in natural systems. We focus primarily on social mammals as these species share the same basic biological features as humans (e.g. lactation, gestation) but also consider examples from birds, a second tetrapod lineage showing multiple evolutions of highly structured social organization (figure 1).

3. Strength and consistency of inequality diverse across mammals

Napoleon (the pig) asserted that 'All animals are equal, but some animals are more equal than others' [34, p. 75] to justify his political ambitions, but this statement is an accurate characterization of the diversity of fairness across animal species as well. In animals, dominance relationships contribute to patterns of inequality [24]. Social dominance can have important consequences for animals, contributing to unequal access to resources [35] and—in some cases—reproductive inequality (skew) [36–38], which varies within and among species (e.g. [39,40]). Because the diversity and evolution of reproductive inequality across humans and other mammals has recently been characterized elsewhere [40] and reproductive skew is discussed extensively in other contributions in this special issue [16,19,41], the first section of this paper focuses on social dominance as a measure of inequality. Social dominance reflects how individuals are organized into a dominance hierarchy based on the outcomes of pairwise agonistic interactions (e.g. wins, losses, and unsolicited appeasements) within a social group [28,42,43]. We sought to quantify the extent to which dominance structures vary within and among species as well as how these structures evolve.

Our initial goal was to investigate whether dominance structures are phylogenetically constrained across (non-domesticated) mammalian species. Drawing from the last century of research on dominance hierarchies, we analysed data that are publicly available from the R-package 'DomArchive' [44]. We focused on whether and how two major aspects of within-group social inequality (or lack thereof)—steepness

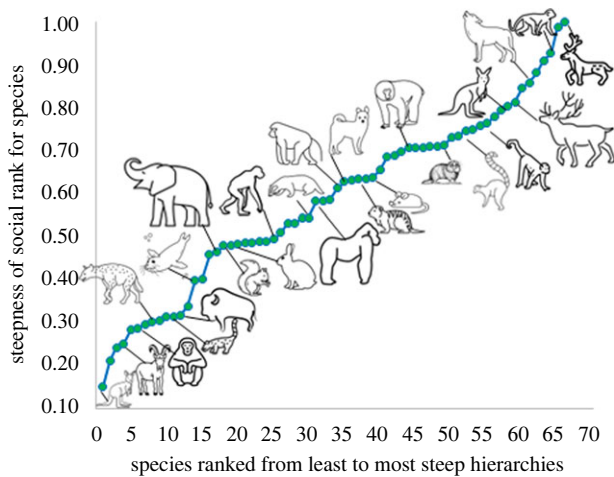


Figure 2. Steepness of dominance hierarchies across 66 species of mammals. For example, the following species are ranked from those with the most shallow to the steepest hierarchies: whiptail wallabies, mountain goats, chimpanzees, white-nosed coatis, bison, harbour seals, African elephant, Albert's squirrel, rabbit, bonobo, European badger, gorilla, chacma baboon, brown hyaena, dwarf mongoose, house mouse, Japanese macaque, Highveld mole rat, ring-tailed lemur, white-faced capuchin, eastern grey kangaroos, snub-nosed monkeys, wolves and sable antelopes (see the electronic supplementary material for the complete list). For visualization purposes only, data were pooled for subspecies or if multiple studies were conducted on the same species to present species-level averages. Domestic species were excluded from the dataset. Sources for species icons: thenounproject.com and Wikimedia commons.

and directional consistency (DC)—varied among and within species of non-human mammals. Steepness, the absolute slope of the straight line fitted to normalized David's scores (a dyadic dominance index) plotted against the subjects' ranks, reflects the degree to which individuals differ in their tendency to win agonistic encounters [45]. DC equals $(H-L)/(H+L)$ based on the wins in the direction of higher (H) minus lower (L) frequency within each dyad and ranges from zero (complete symmetry) to one (completely asymmetric) [46,47]. Briefly, we asked whether steepness or DC was phylogenetically constrained after accounting for the age, sex and environmental context (naturalistic versus captive) for social mammals (see the electronic supplementary material for complete methods) [48].

