The ecology of wealth inequality in animal societies

Eli D. Strauss[1,2,3,4], Daizaburo Shizuka[3]

[1]Department of Collective Behavior, Max Planck Institute of Animal Behavior, Konstanz, Germany

[2]Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany

[3]School of Biological Sciences, University of Nebraska Lincoln, Lincoln, NE

[4]BEACON Center for the Study of Evolution in Action, Michigan State University, Lansing, MI

Corresponding author: Eli Strauss estrauss@ab.mpg.de

Keywords: Wealth inequality, niche construction, social evolution, social mobility, intergenerational wealth transmission, status-seeking behaviour

Abstract

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: (1) developing measures of wealth and inequality as taxonomically broad features of societies, (2) considering how feedback loops link inequality to individual and societal outcomes, (3) exploring the ecological and evolutionary underpinnings of what makes some societies more unequal than others, and (4) 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

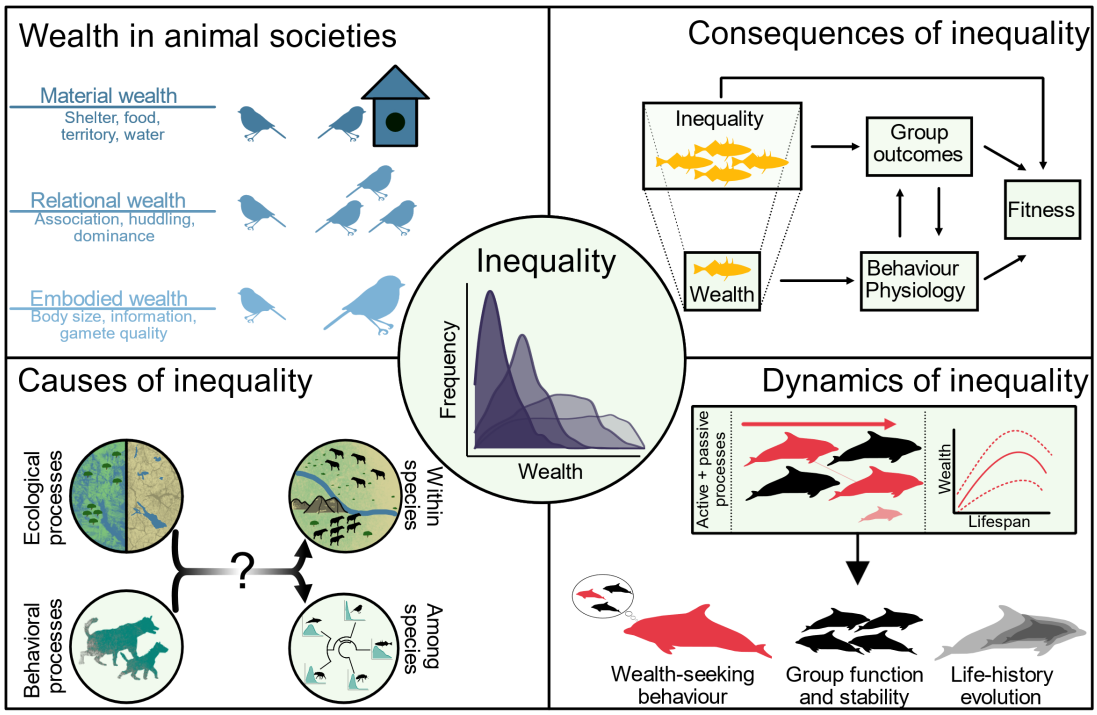
Inequality is a general feature of human and non-human animal societies. Most societies exhibit disparities among individuals' access to resources, physical condition, and social relationships. These disparities can be conceptualized as dimensions of wealth inequality, which translate into differences 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 structure interactions among group-mates and influence social structure and fitness-related outcomes [8]. Sexual selection theory addresses the causes and consequences of inequality on mating success [9], and studies of reproductive skew examine behavioral constraints on inequality in reproduction [10,11]. Research into collective decision-making explores the causes and

consequences of inequality in movement 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 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: (1) developing measures of wealth and inequality as taxonomically broad features of societies, (2) considering how feedback loops link inequality to individual and societal outcomes, (3) exploring the ecological and evolutionary underpinnings of what makes some societies more unequal than others, and (4) studying the long-term dynamics of inequality as a central component of social evolution. Under 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.



