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Review



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Dominance in humans

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Dominance captures behavioural patterns found in social hierarchies that arise from agonistic interactions in which some individuals coercively exploit their control over costs and benefits to extract deference from others, often through aggression, threats and/or intimidation. Accumulating evidence points to its importance in humans and its separation from prestige-an alternate avenue to high status in which status arises from information (e.g. knowledge, skill, etc.) or other non-rival goods. In this review, we provide an overview of the theoretical underpinnings of dominance as a concept within evolutionary biology, discuss the challenges of applying it to humans and consider alternative theoretical accounts which assert that dominance is relevant to understanding status in humans. We then review empirical evidence for its continued importance in human groups, including the effects of dominance-independently of prestigeon measurable outcomes such as social influence and reproductive fitness, evidence for specialized dominance psychology, and evidence for genderspecific effects. Finally, because human-specific factors such as norms and coalitions may place bounds on purely coercive status-attainment strategies, we end by considering key situations and contexts that increase the likelihood for dominance status to coexist alongside prestige status within the same individual, including how: (i) institutional power and authority tend to elicit dominance; (ii) dominance-enhancing traits can at times generate benefits for others (prestige); and (iii) certain dominance cues and ethology may lead to mis-attributions of prestige.

This article is part of the theme issue 'The centennial of the pecking order: current state and future prospects for the study of dominance hierarchies'.

1. Introduction

The concept of dominance plays an important role in animal behaviour, social psychology, developmental psychology and anthropology. Dominant individuals accrue social influence and achieve superior resource access and greater fitness through their greater coercive control over costs and benefits; they maintain their attained rank in a stable hierarchy through intimidation and threats. Individuals who *fear* the *cost-infliction or benefit-withholding capacity* of the dominant in an escalated conflict yield to the dominant in contests, and grant dominants—with resistance when possible—the resources and accoutrements of status. Recently, however, some researchers have raised questions regarding the importance of dominance in structuring social rank in humans [1–3]; they argue that social status in our species has substantially diverged from the patterns observed in other great apes such that coercive routes to status attainment play little to no role in our species.

To address this debate, we review and integrate existing approaches to dominance with an eye on the evolved peculiarities of humans. First, drawing on the conceptual framework of evolutionary game theory, we review when and why social animals might evolve to either fight for dominance or consent to a subordinate status. Second, in light of this framework, we discuss several features of humans that have emerged through culture-gene coevolutionary processes that make it challenging for researchers to isolate and study dominance status. These features include: (i) prestige-based status, a second avenue to

status arising from access to information in the form of knowledge and skills; (ii) social norms that enforce egalitarian relationships, suppress the use of aggression and create opportunities for individuals to leave unequal groups; and (iii) cumulative cultural products like languages and projectile weapons that create challenges for prospective dominants and opportunities for anti-dominance behaviours from subordinates. Third, we review the psychological and behavioural evidence for dominance in humans, drawing evidence from research with infants, children and adults across populations. Finally, we close with a discussion of some of the methodological challenges to studying human status and important areas of focus for future research, such as the differences in how dominance emerges in men and women, and how it interacts with institutions, culture and forms of prestige status.

2. Theorizing dominance

Aggression in group-living animals is often stably patterned, with one member of any given pair tending to be the aggressor towards the other individual, who does not reciprocate, and who often yields valuable resources during contests. This patterning was first highlighted by Schjelderupp-Ebbe [4] among chickens, from which the notion of a *pecking order* derives. Empirically, pairwise dominance relations often form a linear order or *dominance hierarchy* in an enormous range of species, including chimpanzees and bonobos [5–10] and humans [11–17].

Why are dominance hierarchies so common? To address this question, standard evolutionary game theorists developed variants of the hawk-dove game [18,19]. In this game, two players confront each other over a resource, and can choose either a peaceful division (act as doves), where each benefits from half the resource at no cost, or fight for its entirety (act as hawks). However, if one player decides to fight and the other does not, the aggressor takes the resource at no cost. If players could only act in one way permanently, natural selection will favour a mixture of hawks and doves depending on the value of the resource, each individual's chances of winning, and fighting costs. However, if agents can switch, natural selection can favour the use of even arbitrary differences among pairs to coordinate hawk or dove status, thereby preventing fights [20] For example, in the stable state achieved if all players use the bourgeois strategy, the individual who arrives first at the resource receives it (plays hawk) while the later arrivals are doves. This suppresses costly conflicts and permits the bourgeois to drive out pure hawks and doves.