Our comparative analysis of mammalian species (electronic supplementary material, table S1) showed that hierarchies are highly variable across mammals (i.e. hierarchies are shallow in some groups but steep in others; electronic supplementary material, table S2 and figure S1); outcomes of agonistic interactions are consistent in some groups but not others (electronic supplementary material, table S3 and figure S1). Moreover, the degree of steepness or DC for a species is largely independent of phylogenetic constraints (see the electronic supplementary material for full results), and these traits vary considerably across mammalian species (e.g. steepness in figure 2), demonstrating the wide range of interspecific variation along a continuum. If dominance is tied to ecologically conservative traits, or if social structures evolved slowly within species, we would expect a strong pattern of phylogenetic conservatism such that closely related taxa should exhibit similar hierarchy properties. Our comparative analyses indicate quite the opposite, revealing that switches to divergent dominance social structures have occurred repeatedly across mammals (electronic

supplementary material, figure S1), even after controlling for traits of the study groups (e.g. age or sex composition; electronic supplementary material, table S2). Hierarchies were significantly steeper for captive than non-captive groups and interactions were significantly more asymmetric within male-only groups (versus female-only groups) and in captivity (versus in naturalistic settings; electronic supplementary material, tables S2 and S3). Nonetheless, the random effect of species (or in some cases, subspecies) improved the fit of both models (steepness: $X^2 = 39.8$ and DC: $X^2 = 46.2$, $p < 0.0001$ for both), confirming that intraspecific dominance structures were generally similar across study groups.

The lack of evolutionary constraint on dominance structures is inconsistent with the idea that inequity within social systems is an inevitable evolutionary legacy, suggesting instead that diverse and divergent social organization strategies evolve quickly. A possible explanation of this pattern is that animal societies evolve rapidly by drift at a rate that erases the signature of the phylogeny. However, given the well-documented fitness consequences of sociality, this seems unlikely. Alternatively, social systems may evolve rapidly in response to local or shifting fitness optima associated with local resource characteristics. Future studies are required to consider the role of ecological conditions in explaining these patterns. For example, ecological theory predicts intense local competition for patchy, high-quality resources may favour steep and consistent fight outcomes; ecological conditions (e.g. defensibility of food or mates)—as well as the degree of relatedness within groups [49]—are expected to drive variation in hierarchy emergence, particularly in primates [50,51]. Differences between captive and natural settings may reflect limited opportunities for dispersive conflict resolution but an abundance of food in captivity. Additionally, a more nuanced approach that explicitly reveals the role of ecological context contributing to the dominance structures within our broad dataset would be valuable. This could further reveal the mechanisms contributing to (un)equal social structures, including the contexts in which sex differences in power over resources and mates are most likely to emerge [52,53]. Regardless of the drivers of this diversity, these patterns demonstrate the extraordinary breadth of social structures across mammals, the lack of a phylogenetic legacy of social dominance among mammals, and the variability of such structures even within members of the same species. Although social dominance is one major axis of inequality in that it reflects the social structures that contribute to resource access in animal groups, there are multiple mechanisms that contribute to differential access to resources and social support beyond an individual's ability to simply win contests. As discussed in the next section, developmental and social mechanisms often contribute to more or less equal societies (table 1).

4. Developmental and social mechanisms contribute to inequality

Intergenerational transfer of embodied, material and relational wealth contribute to inequality in human and non-human societies [5,20,21]. Here, we focus on a diversity of mechanisms linked to promoting or inhibiting inequality across some of the best-studied examples of social mammals (table 1).

Table 1. Comparative data exemplifying mechanisms of (in)equality across well-studied social mammals.

