

## Review

## Leadership in Mammalian Societies: Emergence, Distribution, Power, and Payoff

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Leadership is an active area of research in both the biological and social sciences. This review provides a transdisciplinary synthesis of biological and social-science views of leadership from an evolutionary perspective, and examines patterns of leadership in a set of small-scale human and non-human mammalian societies. We review empirical and theoretical work on leadership in four domains: movement, food acquisition, within-group conflict mediation, and between-group interactions. We categorize patterns of variation in leadership in five dimensions: distribution (across individuals), emergence (achieved versus inherited), power, relative payoff to leadership, and generality (across domains). We find that human leadership exhibits commonalities with and differences from the broader mammalian pattern, raising interesting theoretical and empirical issues.

### Evolution of Leadership Across Mammalian Societies

**Leadership** (see [Glossary](#)) is a pervasive phenomenon in social species, organizing behaviors ranging from group movement to complex patterns of cooperation and conflict. Despite being an active topic in biological and social sciences, little in the way of theoretical and empirical synthesis exists. Theory and data indicate that leadership is relevant in a variety of contexts of current biological interest, including reproductive skew, the evolution of cooperation, intergroup conflict, and evolved personality differences [1–4]. Biologists have produced a substantial theoretical and empirical literature on hierarchy and decision-making in non-human societies, but focus primarily on leadership during movement [5–9]. By contrast, social scientists have written extensively about leadership in a wide variety of contexts [10,11], but often lack evolutionary perspectives and formal models (but see [12–15]).

This review offers a transdisciplinary synthesis of biological and social-science models of leadership from an evolutionary perspective, and analyzes leadership patterns across a sample of mammalian species. We review evolutionary models of leadership in four domains: group movement, food acquisition, conflict mediation, and between-group interaction ([Box 1](#)). We draw on theoretical work to analyze how leadership varies across these domains for a sample of human and non-human groups. With evolutionary questions in mind, we classify this variation into five dimensions that can be identified across species: **distribution** across individuals (skew), leadership emergence, differential **power**, relative payoff (to leaders versus followers),

### Trends

Leadership is an active research area in both biological and social sciences, but there has been limited synthesis within or across these areas; evolutionary theory can assist with such synthesis, but additional elements are needed for a robust comparative framework.

Variation in leadership can be measured in multiple dimensions, including emergence (how does one become a leader?), distribution (how widely shared is leadership?), power (how much power do leaders wield over followers?), relative benefit (do leaders gain more or less than followers?), and generality (how likely are leaders in one domain, such as movement or conflict resolution, to lead in other domains?).

A comparative framework based on these dimensions can reveal commonalities and differences among leaders in mammalian societies, including human societies.

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### Box 1. Leadership Domains and Dimensions

Leadership and alternative forms of decision-making (e.g., via quorum-sensing) can occur in one or more domains or contexts within social groups. As noted in the main text, collective movement is the domain most commonly treated in the biological literature (both theoretical and empirical), but social scientists as well as some biologists are concerned with leadership phenomena in other domains that have significant fitness implications. For our comparative analysis of mammalian (including human) leadership, we chose to focus on four domains: (i) collective movement, (ii) food acquisition, (iii) within-group conflict resolution, and (iv) between-group interactions (whether peaceful or hostile). The text discusses examples of leadership in each of these domains for a variety of social groups, as well as related theoretical models concerning leadership evolution.

Leadership dimensions involve a more abstract categorization. This can be approached in the form of a set of questions. For any given domain, are there leaders? In a purely egalitarian or democratic decision regime, involving either consensus decision-making or absence of collective behavior, the answer will be 'no'. We recognize that this 'pure' form of consensus may be rare given the pervasiveness of often subtle forms of leadership and influence. If the answer is 'yes' for any given domain, the following questions can be used to characterize different dimensions along which leadership varies:

- (i) *How distributed is leadership?* In other words, what proportion of group membership typically makes a decision in a given domain?
- (ii) *Emergence.* Is leadership achieved (by leader's actions or qualities) or ascribed (by inheritance or some other process not dependent on the individual's actions or qualities)?
- (iii) *How powerful is the leader?* Our definition of power (see [Glossary](#)) does not necessarily entail coercion.
- (iv) *Relative benefit.* Do leaders reap fitness-correlated benefits from their actions equal to, greater than, or less than, that averaged by other group members?
- (v) *Generality.* To what extent does leadership in one domain predict leadership in other domains?

As discussed further in the text, evolutionary theory as well as empirical evidence suggests that these dimensions are not independent of each other; for example, greater power should be (and often is) associated with higher relative payoff to leadership.

and generality across domains (Box 1). We advance the study of leadership by synthesizing its theoretical predictions regarding emergence and maintenance, and establish measurable criteria for comparative study to stimulate empirical and theoretical progress. The hypothesis that humans have evolved unique leadership attributes not found among other mammals (e.g., [3, 15]) remains largely untested because we currently lack suitable comparative frameworks for examining leadership across mammalian societies. One aim of this review is to apply such a framework in a preliminary examination of this hypothesis.

