

Review



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The ecology of wealth inequality in animal societies

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Individuals vary in their access to resources, social connections and phenotypic traits, and a central goal of evolutionary biology is to understand how this variation arises and influences fitness. Parallel research on humans has focused on the causes and consequences of variation in material possessions, opportunity and health. Central to both fields of study is that unequal distribution of wealth is an important component of social structure that drives variation in relevant outcomes. Here, we advance a research framework and agenda for studying wealth inequality within an ecological and evolutionary context. This ecology of inequality approach presents the opportunity to reintegrate key evolutionary concepts as different dimensions of the link between wealth and fitness by (i) developing measures of wealth and inequality as taxonomically broad features of societies, (ii) considering how feedback loops link inequality to individual and societal outcomes, (iii) exploring the ecological and evolutionary underpinnings of what makes some societies more unequal than others, and (iv) studying the long-term dynamics of inequality as a central component of social evolution. We hope that this framework will facilitate a cohesive understanding of inequality as a widespread biological phenomenon and clarify the role of social systems as central to evolutionary biology.

1. Introduction

Inequality is a general feature of human and non-human animal societies. Most societies exhibit disparities in individual access to resources, physical condition and social relationships. These disparities can be conceptualized as dimensions of wealth inequality, which translate into differences in outcomes such as health, longevity and reproductive success, and ultimately influence variation in fitness. Wealth inequality in different dimensions may be driven by similar underlying processes and have shared effects on outcomes. Social systems may also differ in which dimension of wealth most directly influences individual outcomes. An overarching study of the causes and consequences of wealth inequality facilitates comparisons of the mechanisms underlying variation in outcomes in various societies. Such a perspective can interrogate the myriad potential factors that generate and maintain wealth inequality, scrutinize the consequences of wealth inequality in terms of individual health and reproductive outcomes, or investigate how inequality changes across time within a society.

Researchers in both human- and animal-oriented fields are motivated to understand how wealth inequality arises, is sustained and acts as a mechanism underlying disparities in outcomes, but the general emphasis differs across fields. In the study of modern human societies, research often focuses on how wealth inequality influences health and well-being, with the aim of informing policies that reduce disparities and promote the well-being of as many people as possible. Research in evolutionary anthropology and related fields examines the role of inequality in human evolution, including the evolutionary origins of human

societies and the effects of inequality on fitness in humans [1–7]. In studies of animal societies, the focus often takes an explicitly evolutionary biology perspective, focusing on wealth inequality as a mechanism that generates variation in fitness.

Wealth, inequality and their influences on fitness variation have been considered in different contexts within the fields of evolution and ecology. For instance, a century of work has explored how networks of dominance relationships arise from interactions among group-mates and influence social structure and fitness-related outcomes [8]. Sexual selection theory addresses the causes and consequences of inequality in mating success [9], and studies of reproductive skew examine behavioural constraints on inequality in reproduction [10,11]. Research into collective decision-making explores the causes and consequences of inequality in behavioural decisions [12–14]. Woven into these subfields are theories of kin selection and multilevel selection, which seek to identify how individual wealth influences the indirect fitness of other individuals, and how inequalities within and between groups influence evolution. Thus, much work on social evolution has concerned itself with the causes and consequences of wealth inequality, albeit without explicitly referring to the parallel concepts of wealth and inequality that human-oriented fields have more thoroughly explored. Notable exceptions are work on privatization and property by Strassman & Queller [15] and intergenerational wealth transfer by Smith *et al.* [16]. In this paper, we expand on this prior work to provide a more overarching review of the concepts of wealth and inequality in animal societies, and explore how wealth inequality can be a source of social selection [17–19].

Here we present a research agenda for studying wealth inequality within an ecological and evolutionary context. We synthesize concepts, questions and empirical insights from research in animals and humans to investigate the ecological and evolutionary implications of inequality. We show that this ‘ecology of wealth inequality’ approach presents the opportunity to clarify the role of social systems as central to evolutionary biology, and to reintegrate key evolutionary concepts that have often been perceived as alternatives (e.g. trait evolution, niche construction, extended phenotypes) as different dimensions of the wealth–fitness relationship. We identify four key opportunities in the ecological study of inequality: (i) developing measures of wealth and inequality as taxonomically broad features of societies, (ii) considering how feedback loops link inequality to individual and societal outcomes, (iii) exploring the ecological and evolutionary underpinnings of what makes some societies more unequal than others, and (iv) studying the long-term dynamics of inequality as a central component of social evolution. In each section, we review existing work and highlight areas requiring additional empirical and theoretical attention. We aim to motivate a cohesive interdisciplinary approach to understanding inequality as a widespread and diverse biological phenomenon.

2. What are wealth and inequality in animal societies?

Non-humans do not have bank accounts, so how can they be wealthy? Economists and evolutionary anthropologists have long known that wealth can take many forms [20,21]. Wealth manifests in many *currencies*, or quantities of attributes or possessions that impact an individual’s access to

‘valued goods and services’ [22]. Although the currencies of wealth are numerous, they can be pooled into three super-seeding categories (here ‘*aspects*’; figure 1, top left) [4,22,23]. *Material wealth* denotes extrasomatic currencies such as money, land or livestock. *Relational wealth* consists of social connections, often measured as ties in a network of relevant social interactions or relationships such as food sharing, prestige or cooperative hunting. Finally, *embodied wealth* refers to attributes of individuals, such as size, strength or knowledge.

This framework reveals how animal societies are also structured by multiple dimensions of wealth. These same three aspects—material, relational and embodied wealth—are key elements of animal societies and map clearly onto established concepts in ecology and evolution, such as constructed/defended niches, social niches and phenotypic traits. Material wealth currencies include defensible resources such as food items, nest sites and territories, as well as ‘constructed’ resources such as food caches, shelters and nest decorations [15,16]. For instance, material wealth is prominent in acorn woodpeckers (*Melanerpes formicivorus*), which invest heavily both in granary construction (the work of generations of woodpeckers) and in the collection and storage of acorns within the granary [24]. Material wealth may also take the form of empty snail shells occupied by hermit crabs (*Pagurus longicarpus*)—resources that are unequally distributed in quality and directly affect fitness outcomes [25]. Relational wealth describes an individual’s social niche [26], encompassing social relationships and interactions such as grooming, huddling or dominance. Considerable evidence points to the impact that relational wealth has in human and non-human animal societies [6,27,28]. For example, social alliances influence rank and fitness in spotted hyenas (*Crocuta crocuta*) [29]. Embodied wealth is made up of phenotypic currencies such as body size, fat reserves, sperm quality, ornament size, display quality or information. Classic examples of embodied wealth are condition-dependent signals, such as the male house-finch’s (*Carpodacus mexicanus*) bright red plumage [30]. These different aspects of wealth operate concurrently, and biological market theory provides a framework for understanding exchanges in a wealth of different currencies [31].

Wealth inequality describes the spread and skewness of distributions of wealth (figure 1, centre circle) in these different dimensions (box 1). The scale at which inequality is assessed can be tuned flexibly according to the question and the study species. For instance, one can measure inequality among individuals in a society or social group, or among individuals in a population consisting of multiple social groups. When wealth operates at the group level (e.g. group territories, shared food caches), wealth inequality among groups can be assessed at the population level.