Such models frame dominance hierarchies as the product of evolved strategies for resolving disputes over limited resources and for minimizing repeated, escalated conflicts in group-living animals. In these models, the evolutionarily stable strategy¹ under many different conditions predicts that some players will yield resources to specific others, giving rise to a system of dominance rank. The rank order, in turn, can be determined by mechanisms such as mutual assessment of formidability (or *resource-holding-potential*, [21,22]), a physical sign or 'badge' of physical condition [23], the outcome of one or several fights [20,21] or even by some conventional sign such as age, tenure in the group (i.e. *queueing*; e.g. [24]), or inherited status [22,25]. Because top-rankers in a stable hierarchy have access to more resources, these models predict that selective pressure exists for traits that enable competition for high rank. They also predict the evolution of a 'dominance psychology'—those adaptations that enable the behavioural flexibility needed to successfully navigate dominance relations [26].

More recent evolutionary models of resource partitioning in group-living organisms demonstrate how (i) the degree to which dominants benefit from the presence of subordinates and (ii) the relative attractiveness of subordinates' outside options can limit the degree of inequality that dominant individuals can impose on the rest of the group ([27-29] and references therein). Consistent with such models, observational studies suggest that dominance can be complicated by the fact that subordinates benefit dominants by provisioning services (such as grooming, food-sharing, etc.) or by mutualism (through predator detection or cooperation in hunting or warfare). This means that subordinates can punish dominants by withholding or threatening to withhold these benefits. Such leverage [19,30-33]; occurs wherever subordinates provide benefits in such a way that the provisioning cannot be compelled. It influences dominance in great apes [29,33-36], and is probably important among humans [29,37] as we cooperate in domains as diverse as foraging, food-sharing, breeding and warfare and as we often choose to leave groups-which is another way subordinates can harm dominants, which, in the extreme, culminates in ostracism [38]. Pervasive leverage weakens the unidirectionality of aggression or intimidation, increases affiliative and reconciliatory behaviours and reduces rank-based inequality, making dominance hierarchies less despotic and more egalitarian [19,32,39] or less steep [40].

Coalitions between individuals who coordinate their aggression can also influence dominance in many primates [41,42] including humans [43,44]. For example, one type of coalition—the large leveling coalition (defined theoretically as one that reduces rank-associated inequality without changing the rank order; [19,45]), may have been especially important in human evolution [43,44]. Factors that promote the evolution of leveling coalitions—which are all likely to have existed in our evolutionary history, as reviewed later—include lower returns to dominance (low despotism) and lower coalition costs [41,45,46], *synergy* (if coalition strength exceeds the combined strength of its constituents [47,48]), and increasing returns to resource ownership, which makes it in all individuals' interest to reduce within-group inequalities [47].

In short, evolutionary game theory provides a firm foundation for understanding how, when and why dominance hierarchies emerge from social interaction in group-living species. The evolutionarily stable behavioural strategies find their counterparts in a suite of psychological adaptations—a *dominance psychology*—that should be observable in both dominants and subordinates. Dominance arises relationally and is not an individual-level trait, but is often correlated to individual traits such as resource-holding potential and physical size. Furthermore, leverage arising from cooperation, mutualism and outside options, as well as coalitionary dynamics—which are all important in humans—are expected to influence the inequalities associated with dominance and to modify its expression.

3. Challenges to dominance in humans

Although we have every reason to suspect that the evolutionary processes and incentives identified by the logic of the models described above will apply to humans, identifying and studying dominance in our species poses particular challenges owing to the influence of both cultural evolution and culture-gene coevolution. Below, we consider three key factors that have probably shaped our species' genetic evolution and that continue to influence the expression of dominance in the modern world:

- (i) the emergence of a second avenue to high status-prestige, from the uneven distribution of our species' most important non-rival good, *cultural information*, such as knowledge, skills, tactics and techniques;
- (ii) the spread of social norms that favour egalitarian behaviour, suppress aggression and facilitate mobility among groups; and
- (iii) the development of cultural products such as projectile weapons, poisons, languages and cooperative hunting and raiding techniques that influence the balance of power between dominants and subordinates.

We discuss these in the context of contemporary mobile hunter–gatherers, because features of social life among these populations were probably recurrent over at least the middle to later Palaeolithic and may have shaped the evolution of our species' dominance psychology.

Humans have evolved a second avenue for achieving status-prestige, which emerged alongside our species' increasingly sophisticated capacities for cultural learning, including our ability to target our cultural learning specifically at those models most likely to possess adaptive information. Evolutionarily, deference in a prestige hierarchy is exchanged for informational access, and thus comes with learning opportunities-those paying deference get to 'hang out' with the more prestigious [26]. Consequently, high prestige produces feelings of respect and admiration and induces approach towards the prestigious, instead of the fear and avoidance associated with dominance [49]. The dominant and prestigious both enjoy increases in social influence and preferential attention [49,50], but prestige increases social influence through voluntary deference, imitation and true persuasion, whereas dominance relies on force and avoidance of the costs that dominant individuals can inflict [49,51].