### Definitions

The study of collective decision-making suffers from lack of agreement on terminology [16]. Biologists often define leadership as differential influence on group activity, however generated. The usual domain of interest is movement [7], with some additional focus on the duration of activities [6]. By contrast, few social science uses of this term highlight being the first to initiate movement or change activity because this might reflect impatience or need rather than differential influence [17]. Instead, they commonly point to differences in social power, meaning the ability of an individual to induce others to act or believe in a particular way [18]. We define leadership here as non-random differential influence on collective behavior. This differential influence might vary based on visibility, knowledge, or other factors affecting voluntary decisions to follow or emulate. Alternatively, it might depend on **coercion** to control the behavior of subordinates, for which the term '**dominance**' is often employed. This variation in causal mechanisms is one issue we address below.

### Models of Leadership

Members of social species regularly make decisions to coordinate activities with group-mates, including where and when to forage, rest, or move. Formal evolutionary models help reveal the evolutionary causes and consequences of these decisions. Theory predicts that, if accurate information is to be maximized and the cost of differences in individual preferences is to be

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minimized, fully **shared decision-making** should emerge (i.e., no consistent leaders) [19,20]. This raises the puzzle of why leaders often do emerge. However, if time is a crucial factor, consensus decisions can be inefficient, thereby increasing costs for group members. For example, in the presence of significant within-group heterogeneity (defined as variation in preferences, personality traits, and reputation), group decisions by a single leader can be most efficient [21]. Moreover, recent models suggest that leadership can also emerge under the influence of differential information, differential relatedness to group-mates, differential power or resource control, personality variation, imitation, punishment, and **volunteerism**, with varying effects on fitness.

Our ultimate goal is to derive general principles from models of leadership. Whereas the scope of inference from any single mathematical model is limited, comparison of multiple models allows for true insights about biological principles. Although some models span multiple domains, each model depends upon its specific assumptions, which are often domain-specific. Therefore we first organize our review of models according to the four domains noted above before concluding with the overarching conceptual insights to be gained from existing theoretical models.

### Movement

Couzin *et al.* [7] studied group movement when only a few members have information on the location of a resource. If members lack a preferred travel direction, and all individuals attempt to avoid collision while simultaneously maintaining group cohesion, a small proportion (e.g., 5%) of informed individuals can efficiently lead others towards the resource. In a related model [22], individuals can invest in obtaining personal or social information about the resource location. With fitness tradeoffs, the population evolves to be dimorphic, with a small proportion of individuals (leaders) actively acquiring information from the environment but ignoring social information from their group-mates, and the remainder simply follow the leaders. These dynamics are similar to those in other producer–scrounger models [23,24]. Stable differences in propensities to lead dispersal attempts arise when dispersal decreases competition between kin; the net fitness benefits of leadership depend upon the costs of dispersal as well as on the degrees of relatedness and reproductive skew within dispersal groups [25].

Johnstone and Manica [4] modeled an  $N$ -player coordination game with conflicts of interest, and analyzed the emergence and maintenance of two personality types: (stubborn) leaders and (agreeable) followers (see **followership**). Leaders are maintained by frequency-dependent selection. They benefit from imposing their preferences on followers, but fail to coordinate effectively when interacting with other leaders. The fraction of leaders in the population increases with the degree of conflict among group members, with both types being common only at intermediate levels of conflict.

### Resource Acquisition

There are several ways leaders improve the efficiency of resource acquisition, thereby increasing the fitness of group members.

### Leaders as Role Models

In mathematical models of social interactions with a possibility of imitation, leaders (i.e., individuals whose strategies are imitated by the rest of the group) emerge naturally. For example, in a version of the minority game [26,27], individuals chose between two different resources of equal total value, but being in the minority provides an advantage (e.g., because the resource is shared among a smaller number of group-mates). Individuals remember group choices over several rounds and base their decisions on past experiences (individual learning) or choices of others (social learning). Rapid emergence of influence-networks can occur when followers copy

## Glossary

### General Terms

**Coercion:** control of the behavior of others through threats or attacks.

**Collective action problem:** any situation in which multiple individuals would all benefit from a particular action, but difficulties of coordination or of ensuring fair contribution to the costs of the action create obstacles; also known as a 'social dilemma'.

**Coordination problem:** situations in which individual success requires collective action to achieve a goal. These range from contexts of pure coordination, where individuals have the same preference or fitness ranking across outcomes, to cases where individuals have different rankings but still achieve higher payoffs by coordinating on one choice.

**Dominance:** ability to win dyadic agonistic interactions (e.g., contests or unsolicited appeasements), with outcomes determining priority of access to resources or mating.

**Egalitarian group:** a society in which the individuals of the same age-sex category have equal access to and control over resources and/or other individuals within the group (in contrast to a stratified/despotic society).

**Leadership:** non-random differential effect on group behavior of conspecifics through actions evolved or intended to elicit this effect (a glossary of leadership types is given below)

**Power:** the ability of leaders to motivate followers to behave in ways they would otherwise not do, often but not necessarily through coercion.