There is broad consensus in evolutionary theory that material and relational wealth (i.e. constructed and social niches) can influence fitness, drive adaptation and contribute to evolutionary change [44]. Existing biological concepts also describe the transmission of wealth across generations via mechanisms of genetic and epigenetic inheritance, ecological inheritance [45] and social inheritance [46]. Intergenerational transmission of wealth may affect ‘privilege’ as a source of inequality in animal societies [16]. Exploring evolutionary themes such as niche construction and social inheritance from the lens of wealth inequality could provide clarity to debates on how to integrate these dynamics in evolutionary theory [47,48]. Specifically, we argue that the patterns of distribution

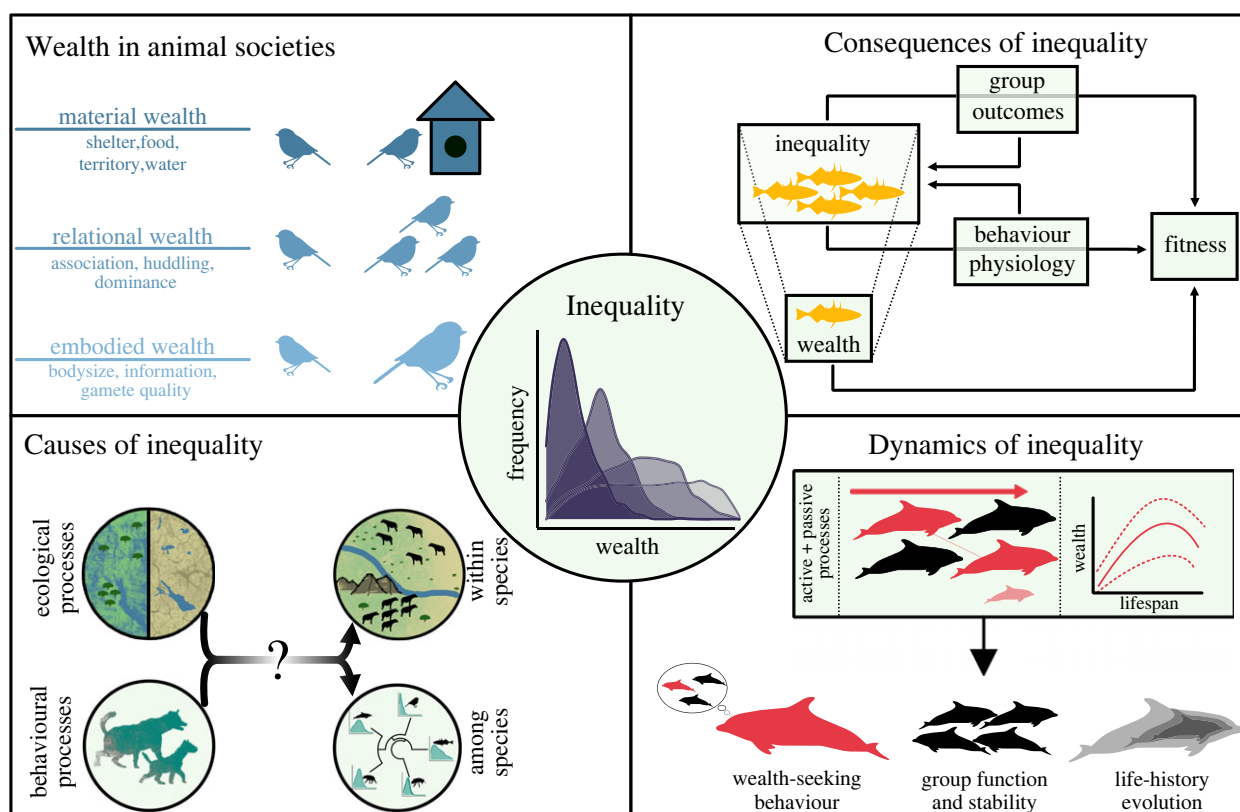


Figure 1. A schematic of the ecology of inequality. Centre circle: inequality describes the distribution of wealth among individuals, which can be measured using metrics borrowed from economics (box 1). Top left: wealth is taxonomically broad and occurs in many currencies, grouped into three aspects. Top right: inequality emerges from individual wealth through bottom-up causation and has a top-down influence on individual outcomes, both directly and via its effects on group outcomes. These effects are independent of the effects of wealth, but can feed back to influence wealth and inequality. Bottom left: multiple ecological (e.g. food/water distribution) and behavioural (e.g. wealth inheritance) processes are hypothesized to influence the amount of inequality in societies, but it is less clear at what scale this influence occurs or to what degree these processes operate across species. Bottom right: inequality is dynamic. Active and passive processes produce changes in wealth within an individual's lifetime and across generations, leading to typical wealth trajectories over the lifespan. The amount, timing and direction of wealth trajectories are expected to exert selection on individuals to optimize their experienced costs and benefits of sociality. (Online version in colour.)

Box 1. Measuring inequality.

Here, we provide a brief introduction to the methods for measuring inequality, intended to introduce the reader to what is an extensive body of literature in economics. Distributions can differ from pure equality in numerous ways [32–35]. When empirical wealth distributions are well described by the functional form of one or more distributions, inequality can be described analytically via the parameters specifying the distribution [36]. Alternatively, inequality can be measured by summarizing the amount of wealth held by individuals in a certain quantile (e.g. the proportion of total wealth held by the wealthiest 10% [37]) or by comparing the wealth of individuals in different quantiles. Finally, 'index' approaches summarize inequality into a single numerical index. The Gini index is the most commonly used metric of inequality, and although most often applied to income, it has also been used to study inequality in distributions of monetary wealth [38], land ownership [23], faculty production by universities [39], body size [40], plant sizes [41] and hermit crab shell sizes [25]. Because a single parameter cannot fully summarize the shape of a distribution, different indices are sensitive to different features of unequal distributions, so caution is warranted when indices disagree [32]. Finally, it is important to note that most of these methods were developed to describe inequality in large nation-states, and methodological challenges remain to facilitate comparative approaches to inequality in smaller societies such as those found in non-human systems [34,35,42,43].

of each aspect of wealth matter, and understanding the structural properties of wealth inequality is key to evolution. For example, niche construction may play a key role in evolution only when the intergenerational transmission of material wealth fundamentally alters how fitness is related to embodied aspects of wealth.

3. What are the consequences of inequality?

Inequality can influence outcomes for individuals directly or by impacting group outcomes (figure 1, top right). There is a

long history of sociological research describing different types of effects of wealth inequality (reviewed in [49]). Most directly, variation in individual wealth may translate into variation in outcomes, and such effects may be linear or non-linear. From an evolutionary ecology perspective, simple effects of wealth on fitness represent selection on various aspects of wealth, such as traits (embodied wealth), resource acquisition and defence (material wealth), or social behaviour (relational wealth). However, sociological approaches to wealth inequality also reveal other effects that may be

relevant to non-human societies. On top of simple wealth effects on outcomes, individuals are influenced by inequality in the distribution of wealth such that two equally wealthy individuals living in societies with different levels of wealth inequality might experience divergent outcomes. Here, we highlight three such effects: (i) the overall level of inequality at the group or society level may have effects beyond an individual's wealth; (ii) behavioural responses to inequality, and (iii) effects of inequality on group persistence or collective action.