Prestige can facilitate coalition formation and collective action [52,53], and such cooperative coalitions often endow prestigious individuals-who naturally emerge as leaderswith the ability to inflict costs. That is, the coalition enables prestigious individuals to behave dominantly towards disloyal followers or even those outside his or her coalition. This means that prestige and dominance status may overlap in some individuals. Similarly, in more complex societies with meritocratic institutions and legally enforced private property, prestige can lead to fame, wealth and institutional power, giving prestigious individuals coercive control over costs and benefits. This again merges prestige and dominance in complex ways [26,54-56]. The diffusion of meritocratic and pluralistic institutions over the last few centuries has probably increased the relative importance of prestige. Therefore, researchers interested in the psychology of status must carefully disentangle prestige and dominance by recognizing how coalitions and institutions can reinforce the relevance of either dominance or prestige, or even induce overlap between the two.

Alongside prestige, cultural evolution and culture-gene coevolution also gave rise to social norms, which came to increasingly shape social life, eventually leading to a norm psychology [57,58]. By contrast to our ape relatives, there is reason to suspect that populations deep in our evolutionary history possessed social norms that promoted egalitarianism and suppressed aggression or coercion [29,37,43,44,59,60]. Aggressive individuals among contemporary huntergatherers, who resort to force and intimidation or violate the autonomy of others, are subjected to social sanctions imposed by the community, with sanctions escalating from criticism, ridicule and ostracism, to execution [43,61-63]. Even behaviours that suggest potential aggression or domineering tendencies (e.g. issuing commands, or selfishness during resource sharing) are closely monitored and sanctioned [44]. Observationally and empirically, dominance and its effects on status vary across contexts, and are especially pronounced in groups with weaker egalitarian norms [64]. Interestingly, prestigious and skilled individuals among hunter-gatherers are commonly targeted by those who wish to remind others of such norms [44]; this, alongside ecological factors, may have forced prestigious hunter-gatherers to be especially generous, forthcoming, and cooperative, limiting the development of self-reinforcing inequalities in prestige in our evolutionary past [65], which is important as the benefits that the prestigious often provide can themselves become the basis for dominant social positions. Our dominance psychology has had to adapt to a norm-governed world where the manipulative use of coercive incentives had to be accomplished more subtly (such as in less overt, physical forms), and within the context of social rules and third-party monitoring.

Over the course of human evolution, norms and institutions pertaining to marriage, exchange and communal rites also promoted 'outside options' for individuals by providing opportunities to move between groups in an ethnolinguistic community [66]. Marriage norms required or encouraged individuals to find partners outside of their local groups, while exchange norms encouraged individuals to maintain ongoing gift-giving relationships with a portfolio of partners, sustaining wide networks of relationships [67]. Communal rituals brought diverse residential groups into periodic contact, which helped keep doors open among residential communities and produced a degree of freedom to move among groups not observed in other socially cooperative species. By providing outside options, these social norms provided further 'leverage' for subordinates and weakened the control of dominants.

Finally, cultural evolution created a variety of cultural products, including communicative repertoires (vocal and sign languages) as well as weapons and tactics, that would have made the project of domination in a mobile hunter–gatherer society very difficult. Language would allow effective subordinate coordination to assassinate aggressive or dominant individuals, and projectile weapons—from atlatls to poisoned arrows—would have reduced the costs of taking down a dominant and increased fighting costs for prospective dominants, especially when combined with ambush tactics developed for hunting or raiding [60,61,63,68].

Owing to the confluence of these factors, dominance is more muted in humans than in other species and can produce more variable effects on status. As noted in [69], 'coercing one's way to power appears to be a relatively

precarious strategy that may yield variable results across time and contexts. While efficacious in certain groups and over certain periods, dominance may fail to deliver in other contexts' [69, p. 240]. The crucial point is that, despite these factors that alter how dominance is expressed in humans and modulate its effects on status, dominance nevertheless constitutes a viable avenue to status in diverse contexts.

4. Dominance in humans: assessing the evidence

As we will show, despite the constraints imposed on dominance by norms, social fluidity, or specific cultural products and its frequent subordination to prestige, dominance continues to play a pervasive role in human social life. We will draw on experimental, observational and anthropological evidence from children and adults from diverse societies to show how dominance reliably impacts social influence, collective decision-making and reproductive fitness in humans, suggesting that dominance continues to contribute pervasively to status asymmetries in our species.