**Prestige:** influence or deference that is freely granted (i.e., not generated by the use of threat or force, in contrast to dominance).

**Shared decision-making:** multiple group members decide on an outcome (via consensus or quorum-sensing), in contrast to unshared decision-making.

**Small-scale society:** a human society consisting of one or a few local communities (several hundred to a few thousand members in total); these tend to be egalitarian, but with some notable exceptions.

**Stratified society:** one in which segments have differential access to and/or control over resources; also known as a despotic society, or a society structured by a dominance hierarchy.

the choices of a small number of individuals with the best strategies (leaders) [27,28]. In a version of the Prisoner Dilemma game with dynamical adjustment of social ties and social learning, adaptation dynamics favor the emergence of highly connected cooperators with high payoffs [29]. These 'leaders' sustain the global cooperative state because their social partners imitate their cooperative strategies. A model of coordination on networks showed that group-mates often emulate individuals (leaders) with privileged information [30]. In a model of how leadership influences group success, players in a multi-player weak-link game become leaders after publicly choosing to contribute before all other players [31,32]; thus, leadership can increase efficiency but not always guarantee success.

### Leaders as Punishers

Punishment has attracted substantial attention as a way to stabilize the production of public goods [33,34]. However, if punishment is costly, it raises a second-order social dilemma because mild cooperators who shirk the costs of punishment will restore the original dilemma to the detriment of all [35]. One solution is to compensate specialized actors (leaders) to administer punishment [36]. Building on patron–client and managerial mutualism models [37], Hooper *et al.* [13] showed that a combination of leaders and followers will outcompete **acephalous** strategies if followers are taxed to pay leaders to efficiently enforce collective action in circumstances where blindly cooperative strategies, peer punishment, or other alternative mechanisms are incapable of efficiently ensuring cooperation. The amount extracted by leaders in the model depends on the cost of the leaders' efforts, and the efficiency of the process of selecting leaders. This model was extended to the specific public good of success in contests over territory [38] as well as applied to agent-based simulations of pre-Hispanic Pueblo societies [39,40].

### Leaders as Managers

A related model assumed that the presence of a leader increases a group's productivity in collective action [41]. Leaders gain more of the reward than the remainder of the group, but they are tolerated because of increased absolute productivity. Leaders are constrained by the fitness followers would gain from leaving the group; as a result, where leadership is efficient and costs of dispersal are high, leaders are able to claim unequal shares of production. This class of models [13,41] is analogous to those of reproductive skew [42–44].

### Leaders as Volunteers

In many public goods games in which the total group benefit is a nonlinear increasing function of the number of contributors, cooperation can sometimes be maintained without genetic relatedness or other forms of assortment [45]. For example, in an  $N$ -person volunteer's dilemma [46], a public good is produced if there are at least  $k$  volunteers (who can be viewed as group leaders); frequency-dependent selection favors a stable mix of volunteers (leaders) and free-riders (followers) [47]. If the benefit of a collective action declines in time [48], altruistic leaders can emerge in groups of non-relatives, and larger group sizes and higher costs of volunteering delay but do not prevent their emergence. In contrast to producer–scrounger models where the producers and scroungers have equal fitness at equilibrium, volunteers (that is, producers) have lower fitness than free-riding group-mates.

### Within-Group Conflict

There is a substantial body of theoretical work on within-group conflicts in which dominant individuals ('leaders') participate in or are targets of coalitionary attacks [49,50]. Coalitions can strongly affect the power of both dominant and subordinate individuals. Within-group competition and conflict can reduce the absolute amount of resources available to the group. In this case, individuals can benefit from investing in a trait ('policing') that simultaneously reduces the relative amount of resource subject to within-group competition and the costs of this competition [51]. If group members vary in relative cost of policing, stronger individuals ('leaders')

**Unshared decision-making:** one or a very few group members make decisions for the group.

#### Types of Leadership

**Acephalous group:** leaderless group; in the human case, one without institutionalized leadership.

**Achieved status:** determined by an individual's abilities, performance or effort (in contrast to ascribed status).

**Ascribed:** assigned at birth or assumed involuntarily later in life (e.g., through maternal rank inheritance based on maternal interventions or bequeathal of resources down a lineage).

**Attribute-based leadership:** determined by the specific traits possessed by a leader (rank, age, tenure, sex, physiological state) when that individual assumes role of leader or follower.

**Delegated leadership:** when a leader has tacit or explicit group consent to act without seeking consensus on each decisions (thus intermediate between pure consensus-based decisions and despotism).

**Despotic leadership:** consistent leadership by a powerful individual or small set of individuals; also termed 'unshared' or 'personal' leadership.

**Distributed leadership:** different individuals lead group action on different occasions, for a given domain, due to fluctuations in motivation, knowledge, or a turn-taking convention; also known as shared leadership.

**Domain-specific leadership:** when an individual's leadership is limited to a specific domain (contrasting with domain-general leadership, as in generalized dominance).

**Followership:** leadership presumed on the basis of others following (e.g., one individual initiates movement and others follow).