Wealth and wealth inequality impact individual health and well-being [28,50–52]. In humans, more unequal societies are often associated with negative individual and societal outcomes [53,54]. An evolutionary comparison across primates, including humans, reveals that life-expectancy increases with lifespan equality, further indicating that inequality covaries with individual outcomes [55]. Inequality negatively impacts health and well-being through behavioural changes [56] or psychosocial stress [57]. In humans, inequality-induced stress is more extreme in societies that are more unequal, even for individuals of high social status [58]. Status-induced stress can affect both low- and high-wealth individuals, and who experiences most stress can depend on the dynamics of the social system [51,59,60]. Overall, widespread association between wealth inequality and individual outcomes supports the hypothesis that living in the context of wealth inequality is a 'fundamental cause' of a suite of negative outcomes [28,56,61].

Individuals attend to inequality within their societies and alter their behaviours accordingly. Experiments in primates, corvids and domestic dogs suggest that the perceived value of a resource is influenced by an individual's observations of the value of the resources their group-mates receive [62]. Individuals often then alter their social behaviour, for example by punishing individuals that receive the higher valued resource [63]. Similarly, subordinate queens of *Polistes fuscatus* wasps greatly increase aggression towards dominants when they perceive that dominants are claiming too unequal a share of reproduction [64]. In humans, an individual's wealth influences their perceptions about the degree of inequality in society [65] and their status-seeking behaviour [66]. In many species, individuals use social information about their status relative to their competitors when making decisions about how and with whom to compete [67]. In sum, intra-group competition and inequality are linked by a feedback loop involving individual perception of their own social status, the social status of others and the amount of inequality in the group. To understand this feedback loop, we should continue to explore how individuals perceive inequality, and how their response to inequality affects social structure. Systems where signals of wealth can be manipulated independently of actual wealth provide a means to experimentally manipulate perceived inequality.

Inequality can influence group outcomes such as group persistence and collective action. Reproductive skew theory [10,11] addresses how inequality in reproduction can affect the productivity or persistence of the group. Inequality can also influence a group's ability to cooperate or achieve collective action. In cooperation experiments with chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and cotton-top tamarins (*Saguinus oedipus*), evidence suggests that species that divide the rewards of cooperation more equally are more likely to show cooperative behaviour [68,69]. Theoretical and empirical studies of collective action problems

(e.g. public goods game) suggest that inequality has complex and often unpredictable effects on cooperative behaviour [70–77]. However, a rough pattern emerges in the literature suggesting that the effect of inequality on cooperation might depend on the type of wealth under consideration. In studies where individuals vary in the resources they can invest in cooperation (i.e. material wealth), inequality typically reduces cooperation [70–72]. However, inequality in social influence can promote cooperation by eliminating free-riders and overcoming coordination challenges [73–77]. Other evidence suggests that inequality can influence group outcomes by improving or impeding the function of groups, for instance by altering costs of coordination, resilience to variable environmental conditions, or ability to compete with other groups [73,75,78,79]. For example, burying beetles (*Nicrophorus nepalensis*) invest more in cooperation in the face of interspecific competitors [80]. A complex relationship between inequality and environment may explain global patterns in the evolution of cooperation: in both *Polistes* wasps and cooperatively breeding birds, the evolution of cooperative groups is associated with the environmental conditions that may increase the need for collective action (e.g. unpredictable environments: [81–83]). Overall, the complex results from theoretical studies suggest a need for empirical work on the links between inequality, individual outcomes and group function in animal systems.

4. What are the causes of inequality?

Multiple behavioural and ecological processes have been hypothesized to influence the amount of wealth inequality within societies, but the extent to which these mechanisms explain variation within versus among species is not fully clear (figure 1, bottom left). Some aspects of inequality seem to be relatively flexible, whereas others are more constrained. For example, in a population of olive baboons (*Papio anubis*) in Kenya, a mass mortality event prompted a long-term shift towards a more tolerant society with more equally distributed stress burdens, perhaps as a result of the death of the individuals that competed most intensely for high status [84]. However, a comparative network motif analysis of dominance hierarchies across many species suggests strong constraints on their structure related to transitivity of dominance relations [85]. Furthermore, in macaques, a suite of behaviours related to inequality in within-group conflict covary across species, producing macaque societies with different 'social styles' and suggesting potential phylogenetic constraints on wealth inequality [86,87]. More longitudinal and phylogenetic studies will be crucial to advance our understanding of plasticity and constraint in inequality across species.

What behavioural and ecological mechanisms influence variation in inequality within and among species? Ecological conditions—such as the patchiness, density and defensibility of resources—have long been hypothesized as a driver of material wealth inequality [1,2,9,88] (but see [89,90]). Additionally, inequality may be influenced by behavioural traits such as levelling coalitions used to control would-be dominants [91], aversion to unequal payoffs [62], preferences regarding perceived inequality [92], status-seeking behaviour [93], visibility of wealth [94] and cognitive processes relating to social competition [67]. Individuals can actively suppress

the wealth of others, as is seen in growth suppression by many fish [95] or the interruption of social bond formation in ravens (*Corvus corax*) [96], or subordinates may voluntarily reduce their own wealth to avoid conflict with group members [97]. Self-reinforcing dynamics—where ‘rich-get-richer’ feedbacks lead wealthy individuals to gain more wealth—can also influence the amount of inequality in societies [98] (see §5). Finally, these behavioural and ecological mechanisms interact. For example, the evolution of male coalitions in primates is explained by resource defensibility [99], and in vulturine guineafowl (*Acryllium vulturinum*), monopolization of clumped resources by dominants can lead to more egalitarian group movement decision-making [13].

Although drivers of inequality may differ among species or wealth aspects, some hypothesized causes of inequality are expected to operate across contexts. For example, the social transfer of wealth is one hypothesized driver of inequality that is likely to operate widely [3,4,16]. In a broad survey of human societies with diverse production systems, the increased fidelity of intergenerational transmission of wealth was associated with more extreme inequality [4,22]. In non-human animals, social inheritance of territory [100,101], knowledge [102,103], social relationships [46] and food caches [24] could provide ample contexts in which to test this hypothesis in diverse systems [16]. For instance, the social inheritance of dominance status in spotted hyenas and Old-World primates may drive inequality in dominance among lineages [29]. In fact, the widespread transmission of wealth across generations points to the evolutionary importance of non-genetic inheritance [45] and selection in response to multigenerational processes [104]. Another broadly operating hypothesized driver of inequality is intergroup conflict. When unequal groups are more effective or willing competitors, selection for success in intergroup conflicts can lead to increased within-group inequality in influence during collective action [79,105,106], and these leaders can also use their influence to increase inequality in other dimensions of wealth [107]. Here there is potential for positive feedback when the individuals that benefit most from intergroup conflict are also effective initiators of these conflicts, as seen in humans and banded mongoose (*Mungos mungo*) [108,109]. Finally, environmental stressors arising from climate change are expected to impact many species, highlighting another potentially broadly acting driver of inequality that we need to better understand. Studying shared processes influencing inequality in diverse wealth currencies and species is key to understanding the evolution of inequality and its role in societies.

5. How does inequality change over time?

Inequality is dynamic: neither the level of inequality nor an individual’s wealth is fixed, and both can change over short or long timescales (figure 1, bottom right). One avenue for understanding these dynamics is through the economic concept of *social mobility*, which describes the dynamics of wealth measured at the individual or lineage level. Aggregating these measures across members of a social group reveals the society-level tendency for individuals or lineages to gain or lose wealth over time, producing more rigid or fluid societies. By integrating over time, social mobility mediates the link between inequality measured at a given time point and the processes or outcomes occurring over individual lifetimes.