From an evolutionary point of view, our baseline expectation should be that humans probably inherited some form of dominance psychology from our shared ancestry with chimpanzees and bonobos, whose social life is strongly shaped by dominance hierarchies [8,19,70-73] Dominance rank is associated among them with both shorter-term social influence, including access to food and mating opportunities [5-7,74], and longer-term outcomes such mating opportunities and fitness [35,75]. Alongside directed movements like chasing and biting as well as cues like peering [8,9], both of our closest relatives acknowledge their place in a stable hierarchy by signalling dominance or submission using arbitrary displays such as pant-grunts [8,19,71,72,76]. Strikingly, aspects of human dominance appear evolutionarily continuous with those in apes, such as attentional mechanisms [77] and some cross-culturally conserved and probably reliably developing ethological displays, which include the pride display (homologous with the bluff display in chimpanzees; [78]) relevant for dominance when accompanying hubristic pride [49], and the shame display (with elements in a variety of primate submission displays, such as crouching or a lowered body posture), which can signal pure subordination, especially in non-western, educated, industrialized, rich and democratic (WEIRD) societies [78-80].

(a) Evidence from infants and children

Studies of infant cognition indicate that the cognitive machinery for mentally representing dominance is used to formulate expectations about the social world in pre-verbal infants as young as 6-10 months of age. Such infants use information about coercive capacity-inferred from attributes such as physical size, strength and formidability-in heuristics to predict patterns of deference and resource acquisition [81-85] (see [86] for a review). Before the end of their first year, infants appear to understand key properties of dominance relations such as transitivity (if A dominates B, and B dominates C, then A also dominates C) and temporal or cross-context stability (if A dominates B today in one domain, A will also dominate B tomorrow in another domain) [81,82,87]. Given how early and reliably these abilities emerge, the cognitive mechanisms for inferring and responding to dominance probably have a shared genetic basis with other primates, who demonstrate many of the same cognitive abilities [10,88].

Children aged 2 to 6 years begin to deploy these cognitive capacities to navigate a social world organized by status hierarchies by using dominance tactics [26]. Dozens of studies show that linear dominance hierarchies reliably develop in peer groups in children as young as two years [13–17]. High rates of agonism in this age group and the frequency of unsupervised play situations with peers or siblings are probably jointly responsible for the strong dominance phenomena observed. Indeed, rates of angry outbursts and physical aggression—kicking, throwing, biting and breaking objects—peak at ages of 2 to 3 years across genders and cultures (with a small male bias; [89,90]). Preschoolers who routinely initiate aggression are reliably recognized by classmates as high status [15].

Nevertheless, the prominence of dominance-related social rank begins to decline from middle childhood onwards, while prestige becomes increasingly important. Cultural norms probably play a key role in this developmental transition. Children in middle childhood readily acquire the social norms of their communities and move towards the behaviours and normative standards of local adults [91-95]. Because children and adults alike are motivated to avoid punishment for norm violations, to the extent that children are part of the local culture, middle childhood marks a critical period of strengthened behavioural adherence to norms that promote egalitarianism and prosociality and suppress the use of coercion. In addition, norm adherence is facilitated by a maturing brain that improves executive functioning, impulse control and emotional regulation [96], and increases risk-aversion [97,98]. Consistent with this, studies reveal a cross-culturally typical trajectory of progressive decline in physical aggression beginning at ages 4 to 5 years and lasting through middle childhood [89,90,99], alongside a concomitant rise in concerns with egalitarianism, fairness and prosociality [91,94,100,101].

Despite this, dominance does not cease to exist in older children and adults and continues to shape status asymmetries along with prestige. In a classic study on German 8 to 11-year olds, Hawley [102] observed children in dyadic play situations. Some children attained influence (here, influential children are those who were observed to spend more time actively playing with an attractive and novel toy that was highly coveted while the other child watched) by deploying prestige through helping, demonstrating useful goal-directed behaviour, or offering advice (social tactics she termed 'prosocial'). Other equally influential children deployed dominance by using physical aggression (e.g. pushing or slapping the partner), by grabbing the toy, or by hurling insults (tactics she termed 'coercive'). Similar evidence comes from studies that apply ethological methods developed for primates to adolescents [11,12]. Savin-Williams [12], for example, found that dominant boys who frequently issued commands, used ridicule, or threatened others with physical aggression tended to prevail in disputes and be regarded as leaders by peers and observers alike.

However, the forms in which dominance is expressed may vary across sex and age. Sex differences in the expression of dominance emerge early in life and persist across age and societies. Whereas males display greater physical and verbal aggression, indirect aggression is more frequently used by females than males [103,104]. Gender norms may combine with any evolved sex differences in traits such as relative

tolerance of physical risk [103,105] to increase the use of physical aggression in men and indirect aggression in women. With respect to age, whereas younger children coerce through physical aggression, older children increasingly deploy non-physical, more normatively acceptable forms of dominance, through verbal or indirect aggression (e.g. use of ridicule, rumor or gossip, or social exclusion; [12,106,107]). Furthermore, older children may learn to deploy a mix of dominance and prestige tactics to maximally influence others' attitudes and behaviours, using simultaneously their threat potential and coercive capacity in conjunction with any valued abilities, knowledge or recognition that they possess. In her work on status hierarchies in late childhood and adolescence, Hawley [108-112] describes individuals who skillfully influence the behaviour of others via both persuasion and force, which she terms 'bistrategic'. She notes: 'bistrategic controllers across all age groups have shown themselves to be the most successful at resource control. Part of their success is due to the fact that they are high in aggression yet mitigate the costs of aggression by employing prosociality' [112, p. 435].