**Institutionalized leadership:** consists of durable positions (regardless of length of tenure of individuals occupying those positions), in contrast to situational leadership.

**Situational leadership:** leadership that arises opportunistically and occurs only in specific situations of short duration; contrasting with institutionalized leadership.

**Volunteerism:** the act of freely proffering services to a group (e.g., agreeing to assume a costly leadership role).

are favored to take on most or all of the policing [52]. For example, game theoretic models used to analyze field data on East African pastoralists showed that wealthy households can afford to enforce conservation of grazing areas, incurring the costs of policing other households from overgrazing [53].

### Between-Group Interactions

Because both conflict and peaceful interactions between groups can produce public goods (e.g., territorial gains), the models reviewed above concerning leaders in collective action can apply in this context. Leaders can also be modeled as volunteers in between-group conflicts. One model [2] predicts that high-ranking individuals (leaders) who usurp a disproportionate share of resources from group-mates will act seemingly altruistically in between-group conflict, expending more effort and often having lower reproductive success than low-ranking group-mates. Similar behavior is expected for individuals with the greatest motivation, strength, or endowments as well as for those paying the lowest costs. Analysis of conflict between **egalitarian groups** showed that, if the collaborative abilities of individuals are relatively low, then the population becomes dimorphic, with a small proportion of 'leaders' contributing to public goods and the rest free-riding [21].

### General Principles

Several general lessons emerge from our theoretical synthesis. First, leaders and followers can emerge naturally as a result of heterogeneity in preferences, motivation, personality, physical characteristics, information available, and other features affecting individual performance in fitness-related activities. Under some conditions, this heterogeneity is predicted to be favored by natural selection. Several models predict relatively low frequencies of leaders, but the results depend on modeling details. Some models also predict that leaders' preferences and choices will strongly control those of followers, but theoretical work on this is very limited. To the extent that differentiation of group members into leaders and followers, and subsequent division of labor between them, is driven by natural selection, leadership tends to be beneficial to both social groups and individual members of these groups. Although sometimes followers can have lower fitness than leaders, this is most likely when the alternatives to accepting the follower's position (e.g., leaving the group or challenging the leader) are more costly. In some situations, group differentiation into leaders and followers is predicted to be maintained by negative frequency-dependent selection, such that both types will have equal fitness at equilibrium. Under other conditions, leaders behave as volunteers and can have lower payoffs than their largely free-riding followers. In sum, there are many ways in which leadership can evolve, some less intuitive than others.

### Empirical Patterns in Leadership

To focus the empirical portion of our review, we compared leadership patterns across mammalian societies by examining leadership in a sample of non-human and human societies (Table 1). We restrict our sample of non-human mammals (NHM) to species for which sufficient data on social interactions of free-living individuals are available. For comparability, we included only **small-scale societies** (SSS) of humans lacking complex political institutions (e.g., more than two formal administrative levels) [11,54]. Our rationale for comparing human and non-human leadership is to help to determine the extent to which a unified evolutionary analysis of mammalian leadership can reveal and explain similarities as well as differences. Although some may assume that leadership among humans is intrinsically unique, we have no *a priori* position on this question, nor on whether we expect greater variation in leadership within or across these groupings (NHM and SSS).

The domains and dimensions delineated in Box 1 provide a useful framework for describing and comparing leadership patterns across societies. We coded each dimension for each domain in our 16 societies according to a five-point rating system (Table S1 in the supplemental information

Table 1. Sixteen Societies Included in the Comparative Analysis<sup>a</sup>

Society	Units for Collective Action (Typical Number of Individuals)
<b>Non-humans</b>	
African elephant ( <i>Loxodonta africana</i> )	Multi-family bond group (25–50), matrilineal family groups (10–20)
Bottlenose dolphin ( <i>Tursiops</i> sp.)	Pod (10–30), alliances (5–14), other subgroups
Chimpanzee ( <i>Pan troglodytes</i> )	Community (46), other subgroups
Lion ( <i>Panthera leo</i> )	Pride (4–18), other subgroups
Meerkat ( <i>Suricata suricatta</i> )	Extended family group ('clans') (20)
Plains zebra ( <i>Equus quagga</i> )	Herd (40), harems (4 adults + offspring)
Spotted hyena ( <i>Crocuta crocuta</i> )	Clans (45–90), other subgroups
White-faced capuchin ( <i>Cebus capucinus</i> )	Multi-male group (5–39)
<b>Humans</b>	
Ache (Paraguay forest)	Residential band (35)
Cheyenne (North American plains)	Tribe (4000), other subgroups
Inuit (Canadian arctic)	Residential band (60)
Kipsigis (Kenyan savannah)	Community (200–300)
Nootka (Canadian Pacific coast)	Winter village (200)
Pimbwe (Tanzanian woodlands)	Tribe (25 000), village (dozens to hundreds)
Shoshone (North American Great Basin)	Camp (10–50), larger temporary aggregations
Tsimane (Bolivian Amazon)	Village (dozens to hundreds)

<sup>a</sup>See the supplemental information online for references and details of the societies sampled.

online), drawing on observational data collected by us or in the published literature (supplemented by consultation with the original field researchers when needed). Each rating is akin to an item on a Likert scale, a measurement tool utilized extensively by psychologists and marketing researchers.

