

(relatively high KLD), the sensory gain is subsequently increased – in the order of hundreds of milliseconds after the event in question is presented [4,5]. Corlett considers that our proposed temporal order places the upweighting of deviant events too late to be adaptive. We agree this would be a concern for delays in the order of trials – like proposed above in the learning literature between predictive and uncertain cues [3] – but less so delays in the order of milliseconds as we propose for perception. Such a delay may be necessary to allow us to achieve adaptive advantages associated with the use of expectations to generate both broadly veridical and informative percepts.

Corlett also suggests that a predictive cancellation mechanism that preemptively suppresses the predicted consequences of action is key for determining whether we were the cause of events in the world and that uncertainty-based inferences are not especially required during action. We challenge both of these points. While we agree that the ‘error’ between expected and actual action outcomes is a vital cue for computing agency, determining agency does not require action predictions to shape the percept in distinct (cancelling) ways. In fact, much recent work – including from our laboratory – suggests that they shape perception similarly to other types of prediction [1] (e.g., [6]). It is important to note that our claims relate solely to sensory prediction mechanisms during action and that sensory suppression generated when we move our eyes or limbs may reflect a nonspecific suppression of all sensory input to a moving body part (Box 1). (While suppression mechanisms may not therefore be predictive, a disruption in them could still lead to the relative upweighting of external sensory evidence when forming perceptual inferences [7].) We believe that the perceptual prediction paradox is still present when predictions are made

during action, as it is crucial for us to generate robust representations of our actions rapidly in the face of sensory noise (veridicality) and remain sensitive to unexpected outcomes that occur as we move (informativeness).

In conclusion, we believe that dialogue between different disciplines in perception and learning sheds complementary light on how animals like us deal with an uncertain environment. These debates reinvigorate older questions about how we continuously forge models of the world around us via our perceptual experiences and raise new questions about how we use these to guide perception of what is here right now.

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## Letter

### Why Social Status Is Essential (But Sometimes Insufficient) for Leadership

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One recurrent feature of social species is the differential degree of deference and advantage conferred on some individuals and denied to others. In recent decades, scholars have made substantial inroads into understanding the psychological foundations of these social asymmetries. Much of this work converges on the notion that social stratification in humans is the result of two distinct forms of status: prestige, or freely conferred deference resulting from the capacity to benefit others and inspire respect; and dominance, or coercive compliance resulting from the capacity to inflict costs and impose fear [1].

In an account consistent with existing work on social hierarchies [1,2], van Vugt and Smith [3] offer an in-depth examination of how prestige and dominance explain leader–follower asymmetries. One conclusion they draw is that ‘not all high-status individuals are therefore leaders, but equally, not all leaders are necessarily high-status individuals’ (p. 954). Although we agree that status and leadership are unlikely to be perfectly correlated, we believe that caution is warranted in consequently inferring a disconnect between status and leadership. In fact, we argue that wielding either dominance or prestige is a necessary, albeit sometimes insufficient, condition for effective leadership, because these two forms of status provide the foundation of a leader’s ability to influence others.

Two insights illustrate why status is crucial for leadership in our species. First, status –

both the prestige and the dominance variety – is a principal means by which leaders emerge. In small, ‘minimal’ laboratory task groups, leaders emerge informally through either respect for their expertise in task-specific knowledge (prestige-based status) or fear and compulsion from a willingness to intimidate and aggress (dominance-based status) [2]. These patterns are also observed in naturalistic groups and communities in the field [4,5], cross-culturally across small-scale societies [1,6], and when leadership becomes formalized, institutional, and collectively acknowledged [7].

Thus, status shapes who emerges as leaders and does not merely correspond with how leadership is exercised, as van Vugt and Smith suggest. Becoming a leader may reciprocally increase status, such as by amplifying one’s coercive threat potential via a newly acquired network of allies. More broadly, persuasion and force are best considered two core mechanisms that generate social asymmetries, including leader–follower asymmetries [1]. Accordingly, the source of climate change activist Greta Thunberg’s leadership is her prestige, resulting from her demonstrated efficacy in contributing to collective action; the deference and attention she receives demonstrate that she is not, as van Vugt and Smith suggest, low status.

Status appears to be important for leadership in many other animal societies as well. Among some primates, leadership is exclusively achieved by those at the very top of the dominance hierarchy, who possess superior fighting ability, size, and strength. However, there is also suggestive evidence for prestige-like processes that promote leadership in several other complex species that demonstrate primitive forms of culture [8]. In orca whales, for example, older females (grandmothers) act as repositories for ecological knowledge and, like prestigious individuals in human societies, transmit valuable know-how to their children

and grandchildren, and provide critical leadership over the pod when foraging for salmon [9]. Thus, although human societies may be unique in the regularity, importance, and scope at which prestige-based status contributes to leadership, the two forms of status may be crucial to leader emergence across many species. In their discussion of leadership in matriarchal animal societies (e.g., orcas, elephants), van Vugt and Smith appear to under-recognize the prestige status of these females and how their prestige is a key source of leadership.

Second, leadership style often changes facultatively within an individual depending on current status and context. For example, business managers are often disinclined towards dominance but, after suffering a loss of prestige, spontaneously resort to force, and seek to regain influence by initiating conflict and waging threats and insults [10]. This finding highlights the necessity of deploying some degree of one form of status or the other to effectively lead and retain the differential influence on which a leader’s privileged position rests.