87

88 **Figure 1**. A schematic of the ecology of inequality. [center circle] Inequality describes the
89 distribution of wealth among individuals, which can be measured using metrics borrowed from
90 economics (Box 1). [top left] Wealth is taxonomically broad and occurs in many currencies, grouped
91 into three aspects. [top right] Inequality emerges from individual wealth through bottom-up causation
92 and has top-down influence on individual outcomes, both directly and via its effects on group
93 outcomes. These effects are independent of the effects of wealth. [bottom left] Multiple ecological
94 (e.g., food/water distribution) and behavioral (e.g., wealth inheritance) processes are hypothesized to
95 influence the amount of inequality in societies, but it's less clear at what scale this influence occurs or
96 to what degree these processes operate across species. [bottom right] Inequality is dynamic. Active
97 and passive processes produce changes in wealth within an individual's lifetime and across
98 generations, leading to typical wealth trajectories over the lifespan. The amount, timing, and direction
99 of wealth trajectories are expected to exert selection on individuals to optimize their experienced costs
100 and benefits of sociality.

101

102 **2. What is wealth and inequality in animal societies?**

Non-humans don't 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 superseding 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 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 multidimensional 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 defendable 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*), who invest heavily in both 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 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]. Biological market theory provides a framework for understanding exchanges in wealth of different currencies

130 [31]. Finally, wealth inequality describes the spread and skewness of distributions of wealth (Figure 1,
131 center circle) in these different dimensions (Box 1).

132 There is broad consensus in evolutionary theory that material and relational wealth (i.e., constructed
133 and social niches) can influence fitness, drive adaptation, and contribute to evolutionary change [32].
134 Existing biological concepts also describe the transmission of wealth across generations via
135 mechanisms of genetic and epigenetic inheritance, ecological inheritance [33], and social inheritance
136 [34]. Intergenerational transmission of wealth may affect "privilege" as a source of inequality in
137 animal societies [16]. Exploring evolutionary themes such as niche construction and social
138 inheritance from the lens of wealth inequality could provide clarity to debates on how to integrate
139 these dynamics in evolutionary theory [35,36]. Specifically, we argue that the patterns of distribution
140 of each aspect of wealth matter, and understanding the structural properties of wealth inequality is key
141 to evolution. For example, niche construction may play a key role in evolution only when the
142 intergenerational transmission of material wealth fundamentally alters how fitness is related to
143 embodied aspects of wealth.

144 **Box 1**

145 Here we provide a brief introduction to the methods for measuring inequality, intended to introduce
146 the reader to what is an extensive body of literature in economics. Distributions can differ from pure
147 equality in numerous ways [37–40]. When empirical wealth distributions are well-described by the
148 functional form of one or more distributions, inequality can be described analytically via the
149 parameters specifying the distribution [41]. Alternatively, inequality can be measured by summarizing
150 the amount of wealth held by individuals in a certain quantile (e.g., the proportion of total wealth held
151 by the wealthiest 10% [42]) or by comparing the wealth of individuals in different quantiles. Finally,
152 "index" approaches summarize inequality into a single numerical index. The Gini index is the most
153 commonly used metric of inequality, and although most often applied to income, it has also been used
154 to study inequality in distributions of monetary wealth [43], land ownership [23], faculty production
155 by universities [44], body size [45], plant sizes [46], and hermit crab shell sizes [25]. Because a
156 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 [37]. 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 [39,40,47,48].