This method is clearly preferable to purely qualitative comparisons, but has significant limitations. One could raise epistemological concerns: do different raters have different implicit norms of reference, for example about what might constitute 'weak' versus 'strong' levels of power? We attempted to minimize this problem by explicit definitions of the possible ratings for each dimension (Table 2), scoring each of the examples in dialogue within our group, and consulting with experts in the field for those groups not studied directly by one of us. We view the empirical portion of this review as a foundational contribution towards a unified approach to studying leadership. Methodologically, it is a survey of current expert opinion on a sample of societies, with the aim of stimulating further research.

Because leadership dimensions (other than generality) can vary independently across domains even in the same society, and leadership can be absent in some domains for a given society, we present the results by domain. For each dimension other than generality, we analyzed ratings to determine whether these varied significantly by leadership domain or society type (i.e., SSS versus NHM) (Table S2).

### Leadership Distribution

The distribution of decision-making within a group (i.e., the proportion of group membership that makes decisions) is of particular interest to biological and social scientists. In the models reviewed above, this can range from individual autonomy through consensus decision-making to despotic control.

Table 2. Rating Codes for Leadership on Mammalian Societies<sup>a</sup>

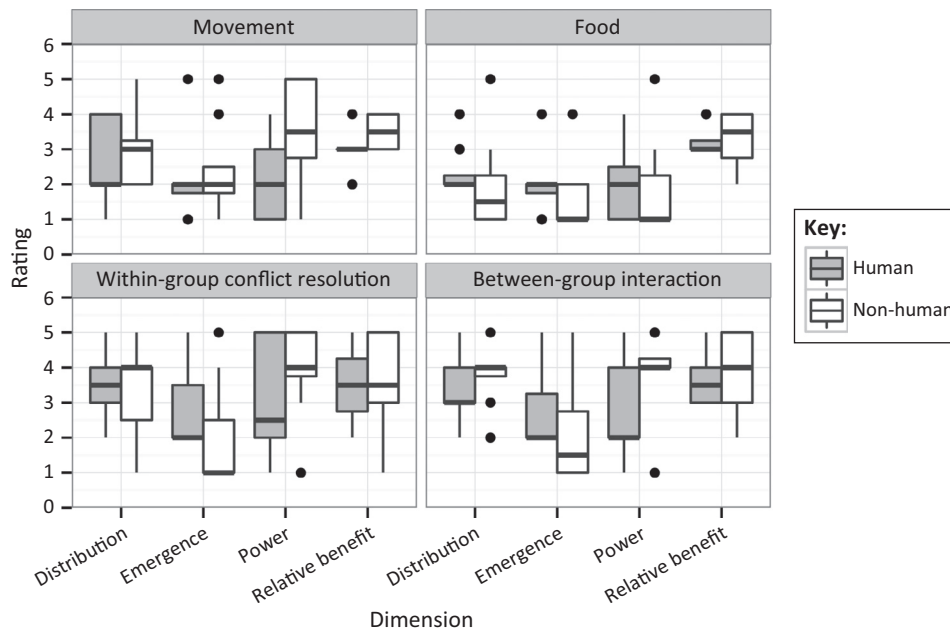
Dimension	Rating Codes and Definitions
Distribution	1 = no leadership (all adults are autonomous in domain X) 2 = semi-autonomy: leadership in domain X is widely shared among a restricted age or sex category (e.g., females usually lead, older adults usually lead) 3 = moderately unshared (roughly the midpoint between 1 and 5) 4 = very unshared (a small number of adults lead in this domain) 5 = highly unshared (one individual usually leads in this domain)
Emergence	1 = leadership fully achievement-based (includes cases where adults are autonomous) 2 = primarily achievement-based (e.g., adults of one age or sex category usually lead, but otherwise leadership is achievement-based) 3 = roughly equal mix of achieved and ascribed (e.g., most competent senior males lead) 4 = primarily ascribed (e.g., leadership inherited by a senior member of chief's family) 5 = fully ascribed (e.g., senior female always leads)
Power	1 = weak or non-existent (adult autonomy, highly democratic decision-making, etc.) 2 = delegated leadership (leaders coordinate or execute decisions most or all agree to) 3 = moderate power (roughly the midpoint between codes 1 and 5) 4 = leaders can coerce or persuade many but not all, or often but not consistently 5 = despotic (leaders consistently coerce or persuade others to follow)
Relative benefit	n.a. = not applicable because no leadership (e.g., full autonomy) 1 = leadership very costly (small payoff relative to that of followers) 2 = leadership somewhat costly, on average 3 = equality (payoff to leadership is roughly the same as the payoff to followers) 4 = leaders gain moderately relative to followers, on average 5 = relative payoff is heavily skewed to leaders
Generality	1 = leadership in one domain rarely predicts leadership in other domains 2 = some correlation (e.g., individuals belonging to one age or sex category usually or always lead in every domain, but the precise identity of leaders varies) 3 = moderate correlation (e.g., consistent across two domains) 4 = strong correlation (e.g., consistent across three domains) 5 = leaders are consistently the same across all domains, independently of distribution (including both cases with consistent autonomy and ones with generalized dominance)

<sup>a</sup>See [Box 1](#) for explanations of each dimension.