species	mechanisms promoting intergenerational inequality		mechanisms promoting equality		
	socioecology	resource (e.g. food, tools, land) transfer (material wealth)	food sharing and adoption of non-kin ^c	fairness—inequity aversion ^d	
chimpanzee (<i>Pan troglodytes</i> spp.)	philopatry, social organization and trophic guild (defendable) ^a	maternal nutrition, stressors (embodied wealth)	revolutionary coalitions and peacekeeping	conflict resolution (forgiveness/reconciliation) ^e	
	male philopatry; mixed sexes; omnivore (most food not defendable)	coalitions (N, R, CH) [54]; maternal presence positively influenced offspring muscle mass [55] and survival [56]	meat-sharing among kin and non-kin; some enforcement via aggression [60,61]	inequity aversion to unequal pay (food) paradigm [64]	post-conflict reconciliation [65–67]
bonobo (<i>Pan paniscus</i>)	male philopatry; mixed sexes; omnivore (most food not defendable)	maternal rank and 'stress' during gestation correlated with offspring stress physiology [57]	mutual tolerance; co-feeding promotes social interactions [69–71]	inequity aversion to unequal pay (food) unclear [64]	post-conflict reconciliation [67]
	both philopatry; mixed sexes; omnivore (most food not defendable)	coalitions (N, R) [54], but they also promote tolerance; maternal presences associated with increased mating, particularly by low and mid-ranking males [68]	feeding promotes social interactions [69–71]	females join forces to protect themselves from harassment by males [72]	post-conflict reconciliation [67]
chacma baboon (<i>Papio ursinus</i>)	both philopatry; mixed sexes; omnivore (most food not defendable)	coalitions (N,R) [73]	tolerated co-feeding limited to kin at playbacks [74]	inequity aversion to unequal pay (food) unclear [64]	post-conflict reconciliation [75]
	females philopatry; mixed sexes; omnivore (most food not defendable)	coalitions (N) [54]; social skills in infants linked to maternal care [76]; maternal sociality predict infant growth and reproduction [77]	mutual feeding tolerance by males of males and females sexes of different ages [60]	cultural shift from competitive to peaceful troop [79]	post-conflict reconciliation [67,80]
olive baboon (<i>P. anubis</i>)	females philopatry; mixed sexes; omnivore (most food not defendable)	mothers experiencing more adversity had increased glucocorticoid levels and reduced offspring survival [78]	tolerance in food sharing present but varies with food type and availability [60]	low and mid-ranking males interrupt consorts by high-ranking males [82]; females join forces for protection against male harassment [83]	post-conflict reconciliation [67,80]
	females philopatry; mixed sexes; omnivore (most food not defendable)	coalitions (N, R, CH) [54]; survival in future generations associated with maternal loss [56]	maternal status predicts son's glucocorticoid concentrations [81]		
yellow baboon (<i>P. cynocephalus</i>)	females philopatry; mixed sexes; omnivore (most food not defendable)	maternal status predicts son's glucocorticoid concentrations [81]			

(Continued.)

Table 1. (Continued.)

species	mechanisms promoting intergenerational inequality		mechanisms promoting equality	
	socioecology	social support ^b , networks, knowledge (relational wealth)	resource (e.g. food, tools, land) transfer (material wealth)	food sharing and adoption of non-kin
Barbary macaque (<i>Macaca sylvanus</i>)	females philopatric; mixed sexes; omnivore (most food not defensible)	coalitions (N, R, CH) [54]		low/mid-ranking males interrupt consorts by high-ranking males [84,85]
	females philopatric; mixed sexes; folivore/frugivore (food mostly not defensible)	coalitions (N, R, CH) [54]		inequity aversion to unequal food reward [86]
	females philopatric; mixed sexes; frugivore (food is defensible)	coalitions (N, R) [54]		inequity aversion to unequal pay (food) paradigm [64]
Japanese macaque (<i>M. fuscata</i>)	females philopatric; mixed sexes; folivore/frugivore (food mostly not defensible)	coalitions (N, R, CH) [54]		inequity aversion to unequal food reward [67]
	females philopatric; mixed sexes; frugivore (food is defensible)	coalitions (N, R, CH) [54]		inequity aversion to unequal food reward [64]
pig-tailed macaque (<i>M. nemestrina</i>)	females philopatric; mixed sexes; folivore/frugivore (food mostly not defensible)	coalitions (N, R) [54]		reciprocal exchange of food among non-kin [87]
	females philopatric; mixed sexes; frugivore (food is defensible)	coalitions (N, R) [54]		tolerated co-feeding between kin and non-kin [88]
bonnet macaque (<i>M. radiata</i>)	females philopatric; mixed sexes; frugivore (food is defensible)	coalitions (N, R) [54]		post-conflict reconciliation [67]
	females philopatric; mixed sexes; frugivore (food is defensible)	coalitions (N, R) [54]		post-conflict reconciliation [67]
tonkean macaque (<i>M. tonkeana</i>)	females philopatric; mixed sexes; frugivore (food is defensible)	coalitions (N, R) [54]		post-conflict reconciliation [67]
	females philopatric; mixed sexes; frugivore (food is defensible)	coalitions (N, R) [54]		post-conflict reconciliation [67]

(Continued.)