Social mobility can vary in the timescale at which it occurs and the processes by which it arises. Intra- and inter-generational mobility classify the generational scale at which mobility occurs. *Intragenerational mobility* describes the degree to which individual wealth changes, producing wealth trajectories over the lifespan. *Intergenerational mobility* refers to the change in wealth within lineages across generations and is the type of social mobility most often studied in humans [110–112]. Examining the correlation between parents’ and offspring’s wealth provides an empirical measure of the extent to which an individual’s position in society is malleable versus predetermined [113]. Increasingly, researchers are expanding the study of intergenerational mobility to include multigenerational effects, such as the effects of grandparents or other more distant kin [114,115].

Processes influencing social mobility can be active or passive: *active mobility* occurs when an individual’s wealth changes with respect to their group-mates by reversing the wealth-ordering of individuals, whereas *passive mobility* occurs as a result of demographic processes such as births and deaths [116]. These demographic processes frequently produce gradual changes that have direct and indirect effects on social structure by removing and replacing individuals and altering existing social relationships [117]. In some cases, demographic changes can push societies over tipping points, or precipitous shifts in social structure that can show hysteresis [118]. Revolutions [119], mass mortality [84,119,120], group fissions [121], the arrival or loss of certain individuals [122–124] and expulsions of group members [125] are examples of active and passive processes that could produce precipitous changes. For instance, social perturbation experiments in captive fish, primates and mice demonstrate how removal of high-status individuals can lead to rapid behavioural, physiological and cognitive changes in other individuals [122–124].

The long-term additive combination of social mobility produces *long-run inequality*, which describes equilibrium patterns of inequality around which a society fluctuates [37,126], assuming such an equilibrium state exists. Understanding where a society sits relative to its expected equilibrium state will require long-term studies in the order of multiple generations. In turn, such work creates opportunities for exploring the forces that lead societies to deviate from or return to their equilibria. This long-run perspective could help us understand when and why societies may have distinctively low social mobility, leading to ‘durable’ inequality [127], or inequality that persists across individuals, time or generations [1]. Durable inequality can give rise to social classes, where individuals of different classes form social networks with different structures, face different mortality sources and cope differently with stressful conditions [60,128,129]. One process producing durable inequality is self-reinforcing dynamics, where already wealthy individuals accrue disproportionately greater wealth [130–133]. Preferential attachment and ‘rich-club effect’ models of social relationships demonstrate how relational wealth can show such self-reinforcing dynamics [134,135]. Frequency-dependent or fluctuating selection may be a counterforce that inhibits the buildup of durable inequality by altering fitness landscapes [136].

Patterns of social mobility may influence the evolution of a wide suite of behavioural strategies such as tolerance and wealth-seeking behaviour, as well as life-history traits related to pace of life (figure 1, bottom right). When upward intra-generational mobility is achieved through active processes,

selection is expected to favour individuals that challenge their group-mates, whereas conflict avoidance and tolerance should be favoured in species where upward intragenerational mobility is achieved through passive processes (e.g. social queuing; [137]). Low intergenerational mobility is expected to amplify selection on traits related to intragenerational mobility, as any changes within a generation are likely to persist and influence future generations. This hypothesized selection driven by social mobility reflects ways in which patterns in the dynamics of social structure can feed back to influence the evolution of individual traits [138], including life-history traits.

Contrasting hypotheses about the influence of social mobility on the stability of social groups highlights potential tradeoffs in the evolution of social structure. On the one hand, some have suggested that upward social mobility is crucial for long-term group stability, as individuals are expected to leave societies where they have no opportunity for wealth acquisition [126]. This pattern of upward mobility is prominent in societies where individuals ‘queue’ for wealth, such as in long-tailed manakins (*Chiroxiphia linearis*) [139], where individuals move up the queue through passive processes (e.g. death of wealthier individuals) [137,139,140]. By contrast, overly frequent active mobility can cause social instability, which is associated with negative consequences for individuals and societies [51,141–143]. These contrasting perspectives emphasize the need for theoretical and empirical work that generates and tests hypotheses about the link between social mobility and the functioning of societies in diverse species.

6. Conclusion and future directions

A key question in ecology and evolution is how the structure of groups arises and impacts the individuals that compose them [138]. Inequality in the distribution of wealth—be it relational, material or embodied—is a group-level feature that is hypothesized to impact individual and group outcomes. Here we coalesce disparate studies of inequality in biological systems into a research framework addressing inequality across ecological and evolutionary contexts and identify three overarching research foci.

First, how does inequality impact individuals beyond the simple effects of individual wealth? Evidence suggests that individuals attend to the amount of inequality within their societies, and that inequality *per se* may have adverse effects for individuals. Here, theoretical work has outpaced empirical work, and examining the impacts of inequality on individual and group outcomes in non-human systems will be fruitful. Experimental studies of inequality in laboratory populations is a promising tool for disentangling the effects of inequality from the effects of wealth. The recent surge in work on social dimensions of health and lifespan in non-human animals promises to shed light on potential avenues by which inequality influences fitness [28].

A second broad aim of the ecology of inequality is to understand the forces that cause inequality, both in the

short term and at evolutionary timescales. Some aspects of inequality can be plastic—even sensitive to the behaviour of a single individual—whereas other aspects of inequality are evolutionarily constrained. The interplay between behavioural processes and environmental conditions (e.g. resource scarcity and competition) fundamentally shapes wealth inequality. Biogeographical and phylogenetic approaches may be useful here for identifying ecological and evolutionary patterns in wealth inequality at a global scale. Finally, feedback loops operating across species and types of wealth might explain why inequality is such a common feature of societies across the animal kingdom.

Third, it is crucial to take a dynamical perspective on inequality to understand selection on individual traits, long-term patterns in inequality, and the stability and persistence of groups. Social mobility—or changes in wealth—can occur owing to various processes and at different timescales, leading to higher-order patterns in inequality among individuals and their descendants, such as social classes or family dynasties. However, very little is known about the existence or implications of these higher-order patterns in inequality in non-human systems. Long-term studies that track groups and their constituents over multiple generations are uniquely situated to address this knowledge gap. Furthermore, we call for theoretical models that explore how lifetime patterns of social mobility impact the evolution of life-history traits and wealth-seeking behaviour.

Inequality is a curiously widespread feature of societies. The framework presented here offers a way forward for exploring the causes of inequality, its impacts on individuals and its role in social evolution. The framework allows inequality to be understood in specific contexts while also providing a means for comparative insight and the identification of general features of inequality operating across species and dimensions of wealth. This approach at once strengthens biological and sociological fields by integrating perspectives and facilitating the exchange of ideas, paving the way for new insights into ecological and evolutionary forces impacting social organisms.

Data accessibility. This article has no additional data.

Authors' contributions. E.D.S.: conceptualization, writing—original draft, and writing—review and editing; D.S.: conceptualization, writing—original draft, and writing—review and editing.