We found a similar overall pattern for SSS and NHM societies, with the majority of societies featuring moderately shared leadership in most domains ([Figure 1](#) and [Table S2](#) for details). Leadership was rated as significantly more concentrated (less shared) in the domains of within-group conflict resolution and between-group interactions than in the other domains. There was no significant effect of society type (SSS vs NHM). However, leadership in domains other than food acquisition is less-evenly distributed in NHM than SSS. Food acquisition and consumption was done individually in most of the NHM societies, but was a cooperative matter within most of the SSS societies [[55,56](#)].

### Leadership Emergence

In some cases, leaders emerge through a process of competition or performance. In others, they are born, not made – by inheritance or some other process independent of their own actions or qualities. Social scientists typically term this contrast **achieved** versus **ascribed leadership status**, labels we adopt here. This ascribed–achieved dimension is a continuum which for convenience we divide into five steps ([Table 2](#)). Even in the same society, leadership in one domain can be primarily achieved even though in another domain it is ascribed. In common with many other status differences, leadership is often correlated with age, as one builds up experience, alliances, and/or competitive ability; we classify this as achieved status, unless there is an invariant seniority rule (e.g., the oldest female always leads). Mathematical models reviewed above, however, focus exclusively on achieved leadership status.



Trends in Ecology &amp; Evolution

Figure 1. Ratings for Leadership Dimensions in Non-Human Mammals (white) and Small-Scale Human Societies (shaded) in Each of the Four Leadership Domains. In each case, the central dark bar represents the median and the box the inter-quartile range.

Our ratings of the 16 societies indicate that most exhibit achieved leadership in the majority of domains (Figure 1). There are no systematic differences across domains in this dimension. We found greater variability within categories (SSS, NHM) than between them, although NHM societies are somewhat more achievement-based than SSS in domains other than movement. Spotted hyenas and the Nootka (Northwest Coast Indians) are clear outliers with highly ascribed (inherited) leadership in all domains.

#### Differential Power

We define power as the ability to motivate others to behave in ways they would otherwise not via mechanisms of coercion, persuasion, or **prestige**. Leaders in SSS are often particularly skilled at using rhetoric to express common goals and to persuade and inspire followers [57]. Few mathematical models explicitly allow for evolving power of leaders (see above), predicting that leaders' actions will have substantial effects on followers unless the latter form coalitions.

The ratings suggest that leaders are generally less powerful in SSS than NHM except in the food-acquisition domain, where adult NHMs are often autonomous (Figure 1). Anthropological research indicates that the smallest-scale societies of low-density foragers or horticulturalists have less-powerful leaders than other human societies, a generalization borne out in our sample (see ratings for Ache, Inuit, Shoshone, and Tsimane, Table S2). There are also significant differences across domains, with leaders being rated more powerful in within- and between-group interactions, and less powerful for movement and food.

#### Relative Benefit

Do leaders reap fitness payoffs from their actions equal to, greater than, or less than those averaged by other group members? Although intuition might suggest that leaders gain disproportionate payoffs, several models predict otherwise. If payoffs are frequency-dependent (e.g., leadership traits are favored when rare, but deleterious when common), fitnesses of leaders and



followers will be equal at equilibrium. Self-serving leaders can be thwarted by coalitions of the less powerful, or (particularly in human societies) by rules that remove them from power; one mechanism to ensure that this is through **delegated leadership**, by which leaders serve the larger group and have only limited autonomy to pursue their own interests.

The evidence from our 16 societies shows greater similarity between NHM and SSS in this dimension than in any other (Figure 1). Notably, across most of our cases, leaders gain fitness-related payoffs equal to or only modestly better than followers. A handful of cases exhibit negative returns to leadership (i.e., apparent altruism or exploitation by followers), as documented among lions [58]. Neither domain nor society type has a significant effect on ratings for relative benefit (Table S2).

### Generality

Leadership is **domain-specific** in some groups, but fairly generalized in others [59]. We therefore asked if individuals who lead in one domain are likely to exercise leadership in other domains. We expected societies with strong dominance hierarchies or charisma-based leadership would exhibit higher generality than societies with widely distributed leadership. We only located one modeling study allowing for the effects of leaders over multiple domains (within- and between-group conflicts [2]), and therefore no model-based generalizations are possible yet.