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 nonlinear. From an evolutionary ecology perspective, such simple effects of wealth inequality on fitness represents selection on various aspects of wealth, such as traits (embodied wealth), resource acquisition and defense (material wealth), or social behavior (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: (1) multilevel effects of inequality such that the overall level of inequality at the group or society level may have effects beyond an individual's wealth; (2) behavioral responses to inequality; and (3) effects of inequality on group persistence or collective action.

Inequality at multiple levels (i.e., overall level of inequality of a community, as well as individual's relative position within the community) impacts 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 life-span equality, further indicating that inequality covaries with individual outcomes [55]. Inequality negatively impacts health and well-being through behavioral 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 behaviors 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 behavior, for example by punishing individuals who 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 independent 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, bonobos, and cottontop tamarins, evidence suggests that species that divide the rewards of cooperation more equally are more likely to show cooperative behavior [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 behavior [70–77]. However, a rough pattern emerges in the literature

211 suggesting that the effect of inequality on cooperation might depend on the type of wealth under
212 consideration. In studies where individuals vary in the resources they can invest in cooperation (i.e.,
213 material wealth), inequality typically reduces cooperation [70–72]. However, inequality in social
214 influence can promote cooperation by eliminating free-riders and overcoming coordination challenges
215 [73–77]. Other evidence suggests that inequality can influence group outcomes by improving or
216 impeding the function of groups, for instance by altering costs of coordination, resilience to variable
217 environmental conditions, or ability to compete with other groups [73,75,78,79]. For example,
218 burying beetles (*Nicrophorus nepalensis*) invest more in cooperation in the face of interspecific
219 competitors [80]. A complex relationship between inequality and environment may explain global
220 patterns in the evolution of cooperation: in both *Polistes* wasps, and cooperatively breeding birds, the
221 evolution of cooperative groups are associated with the environmental conditions that may increase
222 the need for collective action (e.g., unpredictable environments: [81–83]). Overall, the complex
223 results from theoretical studies suggest a need for empirical work on the links between inequality,
224 individual outcomes, and group function in animal systems.

225

226 **4. What are the causes of inequality?**

227 Multiple behavioral and ecological processes have been hypothesized to influence the amount of
228 wealth inequality within societies. but the extent to which these mechanisms explain variation within
229 vs. among species is not fully clear (Figure 1, bottom left). Some aspects of inequality seem to be
230 relatively flexible, whereas others are more constrained. For example, in a population of olive
231 baboons (*Papio anubis*) in Kenya, a mass-mortality event prompted a long-term shift towards a more
232 tolerant society with more equally distributed stress burdens, perhaps as a result of the death of the
233 individuals who competed most intensely for high status [84]. However, a comparative network motif
234 analysis of dominance hierarchies across many species suggests strong constraints on their structure
235 related to transitivity of dominance relations [85]. Furthermore, in macaques, a suite of behaviors
236 related to inequality in within-group conflict covary across species, producing macaque societies with
237 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 behavioral 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 behavioral traits such as leveling coalitions used to control would-be dominants [91], aversion to unequal payoffs [62], preferences regarding perceived inequality [92], status seeking behavior [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 Section 5). Finally, these behavioral 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 equal 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, 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 [34], 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 [33] 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 who 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 position within it are 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.

Social mobility can vary in the timescale at which it occurs and the processes by which it arises. Intra- and intergenerational 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 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].

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

304 The long-term additive combination of social mobility produce *long-run inequality*, which
305 describes equilibrium patterns of inequality around which a society fluctuates [42,126], assuming
306 such an equilibrium state exists. Understanding where a society sits relative to its expected
307 equilibrium state will require long-term studies on the order of multiple generations. In turn, such
308 work creates opportunities for exploring the forces that lead societies to deviate from or return to their
309 equilibria. This long-run perspective could help us understand when and why societies may have
310 distinctively low social mobility, leading to 'durable' inequality [127], or inequality that persists
311 across individuals, time, or generations [1]. Durable inequality can give rise to social classes, where
312 individuals of different classes form social networks with different structures, face different mortality
313 sources, and cope differently with stressful conditions [60,128,129]. One process producing durable
314 inequality is self-reinforcing dynamics, where already wealthy individuals accrue disproportionately
315 greater wealth, [130–133]. Preferential attachment and "rich-club effect" models of social
316 relationships demonstrate how relational wealth can show such self-reinforcing dynamics [134,135].
317 Frequency-dependent or fluctuating selection may be a counterforce that inhibits the buildup of
318 durable inequality by altering fitness landscapes [136].

