Supplementary Material
Leadership in Mammalian and Small-Scale Human Societies

Jennifer E. Smith[1], Sergey Gavrilets[2], Monique Borgerhoff Mulder[3], Paul Hooper[4], Claire El Mouden[5], Daniel Nettle[6], Christoph Hauert[7], Kim Hill[8], Susan Perry[9], Anne E. Pusey[10], Mark van Vugt[11], Eric Alden Smith[12]

[1] Mills College, Department of Biology, Oakland, CA 94613, USA
[2] University of Tennessee, Departments of Ecology & Evolutionary Biology and Mathematics and National Institute for Mathematical and Biological Synthesis, Knoxville, TN 37996, USA
[3] University of California at Davis, Department of Anthropology and Center for Population Biology, Davis, CA 95616, USA
[4] Emory University, Department of Anthropology, Atlanta, GA 30322, USA
[5] University of Oxford, Department of Zoology, Oxford OX1 3PS, UK
[6] Newcastle University, Centre for Behavior and Evolution and Institute of Neuroscience, Newcastle NE2 4HH, UK
[7] University of British Columbia, Departments of Mathematics and Zoology, Vancouver, BC V6T 1Z2, Canada
[8] Arizona State University, Institute of Human Origins and School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85281, USA
[9] University of California Los Angeles, Department of Anthropology, Los Angeles, CA 90095
[10] Duke University, Department of Evolutionary Anthropology, Durham, NC 27708, USA
[11] Department of Experimental and Applied Psychology, VU University Amsterdam, the Netherlands and Institute for Cognitive and Evolutionary Anthropology, University of Oxford, UK
[12] University of Washington, Department of Anthropology, Seattle, WA 98195-3100, USA

Corresponding authors:
Eric Alden Smith (easmith@uw.edu) and Jennifer E. Smith (jesmith@mills.edu)

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Table S1. Full ratings for the sixteen-society sample, by domain and dimension.

Mammalian species	Dimension	Group Movement	Food acquisition	Within-group conflict	Between-group interactions
African elephants	Distribution	5	1	1	5
	Power	5	1	5	5
	Emergence	5	1	1	5
	Relative benefit	3	n.a.	3	5
	Generality	5	[same in all domains, by definition]		
African lions	Distribution	2	3	1	2
	Power	1	1	1	1
	Emergence	2	2	2	2
	Relative benefit	3	3	1	2
	Generality	2	[same in all domains, by definition]		
Bottlenose dolphins	Distribution	4	5	4	4
	Power	5	5	4	4
	Emergence	1	1	1	1
	Relative benefit	4	4	3	3
	Generality	4	[same in all domains, by definition]		
Chimpanzees[a]	Distribution	2	1	4	3
	Power	3	1	4	4
	Emergence	2	1	1	1
	Relative benefit	3	n.a.	4	4
	Generality	3	[same in all domains, by definition]		
Plains zebra	Distribution	3	1	3	4
	Power	5	1	3	4
	Emergence	2	1	4	1
	Relative benefit	4	n.a.	3	3
	Generality	3	[same in all domains, by definition]		
Meerkats	Distribution	3	2	5	4
	Power	2	3	5	5
	Emergence	2	2	1	1
	Relative benefit	3	4	5	4
	Generality	5	[same in all domains, by definition]		

Spotted hyenas	Distribution	3	2	4	4
	Power	4	2	5	4
	Emergence	4	4	5	5
	Relative benefit	4	2	5	5
	Generality	5	[same in all domains, by definition]		
White-faced capuchins	Distribution	2	1	4	4
	Power	3	1	4	4
	Emergence	1	1	1	2
	Relative benefit	4	n.a.	5	5
	Generality	4	[same in all domains, by definition]		

Small-scale society	**Dimension**	**Group Movement**	**Food acquisition**	**Within-group conflict**	**Between-group interactions**
Ache	Distribution	4	2	4	2
	Power	2	1	1	1
	Emergence	2	1	2	2
	Relative benefit	2	3	2	3
	Generality	3	[same in all domains, by definition]		
Cheyenne	Distribution	4	3	4	3
	Power	3	4	5	4
	Emergence	2	2	3	3
	Relative benefit	3	3	2	4
	Generality	4	[same in all domains, by definition]		
Inuit	Distribution	2	2	3	3
	Power	2	2	3	2
	Emergence	2	2	2	2
	Relative benefit	3	3	4	4
	Generality	4	[same in all domains, by definition]		
Kipsigis	Distribution	2	2	3	4
	Power	3	2	2	2
	Emergence	2	2	2	2
	Relative benefit	3	4	3	3
	Generality	2	[same in all domains, by definition]		

