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Invited Ideas
The nature of privilege: intergenerational wealth in animal societies

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Wealth inequality is widespread across human societies, from pastoral and small-scale agricultural groups to large modern social structures. The intergenerational transfer of wealth privileges some individuals over others through the transmission of resources external to an individual organism. Privileged access to household wealth (e.g., land, shelter, silver) positively influences the destinies of some (and their descendants) over others in human societies. Strikingly parallel phenomena exist in animal societies. Inheritance of nongenetic commodities (e.g., a nest, territory, tool) external to an individual also contributes greatly to direct fitness in animals. Here, we illustrate the evolutionary diversity of privilege and its disparity-generating effects on the evolutionary trajectories of lineages across the Tree of Life. We propose that integration of approaches used to study these patterns in humans may offer new insights into a core principle from behavioral ecology—differential access to inherited resources—and help to establish a broad, comparative framework for studying inequality in animals.

Key words: **comparative evolution, cooperation, inequality, niche construction, social network, territory defense.**

Wealth inequality exerts a powerful influence on the health (e.g., Deaton 2013) and opportunities (e.g., Khan 2021) of individuals around the globe, and occurs when humans have differential access to—and variation in—three classes of wealth: (1) material (resources accumulated in the environment), (2) embodied (individual differences in size, strength, skill, or knowledge), and (3) relational wealth (social connections and capital; Kaplan 1996; Borgerhoff Mulder et al. 2009). In humans, unequal distributions of material wealth contribute most strongly to this imbalance (Bowles et al. 2010; Smith, Borgerhoff Mulder, et al. 2010) from small-scale agricultural and pastoral societies (Borgerhoff Mulder et al. 2009) to residents living in modern cities (Schell et al. 2020). The intergenerational transfer of material wealth can shape divergent destinies (Flannery 2012; Kohler et al. 2017), contribute to the economic concept of intergenerational wealth mobility (Solon 1992, 2002; Corak 2013; Chetty et al. 2014), and even alter the evolutionary trajectories across human societies (Smith, Borgerhoff Mulder, et al. 2010).

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THE PHYLOGENY OF PRIVILEGE

The concept of privilege—differential access to inherited resources—is familiar in the context of human economic and social systems, but many other animals also transfer some forms of wealth across generations. Although some of these examples are well known to workers within particular animal systems, there have been few efforts to understand the implications of privilege within a comparative evolutionary context. In this piece, we argue that the tools used to study wealth cross-culturally within humans, when integrated with comparative phylogenetic approaches, may yield powerful new insights into privilege dynamics in animal societies.

Cultural and historical factors shape the expression of privilege in human societies. Yet, parallels exist in how privilege emerges in both human and animal societies. In animal societies, wealth comes in the form of transgenerational effects of parental care (Champagne 2008) or social networks (Ilany and Akçay 2016; Ilany et al. 2021), but also the direct transfer of material wealth via nongenetic inheritance (Emlen 1991; Ragsdale 1999). Here, we illustrate the evolutionary diversity of material wealth transfer (a form of privilege that is ubiquitous across species of animals, Figure 1), and its disparity-generating effects in five divergent taxonomic lineages of animals (Figure 2). We also propose new directions for its comparative study.