Patterns of social mobility may influence evolution of a wide suite behavioral strategies such as tolerance and wealth-seeking behaviour, as well as life-history traits related to pace-of life (Figure 1, bottom right). Where upward intragenerational mobility is achieved through active processes, selection is expected to favor individuals who challenge their groupmates, whereas conflict avoidance and tolerance should be favored 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]. In 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. Conclusions and future directions

A key question in ecology and evolution is how the structure of groups arise and impact the individuals that comprise 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 lab 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 behavior of a single individual—whereas other aspects of inequality are evolutionarily constrained. The interplay between behavioral processes and environmental conditions (e.g., resource scarcity, 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 due 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 lifetime patterns of social mobility impact the evolution of life-history traits and wealth-seeking behavior.

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 is built upon a multidimensional concept of wealth, which 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. 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.

Author Contributions

Both authors contributed to all aspects of the manuscript.

Funding

This work was supported by the University of Nebraska-Lincoln Population Biology Program of Excellence; NSF Grant OIA 0939454 via "BEACON: An NSF Center for the Study of Evolution in Action;" the Alexander von Humboldt Foundation.

Acknowledgements

Thanks to Monique Borgerhoff Mulder, Mauricio Cantor, Danai Papageorgiou, members of the UNL School of Biological Sciences Behavior Group, three anonymous reviewers, and the editor for helpful comments on prior versions of this manuscript.

1. 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)

2. Haynie HJ *et al.* 2021 Pathways to social inequality. *Evol. Hum. Sci.* **3**, 1–14. (doi:10.1017/ehs.2021.32)

3. Shennan S. 2011 Property and wealth inequality as cultural niche construction. *Philos. Trans. R. Soc. B Biol. Sci.* **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. *Philos. Trans. R. Soc. B Biol. Sci.* **364**, 3289–3299. (doi:10.1098/rstb.2009.0115)

6. Von Rueden CR, Jaeggi A V. 2016 Men's status and reproductive success in 33 nonindustrial societies: Effects of subsistence, marriage system, and reproductive strategy. *Proc. Natl. Acad. Sci. U. S. A.* **113**, 10824–10829. (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. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **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:DOI: 10.1126/science.327542)

10. Vehrencamp SL. 1983 A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* **31**, 667–682.

11. Clutton-Brock TH. 1998 Reproductive skew, concessions and limited control. *Trends Ecol.*

Evol. **13**, 288–292.

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**, 1–8. (doi:10.1126/sciadv.aba5881)

14. Conradt 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 Edmund D III. 2010 Interacting phenotypes and the evolutionary process. III. Social evolution. *Evolution (N. Y).* **64**, 2558–2574.

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: W. Strahan and T. Cadell.

21. Weber M. 2010 The distribution of power within the community: Classes, Stände, Parties by Max Weber. *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.* **50**, iii–115. (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. its 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**, 1–12. (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.* **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. Scott-Phillips TC, Laland KN, Shuker DM, Dickins TE, West SA. 2014 The niche construction perspective: A critical appraisal. *Evolution (N. Y).* **68**, 1231–1243. (doi:10.1111/evo.12332)

33. Odling-Smee J, Laland K. 2011 Ecological inheritance and cultural inheritance: What are they

464 and how do they differ? *Biol. Theory* **6**, 220–230. (doi:10.1007/s13752-012-0030-x)