Nevertheless, children continue to refine their ability to assess and distinguish prestige and dominance with learning and developmental age, facilitated by an improved cognitive understanding of the benefits and costs associated with deference. One study of British and Chinese children [113] showed that 5-year-olds demonstrate some ability to distinguish between dominance and prestige—mentally associating prestige with being liked and dominance with being feared—but also that they occasionally conflate the two strategies. By contrast, these mistakes are virtually absent among 10-year-olds, who consistently distinguish the two kinds of status.

(b) Evidence from adults

In adults, dominance reliably affects collective decisionmaking and is associated with higher perceived and empirically measured influence in naturalistic groups in both large- and small-scale societies [50,51,64,114-117]. Much of this literature focuses on cross-sectional correlations, or the impact of dominant behaviours in more ephemeral interactions; such studies are nevertheless important as they demonstrate the efficacy of the interactional mechanisms underlying dominance to produce social influence over the very short term and in novel social groups and contexts. Longitudinal studies further demonstrate the cumulative impact of such mechanisms: McClanahan et al. [64] followed over 350 MBA students who were assigned to five to six member teams to collaborate intensively over one month. Dominance, as evaluated by team members at the time of group formation, predicts exercising greater influence a month later, again as evaluated by team members at project completion. Moreover, the influence of dominant individuals rose over the period examined, as evidenced by the positive effect of initial dominance on subsequent influence after accounting for initial influence, which documents change in influence across time. In a very long-term field study, Anderson et al. [118] found that dominant-aggressive behaviours predict greater other-rated power and the attainment of organizational rank in corporate settings in a large dataset of over 14 years.

Among small-scale societies, proxies for dominance such as physical formidability and size predict multiple dimensions of social status for males, such as getting one's way in a dispute (a context directly relevant to contest-based theories of dominance) among the Tsimane [119,120]. These proxies also predict quantity of social support and the likelihood of winning fights [119]. Tellingly, dominance does not increase the dimension of respect in that study, suggesting that the independent effect of physical formidability on the multiple dimensions of social status was generated entirely by mechanisms that do not increase the respect accorded to the physically powerful (i.e. that cost-infliction abilities have a direct impact on status independent of the prestige that they can bring). Dominance also increases the likelihood of leadership among the Chabu (an Ethiopian population of former hunter-gatherers), especially among men [55]. In a cross-cultural study using an ethnographic dataset, dominance as evaluated by terms indicating coercive authority contributes to leadership in 59% of the traditional societies surveyed [55]. The longitudinal impacts of dominance (as opposed to its cross-sectional correlations) in non-WEIRD societies is relatively understudied and a promising research topic. Owing to the lower levels of relational mobility in small-scale societies, which reduces the leverage subordinates can exert over dominants (since they cannot leave groups readily and have few outside options), one can expect dominance to have an even larger impact on social influence and rank in small-scale, non-WEIRD than in WEIRD societies, where relational mobility may diminish the long-term efficacy of dominant behaviours as a path to high status in some contexts [117]. Future studies may also better target the issue that proxies for cost-infliction abilities used in field studies in non-WEIRD contexts may generate status via other pathways (such as physical formidability increasing hunting ability), for example by analysing its impacts on multiple dimensions of social status like in [119].

As reviewed previously, high-status individuals have greater reproductive success than lower status males in diverse species of primates. Paralleling this, dominance contributes to male fitness in small-scale human societies. To illustrate this, we estimate the effect of dominance and prestige status on men's reproductive success through reanalysis of von Rueden & Jaeggi's [121] meta-analytic study of fertility in 46 studies across 33 non-industrial societies. While the confidence intervals are wide, highlighting the need for more studies or studies with larger sample sizes, dominance-as proxied by physical formidability in existing studies-as well as prestige, proxied here by hunting ability, contributes significantly to increased fitness as measured by the number of surviving children (Zr = 0.18)and 0.30, respectively²; electronic supplementary material, figure S1). However, because only a small handful of studies had measured proxies of both dominance and prestige, we estimate separately in these models the effect of each form of status on fitness (i.e. not controlling for each other). Physical formidability is an imperfect and crude measure of dominance, but may be the best proxy available from the literature for cost-infliction abilities, in terms of its representation across studies and the directness of its relationship to cost-infliction in the context of small-scale societies. Hunting ability, on the other hand, is everywhere strongly associated with prestige in the ethnographic record ([26, §5.a.a] and references therein, [116, §3] and references therein). Our

analysis here highlights the pressing need for field studies in small-scale societies that use measures more precisely targeting dominance and prestige simultaneously and their impacts on status and fitness outcomes (like in [55]).