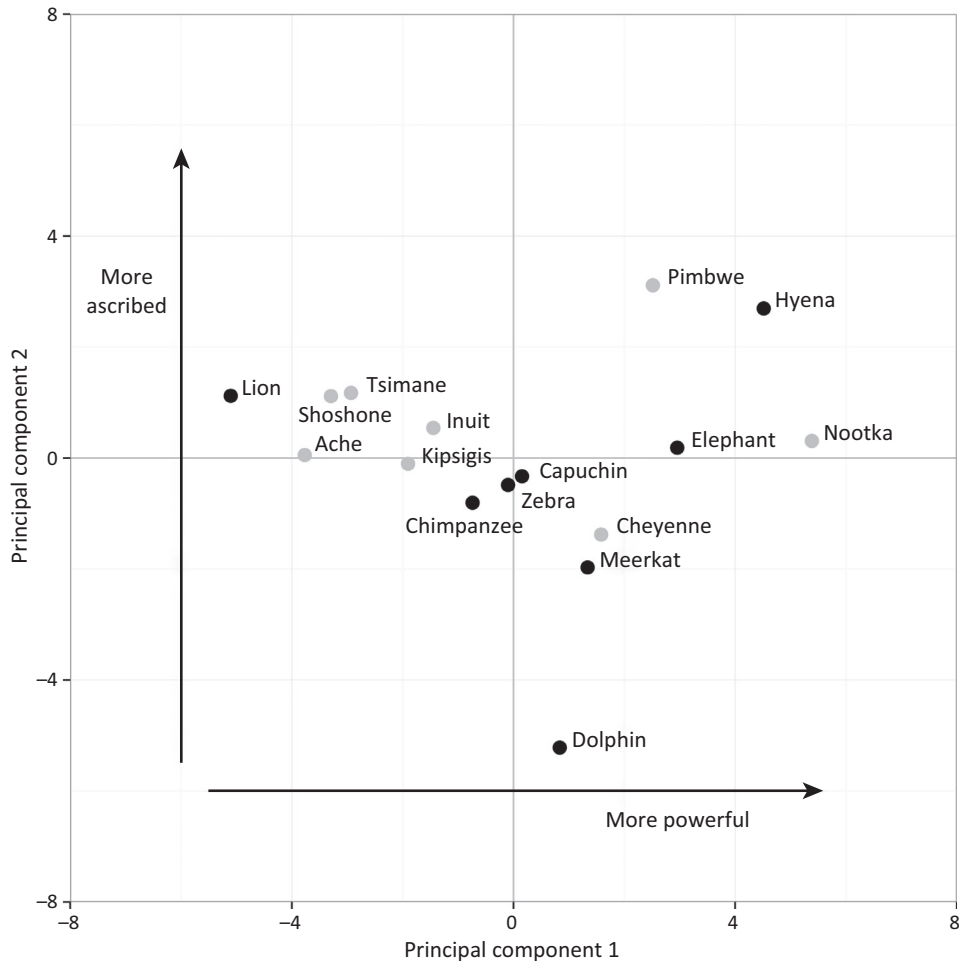
We found that leadership is somewhat more generalized in NHM societies than in SSS; this was true for both median ratings (median = 4 for NHM, versus 3 for SSS) as well as the range across societies (three NHM but no SSS societies were rated 5, whereas three SSS but no NHM societies rated 2; Table S2). As expected, societies with marked dominance hierarchies (e.g., capuchins, meerkats, hyenas) exhibit greater leadership generality across domains, reflecting the fact that high-ranking individuals typically occupy most leadership roles.

### Cross-Domain Synthesis

Because several of the rating dimensions are intercorrelated, we employed principal components analysis to reduce the dimensions of the correlation matrix. The first two principal components accounted for 55% of the variation. The first (39% of the variation) loaded substantially on all variables, but was specifically associated with leaders being powerful, leadership being concentrated, and the benefits of leadership being relatively large across domains. We thus named this principal component 'power'. The second principal component (16% of the variation) specifically identified variables relating to 'emergence': societies scoring highly on this principal component had leaders whose role was more ascribed, whereas those with low scores had leadership that was more achievement-based. Figure 2 reveals no systematic divergence between human and non-human mammals; some SSS have low leadership power scores while others have some of the highest. There is similar variation amongst SSS for the emergence dimension.

### Towards a Unifying View of Leadership

Examination of leadership in a sample of NHM and human SSS in a cross-species framework revealed some suggestive patterns. We found significant variation across domains for two dimensions, distribution and power, with leadership being the most concentrated and powerful in conflict mediation and between-group interactions. Comparing humans to other mammalian species in our sample, we found both similarities and differences. Despite common assumptions often made around the notion of human uniqueness, interestingly, we found no clear divide between human and non-human social mammals with respect to the emergence of leadership in this exploratory analysis. Instead, both NHM and SSS leadership is based more on individual achievement than on ascribed (inherited) status, although exceptions to this pattern should motivate future theoretical and empirical analyses. In addition, both NHM and SSS leaders tend



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Figure 2. Position of Each Sample Society in the 2D Space Defined by the First Two Principal Components Extracted from the Set of Ratings for Four Dimensions (Excluding Generality) in All Four Domains.

to wield more power in the domains of within-group conflict-resolution and between-group interactions, consistent with theoretical analyses of the importance of multilevel selection [60] as well as within-group dynamics [2]. Furthermore, the paucity of coercive leadership in small-scale (but not complex) human societies is arguably similar to the way NHM use communicative or passive mechanisms, but rarely coercion, to recruit followers [9]. These continuities between humans and other mammals in leadership patterns likely reflect shared evolved cognitive mechanisms governing dominance–subordination, alliance formation, and decision-making [3,15].