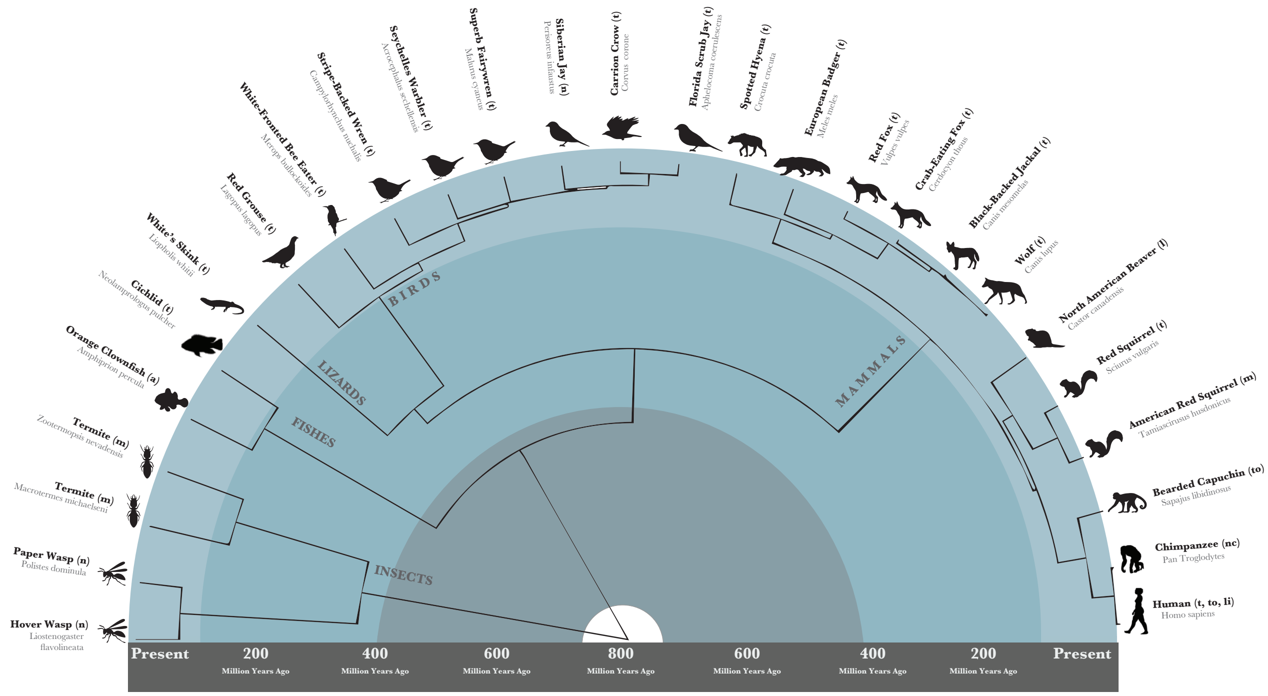

Figure 1

The intergenerational transfer of material wealth is widespread across the Tree of Life, with taxonomic examples ranging from social insects and fish to mammalian carnivores and primates, including humans. Examples of commodities transferred from one generation to the next include a (n) nest, (m) mound, (a) anemone, (t) territory, (l) lodge, (m) midden, (to) tools, (nc) natal community, and (li) livestock (see Supporting Information for full references and additional details).

Intergenerational transfer of material wealth within family lineages

Intergenerational transfer of material wealth can drive inequality within family lineages of animals. In North American red squirrels (*Tamiasciurus hudsonicus*), a mother may store spruce cones on her territory and privilege her daughter by bequeathing a rich territory to her; daughters who receive these resources survive longer and reproduce earlier than those without (Smith 1968). Male food hoarders can also influence the lifetime fitness of subsequent owners of middens and these effects persist across multiple owners (Fisher et al. 2019). Because these food hoards outlive their owners, these indirect effects alter the environments that others experience. Thus, when some offspring receive a cone stash and others do not, this perpetuates inequality across generations privileging some individuals over others. Whereas many species, including the red squirrels described here, modify their local resource distributions (Laland et al. 1999; Olding-Smee 2012), studying the evolutionary dynamics associated with the intergenerational transfer of these constructed niches requires explicit study within a comparative framework.