Similar evidence comes from other work that captures nonphysical elements of dominance. Consider how, for example, a quantitative study of ethnographic records from 59 nonindustrial population reveals that members of the community who are aggressive or exercise coercive authority (dominant) tend to have multiple mating partners (polygynous) and higher quality spouses [55]. Similarly, among the Chabu, men who are feared (dominant) have more current spouses and more marriages over the lifetime, although in these data a higher number of mating partners do not necessarily translate into more surviving children [55]. In contemporary WEIRD societies marked by low fertility norms, statusoften indexed by income and wealth in studies, thus conflating dominance and prestige [122]-has a zero or weak positive association with male reproductive success, but a more variable and often negative effect on female fitness [123-125].

The different psychologies evoked by the two forms of status should also make us expect that the pathways through which dominance and prestige increases fitness may differ. For example, evidence from the Tsimane shows that men with either forms of status have a higher number of surviving offspring for their age; however, dominant men-as indexed by their greater physical formidability-marry younger wives and (like prestigious men) have more extra-marital affairs, whereas prestigious men marry at an earlier age and their offspring experience lower childhood mortality [120]. Other evidence from WEIRD societies, indicates that while women prefer prestigious men over dominant men when evaluating romantic partners, particularly in long-term relationships, greater dominance is selectively preferred in the context of short-term relationships [126-129]. Traits supporting high dominance attainment may also support intrasexual competition, and many traits that serve as dominance signals, such as vocal pitch and physical formidability, are sexually selected in men in both small-scale [130,131] and large-scale societies [126-129,132]. The effects of status on female fitness, despite being consistently positive in most female mammals, is more variable in human societies and less well-studied [133].

An accumulating body of evidence strongly indicates that multiple verbal, nonverbal and physical cues reliably signal dominance or domineering intentions in human adults and are interpreted as such; by contrast, prestige is associated with a distinct set of ethological and physical cues. For example, in both small and large scale societies, experiments and field observations indicate that appearing physically formidable is associated with greater dominance status [119,120,134,135]. Similarly, among non-verbal behaviours, dominance is associated with physical expansiveness and a downward head tilt [136] while prestige is associated with signals of confidence (e.g. upward head tilt, erect torso and smile). The combination of physical traits and non-verbal cues may shape initial expectations of dominance in rapid, highly automatic processes that involves little conscious cognition (at first glance) and interactants may be able to extract so much non-verbal information before any verbal exchange that subsequent verbal interactions do not modify initial dominance ratings [137].

More subtly, dominance and prestige also produce different verbal behaviours in humans. Dominance is associated with aggressive attempts to take up conversational space, overt signalling of one's own importance, exaggeration of one's own contributions, attempts to manipulate and exploit [49,51] as well as lowered vocal pitch [114,132]. Lower unmodulated vocal pitch predicts higher assessed dominance through its influence on perceived threat potential in small and large-scale societies [127,138]. Dynamic lowering of pitch also predicts higher assessed dominance and is interpreted by others as signalling intent to pursue a dominance-based strategy to attain social rank [114,139]. Interestingly, men modulate their vocal pitch in response to their self-perceived physical dominance relative to a male competitor [127,140]-an example of social dynamics and assessment influencing levels of expressed dominance. By contrast, prestige is associated with self-deprecation, praise for others and an open conversational style that invites criticism, signals respect for others' opinions and respect for group consensus [49,51]. Prestige also heightens voice [114].

As human relationships come with extensive benefits, strategic behaviours or social tactics in such relationships can also correlate with dominance and prestige. Dominance is associated with both coercive and complaisant (gaining influence by pleasing others) social tactics, in line with its dependence on perceived cost-infliction abilities, but prestige is associated with the use of only complaisant tactics in a WEIRD sample [141]. The combination of complaisance and coercion suggests that benefit provisioning may facilitate dominance-pursuit if it increases the future effectiveness of benefit-withholding as a threat. That the calculus of costs and benefits may easily blur the line between a benefits-provisioning account for prestige on one hand, and dominance on the other, points to the fact that the informational goods theory more clearly distinguishes prestige from dominance by highlighting the non-rivalrous and non-zero sum nature of the exchange between the prestigious and their followers.