On the other hand, SSS leaders in our sample generally wield less power than do NHM leaders, and leadership is marginally more domain-general in the societies of NHM than in SSS. These differences reflect a tendency for humans to develop role specialization and depend less on dominance as the basis for leadership, which arguably indicates significant evolutionary divergences between humans and NHM [61,62]. Even in the least complex human societies, the scale of collective action (for food acquisition and distribution, conflict mediation, and between-group interactions) is greater and presumably more crucial for survival and reproduction [13,54,63].

We hypothesize that the factors causing human leadership to potentially diverge from the prevailing mammalian patterns are those responsible for other aspects of human uniqueness [64], but additional empirical tests are clearly warranted to investigate this possibility. Biologically evolved characteristics facilitating syntactic language and high-volume cumulative cultural transmission underpin the development of norms and institutions shaping all aspects of human social behavior [63,65–67], including leadership [68]. Human socioeconomic systems are characterized by massive flows of goods and services among large numbers of individuals who are often non-kin. Such a social system appears to favor the emergence of mechanisms to solve complex **coordination problems** [69]. Human cognitive capacities for planning and communication facilitate solution of more challenging **collective action problems** that benefit most members of the cooperative social units [21,67]. In such contexts, coercion is not necessary to motivate group members to follow leaders [13].

Our review reveals notable gaps in leadership studies that differ for SSS and NHM (see Outstanding Questions). Leadership has rarely been quantified in domains beyond group movement for even the best-studied NHM. Future studies should investigate the degree to which this lacuna in the literature reflects actual patterns of leadership in NHM. In SSS, leadership is poorly described in the domains of movement and food acquisition, perhaps because of the rarity of formal leadership roles; here again new studies will be necessary to examine the dimensions of collective decision-making in these domains. We also have little systematic understanding of the variable fitness costs and benefits associated with leadership status in SSS [68] or NHM societies [9]. Existing theoretical work spans multiple domains of leadership, but most focuses on only three dimensions of leadership: distribution, emergence, and payoffs. An important direction for future theoretical work is to provide modeling guidance on evolutionary processes driving variation in the power of leaders and the generality of leadership across multiple domains. We hope this review helps to stimulate greater integration of empirical work and model-building on this emerging research topic.

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### Supplemental Information

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### Outstanding Questions

The evolution of leadership is a rapidly-growing area of interest in both biological and social sciences (and particularly in transdisciplinary work that cuts across the boundary between them). Here we simply list some of the outstanding questions that have yet to be addressed in a systematic way.

What drives variation in leadership patterns across species or cultures? For the distribution dimension, it seems clear that neither consensus-based nor concentrated leadership constitute inevitable equilibria, but rather reflect different points on a dynamic continuum maintained by some combination of internal and external tradeoffs and opportunities. Although widely distributed decision-making may maximize efficiency under some conditions, it can be very inefficient under others. In addition, heterogeneity among individuals in ability, motivation, and inherited status or resources may concentrate leadership.

Is the predominance of female leadership by adults seen in our sample of NHM generalizable to other species? Is the bias towards male leadership seen in our SSS sample a robust contrast? Salient attributes such as age and sex have yet to be systematically quantified across species within a phylogenetically controlled context, despite our efforts here. Understanding **attribute-based leadership** should facilitate the development of mechanistically inspired hypotheses, and illuminate the cognitive basis of leadership traits.

We summarize evidence that benefits are fairly evenly divided between leaders and other group members. However, this might reflect the fact that we differentiate leadership from dominance, as well as restricting human cases to small-scale societies. Under what conditions can individuals convert leadership into **despotism**? Many social scientists are currently interested in the dark side of leadership, when leaders exploit followers (see next point). There is also keen interest in the evolutionary origins of charismatic leadership, where followers voluntarily obey leaders because of some quality they signal (which immediately suggests the relevance of signaling theory, as yet barely exploited in leadership studies).

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If, as we argue, leadership evolves by natural selection, one might expect the existence of special, conditionally expressed adaptations that increase the efficiency of both leaders and followers in their respective roles. For example, followers might evolve to be less 'rebellious' (or more willing to accept their role) and leaders more pro-social. Alternatively, a different trajectory might arise, where leaders evolve to be more powerful and manipulative ('Machiavellian'), and followers more suspicious and stubborn. One can arguably find evidence for both trajectories in the historic and ethnographic record of humans, and also in studies of other mammals.

What accounts for the transition from acephalous societies to more-complex and **stratified societies** in human history? This question has preoccupied scholars from Hobbes and Marx to more contemporary analyses drawing on evolutionary game theory and cultural transmission dynamics. Do comparisons with (generally acephalous) mammalian cases offer any insights? Are any of the models of leadership summarized in our review sufficient to address this question? What are the causes and consequences of the shift from informal or **situational leadership** to **institutionalized** forms in human history, and do these have any non-human analogs?

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