Table 1. (Continued.)

species	mechanisms promoting intergenerational inequality		mechanisms promoting equality	
	socioecology	social support ^b , networks, knowledge (relational wealth)	resource (e.g. food, tools, land) transfer (material wealth)	revolutionary coalitions and peacekeeping
tufted (brown) capuchin monkey (<i>Sapajus apella</i>)	females philopatric; mixed sexes; omnivore (most food not defensible)	coalitions (N) [54]		inequity aversion to unequal pay (food) paradigm [64]
bearded capuchin monkey (<i>Cebus libidinosus</i>)	females philopatric; mixed sexes; folivore/frugivore (food mostly not defensible)	accumulation of stone tools and anvils [92]		inequity aversion to unequal pay (food) paradigm [64] prevents conflict [91]
grey wolf (<i>Canis lupus</i>)	females philopatric; mixed sexes; carnivore (food is defensible)	coalitions (N, R) [54]; large size combined favours rapid neonatal growth [93]	territories passed from one generation to next along maternal line [94]	co-feeding tolerated within a closely related wolf pack [95]
African wild dog (<i>Lycan pictus</i>)	neither sex philopatric; mixed sexes; carnivore (food is defensible)	coalitions (N, R) [54]		food sharing among closely related group members [60]; adoption common [98]
African lion (<i>Panthera leo leo</i>)	females philopatric; mixed sexes; carnivore (food is defensible)	coalitions (N) [54]		food sharing among females join forces to reduce infanticide [99]
spotted hyaena (<i>Crocuta crocuta</i>)	females philopatric; mixed sexes; carnivore (food is defensible)	mechanisms promoting intergenerational inequality: coalitions (N, R, CH) [54]; maternal rank-inheritance [100]; rank-based social network inheritance [101]	territory inheritance by philopatric females and priority of access to high-ranking individuals [103]	rank-changing revolutionary coalitions increase social mobility with intergenerational fitness benefits. [106]

(Continued.)

Table 1. (Continued.)

species	mechanisms promoting intergenerational inequality		mechanisms promoting equality					
	socioecology	social support ^b , networks, knowledge (relational wealth)	maternal nutrition, stressors (embodied wealth)	resource (e.g. food, tools, land) transfer (material wealth)	food sharing and adoption of non-kin ^c	revolutionary coalitions and peacekeeping	fairness—inequity aversion ^d	conflict resolution (forgiveness/reconciliation) ^e
banded mongoose (<i>Mungos mungo</i>)	philopatry, social organization and trophic guild (defendable) ^a	both or neither sex (varies by group) philopatric; mixed sexes; insectivore (food is not defendable)	coalitions (R) [73]; escorted pups heaviest at maturity and increased reproductive success [108]	supplemental food prenatally increased offspring lifespan and post-natally increased lifetime reproductive success [18]	tolerance of food sharing among close relatives [109]; equitably allocate care among group-mates when kinship masked [110]	food sharing and adoption of non-kin ^c	dispersive conflict resolution via evictions from group [111]	conflict resolution (forgiveness/reconciliation) ^e
wild horse (<i>Equus caballus</i>)	neither philopatric; mixed sexes; herbivore (food is not defendable)	coalitions (N) [54]	coalitions (N) [54]		low and mid-ranking males interrupt consorts by high-ranking males [112]		post-conflict reconciliation [113]	
bottlenose dolphin (<i>Tursiops truncatus</i>)	both sexes philopatric; mixed sexes; piscivore (food is not defendable)	coalitions (N) [54]	coalitions (N) [54]				post-conflict reconciliation [114]	
Indo-Pacific dolphin (<i>T. aduncus</i>)	both sexes philopatric; mixed sexes; piscivore (food is not defendable)	coalitions (N) [73]	coalitions (N) [73]		low and mid-ranking males interrupt consorts by high-ranking males [115]		post-conflict reconciliation [116]	
killer whale (<i>Orcinus orca</i>)	both sexes philopatric; mixed sexes; piscivore /carnivore (most food is not defendable)	intergenerational transfer of ecological knowledge [117] increases survival of grandoffspring [118]	poor maternal nutrition negatively affects foetal brains [119]	tolerance of co-feeding by non-kin, including feeding by other pods [120,121]			post-conflict reconciliation [122]	

^aPhilopatry scored as females (F), males, (M), both (B) or neither (N) sex remaining at home into adulthood; social organization reflects the sex composition of adults in the group, where 'mixed' refers to multiple adult males and females in the group; trophic guild reflects the typical diet for a species and whether that food is defendable (yes = defendable; no = non-defendable), for complete set of references, see [54]. For brevity, whenever possible, we cited early review papers.