Dominance and prestige are also associated with distinct emotional and motivational states, at least in WEIRD societies. Dominance is associated with a facet of pride-hubristic pridecapturing narcissism, arrogance and egotism-which are states that may support the antisocial behaviours, manipulation and strategic lying associated with pursuing dominance rank [49]. By contrast, prestige is associated with authentic pride, stemming from genuine accomplishment, which may adaptively facilitate or signal motivation, humility and prosociality [142]. Anger may also help dominants credibly signal their commitment to inflict costs or withhold benefits, attracting subordinate attention and improving their bargaining position [143]. Anger independently promotes dominance-seeking behaviour [144], and often co-occurs with shame; the two emotions are strongly correlated [78], and they may jointly motivate people to counter threats to dominance status. Low dominance rank heightens sensitivity to social threats and increases social inhibition, but high dominance blunts such sensitivity, promotes approach behaviours and reduces inhibitionattentional and behavioural biases that may be adaptive to different levels of social privilege [145,146].

5. Discussion

The evidence reviewed above indicates that dominance continues to be a viable route to rank acquisition, impacting

both social influence and fitness in humans across a wide range of contexts, and plays a role in human status asymmetries from the youngest of ages. However, the human-specific complications presented in this review cannot be overlooked. First, we comment on some important methodological and theoretical issues with research programmes that attempt to measure dominance in our species. Second, we look into gender-specific effects of dominant strategies for rank acquisition. Also finally, because norms may place bounds on the effectiveness of coercion-based strategies to rank attainment or even modify their function, we lay out the evidence for three social dynamics that influence dominance attainment and their interaction with prestige, and use concepts previously developed to consider how socioecological and institutional factors affect when and how dominant individuals can attain influence.

(a) Theoretical and methodological challenges

Because dominance produces status or influence over others' actions that is achieved against anothers' preferences, survey measures that tap the colloquial understanding of 'social influence' or 'status' or that rely on the definition of status in social psychology (which involves gaining deference through changing another's preferences; [51]) may fail to capture the full impact of dominance. Indeed, a recent highprofile analysis of questionnaire responses [3] found across a range of large-scale societies, that people rated dominant traits (defined by 'cost-infliction inclinations and abilities') to have weak or no impact on social influence after controlling for prestigious traits (benefit-provisioning inclinations and abilities). However, in several follow-up studies, Cheng et al. [147] demonstrated that the descriptors of the dependent variable (social influence) in the study strongly activated prestige-related concepts, which would make 'prestige' appear more important in the results. Translations often magnified this problem by using synonyms for 'reputation' and sometimes 'prestige' itself in the target language for the dependent variable. Additionally, the analyses suffered from high collinearity between dominance and prestige, which rendered any firm conclusions inappropriate. However, reanalyses designed to address this issue revealed an important role for dominance, albeit less than for prestige-which is not unexpected given the translation process and the semantics of words used for the dependent variable. For the reasons we have described, prestige may often be more important than dominance in many contexts, but as we have reviewed, dominance continues to play an important role.

Studies of non-human primates use multiple measures of dominance, such as resource control after competitive bouts, or directionality of aggression and formal dominance signals. These measures usually correlate, but not always, leading to doubts about construct validity in some species [148]. Nevertheless, recent research in humans that treats dominance as a trait reflecting stable individual differences in ability and tendency to use force-based strategies for rank pursuit [49] generally finds very high inter-rater correlations of subject's dominance (approx. 78–0.88 in [49]; greater than 0.8 in [51]), and Cronbach's alpha (0.83 in [56]; 0.83–0.93 in [51]; 0.86 in [115]), indicating that naturalistic groups reach nearconsensus on a dominance construct that demonstrates excellent validity according to standard psychological criteria. Empirically, measured dominance and prestige tend to be uncorrelated (r = 0.03-0.12 in [49]; r = 0.01 in [51] r = -0.12-0.17 in [117]) or negatively correlated (e.g. [129]), which means that the high level of collinearity that people believe exists between prestige and dominance in [3] may not be empirically reflected in naturalistic groups in the laboratory or the field. An older tradition in the measurement of dominance inspired by primate ethology uses purely relational measures (such as the direction of unreciprocated agonistic behaviours) to measure dominance as an emergent phenomenon specific to a group, which is closer to the theoretical foundations of dominance as a concept. When used together with survey-assessed trait dominance, relational and trait dominance strongly correlate, regardless of whether the survey is filled by observers or by group participants [12]. Overall, the evidence points to the importance of avoiding self-report measures in favour of integrating both otherreport measures and ethological observations to produce secure measurements of the dominance construct.

(b) Gender-specific effects

Current research supports the view that dominance plays a role in status attainment for both men and women in same and mixed-gender contexts [51,64,115,117,118]. However, evidence exists for gender-specificity in the way dominance impacts social status. For example, in a study of status among same-sex face-to-face groups in Canada [51], women perceived as dominant were deemed less likeable by other women (r = -0.24, p = 0.025), whereas dominant men incurred little to no social penalty (r = 0.08, p = 0.43). Among the egalitarian Chabu in Ethiopia, dominance contributed less to leadership attainment among women than among men [55].