The material transfer of (nongenetic) material wealth contributes to the extinction (vs. expansion) of family lineages and advantage individuals of the philopatric (vs. dispersing) sex across species. For spotted hyenas (*Crocuta crocuta*), individuals from multiple maternal lineages join forces to defend a shared territory, but high-born philopatric females and their descendants have privileged access to resources within them (Holekamp et al. 2012) (Figure 2). Differential access promotes the extinction of nonprivileged family lineages but expands land ownership by privileged animals; these effects are further ameliorated by differential access to social support within groups (Smith, Van Horn, et al. 2010; Strauss and Holekamp 2019). In contrast, territory acquisition by a young male red grouse (*Lagopus lagopus scotica*) is impacted by paternal presence (Watson et al. 1994) (Figure 2). Philopatric sons with nearby fathers gain larger and more defended territories than individuals whose fathers are no longer alive. Thus, the comparative study of wealth transfer across animals should therefore offer insights into the evolutionary dynamics of family groups and the consequences of sex-biased dispersal in animals.

The transgenerational use of activity sites can also contribute to the accumulation of stone tools within lineages. Taï Chimpanzees (*Pan troglodytes verus*) (Mercader et al. 2002) and bearded capuchin monkeys (*Cebus libidinosus*) (Elisabetta et al. 2013) inherit tools produced at nut-cracking sites via the paternal and maternal lines, respectively. Individuals that inherit are advantaged over others who do not in terms of their ability to gain access to key food resources; these beneficial effects are further compounded through the transfer of social information (e.g., traditions for how to use inherited materials) across generations. These examples shed light on the direct and indirect role of wealth transfer in shaping legacies of inequality along bloodlines over multiple time scales. These effects of intergenerational wealth mobility are likely stronger for some species than for others, as we discuss below, and therefore should be the subject of a quantitative study by behavioral ecologists to understand the breadth of their influence.

Intergenerational transfer of material wealth among non-kin

Intergenerational transfer of material wealth is not limited to genetic relatives within animal societies and can impose similar disparity-generating effects through preferential treatment by non-kin. For instance, privileged access to shelter (e.g., a nest) can transcend bloodlines in European paper wasps (*Polistes dominula*). Inheritance of built structures from kin or non-kin advantage wasps fortunate enough to receive them (Leadbeater et al. 2011). As a result, females who share nests with others are more likely to inherit structures and produce offspring than less privileged lone females. Within some termite societies structures