^bIntragroup coalition formation during which coalitionary supported was nepotistic (N; kin-biased) and whether coalitionary aggression was directed towards subordinate targets to reinforce (R) and/or towards dominant to challenge (CH) the status quo [54,73].

^cFood sharing [60].

^dInequity aversion [64].

^eReconciliation [67].

(a) Maternal nutrition and stressors contribute to embodied wealth

In human societies around the world, the strongest predictor of undernutrition before, during and after pregnancy is poverty. Women without resources are less likely to have access to sufficient high-quality nutrition during these critical periods, compromising the immunological, neurological, metabolic and reproductive health throughout their, and perhaps their offspring's, lives [123–125]. Mounting evidence links high-quality maternal nutrition before and during human pregnancy to enhanced adult health outcomes in the developing fetus [126–128]. These include a lower incidence of diseases most linked to morbidity and mortality in humans. The quality of gestational nutrition also shapes pregnancy outcomes with superior nutrition linked to reduced risk of preterm delivery and forms of gestational hypertension. Additional research points to a linkage between quality preconception nutrition and long-term health benefits for the fetus through its life course [129].

Some mechanisms underlying these connections involve transgenerational epigenetic changes and the vertical transfer of beneficial microbiota during pregnancy and lactation. Transfer of immunities during and following pregnancy sets up a neonate not only for early resistance to pathogens but also shapes microbial endophenotypes increasingly linked to a range of consequential adult health effects [130–132]. Access to several nutrients, including fat, protein, vitamin B12, iron, zinc and iodine, impacts neonatal brain development and cognition. Humans whose mothers have greater access to diets rich in these and other nutrients appear to enjoy a number of neurological and cognitive benefits [130]. Undernutrition *in utero* disadvantages individuals whose low birth weights may be followed by stunted growth, shorter adult height and reduced economic outcomes [123,124,133].

It is well documented that maternal 'stress', reflected by high levels of glucocorticoids (GCs) during gestation, is linked to numerous effects on infant physiology that often extend into adulthood, and sometimes intergenerational effects for humans [134]. Similar effects have been shown for many other mammals as well. For example, maternal 'stress' experienced during gestation from snowshoe hares (*Lepus americanus*) [135] to monkeys [136] and apes [57] is often related to offspring stress physiology. Olive baboons (*Papio anubis*) with mothers who experienced more adversity, for example, also had increased GCs and reduced lifespans [78]. However, links between GCs and key traits (e.g. reproduction, health disparities) vary across and within species [137,138].

In some mammals, a parallel relationship exists between a female's nutritional resources and the health and reproductive success of her offspring. These differences in access can impose transgenerational effects on parental care [139], privileging some individuals over others. Evidence for such effects includes data from a mammalian carnivore, the spotted hyaena (*Crocuta crocuta*; figure 1). The quality of maternal nutrition, so often linked to a female's social rank and access to resources, places hyaena offspring at an advantage or disadvantage from its earliest days [103]. Young hyaenas born to high-ranking mothers are the beneficiaries of a nutritional 'silver spoon effect' during both gestation and lactation with long-lasting effects later in life [102]. Compared to offspring of low-ranking mothers, nutrition-advantaged offspring are weaned at earlier ages [140,141], enjoy enhanced immune

systems [142] and grow faster [143]. Earlier consumption of meat may provide an early growth and size advantage for these cubs. Hyaena mothers with reduced access to food may also experience greater stress [144], exposing neonates of low-ranking mothers to elevated cortisol levels which influence the size, strength and immunocompetence of young cubs.

Do the offspring of stressed or malnourished mothers have any available mechanisms to cope with this form of disadvantage? Emerging evidence documents a great deal of behavioural and physiological plasticity associated with an animal's social rank [145]. A comparative study across mammals shows that offspring exposure to prenatal stress causes numerous effects in infant physiology that extend well into adulthood [146]. For instance, macaque offspring exposed to prenatal stress respond to reduced maternal investment through accelerated growth despite reduced motor skills and immune function [147]. Thus, across mammals, young may adjust—at least to some extent—to make the best of a challenging start [146].