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

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References

- Mattison SM, Smith EA, Shenk MK, Cochrane EE. 2016 The evolution of inequality. *Evol. Anthropol. Issues News Rev.* **25**, 184–199. (doi:10.1002/evan.21491)
- Haynie HJ *et al.* 2021 Pathways to social inequality. *Evol. Hum. Sci.* **3**, e35. (doi:10.1017/ehs.2021.32)
- Shennan S. 2011 Property and wealth inequality as cultural niche construction. *Phil. Trans. R. Soc. B* **366**, 918–926. (doi:10.1098/rstb.2010.0309)

4. Borgerhoff Mulder M *et al.* 2009 Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. *Science* **326**, 682–688. (doi:10.1126/science.1178336)
5. Kaplan HS, Hooper PL, Gurven M. 2009 The evolutionary and ecological roots of human social organization. *Phil. Trans. R. Soc. B* **364**, 3289–3299. (doi:10.1098/rstb.2009.0115)
6. Von Rueden CR, Jaeggi AV. 2016 Men's status and reproductive success in 33 nonindustrial societies: effects of subsistence, marriage system, and reproductive strategy. *Proc. Natl Acad. Sci. USA* **113**, 10 824–10 829. (doi:10.1073/pnas.1606800113)
7. Gintis H, van Schaik C, Boehm C. 2015 Zoon politikon: the evolutionary origins of human political systems. *Curr. Anthropol.* **56**, 327–353. (doi:10.1086/681217)
8. Strauss ED, Curley JP, Shizuka D, Hobson EA. 2022 The centennial of the pecking order: current state and future prospects for the study of dominance hierarchies. *Phil. Trans. R. Soc. Lond. B* **377**, 20200432. (doi:10.1098/rstb.2020.0432)
9. Emlen ST, Oring LW. 1977 Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223. (doi:10.1126/science.327542)
10. Vehrencamp SL. 1983 A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* **31**, 667–682. (doi:10.1016/S0003-3472(83)80222-X)
11. Clutton-Brock TH. 1998 Reproductive skew, concessions and limited control. *Trends Ecol. Evol.* **13**, 288–292. (doi:10.1016/S0169-5347(98)01402-5)
12. Strandburg-Peshkin A, Farine DR, Couzin ID, Crofoot MC. 2015 Shared decision-making drives collective movement in wild baboons. *Science* **348**, 1358–1361. (doi:10.1126/science.aaa5099)
13. Papageorgiou D, Farine DR. 2020 Shared decision-making allows subordinates to lead when dominants monopolize resources. *Sci. Adv.* **6**, eaba5881. (doi:10.1126/sciadv.aba5881)
14. Conratt L, Roper TJ. 2005 Consensus decision making in animals. *Trends Ecol. Evol.* **20**, 449–456. (doi:10.1016/j.tree.2005.05.008)
15. Strassmann JE, Queller DC. 2014 Privatization and property in biology. *Anim. Behav.* **92**, 305–311. (doi:10.1016/j.anbehav.2014.02.011)
16. Smith JE, Natterson-Horowitz B, Alfaro ME. 2022 The nature of privilege: intergenerational wealth in animal societies. *Behav. Ecol.* **33**, 1–6. (doi:10.1093/beheco/arab137)
17. Wolf JB, Brodie ED, Moore AJ. 1999 Interacting phenotypes and the evolutionary process. II. Selection resulting from social interactions. *Am. Nat.* **153**, 254–266. (doi:10.1086/303168)
18. McGlothlin JW, Moore AJ, Wolf JB, Brodie III ED. 2010 Interacting phenotypes and the evolutionary process. III. Social evolution. *Evolution* **64**, 2558–2574. (doi:10.1111/j.1558-5646.2010.01012.x)
19. West-Eberhard MJ. 1983 Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**, 155–183. (doi:10.1086/413215)
20. Smith A. 1776 *An inquiry into the nature and causes of the wealth of nations*. London, UK: W. Strahan and T. Cadell.
21. Weber M. 2010 The distribution of power within the community: classes, stände, parties. *J. Class. Sociol.* **10**, 137–152. (doi:10.1177/1468795X10361546)
22. Bowles S, Smith EA, Borgerhoff Mulder M. 2010 The emergence and persistence of inequality in premodern societies. *Curr. Anthropol.* **51**, 117–118. (doi:10.1086/649567)
23. Smith EA, Borgerhoff Mulder M, Bowles S, Gurven M, Hertz T, Shenk MK. 2010 Production systems, inheritance, and inequality in premodern societies. *Curr. Anthropol.* **51**, 85–94. (doi:10.1086/649029)
24. MacRoberts MH, MacRoberts BR. 1976 Social organization and behavior of the acorn woodpecker in central coastal California. *Ornithol. Monogr.*, no. 21. (doi:10.2307/40166738)
25. Chase ID, Douady R, Padilla DK. 2020 A comparison of wealth inequality in humans and non-humans. *Phys. A Stat. Mech. Appl.* **538**, 122962. (doi:10.1016/j.physa.2019.122962)
26. Saltz JB, Geiger AP, Anderson R, Johnson B, Marren R. 2016 What, if anything, is a social niche? *Evol. Ecol.* **30**, 349–364. (doi:10.1007/s10682-015-9792-5)