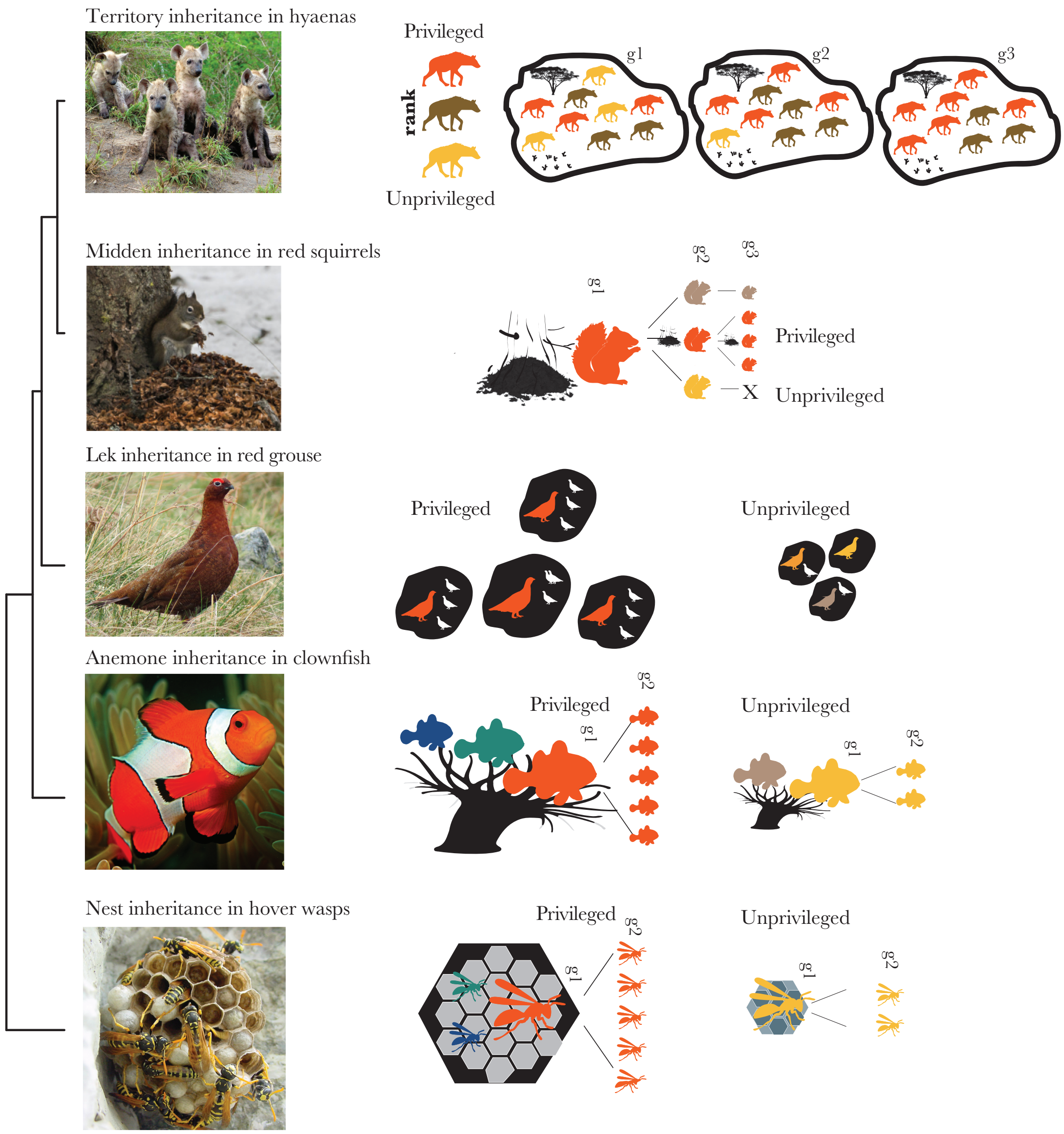

Figure 2

Salient examples of commodities privileged to some but not others via the intergenerational transfer of material wealth include access to land, shelter, and stockpiles of food. This differential access produces compounding effects over multiple generations (from g_1 to g_{1+n}) that privilege some family lineages over others. For example, some (b) North American red squirrels (g_1) transfer stores of acorns (middens) to one individual (g_2) but not to others, imposing differential fitness outcomes on young squirrels that perpetuate across future generations (g_3). In a fish species (d), inheritance of high quality (larger) anemones privileges some clown anemonefish over others, influencing the fates of the next generation of fishes. Examples also involve birds, such as in the red grouse (c); sons gain privileged positions on leks, and thus mating opportunities, when their father is nearby and after he dies such that land ownership is passed on from one generation to the next via the paternal line (Photo by Craig Jones). In a social carnivore, the spotted hyena (a), offspring inherit their social rank from their mothers within the maternal line (matriline) and priority of access to ephemeral food within shared territories. As a result, full family lines within this species increase in their representation over time whereas other lineages decrease in numbers or even go extinct over time. Similar patterns exist in some social insects (e) for which some privileged wasps inherit nests while others do not, benefiting some lineages over others to further perpetuate the cycle of privilege. All other photos reproduced with permission through creative commons license.

may be inherited from kin, but inheritance can also occur when different lineages merge to share "real estate" (Thorne et al. 2003). The merging of families accelerates inheritance, increasing opportunities for resource acquisition for future generations, benefiting some termite lineages over others to further perpetuate the cycle of privilege. In some cases, disadvantaged individuals wait for privileged individuals to perish, as occurs, for example, in the clown anemonefish (*Amphiprion percula*) which lives in groups composed of non-relatives (Buston 2004). The non-breeding fish queue to inherit high-quality anemones from non-kin, but not all individuals inherit, and these effects can compound across multiple generations. Further inquiry into understanding selective processes shaping resource transfer among non-kin within a comparative perspective could offer new insights into the evolutionary origins of cooperation among non-relatives.