465 34. Ilany A, Akçay E. 2016 Social inheritance can explain the structure of animal social networks.
466 *Nat. Commun.* **7**, 12084. (doi:10.1038/ncomms12084)

467 35. Laland K, Uller T, Feldman M, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee
468 J. 2014 Does evolutionary theory need a rethink? *Nature* **514**, 161–164.
469 (doi:10.1038/514161a)

470 36. Wray GA, Hoekstra HE, Futuyma DJ, Lenski RE, Mackay TFC, Schluter D, Strassmann JE.
471 2014 Does evolutionary theory need a rethink?-COUNTERPOINT No, all is well. *Nature* **514**,
472 161–164. (doi:10.1038/514161a)

473 37. Cowell F. 2011 *Measuring Inequality*. Third edit. Oxford University Press.
474 (doi:10.1093/acprof:osobl/9780199594030.001.0001)

475 38. De Maio FG. 2007 Income inequality measures. *J. Epidemiol. Community Health* **61**, 849–
476 852. (doi:10.1136/jech.2006.052969)

477 39. Kokko H, Mackenzie A, Reynolds JD, Lindström J, Sutherland WJ. 1999 Measures of
478 inequality are not equal. *Am. Nat.* **154**, 358–382. (doi:10.1086/303235)

479 40. Ross CT, Jaeggi A V., Borgerhoff Mulder M, Smith JE, Smith EA, Gavrilets S, Hooper PL.
480 2020 The multinomial index: a robust measure of reproductive skew. *Proc. R. Soc. B Biol. Sci.*
481 **287**, 20202025.

482 41. Inoue JI, Ghosh A, Chatterjee A, Chakrabarti BK. 2015 Measuring social inequality with
483 quantitative methodology: Analytical estimates and empirical data analysis by Gini and k
484 indices. *Phys. A Stat. Mech. its Appl.* **429**, 184–204. (doi:10.1016/j.physa.2015.01.082)

485 42. Piketty T, Saez E. 2014 Income inequality in Europe and the United States,. *Science.* **344**,
486 838–843. (doi:10.1126/science.1251936)

487 43. Keister LA, Moller S. 2000 Wealth inequality in the United States. *Annu. Rev. Sociol.* **26**, 63–

488 81. (doi:10.1146/annurev.soc.26.1.63)

489 44. Clauset A, Arbesman S, Larremore DB. 2015 Systematic inequality and hierarchy in faculty
490 hiring networks. *Sci. Adv.* **1**, 1–7. (doi:10.1126/sciadv.1400005)

491 45. Dobson AP. 1986 Inequalities in the individual reproductive success of parasites. *Parasitology*
492 **92**, 675–682. (doi:10.1017/S0031182000065537)

493 46. Damgaard C, Weiner J. 2000 Describing inequality in plant size or fecundity. *Ecology* **81**,
494 1139–1142. (doi:10.1890/0012-9658(2000)081[1139:DIIPSO]2.0.CO;2)

495 47. Bowles S, Fochesato M, Bogaard A. 2019 Comparing ancient inequalities: the challenges of
496 comparability, bias and precision. *Antiquity* **370**, 853–869.

497 48. Bowles S, Carlin W. 2020 Inequality as experienced difference: A reformulation of the Gini
498 coefficient. *Econ. Lett.* **186**, 108789. (doi:10.1016/j.econlet.2019.108789)

499 49. Neckerman KM, Torche F. 2007 Inequality : Causes and consequences. *Annu. Rev. Sociol.* **33**,
500 335–357.

501 50. Marmot MG *et al.* 1991 Health inequalities among British civil servants: the Whitehall II
502 study. *Lancet* **337**, 1387–1393. (doi:10.1016/0140-6736(91)93068-K)

503 51. Sapolsky RM. 2005 The influence of social hierarchy on primate health. *Science.* **308**, 648–
504 652.