27. Silk JB. 2007 Social components of fitness in primate groups. *Science* **317**, 1347–1351. (doi:10.1126/science.1140734)
28. Snyder-Mackler N *et al.* 2020 Social determinants of health and survival in humans and other animals. *Science* **368**, eaax9553. (doi:10.1126/science.aax9553)
29. Strauss ED, Holekamp KE. 2019 Social alliances improve rank and fitness in convention-based societies. *Proc. Natl Acad. Sci. USA* **116**, 8919–8924. (doi:10.1073/pnas.1810384116)
30. Hill GE. 1990 Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Anim. Behav.* **40**, 563–572. (doi:10.1016/S0003-3472(05)80537-8)
31. Noë R, Hammerstein P. 1995 Biological markets. *Trends Ecol. Evol.* **10**, 336–339. (doi:10.1016/S0169-5347(00)89123-5)
32. Cowell F. 2011 *Measuring inequality*, 3rd edn. Oxford, UK: Oxford University Press.
33. De Maio FG. 2007 Income inequality measures. *J. Epidemiol. Commun. Health* **61**, 849–852. (doi:10.1136/jech.2006.052969)
34. Kokko H, Mackenzie A, Reynolds JD, Lindström J, Sutherland WJ. 1999 Measures of inequality are not equal. *Am. Nat.* **154**, 358–382. (doi:10.1086/303235)
35. Ross CT, Jaeggi AV, Borgerhoff Mulder M, Smith JE, Smith EA, Gavrilets S, Hooper PL. 2020 The multinomial index: a robust measure of reproductive skew. *Proc. R. Soc. B* **287**, 20202025. (doi:10.1098/rspb.2020.2025)
36. Inoue JI, Ghosh A, Chatterjee A, Chakrabarti BK. 2015 Measuring social inequality with quantitative methodology: analytical estimates and empirical data analysis by Gini and k indices. *Phys. A Stat. Mech. Appl.* **429**, 184–204. (doi:10.1016/j.physa.2015.01.082)
37. Piketty T, Saez E. 2014 Income inequality in Europe and the United States. *Science* **344**, 838–843. (doi:10.1126/science.1251936)
38. Keister LA, Moller S. 2000 Wealth inequality in the United States. *Annu. Rev. Sociol.* **26**, 63–81. (doi:10.1146/annurev.soc.26.1.63)
39. Clauset A, Arbesman S, Larremore DB. 2015 Systematic inequality and hierarchy in faculty hiring networks. *Sci. Adv.* **1**, e1400005. (doi:10.1126/sciadv.1400005)
40. Dobson AP. 1986 Inequalities in the individual reproductive success of parasites. *Parasitology* **92**, 675–682. (doi:10.1017/S0031182000065537)
41. Damgaard C, Weiner J. 2000 Describing inequality in plant size or fecundity. *Ecology* **81**, 1139–1142. (doi:10.1890/0012-9658(2000)081[1139:DIIPSO]2.0.CO;2)
42. Bowles S, Fochesato M, Bogaard A. 2019 Comparing ancient inequalities: the challenges of comparability, bias and precision. *Antiquity* **370**, 853–869. (doi:10.15184/aqy.2019.106)
43. Bowles S, Carlin W. 2020 Inequality as experienced difference: a reformulation of the Gini coefficient. *Econ. Lett.* **186**, 108789. (doi:10.1016/j.econlet.2019.108789)
44. Scott-Phillips TC, Laland KN, Shuker DM, Dickens TE, West SA. 2014 The niche construction perspective: a critical appraisal. *Evolution* **68**, 1231–1243. (doi:10.1111/evo.12332)
45. Odling-Smee J, Laland K. 2011 Ecological inheritance and cultural inheritance: what are they and how do they differ? *Biol. Theory* **6**, 220–230. (doi:10.1007/s13752-012-0030-x)
46. Ilany A, Akçay E. 2016 Social inheritance can explain the structure of animal social networks. *Nat. Commun.* **7**, 12084. (doi:10.1038/ncomms12084)
47. Laland K, Uller T, Feldman M, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J. 2014 Does evolutionary theory need a rethink? *Nature* **514**, 161–164. (doi:10.1038/514161a)
48. Wray GA, Hoekstra HE, Futuyma DJ, Lenski RE, Mackay TFC, Schluter D, Strassmann JE. 2014 Does evolutionary theory need a rethink? [counterpoint] No, all is well. *Nature* **514**, 161–164. (doi:10.1038/514161a)
49. Neckerman KM, Torche F. 2007 Inequality: causes and consequences. *Annu. Rev. Sociol.* **33**, 335–357. (doi:10.1146/annurev.soc.33.040406.131755)
50. Marmot MG *et al.* 1991 Health inequalities among British civil servants: the Whitehall II study. *Lancet* **337**, 1387–1393. (doi:10.1016/0140-6736(91)93068-K)
51. Sapolsky RM. 2005 The influence of social hierarchy on primate health. *Science* **308**, 648–652. (doi:10.1126/science.1106477)
52. Jaeggi AV *et al.* 2021 Do wealth and inequality associate with health in a small-scale subsistence society? *eLife* **10**, e59437. (doi:10.7554/eLife.59437)
53. Pickett KE, Wilkinson RG. 2015 Income inequality and health: a causal review. *Social Sci. Med.* **128**, 316–326. (doi:10.1016/j.socscimed.2014.12.031)