A COMPARATIVE PERSPECTIVE ON WEALTH INEQUALITY

Recently, parallels in the linkage between social inequality, health, and survival have been demonstrated in animal societies

(Snyder-Mackler et al. 2020). This discovery illustrates how wealth and access govern well-being across many social animals, humans included, but we have a poor understanding of whether shared mechanisms underlie these inequalities. One reason is that behavioral ecologists tend to focus on the consequences of inheritance for individual-level fitness rather than on what causes the gains or losses of wealth inheritance across species.

We propose identifying these commonalities as an important first step toward understanding the drivers of privilege in the natural world. Comparative study of privilege in animal societies may yield a greater understanding of (1) the deep evolutionary roots of wealth inequality across the Tree of Life, (2) how advantages for some but not other individuals perpetuate privilege to create and sustain a landscape of inequality, (3) how multigenerational inequality and its compounding of advantages for some contribute to unequal playing fields across multiple species, including our own.

Such insights would reveal how the transfer of territory and other material commodities influence evolutionary trajectories, including its effects on mating strategies, dispersal decisions, the timing of reproduction, group size, intergroup relationships, social dynamics, and habitat selection as well as its effects on speciation or vulnerability to extinction. By elucidating these associations, we might begin to understand the conditions producing more or less even playing fields in the natural world, contributing to a deeper understanding of the general processes across species that (de)stabilize dominance hierarchies, for example.

A transdisciplinary perspective to explain animal inequality

More generally, we highlight the need to test theories from the social sciences using natural history information from across the Tree of Life. Robust measures of reproductive inequality (e.g., Ross et al. 2020) and data from long-term studies of marked individuals (Lindenmayer et al. 2012) now make such comparisons possible across multiple species of animals. One major avenue forward is to draw from anthropological approaches used to study such patterns of intergenerational wealth transfer in humans (e.g., Mattison et al. 2016) to systematically study parallel processes in non-human animals. For example, a cross-cultural comparison of premodern human societies reveals that the relative importance of material, embodied, and relational wealth and the extent of intergenerational wealth transfer differs across societal types (Smith, Borgerhoff Mulder, et al. 2010). Importantly, high wealth inequality within human societies positively predicts the occurrence of such intergenerational transfer.

Although material wealth transfer is theoretically possible for any species for which valuable resources exceed an individual's lifespan, our framework explicitly draws upon three principles derived from studies of human ecology. First, wealth transfer is expected to be more profitable and therefore evolve more often for species that depend upon stationary resources, such as permanent shelters. Second, privilege is expected to be most common for species that depend upon saturated habitats with predictable and concentrated resources, such as species that endure for multiple generations at high-quality territories or oviposition sites. Third, we expect that highly transient species—or members of the dispersing sex for species with sex-biased dispersal—will be less likely to accumulate, defend, and transfer material property (e.g., tools, food caches) from one generation to the next than more sedentary or territorial ones. Thus, understanding the degree of material wealth transfer across animals that vary in patterns of space use will contribute more broadly to our understanding of the principles governing movement ecology (Nathan et al. 2008).

A transdisciplinary perspective suggests biologists should study the extent to which various classes of wealth (e.g., material, embodied, relational) interact—or act on their own—to contribute to inequality in animals. For example, among the Pimbwe of Tanzania, a horticultural population in East Africa, material *and* relational—but to a lesser extent embodied (a person's strength, skill, or knowledge; Kaplan 1996)—wealth strongly influence reproductive success (Borgerhoff Mulder and Beheim 2011). We might predict similar patterns across non-human animals such that the relative contributions of each wealth class co-varies with the social and ecological traits of a species. Moreover, we predict the compounding effects of privilege to be most pronounced for species with both the intergenerational transfer of material (e.g., territory, stone tools) *and* relational (e.g., social networks, teaching) wealth, such as in the societies of spotted hyenas, chimpanzees, and capuchins.