Although we view high status as essential for seeking and exercising leadership, at times high-status individuals may nonetheless fail to acquire leadership, or effectively lead. van Vugt and Smith’s analysis of this puzzle rightly focuses on the under-representation of prestigious women in leadership positions, but overlooks other relevant interindividual differences and cultural factors. For example, leadership acquisition depends in part on motivation and political will and ambition [11], expressed in a willingness to out-compete other high-status individuals with leadership aspirations. In some traditional societies, ‘Big Men’ with substantial prestige compete with other prestigious Big Men for leadership through generosity (e.g., throwing feasts, giving away wealth), contributing to collective action, and building alliances, which further augment their influence to attract more followers [12].

Another factor that can moderate the impact of status on leadership is culture, particularly cultural norms that exalt social and political equality, which can suppress the emergence of dominant leaders. Among the most egalitarian hunter-gatherers, coercive dominance is uncommon, owing to an exceptionally strong cultural emphasis on individual autonomy, a sharing ethos, and leveling efforts to limit the power of would-be aggrandizers [13]. Similarly, modern workplaces with effective antibullying sanctions may curtail the ascension of dominant employees. Finally, institutions and organizations may express variable, idiosyncratic criteria for advancement to leadership (e.g., in mobs and street gangs, a fearsome reputation may be a particularly effective means to rise through the ranks). Across these contexts, both dominance and prestige may each become more weakly associated with leadership.

Taken together, these considerations suggest that individuals lacking prestige to attract followers or coercive dominance to compel compliance are unlikely to ascend to leadership, and leaders without either source of influence will tend to fail. Possessing one or the other form of status is therefore likely to be a necessary but insufficient condition for leadership. Further work is needed to examine the constellation of factors and mechanisms that multiply determine success in competition for leadership, including why high-status individuals at times fail to be promoted to top leadership.

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## Letter

# Leadership and Status in Mammalian Societies: Context Matters

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It is widely recognized that within mammalian societies an individual may be simultaneously a leader of collective behavior and hold a position of high status. Drawing from a comparative perspective, we recently suggested that some leaders are of low status or emerge in egalitarian societies lacking dominance hierarchies [1]. Furthermore, we noted that some high-ranking individuals, despite their priority access to

resources and ability to evoke submissive behaviors or win dyadic competitions, have little or no influence on collective group behavior [1].

Importantly, our recent article identifies some conceptual and empirical challenges regarding status and leadership when viewed through a comparative lens. Biological and social science literatures sometimes apply different definitions, which hinders progress. Dual models of human status [2] are based on three components: (i) priority access to limited resources, (ii) ability to win dyadic contests over resources, and (iii) relative influence on group decisions. However, only this third component describes activities that are associated across species with leadership [3]. In other words, as applied across species, leadership implies only that an individual has a disproportional influence on collective behaviors (e.g., group foraging, movements, conflict resolution, and between-group conflicts). Thus, whereas leadership refers to influence in a decision-making hierarchy, dominance status refers to a position within a resource hierarchy. Moreover, dominance status is relational within a pair of individuals and, in many cases, these pairwise relations are not necessarily transitive across group members (e.g., nonlinear or nontransitive resource hierarchies) [4]. By contrast, leadership status refers simply to whether an individual currently occupies a position in which they impose disproportional influence on group decisions. Our dual model approach to leadership therefore focuses solely on an individual's influence on collective behavior and emphasizes the value of this distinction in contributing to our understanding of the general principles and evolutionary origins of leadership.

Although Cheng and Tracy [5] agree with us that not all high-status individuals are leaders, they question whether low-status individuals can be leaders and the extent

to which it is possible to disentangle notions of status and leadership. The comparative perspective offers insights into the empirical need to separate leadership and status. For example, hungry fish [6] or thirsty zebra [7] lead collective movements until their physiological needs are met, but this has no impact on their standing within their group. Moreover, mammals living in egalitarian societies also have leadership in collective behaviors despite a lack of status differences among group members [3]. Thus, leadership and status should be assessed independently – even if some individuals are both leaders and of high status at the same time. Recognition of this will push the field forward, permitting: (i) comparative studies to quantify each attribute's effect on collective behavior and (ii) research on humans to explore when leadership (e.g., influencing collective behavior) is displayed by low-status group members (e.g., children), members of low-status groups (e.g., lower socioeconomic classes, minority groups), or members of strictly egalitarian groups.

Leadership styles and, by extension, who is most likely to occupy a leadership role within a society, are often context dependent and variable over time. Our article highlights the ubiquity of this phenomenon in mammalian societies, noting that these context-dependent patterns across mammals (including humans) offer an understanding of the flexible nature of leadership. We point to this fluidity by explaining that the traits of individuals occupying leadership roles in mammalian societies often vary within species across four major contexts: collective movements, group foraging, within-group conflict resolution, and between-group conflicts [1,3]. Spotted hyenas offer a salient example of how the traits of individuals that emerge as leaders vary across context and time – even within a single species in which dominance status strongly influences many aspects of its social lives (Box 1).