54. Wilkinson RG, Pickett KE. 2009 Income inequality and social dysfunction. *Annu. Rev. Sociol.* **35**, 493–511. (doi:10.1146/annurev-soc-070308-115926)
55. Colchero F *et al.* 2016 The emergence of longevous populations. *Proc. Natl Acad. Sci. USA* **113**, E7681–E7690. (doi:10.1073/pnas.1612191113)
56. Pepper GV, Nettle D. 2017 The behavioural constellation of deprivation: causes and consequences. *Behav. Brain Sci.* **40**, e314. (doi:10.1017/S0140525X1600234X)
57. Rodríguez-Bailón R, Sánchez-Rodríguez Á, García-Sánchez E, Petkanopoulou K, Willis GB. 2020 Inequality is in the air: contextual psychosocial effects of power and social class. *Curr. Opin. Psychol.* **33**, 120–125. (doi:10.1016/j.copsyc.2019.07.004)
58. Buttrick NR, Oishi S. 2017 The psychological consequences of income inequality. *Social Pers. Psychol. Compass* **11**, e12304. (doi:10.1111/spc3.12304)
59. Gesquiere LR, Learn NH, Simao MCM, Onyango PO, Alberts SC, Altmann J. 2011 Life at the top: rank and stress in wild male baboons. *Science* **333**, 357–360. (doi:10.1126/science.1207120)
60. Kessler RC, Price RH, Wortman CB. 1985 Social factors in psychopathology: stress, social support, and coping processes. *Annu. Rev. Psychol.* **36**, 531–572. (doi:10.1146/annurev.ps.36.020185.002531)
61. Link BG, Phelan J. 1995 Social conditions as fundamental causes of disease. *J. Health Soc. Behav.* **1995**(Extra issue), 80–94. (doi:10.2307/2626958)
62. Brosnan SF, De Waal FBM. 2014 Evolution of responses to (un)fairness. *Science* **346**, 1251776. (doi:10.1126/science.1251776)
63. Leimgruber KL, Rosati AG, Santos LR. 2016 Capuchin monkeys punish those who have more. *Evol. Hum. Behav.* **37**, 236–244. (doi:10.1016/j.evolhumbehav.2015.12.002)
64. Reeve HK, Nonacs P. 1992 Social contracts in wasp societies. *Nature* **359**, 823–825. (doi:10.1038/359823a0)
65. Rodríguez-Bailón R, Bratanova B, Willis GB, Lopez-Rodríguez L, Sturrock A, Loughnan S. 2017 Social class and ideologies of inequality: how they uphold unequal societies. *J. Social Issues* **73**, 99–116. (doi:10.1111/josi.12206)
66. Belmi P, Laurin K. 2016 Who wants to get to the top? Class and lay theories about power. *J. Pers. Social Psychol.* **111**, 505–529. (doi:10.1037/pspi0000060)
67. Hobson EA, Mønster D, DeDeo S. 2021 Aggression heuristics underlie animal dominance hierarchies and provide evidence of group-level social information. *Proc. Natl Acad. Sci. USA* **118**, e2022912118. (doi:10.1073/pnas.2022912118)
68. Cronin KA, Sánchez A. 2012 Social dynamics and cooperation: the case of nonhuman primates and its implications for human behavior. *Adv. Complex Syst.* **15**, 1250066. (doi:10.1142/S021952591250066X)
69. Hare B, Melis AP, Woods V, Hastings S, Wrangham R. 2007 Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Curr. Biol.* **17**, 619–623. (doi:10.1016/j.cub.2007.02.040)
70. Fung JMY, Au WT. 2014 Effect of inequality on cooperation: heterogeneity and hegemony in public goods dilemma. *Org. Behav. Hum. Decis. Process.* **123**, 9–22. (doi:10.1016/j.obhdp.2013.10.010)
71. Hargreaves Heap SP, Ramalingam A, Stoddard BV. 2016 Endowment inequality in public goods games: a re-examination. *Econ. Lett.* **146**, 4–7. (doi:10.1016/j.econlet.2016.07.015)
72. Hauser OP, Hilbe C, Chatterjee K, Nowak MA. 2019 Social dilemmas among unequals. *Nature* **572**, 524–527. (doi:10.1038/s41586-019-1488-5)
73. Gavrilets S, Fortunato L. 2014 A solution to the collective action problem in between-group conflict with within-group inequality. *Nat. Commun.* **5**, 3526. (doi:10.1038/ncomms4526)
74. Glowacki L, von Rueden C. 2015 Leadership solves collective action problems in small-scale societies. *Phil. Trans. R. Soc. B* **370**, 20150010. (doi:10.1098/rstb.2015.0010)
75. Hooper PL, Kaplan HS, Boone JL. 2010 A theory of leadership in human cooperative groups. *J. Theor. Biol.* **265**, 633–646. (doi:10.1016/j.jtbi.2010.05.034)
76. Santos FC, Santos MD, Pacheco JM. 2008 Social diversity promotes the emergence of cooperation in public goods games. *Nature* **454**, 213–216. (doi:10.1038/nature06940)
77. Van Vugt M, Smith JE. 2019 A dual model of leadership and hierarchy: evolutionary synthesis. *Trends Cogn. Sci.* **23**, 952–967. (doi:10.1016/j.tics.2019.09.004)
78. Perret C, Hart E, Powers ST. 2020 From disorganized equality to efficient hierarchy: how group size drives the evolution of hierarchy in human societies. *Proc. R. Soc. B* **287**, 20200693. (doi:10.1098/rspb.2020.0693)
79. Rogers DS, Deshpande O, Feldman MW. 2011 The spread of inequality. *PLoS ONE* **6**, e24683. (doi:10.1371/journal.pone.0024683)
80. Liu M, Chen BF, Rubenstein DR, Shen SF. 2020 Social rank modulates how environmental quality influences cooperation and conflict within animal societies: dominance and cooperation. *Proc. R. Soc. B* **287**, 20201720. (doi:10.1098/rspb.2020.1720)
81. Rubenstein DR, Lovette IJ. 2007 Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.* **17**, 1414–1419. (doi:10.1016/j.cub.2007.07.032)
82. Griesser M, Drobniak SM, Nakagawa S, Botero CA. 2017 Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLoS Biol.* **15**, e2000483. (doi:10.1371/journal.pbio.2000483)
83. Sheehan MJ, Botero CA, Hendry TA, Sedio BE, Jandt JM, Weiner S, Toth AL, Tibbetts EA. 2015 Different axes of environmental variation explain the presence vs. extent of cooperative nest founding associations in *Polistes* paper wasps. *Ecol. Lett.* **18**, 1057–1067. (doi:10.1111/ele.12488)
84. Sapolsky RM, Share LJ. 2004 A pacific culture among wild baboons: its emergence and transmission. *PLoS Biol.* **2**, e106. (doi:10.1371/journal.pbio.0020106)
85. Shizuka D, McDonald DB. 2015 The network motif architecture of dominance hierarchies. *J. R. Soc. Interface* **12**, 20150080. (doi:10.1098/rsif.2015.0080)
86. Thierry B, Aureli F, Nunn CL, Petit O, Abegg C, de Waal FBM. 2008 A comparative study of conflict resolution in macaques: insights into the nature of trait covariation. *Anim. Behav.* **75**, 847–860. (doi:10.1016/j.anbehav.2007.07.006)
87. Thierry B. 2013 Identifying constraints in the evolution of primate societies. *Phil. Trans. R. Soc. B* **368**, 20120342. (doi:10.1098/rstb.2012.0342)
88. Wrangham RW. 1980 An ecological model of female-bonded primate groups. *Behaviour* **75**, 262–300. (doi:10.1163/156853980X00447)
89. Clutton-Brock TH, Janson C. 2012 Primate socioecology at the crossroads: past, present, and future. *Evol. Anthropol.* **21**, 136–150. (doi:10.1002/evan.21316)
90. Thierry B. 2008 Primate socioecology, the lost dream of ecological determinism. *Evol. Anthropol.* **17**, 93–96. (doi:10.1002/evan.20168)
91. Boehm C *et al.* 1993 Egalitarian behavior and reverse dominance hierarchy. *Curr. Anthropol.* **34**, 227–254. (doi:10.1086/204166)
92. Kleppelø TH, Czajkowski NO, Vassend O, Røysamb E, Eftedal NH, Sheehy-Skeffington J, Kunst JR, Thomsen L. 2019 Correlations between social dominance orientation and political attitudes reflect common genetic underpinnings. *Proc. Natl Acad. Sci. USA* **116**, 17 741–17 746. (doi:10.1073/pnas.1818711116)
93. Mitchell RL, Bae KK, Case CR, Hays NA. 2020 Drivers of desire for social rank. *Curr. Opin. Psychol.* **33**, 189–195. (doi:10.1016/j.copsyc.2019.07.027)
94. Marshall HH *et al.* 2021 A veil of ignorance can promote fairness in a mammal society. *Nat. Commun.* **12**, 3717. (doi:10.1038/s41467-021-23910-6)
95. Hamilton IM, Benincasa MD. 2022 Emergence of size-structured dominance hierarchies through size-dependent feedback. *Phil. Trans. R. Soc. B* **377**, 20200449. (doi:10.1098/rstb.2020.0449)
96. Massen JJM, Szpil G, Spreafico M, Bugnyar T. 2014 Ravens intervene in others' bonding attempts. *Curr. Biol.* **24**, 2733–2736. (doi:10.1016/j.cub.2014.09.073)
97. Heg D, Bender N, Hamilton I. 2004 Strategic growth decisions in helper cichlids. *Proc. R. Soc. Lond. B* **271**, S505–S508. (doi:10.1098/rsbl.2004.0232)
98. Diprete TA, Eirich GM. 2006 Cumulative advantage as a mechanism for inequality: a review of theoretical and empirical developments. *Annu. Rev. Sociol.* **32**, 271–297. (doi:10.1146/annurev.soc.32.061604.123127)
99. Bissonnette A, Franz M, Schülke O, Ostner J. 2014 Socioecology, but not cognition, predicts male coalitions across primates. *Behav. Ecol.* **25**, 794–801. (doi:10.1093/beheco/aru054)
100. Woolfenden GE, Fitzpatrick JW. 1978 The inheritance of territory in group-breeding birds. *Bioscience* **28**, 104–108. (doi:10.2307/1307423)
101. Clarke PMR, McElreath MB, Barrett BJ, Mabry KE, McElreath R. 2018 The evolution of bequeathal in