505 52. Jaeggi A V. *et al.* 2021 Do wealth and inequality associate with health in a small-scale
506 subsistence society? *Elife* **10**, 1–28. (doi:10.7554/eLife.59437)

507 53. Pickett KE, Wilkinson RG. 2015 Income inequality and health: A causal review. *Soc. Sci.*
508 *Med.* **128**, 316–326. (doi:10.1016/j.socscimed.2014.12.031)

509 54. Wilkinson RG, Pickett KE. 2009 Income inequality and social dysfunction. *Annu. Rev. Sociol.*
510 **35**, 493–511. (doi:10.1146/annurev-soc-070308-115926)

511 55. Colchero F *et al.* 2016 The emergence of longevous populations. *Proc. Natl. Acad. Sci. U. S.*

512 *A.* **113**, E7681–E7690. (doi:10.1073/pnas.1612191113)

513 56. Pepper G V., Nettle D. 2017 The behavioural constellation of deprivation: Causes and
514 consequences. *Behav. Brain Sci.* **40**. (doi:10.1017/S0140525X1600234X)

515 57. Rodríguez-Bailón R, Sánchez-Rodríguez Á, García-Sánchez E, Petkanopoulou K, Willis GB.
516 2020 Inequality is in the air: contextual psychosocial effects of power and social class. *Curr.*
517 *Opin. Psychol.* **33**, 120–125. (doi:10.1016/j.copsyc.2019.07.004)

518 58. Buttrick NR, Oishi S. 2017 The psychological consequences of income inequality. *Soc.*
519 *Personal. Psychol. Compass* **11**, 1–12. (doi:10.1111/spc3.12304)

520 59. Gesquiere LR, Learn NH, Simao MCM, Onyango PO, Alberts SC, Altmann J. 2011 Life at the
521 top: Rank and stress in wild male baboons. *Science.* **333**, 357–360.
522 (doi:10.1126/science.1207120)

523 60. Kessler RC, Price RH, Wortman CB. 1985 Social factors in psychopathology: Stress, social
524 support, and coping processes. *Annu. Rev. Psychol.* **36**, 531–572.
525 (doi:10.1146/annurev.ps.36.020185.002531)

526 61. Link BG, Phelan J. 1995 Social conditions as fundamental causes of disease. *J. Health Soc.*
527 *Behav.* , 80–94.

528 62. Brosnan SF, De Waal FBM. 2014 Evolution of responses to (un)fairness. *Science.* **346**.
529 (doi:10.1126/science.1251776)

530 63. Leimgruber KL, Rosati AG, Santos LR. 2016 Capuchin monkeys punish those who have
531 more. *Evol. Hum. Behav.* **37**, 236–244. (doi:10.1016/j.evolhumbehav.2015.12.002)

532 64. Reeve HK, Nonacs P. 1992 Social contracts in wasp societies. *Nature* **359**, 823–825.
533 (doi:10.1038/359823a0)

534 65. Rodriguez-Bailon R, Bratanova B, Willis GB, Lopez-Rodriguez L, Sturrock A, Loughnan S.
535 2017 Social class and ideologies of inequality: How they uphold unequal societies. *J. Soc.*

536 *Issues* **73**, 99–116. (doi:10.1111/josi.12206)

537 66. Belmi P, Laurin K. 2016 Who wants to get to the top? Class and lay theories about power. *J.*
538 *Pers. Soc. Psychol.* **111**, 505–529. (doi:10.1037/pspi0000060)

539 67. Hobson EA, Mønster D, DeDeo S. 2021 Aggression heuristics underlie animal dominance
540 hierarchies and provide evidence of group-level social information. *Proc. Natl. Acad. Sci. U.*
541 *S. A.* **118**, 1–9. (doi:10.1073/pnas.2022912118)

542 68. Cronin KA, Sánchez A. 2012 Social dynamics and cooperation: The case of nonhuman
543 primates and its implications for human behavior. *Adv. Complex Syst.* **15**, 1–21.
544 (doi:10.1142/S021952591250066X)