We expect feedback loops to occur for these processes. In some cases, cultural traditions or norms promoting equity may also limit the accumulation of privilege across time, but generally feedback loops are expected to reinforce intergenerational privilege. For example, positive assortment in mate and partner choice might increase the association between one generation's accumulation of wealth and the next. Thus, developmental effects of privileged offspring may be associated with genotypic and phenotypic differences that contribute to differential reproductive outcomes among non-human animals. Positive feedback loops between the individual and social environment may also attenuate the strength of inequality within social systems across time through winner–loser effects (Lihoreau et al. 2021). In social species, winning access to resources can increase the likelihood that an individual will win again and, thus, their ability to accumulate more wealth in the future; in contrast, losers become less likely to win and less likely to accumulate wealth. Biologists should therefore leverage data from long-term studies of animals to understand the extent to which inheritance systems maintain differences across generations via positive feedback loops to generate and reinforce intergenerational privilege.

A phylogenetic toolkit for understanding the ecology of privilege

Clearly, biologists know a great deal about how resource use of animals varies with diet type (e.g., carnivore vs. herbivore), modes and intensity of competition (e.g., contest vs. scramble competition), dispersal patterns (e.g., philopatric vs. dispersing), space use (e.g., transient vs. residential or territorial) as well as social structures (e.g., despotic to egalitarian) and mating systems (e.g., monogamous vs. polygamous). As a discipline, behavioral ecologists are well equipped to examine the relative importance of these factors in the lives of animals to identify the universal factors driving intergenerational wealth transfer within (and potentially across) family lines. Insights from the study of humans generate multiple testable predictions, several of which we outline below.

Variation in patterns of resource use and defense may explain patterns of intergenerational wealth transfer across animals. For example, evidence from human societies that vary in their foraging ecologies (Smith, Borgerhoff Mulder, et al. 2010) suggests that intergenerational transfer of wealth is likely for species with intense feeding competition, such as in social carnivorans (Smith et al. 2012). Moreover, data from nearly ninety hunter–gather societies reveal a strong correlation between the reliance upon clumped, defensible resources (e.g., wild salmon vs. wild plant resources) and institutionalized wealth inequality (Smith and Codding 2021). Thus, we might also expect increased inequality in territorial species with contest competition versus more transient ones with scramble competition.

The life history traits and mating systems of animals should also strongly predict patterns of intergenerational wealth transfer in animals. That is, the philopatric sex should generally have more opportunities to accumulate intergenerational wealth, particularly within family lines (e.g., within matrilines) for philopatric animals residing in the same area for multiple generations. Although mating systems are also expected to vary with wealth inequality, the directions of these relationships are less clear from this transdisciplinary lens. Somewhat paradoxically, as humans transitioned from egalitarian horticultural populations to more unequal agricultural ones, they shifted from polygynous to monogamous mating systems (Ross et al. 2018). However, for birds and mammals, polygyny (e.g., multiple females and one male) is generally more common and more pronounced within populations for which males vary greatly in control over access to limited resources (e.g., nesting sites, food; Verner and Wilson 1966; Orians et al. 1969). Future studies should therefore study the extent to which various life history traits and aspects of mating systems explain patterns of intergenerational wealth transfer across animals.

Going forward, behavioral ecologists now possess the quantitative tools and detailed data sets to ask these and related questions across animals. By drawing insights across populations of the same species experiencing different ecological conditions and across multiple biological species, we will be able to explain how variation in ecological and social traits explain the presence/absence and intensity of intergenerational wealth transfer within a phylogenetic context. The systematic lines of inquiry proposed here should therefore start to reveal which ecological drivers contribute to intergenerational wealth transfer and reveal the fundamental principles underlying wealth inequality across the Tree of Life.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

AUTHOR CONTRIBUTIONS

All authors contributed to writing this paper. J.E.S. and B.N.H. are shared first authors.

Data availability: No original data are included in this manuscript. All information for the phylogeny is provided in our, Supporting Information section, to be posted online, pending acceptance.

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