Nootka	Distribution	4	4	5	4
	Power	4	4	5	4
	Emergence	5	4	5	4
	Relative benefit	4	4	5	5
	Generality	4	[same in all domains, by definition]		
Pimbwe	Distribution	1	2	4	5
	Power	1	2	5	5
	Emergence	1	2	5	5
	Relative benefit	3	3	5	4
	Generality	3	[same in all domains, by definition]		
Shoshone	Distribution	2	2	2	3
	Power	1	1	2	2
	Emergence	1	1	2	2
	Relative benefit	3	3	4	3
	Generality	3	[same in all domains, by definition]		
Tsimane	Distribution	2	2	3	3
	Power	1	1	2	2
	Emergence	2	2	2	2
	Relative benefit	3	3	3	3
	Generality	2	[same in all domains, by definition]		

[a] Ratings for chimpanzee food acquisition are for typical diet; ratings for hunted food, which constitutes <5% of dietary intake, are 4, 4, 2, 4, 3 for each dimension (in the order listed in the table).

Statistical analyses of variation in mammalian leadership patterns

As discussed in the main text, we coded each dimension of each leadership domain in our sixteen societies according to a five-point rating system. Thus, each rating is akin to an item on a Likert scale, a measurement tool utilized extensively by psychologists and survey researchers [S1, S2]. The rating protocol is detailed in Table 2 of the main text. The total sample thus consisted of four ratings (one for each dimension) for each of four leadership domains associated with each of the sixteen societies, except for some societies evaluated in the food domain. That is, leadership was deemed to be non-applicable in the domain of food for elephants, zebra, chimpanzees and capuchins; most foraging is equally distributed in these societies. In addition, we had a single rating per society for the domain-generality of leadership.

To determine whether ratings varied significantly by leadership domain or by type of society (i.e., small-scale societies (SSS) of humans versus non-human mammals [NHM]), we analyzed the 64 ratings given for each dimension using non-parametric (Kruskal-Wallis) tests. The results are detailed in Table S2. Ratings differed significantly across domains for two of the four dimensions, namely Distribution and Power, but not for Emergence or Relative Benefit. SSS differed significantly from NHM for Emergence, and there was a marginally non-significant difference for Power. Differences between SSS and NHM were not statistically significant for Distribution, Relative Benefit, or Generality.

Table S2. Statistical analyses of variation in leadership across the sixteen-society sample.

Dimension	Domain[a]	Type[b]
Distribution	$\chi^2_3 = 13.59$, $p < 0.01$	$\chi^2_1 = 0.04$, $p = 0.85$
Power	$\chi^2_3 = 9.67$, $p = 0.02$	$\chi^2_1 = 3.37$, $p = 0.07$
Emergence	$\chi^2_3 = 2.58$, $p = 0.46$	$\chi^2_1 = 4.83$, $p = 0.03$
Relative benefit	$\chi^2_3 = 3.32$, $p = 0.35$	$\chi^2_1 = 1.73$, $p = 0.19$
Generality[c]	---	$\chi^2_1 = 1.58$, $p = 0.21$

[a] Kruskal-Wallis tests of whether ratings for the given dimension varied significantly across different domains

[b] Kruskal-Wallis tests of whether ratings for the given dimension varied significantly across the two types of society (non-human mammals versus small-scale human societies)

[c] Since by definition generality ratings for any of the sample are constant across domains, only variation across type of society was tested

The principal components analysis described in the main text was performed using the 'princomp' function in the statistical programming language *R*. The dataset was the sixteen ratings given for each of the sixteen societies (not including the single rating per society for domain-generality). The princomp function produces an unrotated principal components analysis with as many components as there are variables (16 in this case). The first two components accounted for 39.34% and 16.06% of the total variation, respectively. The components were named by inspection of the component loadings for each variable. The scores of each society on these two principal components were used to produce figure 2.