545 69. Hare B, Melis AP, Woods V, Hastings S, Wrangham R. 2007 Tolerance allows bonobos to
546 outperform chimpanzees on a cooperative task. *Curr. Biol.* **17**, 619–623.
547 (doi:10.1016/j.cub.2007.02.040)

548 70. Fung JMY, Au WT. 2014 Effect of inequality on cooperation: Heterogeneity and hegemony in
549 public goods dilemma. *Organ. Behav. Hum. Decis. Process.* **123**, 9–22.
550 (doi:10.1016/j.obhdp.2013.10.010)

551 71. Hargreaves Heap SP, Ramalingam A, Stoddard B V. 2016 Endowment inequality in public
552 goods games: A re-examination. *Econ. Lett.* **146**, 4–7. (doi:10.1016/j.econlet.2016.07.015)

553 72. Hauser OP, Hilbe C, Chatterjee K, Nowak MA. 2019 Social dilemmas among unequals.
554 *Nature* **572**, 524–527. (doi:10.1038/s41586-019-1488-5)

555 73. Gavrilets S, Fortunato L. 2014 A solution to the collective action problem in between-group
556 conflict with within-group inequality. *Nat. Commun.* **5**, 3526. (doi:10.1038/ncomms4526)

557 74. Glowacki L, von Rueden C. 2015 Leadership solves collective action problems in small-scale
558 societies. *Philos. Trans. R. Soc. B Biol. Sci.* **370**. (doi:10.1098/rstb.2015.0010)

559 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. *Proceedings. Biol. Sci.* **287**, 20200693. (doi:10.1098/rspb.2020.0693)

79. Rogers DS, Deshpande O, Feldman MW. 2011 The spread of inequality. *PLoS One* **6**. (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 Biol. Sci.* **287**. (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)

584 85. Shizuka D, McDonald DB. 2015 The network motif architecture of dominance hierarchies. *J.*
585 *R. Soc. Interface* **12**, 20150080.

586 86. Thierry B, Aureli F, Nunn CL, Petit O, Abegg C, de Waal FBM. 2008 A comparative study of
587 conflict resolution in macaques: insights into the nature of trait covariation. *Anim. Behav.* **75**,
588 847–860. (doi:10.1016/j.anbehav.2007.07.006)

589 87. Thierry B. 2013 Identifying constraints in the evolution of primate societies. *Philos. Trans. R.*
590 *Soc. Lond. B. Biol. Sci.* **368**, 20120342.

591 88. Wrangham RW. 1980 An ecological model of female-bonded primate groups. *Behaviour* **75**,
592 262–300.

593 89. Clutton-Brock TH, Janson C. 2012 Primate socioecology at the crossroads: Past, present, and
594 future. *Evol. Anthropol.* **21**, 136–150. (doi:10.1002/evan.21316)

595 90. Thierry B. 2008 Primate socioecology, the lost dream of ecological determinism. *Evol.*
596 *Anthropol.* **17**, 93–96. (doi:10.1002/evan.20168)

597 91. Boehm C *et al.* 1993 Egalitarian behavior and reverse dominance hierarchy. *Curr. Anthropol.*
598 **34**, 227–254.

599 92. Kleppestø TH, Czajkowski NO, Vassend O, Røysamb E, Eftedal NH, Sheehy-Skeffington J,
600 Kunst JR, Thomsen L. 2019 Correlations between social dominance orientation and political
601 attitudes reflect common genetic underpinnings. *Proc. Natl. Acad. Sci. U. S. A.* **116**, 17741–
602 17746. (doi:10.1073/pnas.1818711116)

603 93. Mitchell RL, Bae KK, Case CR, Hays NA. 2020 Drivers of desire for social rank. *Curr. Opin.*
604 *Psychol.* **33**, 189–195. (doi:10.1016/j.copsyc.2019.07.027)