Beyond these early life effects, many mammals often depend upon their mothers long after weaning. Comparative data across seven species of primates offer some insights into the intergenerational effects of maternal loss on offspring fitness [56]. Offspring survival for most species was lower in the years immediately prior to a mother's death despite mothers still being alive [56]. Beyond this, for several species of monkeys with social structures ranging from egalitarian to despotic, early maternal death experienced in one generation was also associated with reduced offspring survival in the next [56]. Similarly strong intergenerational effects may indeed be present in non-primate mammals, particularly others with slow life histories.

(b) Resource inheritance contributes to material wealth

Parallels also exist in how resource distributions emerge in human and non-human societies. Links among social inequality, health and survival have been demonstrated for both human and non-human mammals [148]. Cultural and historical factors, including systemic (institutional) racism [15,149,150], contribute to inequality in human societies through forms of oppression, privileging some individuals over others. In other social mammals, wealth (resources) can be also acquired from the direct transfer of material wealth via non-genetic inheritance of material goods [151,152], such as a defended, high-quality real estate to perpetuate legacies of inequality across generations. Among others, wolves [94], lions [153], hyaenas [103] and chimpanzees [59] transfer territories from one generation to the next such that wealth accumulates in some family lines but less so for others.

Resource inheritance, when coupled with social learning and cultural traditions, can further perpetuate patterns of reproductive inequality [151]. Material transfer of resources and social knowledge of how to use materials (relational wealth, as discussed in the next section) can be transferred from one generation to the next. For example, Tai chimpanzees (*Pan troglodytes versutus*) [58] and bearded capuchin monkeys (*Cebus libidinosus*) [92] inherit tools and social knowledge of how to use them. Individuals that inherit physical tools (e.g. stones) are advantaged over others who do not, and these beneficial effects are further compounded through the transfer of social information (e.g. traditions for how to use inherited materials) across generations. Still, some tools used by animals—from corvids to dolphins and apes—are ephemeral;

the short-lived nature of ephemeral tools (i.e. sticks, sponges) can limit their intergenerational transfer [154], and tool use is not always socially learned [155]. Thus, although material inheritance when combined with social inheritance can strongly privilege some over others, the extent of these effects varies and warrants further study.

(c) Intergenerational social support as a form of relational wealth

Coalitions and alliances are major forms of social support that influence an individual animal's social status [54,73,156,157]. Intragroup coalitions form when two or more individuals join forces to direct aggression towards another group member. This cooperative behaviour powerfully influences social structures of carnivores (e.g. spotted hyaenas [73,100,158,159], African wild dogs (*Lycaon pictus*) [160]), ungulates (e.g. fallow deer; *Dama dama* [161]) and primates (e.g. macaques [162], chimpanzees [163,164] and baboons [165]; table 1). Specifically, individuals benefit from intragroup coalitions that reinforce their own dominance and privilege their genetic relatives [73,166–168]. In the societies of spotted hyaenas [100], as well as those of yellow baboons (*P. cynocephalus*) [169], stump-tail macaques (*Macaca arctoides*) [170] and vervet monkeys (*Chlorocebus pygerythrus*) [171,172]), young inherit status from mothers through maternal rank 'inheritance,' a non-genetic mechanism of socially learned status based on repeated maternal support. Thus, rank can be independent of an individual's size or fighting ability but flexible in that it is socially learned and these effects can be further ameliorated by differential social support into adulthood [73,106].

Group stability and associated dominance structures may be maintained or disrupted over time. For example, to compensate for rank instability owing to the loss of a keystone individual, baboons and macaques sometimes compensate through their proximity network [173] or policing [174], respectively. Among birds, ravens (*Corvus corax*) also maintain group stability through social interventions that prevent others from forming competitive alliances [175]. When social mammals inherit their social networks, this can reinforce systems of social support or isolation [101,176], but social mechanisms can also promote cultural shifts. In one baboon troop, the loss of dominant males contributed to a multigenerational shift from a competitive to a peaceful culture [79]. Yet, social networks are not always passed down from one generation to the next even in species with maternal rank inheritance (e.g. vervets) [177], further highlighting the breadth of ways social behaviour emerges to contribute to more or less equal societal structures. Taken together, these lines of evidence highlight the enormous amount of inter- and intra-specific variation in these emergent social processes, the limits of social inheritance and opportunities for behavioural flexibility across social mammals.