Background information on the sixteen-society sample

The ratings of leadership patterns across the sixteen species in our sample are based on detailed observational studies in naturalistic settings. The following sketches provide contextual information to illustrate the basis for our ratings (detailed in Table S1).

Non-human mammals

African elephants (*Loxodonta africana*). Elephants live in matriarchal societies with herds, bond groups, and clans of related females. Adult female elephants live in core social groups, called families. Families are comprised of predictable sets of individuals, comprised of mothers, their adult daughters and their offspring. Core groups may contain 1–20 adult females and their immature offspring. At maturity, males disperse and females generally remain with their natal core social group. Immigrant males separate from the main herd either in bachelor groups or on their own, with the oldest males being socially-dominant. Over the course of hours, days or weeks, core groups temporarily fission into smaller subgroups or whole core groups may fuse to form a larger group with adult females from other core groups across the population. Because elephants grow larger with age, size-based dominance is mainly attributed to the age of adults. The matriarch is the oldest adult female in the social unit, and she is primarily responsible for leadership across domains.

Group movement: Matriarchs lead the activity, direction and rates of group movements. If the matriarch moves, then the rest of the family follows close behind her. Within families, calves tend to follow their mothers. Everyone benefits equally from following the matriarch.

Food acquisition: Elephants are herbivores that feed primarily on grasses and herbs in the rainy season and on woody plants in the dry season. When adult females stop to be feed, others in the core group spread out and also start to forage. However, leadership is generally distributed during foraging because there is no food sharing and food is acquired on an individual basis.

Within-group conflict: Elephants intervene during within-group conflict to stop fights. Although participants in fights are variable over time, coalitionary allies generally are limited to genetically-related individuals of the same sex. Allomothers also intervene on behalf of calves.

Between-group interactions: Matriarchs take the lead during between-group conflicts.

References: See [S3-6] for further information underlying our ratings.

African lions (*Panthera leo*). Lions are the largest of the African carnivores. These long-lived social carnivores reside in egalitarian prides comprised of 3-12 females and 1-7 males. Females are generally close relatives living in matriarchal societies with communal care and allonursing. Males are often, but not always, related brothers that form stable coalitions within groups. Lions live in residential prides that defend territories large enough to support large numbers of prey. Males are larger than females, engaging in intense male mating competition.

Group movement: Adult females are most likely to be followed by immature lions, but among adult females, there is no evidence that particular individuals are most likely to be a followed.

Food acquisition: Leadership roles during hunting are consistent regardless of prey item hunted and adult females produce food more often than do adult males. Lion societies are egalitarian, so leaders have limited power in who initiates hunting and everyone benefits from hunting efforts. Males do often feed before females do at kills. Lions typically follow anyone that is actively hunting (mainly adult females). For small prey, lions hunt individually and do not share. For intermediate size prey, there is conflict as one lion must suffocate the prey, but while they do that others can start eating the intestines, which are highly nutritious. The lion that did the kill gets very ‘angry’ at this and hisses and growls, but to no avail. They end up with meat, but of lower quality, as by the time the animal is suffocated, the whole pride will be feeding. For larger prey, there is no conflict as every member can eat more than their fill.

Within-group conflict: Lions do not intervene in fights within the group.

Between-group interactions: Between-group conflict is very important in lions with both sexes forming coalitions against members of other prides. There are typically consistent roles during between-group conflicts, with some lions acting as leaders, some acting as laggards, and others performing a mixed strategy of context-dependent helping. Although individuals are consistent in the degree to which they help, age, body size and reproductive state fail to explain these patterns. Leaders are typically followed. Although the mechanisms by which individuals

take on these roles is poorly understood, differences may be attributed to personalities.

References: See [S6-8] for further information underlying our ratings for lions.

Bottlenose dolphins (*Tursiops sp.*). Bottlenose dolphins live in open, fission-fusion societies, called pods, comprised of typically 10-30 members, but group sizes range from several to over 1,000 individuals. Dolphins feed primarily upon fish and often cooperatively hunt fish using echolocation. Group movements are coordinated through acoustic and visual signals, with key individuals leading most movement. Adult males of Shark Bay, Australia form particularly large super-alliances with multiple levels of cooperation and form coalitions to acquire mates. Leadership is often biased towards a select few adult individuals, most of whom are males. Overall, adult males take on leadership roles in virtually all contexts.