605 94. Marshall HH *et al.* 2021 A veil of ignorance can promote fairness in a mammal society. *Nat.*
606 *Commun.* **12**. (doi:10.1038/s41467-021-23910-6)

607 95. Hamilton IM, Benincasa MD. 2022 Emergence of size-structured dominance hierarchies

through size-dependent feedback. *Philos. Trans. R. Soc. B Biol. Sci.* **377**. (doi:10.1098/rstb.2020.0449)

96. Massen JJM, Szipl 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. London. Ser. B Biol. Sci.* **271**. (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**, 10594–10607. (doi:10.1002/ece3.4549)

102. Brent LJN, 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. U. S. A.* **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 Biol. Sci.* **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. Organ.* **126**, 75–88. (doi:10.1016/j.jebo.2015.09.002)

106. Turchin P, Gavrilets S. 2009 Evolution of complex hierarchical societies. *Soc. 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 Biol. Sci.* **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. U. S. A.* **117**, 29759–29766. (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. (doi:https://www.jstor.org/stable/2117312)

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 Biol. Sci.* **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 Univeristy 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 Biol. Sci.* **287**, 1–9. (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. *Philos. Trans. R. Soc. B Biol. Sci.* **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 Biol. Sci.* **272**, 1091–1099. (doi:10.1098/rspb.2004.3019)

680 125. Larson SM, Ruiz-Lambides A, Platt ML, Brent LJN. 2018 Social network dynamics precede a
681 mass eviction in group-living rhesus macaques. *Anim. Behav.* **136**, 185–193.
682 (doi:10.1016/j.anbehav.2017.08.019)

683 126. Sun L, Xia DP, Sun S, Sheeran LK, Li JH. 2017 The prospect of rising in rank is key to long-
684 term stability in Tibetan macaque society. *Sci. Rep.* **7**, 1–8. (doi:10.1038/s41598-017-07067-1)

685 127. Tilly C. 1998 *Durable inequality*. University of California Press.

686 128. Carey RM, Markus HR. 2017 Social class shapes the form and function of relationships and
687 selves. *Curr. Opin. Psychol.* **18**, 123–130. (doi:10.1016/j.copsyc.2017.08.031)

688 129. House JS, Lepkowski JM, Kinney AM, Mero RP, Kessler RC, Herzog AR. 1994 The social
689 stratification of aging and health. *J. Health Soc. Behav.* **35**, 213. (doi:10.2307/2137277)

690 130. Bol T, De Vaan M, Van De Rijt A. 2018 The Matthew effect in science funding. *Proc. Natl.*
691 *Acad. Sci. U. S. A.* **115**, 4887–4890. (doi:10.1073/pnas.1719557115)

692 131. Merton RK. 1968 The Matthew Effect in Science: The reward and communication systems of
693 science are considered. *Science.* **159**, 56–63. (doi:10.1126/science.159.3810.56)

694 132. van de Rijt A, Kang SM, Restivo M, Patil A. 2014 Field experiments of success-breeds-
695 success dynamics. *Proc. Natl. Acad. Sci.* **111**, 6934–6939. (doi:10.1073/pnas.1316836111)

696 133. Dugatkin LA, Druen M. 2004 The social implications of winner and loser effects. *Proc. R.*
697 *Soc. B Biol. Sci.* **271**, 488–489. (doi:10.1098/rsbl.2004.0235)

698 134. Barabási A-L, Albert R. 1999 Emergence of scaling in random networks. *Science.* **286**, 509–
699 512. (doi:10.1126/science.286.5439.509)

700 135. Colizza V, Flammini A, Serrano MA, Vespignani A. 2006 Detecting rich-club ordering in
701 complex networks. *Nat. Phys.* **2**, 110–115. (doi:10.1038/nphys209)

702 136. Nosil P, Villoutreix R, De Carvalho CF, Farkas TE, Soria-Carrasco V, Feder JL, Crespi BJ,
703 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. B Biol. Sci.* **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.* , 1–18. (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.