5. Mechanisms of fairness and equality in nature

A sense of fairness has long been believed to be a necessary precursor for the emergence of cooperation in particular and equality in general within human social groups. In this paper, we focus on four major mechanisms of fairness that promote equity within animal societies and highlight examples from social mammals (table 1). Levelling mechanisms include food sharing and adoption of non-kin, revolutionary coalitions, conflict resolution and inequity aversion.

(a) Food sharing and adoption

Food sharing, defined as the unresisted transfer of food from one food-motivated individual to another, can promote equal access to limited food resources [60,178]. A comparative approach reveals that energetically costly food sharing among unrelated adults has evolved in a range of social species [60,179,180]. Food-sharing among unrelated primates is limited, but information on food sharing among chimpanzees and bonobos (*Pan paniscus*) is particularly well documented. Chimpanzees, for example, tolerate meat-sharing among community members [181–186], which can be enforced via aggression [61,187]. By contrast, bonobos share food in the absence of conflict [70] and their co-feeding among non-kin enhances social interactions [69,71]. Many baboons and social carnivores share food (table 1), particularly with close kin [166]; brown capuchins (*Cebus apella*) [188], ravens [189] and long-tailed macaques (*M. fascicularis*) [87] also share with non-kin. Moreover, mutual tolerance between males and females maintains social bonds in Guinea baboons (*P. papio*) [190] to domestic dogs (*Canis lupus familiaris*) [191]. Vampire bats (*Desmodus rotundus*) only feed on blood and will die after as little as 70 hours of fasting; roost-mates cooperate by regurgitating blood meals to kin and non-kin [192]. Killer whales (*Orcinus orca*) also share food with non-kin, including with whales belonging to other groups [121,193]. When cooperatively breeding banded mongooses (*Mungos mungo*) lack information regarding kinship they actively provide postnatal care to the most disadvantaged group-mates [110]. That is, only when knowledge about personal gains is masked, mongooses promote fairness, a finding consistent with the classic philosophical notion that a 'veil of ignorance' (hidden reward distributions) promotes fair, equitable outcomes in human societies.

Adoption occurs when adult animals allocate care to young individuals that are not their offspring, an altruistic act documented for multiple species of waterfowl [194] to social carnivores [104]. Snow geese (*Anser caerulescens caerulescens*), for example, regularly adopt eggs laid by conspecifics [195], and one study showed that adoption in African wild dogs occurred in at least one quarter of the packs [98]. For spotted hyaenas, only 13 cases of adoptions have been reported [104], all at a single study site despite their long-term study in multiple areas. Interestingly, postnatal maternal care by surrogate hyaena mothers levelled the playing field of previously orphaned cubs; the social rank of adopted offspring resembled that of their surrogate mothers and persisted into adulthood [104], elucidating how social learning can contribute to inequality in convention-based societies [106].

(b) Revolutionary coalitions

The social lives of animals are by no means fixed but instead are often malleable, subject to cultural shifts based on the outcomes of coalitionary aggression or peacekeeping mechanisms from within. Revolutionary coalitions occur when both partners rank below their target. These can involve enormous immediate risks—but potentially high pay-offs—and often require an understanding of social dynamics [156,196,197]. Although revolutionary coalitions, also called all up coalitions, are always directed up the hierarchy towards dominants, they may either be levelling (i.e. change the pay-off distribution without shifting dominance rank relationships) or rank-changing (i.e. promote rank-reversals within a dominance hierarchy) coalitions [198].

Levelling coalitions permit at least one member of a coalition to obtain access to a mate without influencing the dominance structure [198]. For example, several species of macaques form levelling coalitions in which males selectively recruit allies that outrank themselves and their opponents [60,183]. Low and mid-ranking males may join forces against higher ranking males to gain mating opportunities (e.g. monkeys [82,84,85,199], horses [112], dolphins [115]). Low-ranking yellow baboons, for example, join forces against highest-ranking males [82,200–203] to increase their mating success. Females also join forces to blunt male power and offer protection from harassment or infanticide (e.g. bonobos [72], baboons [83] and lions [99]).