- stable habitats. *Ecol. Evol.* **8**, 10 594–10 607. (doi:10.1002/ece3.4549)
102. Brent LNJ, Franks DW, Foster EA, Balcomb KC, Cant MA, Croft DP. 2015 Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Curr. Biol.* **25**, 746–750. (doi:10.1016/j.cub.2015.01.037)
103. Krützen M, Mann J, Heithaus MR, Connor RC, Bejder L, Sherwin WB. 2005 Cultural transmission of tool use in bottlenose dolphins. *Proc. Natl Acad. Sci. USA* **102**, 8939–8943. (doi:10.1073/pnas.0500232102)
104. Haaland TR, Wright J, Ratikainen II. 2019 Bet-hedging across generations can affect the evolution of variance-sensitive strategies within generations. *Proc. R. Soc. B* **286**, 20192070. (doi:10.1098/rspb.2019.2070)
105. Makowsky MD, Smaldino PE. 2016 The evolution of power and the divergence of cooperative norms. *J. Econ. Behav. Org.* **126**, 75–88. (doi:10.1016/j.jebo.2015.09.002)
106. Turchin P, Gavrilets S. 2009 Evolution of complex hierarchical societies. *Social Evol. Hist.* **8**, 167–198.
107. Powers ST, Lehmann L. 2014 An evolutionary model explaining the Neolithic transition from egalitarianism to leadership and despotism. *Proc. R. Soc. B* **281**, 20141349. (doi:10.1098/rspb.2014.1349)
108. Doğan G, Glowacki L, Rusch H. 2018 Spoils division rules shape aggression between natural groups. *Nat. Hum. Behav.* **2**, 322–326. (doi:10.1038/s41562-018-0338-z)
109. Johnstone RA, Cant MA, Cram D, Thompson FJ. 2020 Exploitative leaders incite intergroup warfare in a social mammal. *Proc. Natl Acad. Sci. USA* **117**, 29 759–29 766. (doi:10.1073/pnas.2003745117)
110. Chetty R, Hendren N, Kline P, Saez E. 2014 Where is the land of opportunity? The geography of intergenerational mobility in the United States. *Q. J. Econ.* **129**, 1553–1623. (doi:10.1093/qje/qju022)
111. Solon G. 1992 Intergenerational income mobility in the United States. *Am. Econ. Rev.* **82**, 393–408.
112. Corak M. 2013 Income inequality, equality of opportunity, and intergenerational mobility. *J. Econ. Perspect.* **27**, 79–102. (doi:10.1257/jep.27.3.79)
113. Bowles S, Gintis H. 2002 The inheritance of inequality. *J. Econ. Perspect.* **16**, 3–30. (doi:10.1257/089533002760278686)
114. Chan TW, Boliver V. 2013 The grandparents effect in social mobility: evidence from British birth cohort studies. *Am. Sociol. Rev.* **78**, 662–678. (doi:10.1177/0003122413489130)
115. Pfeffer FT. 2014 Multigenerational approaches to social mobility. A multifaceted research agenda. *Res. Soc. Stratif. Mobil.* **35**, 1–12. (doi:10.1016/j.rssm.2014.01.001)
116. Strauss ED, Holekamp KE. 2019 Inferring longitudinal hierarchies: framework and methods for studying the dynamics of dominance. *J. Anim. Ecol.* **88**, 521–536. (doi:10.1111/1365-2656.12951)
117. Shizuka D, Johnson AE. 2020 How demographic processes shape animal social networks. *Behav. Ecol.* **31**, 1–11. (doi:10.1093/beheco/arz083)
118. Pruitt JN *et al.* 2018 Social tipping points in animal societies. *Proc. R. Soc. B* **285**, 20181282. (doi:10.1098/rspb.2018.1282)
119. Scheidel W. 2017 *The great leveler: violence and the history of inequality from the Stone Age to the twenty-first century*. Princeton, NJ: Princeton University Press.
120. Evans JC, Liechti JI, Boatman B, König B. 2020 A natural catastrophic turnover event: individual sociality matters despite community resilience in wild house mice. *Proc. R. Soc. B* **287**, 20192880. (doi:10.1098/rspb.2019.2880)
121. Dittus WPJ. 1988 Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. *Anim. Behav.* **36**, 1626–1645. (doi:10.1016/S0003-3472(88)80104-0)
122. Wallace KJ, Choudhary KD, Kutty LA, Le DH, Lee MT, Wu K, Hofmann HA. 2022 Social ascent changes cognition, behaviour and physiology in a highly social cichlid fish. *Phil. Trans. R. Soc. B* **377**, 20200448. (doi:10.1098/rstb.2020.0448)
123. Williamson CM, Romeo RD, Curley JP. 2017 Dynamic changes in social dominance and mPOA GnRH expression in male mice following social opportunity. *Horm. Behav.* **87**, 80–88. (doi:10.1016/j.yhbeh.2016.11.001)
124. Flack JC, Krakauer DC, De Waal FBM. 2005 Robustness mechanisms in primate societies: a perturbation study. *Proc. R. Soc. B* **272**, 1091–1099. (doi:10.1098/rspb.2004.3019)
125. Larson SM, Ruiz-Lambides A, Platt ML, Brent LNJ. 2018 Social network dynamics precede a mass eviction in group-living rhesus macaques. *Anim. Behav.* **136**, 185–193. (doi:10.1016/j.anbehav.2017.08.019)
126. Sun L, Xia DP, Sun S, Sheeran LK, Li JH. 2017 The prospect of rising in rank is key to long-term stability in Tibetan macaque society. *Scient. Rep.* **7**, 7082. (doi:10.1038/s41598-017-07067-1)
127. Tilly C. 1998 *Durable inequality*. Berkeley, CA: University of California Press.
128. Carey RM, Markus HR. 2017 Social class shapes the form and function of relationships and selves. *Curr. Opin. Psychol.* **18**, 123–130. (doi:10.1016/j.copsyc.2017.08.031)
129. House JS, Lepkowski JM, Kinney AM, Mero RP, Kessler RC, Herzog AR. 1994 The social stratification of aging and health. *J. Health Soc. Behav.* **35**, 213. (doi:10.2307/2137277)
130. Bol T, De Vaan M, Van De Rijdt A. 2018 The Matthew effect in science funding. *Proc. Natl Acad. Sci. USA* **115**, 4887–4890. (doi:10.1073/pnas.1719557115)
131. Merton RK. 1968 The Matthew effect in science: the reward and communication systems of science are considered. *Science* **159**, 56–63. (doi:10.1126/science.159.3810.56)
132. van de Rijdt A, Kang SM, Restivo M, Patil A. 2014 Field experiments of success-breeds-success dynamics. *Proc. Natl Acad. Sci. USA* **111**, 6934–6939. (doi:10.1073/pnas.1316836111)
133. Dugatkin LA, Druen M. 2004 The social implications of winner and loser effects. *Proc. R. Soc. B* **271**, 488–489. (doi:10.1098/rsbl.2004.0235)
134. Barabási AL, Albert R. 1999 Emergence of scaling in random networks. *Science* **286**, 509–512. (doi:10.1126/science.286.5439.509)
135. Colizza V, Flammini A, Serrano MA, Vespignani A. 2006 Detecting rich-club ordering in complex networks. *Nat. Phys.* **2**, 110–115. (doi:10.1038/nphys209)
136. Nosil P, Villoutreix R, De Carvalho CF, Farkas TE, Soria-Carrasco V, Feder JL, Crespi BJ, Gompert Z. 2018 Natural selection and the predictability of evolution in *Timema* stick insects. *Science* **359**, 765–770. (doi:10.1126/science.aap9125)
137. Kokko H, Johnstone RA. 1999 Social queuing in animal societies: a dynamic model of reproductive skew. *Proc. R. Soc. Lond. B* **266**, 571–578. (doi:10.1098/rspb.1999.0674)
138. Cantor M *et al.* 2020 The importance of individual-to-society feedbacks in animal ecology and evolution. *J. Anim. Ecol.* **90**, 27–44. (doi:10.1111/1365-2656.13336)
139. McDonald DB. 1993 Delayed plumage maturation and orderly queues for status: a manakin mannequin experiment. *Ethology* **94**, 31–45. (doi:10.1111/j.1439-0310.1993.tb00545.x)
140. Duncan C, Gaynor D, Clutton-Brock TH. 2018 The importance of being beta: female succession in a cooperative breeder. *Anim. Behav.* **146**, 113–122. (doi:10.1016/j.anbehav.2018.10.013)
141. Beaulieu M, Mboumba S, Willaume E, Kappeler PM, Charpentier MJE. 2014 The oxidative cost of unstable social dominance. *J. Exp. Biol.* **217**, 2629–2632. (doi:10.1242/jeb.104851)
142. Carvalho RR, Palme R, da Silva Vasconcellos A. 2018 An integrated analysis of social stress in laying hens: the interaction between physiology, behaviour, and hierarchy. *Behav. Processes.* **149**, 43–51. (doi:10.1016/j.beproc.2018.01.016)
143. Kaburu SSK, Inoue S, Newton-Fisher NE. 2013 Death of the alpha: within-community lethal violence among chimpanzees of the Mahale Mountains National Park. *Am. J. Primatol.* **75**, 789–797. (doi:10.1002/ajp.22135)