One potential explanation for this comes from social role theory [149]: women's lower status across societies results from social norms emphasizing that women ought to be communal-warm, nurturing, kind-while men should strive to be agentic-assertive, authoritative and independent [150-152]. A proclivity to sanction gender norm violations [153,154] may result in backlash against women who exercise dominance, who are often described by scholars as overly agentic relative to norm expectations [155-158]. Backlash occurs even when dominant women seek to lead groups with communal and other-serving (stereotypically feminine) goals [159], and among same-sex sanctioners [160]. Alternatively, because men and women may have tended to solve problems in different social domains over evolutionary history, dominance may be a more socially valued trait in men than in women for both cultural and biological reasons [161]-a hypothesis that may be tested with further crosscultural research.

(c) The social dynamics of prestige and dominance

While prestige and dominance coexist as pathways to status in humans, they need not operate independently. Many high-status individuals may derive influence from *both* prestige and dominance processes. This is especially important given the factors reviewed that limit the effectiveness of coercive tactics alone. Alongside the more straightforward process where subordinates are compelled into compliance exclusively via coercive threats, three mechanisms may produce an overlap between dominance and prestige status components. First, culturally evolved institutional hierarchies may grant formal leaders, managers and other authorities power through control over rewards and punishments, which creates the conditions for dominance via coercive threats; institutionally powerful individuals tend to resort to dominant social tactics especially when prestige is lost [162]. Because such positions may in some societies be attained (or be assumed to be attained) through skill, competence or knowledge, high-status authorities may demonstrate prestige ethology even as they keep aggressive or coercive tactics in their toolboxes for use in limited occasions. Such roles may exist even in egalitarian societies, for example among shamans, who tend to be simultaneously respected and feared [56,163].

Second, traits, attributes and motivations that generate coercive threat may themselves constitute valued abilities worthy of emulation or deference in some situations. Physically formidable men may be seen as more capable of generating benefits for in-group members through their perceived capacity to punish free-riders, to facilitate intergroup competition [134,164,165] or to compel broader coalitional support from others [1,52].

Third, displays of confidence, which are frequent among dominant individuals [166] can lead to an undeserved prestigious reputation relative to their true skill. This will depend on the quality of information on other's skill levels, meaning that this mechanism is more likely to operate in complex large-scale societies with high levels of specialization and where ephemeral interactions with strangers are important.

6. Conclusion

Convergent evidence from multiple disciplines and from studies across ages, sexes and cultures, show that agonistic and aggressive forms of rank-pursuit involving the deployment of cost-infliction or benefit-withholding strategies continues to be a viable route to social status in humans. Norm-governed coalitionary behaviours and human-specific ecological factors strongly temper and modify the expression of dominance in our species, but the fundamental strategic calculus rooted in game theory, where individuals who are more willing and able to inflict costs in protracted conflicts have resources ceded to them and gain influence, continues to hold, and is required to explain empirically measured social asymmetries and fitness differentials across societies and contexts. Furthermore, developmental and comparative studies demonstrate that the cognitive, emotional and

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motivational mechanisms that constitute a 'dominance psychology', as well as multiple aspects of human dominance ethology, appear to be cross-culturally stable, to demonstrate phylogenetic continuity with similar phenomena in great apes, and to emerge early in development. This strongly indicates that dominance has played and continues to play a role in structuring our social environments and shaping our psychology.

Some important open questions are how much dominance affects the fitness of women, and whether the dominance cues in women are identical to those that strongly affect assessed dominance in men. How institutional, socioecological and cultural factors affect the success of either dominance or prestige-based strategies for rank-pursuit, and how they may affect the specific mechanisms that confer dominance or prestige (or both) on certain individuals, remain a fruitful avenue for future research.

Data accessibility. The data analysed for electronic supplementary material figure S1 in this paper are from [121]. Link: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5047206/. The specific data file is freely available at this link: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5047206/bin/pnas.1606800113.sd01.xlsx. Code for the analysis of electronic supplementary material figure S1 is at this link: https://osf.io/87zxf/.

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Endnotes

¹The evolutionary stable strategy in any system is the *strategy* (pattern of choices in a *game*, where agents pick from a list of options; the payoffs are dependent on both self's and other's choices in the matrix of options) that has the following two properties: (i) it is a *Nash equilibrium*: when all players play according to the equilibrium strategy, no player can improve their outcomes by switching to an alternate strategy; and (ii) it is *evolutionarily stable*; when all players play according to the equilibrium strategy, no other strategies can be evolutionarily favoured, because natural selection keeps the equilibrium strategy in place.

²Fisher's Z-transformed effect size.

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