Rank-changing coalitions can improve an individual's position in its dominance hierarchy, affecting lifetime reproductive success, and restructure the group's dominance hierarchy through rank reversals [198]. Although rare, rank reversals contribute to revolutionary social change with major fitness consequences for the individuals involved and have compounding intergenerational effects [106]. For example, in spotted hyaenas, individuals that repeatedly form coalitions with top allies improve their upwards social mobility [106] (table 1). In several macaque species, although rare, mother–daughter reversals are achieved via coalitionary overthrows (e.g. [204,205]). Thus, coalitions can influence the distribution of resources to promote equality by dismantling current structures.

(c) Conflict resolution

Forgiveness has profound consequences on multiple aspects of social life for humans, from family relationships to the political alliances among nations [206]. Other social mammals have also evolved a suite of behavioural mechanisms to mitigate conflict within groups and thereby reduce escalated aggression when conflicts of interest emerge [28,207,208]. For example, mountain gorillas (*Gorilla beringei beringei*) embrace [209], chimpanzees kiss [210] and bonobos massage genitals [211]. These gestures help to reduce immediate injury and promote sociopositive interactions, thereby increasing group cohesion. Because the strength of social bonds can predict future cooperation (e.g. [212]), repair of relationships can more broadly promote future opportunities for cooperation between former opponents. Evidence for reconciliation is now vast, occurring across many social mammals (table 1) as well as in some birds (e.g. ravens [213] and monk parakeets (*Myiopsitta monachus*) [214]). Reconciliation may be a common feature in groups of animals with repeated interactions.

(d) Inequity aversion

A major requirement for equality within groups is the ability for conspecifics to share the pay-offs associated with cooperative behaviours. The evolutionary benefits of sensitivity to (in)equity include the ability to recognize when individuals receive less than their partners. Although a sense

of fairness has long been considered an important aspect of economic decision-making in humans [215], with empathy for victims present in young human infants [216], understanding fairness—defined as the redistribution of resources to reduce initial inequalities [110]—in non-human animals is challenging. One major tool used to gain insights into the concept of fairness is to measure the behavioural reactions by animals exposed to situations in which one individual receives more or less than the other individual. Brosnan & de Waal [217] designed one such paradigm to show that brown capuchin monkeys refused a food reward associated with unfair offers (e.g. grapes versus cucumbers; table 1). Subsequent tests reveal that this form of inequity aversion is most pronounced in species that cooperate, especially those who do so outside of mating or kinship [64,218], such as occurs in chimpanzees [219,220] (but see: [221] for evidence of indifference to welfare of non-kin), long-tailed macaques [222] and corvids (e.g. crows, ravens) [223]. Moreover, social mammals from rats [224] to dogs [225] are also averse to inequity. Evidence for bonobos is equivocal [226] with data limited by small sample sizes [227]. However, there is little evidence for inequity aversion in non-cooperative species [228–230]. In summary, this trait coevolves with cooperation to reduce inequality in social mammals and has deep evolutionary roots.

6. Conclusion

Overall, we showed that multiple features characterizing dominance hierarchies (one measure of inequality in animals) are not evolutionary constrained, highlighting the enormous flexibility of social systems. We also documented that a diversity of mechanisms emerge across species to promote more or less equal social systems. These mechanisms may offer new ways to understand peacekeeping and conflict across mammalian societies and perhaps even help to offer insights into human inequality.

Data accessibility. All data from the freely available online archive. For details, see [44].

Data and all R-code for statistical analyses is included in the electronic supplementary material [48].

Authors' contributions. J.E.S.: conceptualization, data curation, investigation, methodology, project administration, supervision, visualization, writing—original draft, writing—review and editing; B.N.-H.: investigation, writing—original draft; M.M.M.: data curation, investigation, writing—review and editing; M.E.A.: formal analysis, writing—review and editing.

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

Conflict of interest declaration. We declare we have no competing interests.

Funding. This research was supported by a Student-Faculty Research Collaboration Grant to M.M.M. and J.E.S. from the Office of Research and Sponsored Programs at the University of Wisconsin - Eau Claire.

Acknowledgements. We acknowledge our positionality and privilege in having the opportunity to write this article. We are grateful to Christopher Schell and Ambika Kamath for thoughtful conversations and feedback that helped to shape the framing and content of this article.

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