Group movement: Select males, presumably with the most knowledge, initiate most traveling bouts by performing side flops. Initiation predicts travelling order and others therefore largely follow a small number of adult male leaders. Adult females, however, perform upside-down lobtails to terminate traveling bouts. Leadership is achieved by adults via social contests or prestige. Leaders are relatively constant across a wide range of group sizes. All dolphins appear to benefit equally from these unshared decisions.

Food acquisition: In Cedar Key, Florida, role specialization has been observed such that one individual consistently acts as the 'driver', herding the fishes in a circle toward the remaining 'barrier' dolphins. Thus, these dolphins show consistent "leaders" within the context of group hunting. The relative benefits of leadership during foraging remains somewhat unclear. Leadership is most likely achieved rather than inherited. Additional study of this phenomenon is required to ascertain if drivers are always adults and to understand the extent to which leadership during hunting occurs in other populations.

Within-group conflict: Adult males, but not females, engage in third-party interactions, cooperating during mating and using aggression to reinforce male-male alliances. Adult male leaders and followers take turns mating with females and therefore equally benefit from leadership. Leadership is achieved with adult males gaining leadership in alliances as they age.

Between-group interactions: Adult males form multiple levels of alliances despite living in open, unbounded societies lacking clear territorial boundaries and frequent between-group interactions. Alliances show extensive overlap in the mating season. Adult males achieve status over time rather than inheriting it. It is likely that all group members benefit from leadership during between-group interactions but more research is needed to confirm this.

References: See [S9-13] for further information underlying our dolphin ratings.

Chimpanzee (*Pan troglodytes*). Chimpanzees live in permanent social groups, called communities, of up to 200 individuals (mean 46), which are fission-fusion societies. Males are philopatric while most females transfer to other communities before breeding. Males are more social than females, spending most of their time in mixed-sex parties and ranging widely. They jointly defend the community territory by patrolling the boundary, behaving aggressively toward neighbors and even killing them when one side greatly outnumbers the other. Range expansion increases access to food and shortens female inter-birth intervals. Females forage in smaller parties except when sexually receptive and in some populations spend over 40% of their time alone or with their dependent young in small overlapping core areas within the community range. As ripe fruit specialists, chimpanzees spend about 90% of their feeding time on plant material and the rest on insects and meat. They hunt mammals such as red colobus monkeys and the meat is shared. Males form a linear dominance hierarchy. The median tenure length of the alpha male is about 5 years but tenure can extend beyond 20 years. Males compete aggressively for dominance and become alpha through their own efforts. Alpha males father more offspring than others but low ranking males gain more paternity than a strict priority of access model predicts. There is considerable variation in the extent to which alphas behave as leaders. Dominance rank differences also exist among females, but are harder to discern.

Group movement: Because of the fission-fusion nature of the society, group composition of foraging parties varies markedly and leadership has yet to be studied systematically. Immatures generally follow their mothers. At Mahale Mountains, Tanzania, old individuals are considered influential in group travel. For a period at Tai forest, Ivory Coast, the alpha male appeared to determine the activity and direction of movement of his and other parties through the pattern and sequence in which he drummed on tree buttresses. At Bossou, Guinea, over a 4 month study, adult males led the progression when the small community crossed roads and the alpha male usually took up the rear when crossing the busiest road.

Food acquisition: Feeding on plant and insect resources is individual and leadership is necessarily distributed. Most hunting of mammals is done by males in groups but the extent to which hunting is collaborative is debated. Some males are more active or successful hunters than others. At Tai, the alpha male was the most successful hunter. In two communities (Kanyawara in Kibale forest, Uganda, and Kasekela in Gombe National Park, Tanzania) the presence of a small number of "impact males" that were not always the alpha male strongly determined whether a hunt took place or not and impact males were most likely to initiate hunts. Some males are better than others at maintaining or getting access to meat after a hunt, often by seizing it from the hunter if they didn't make the kill themselves. At Mahale, the alpha male consistently possessed meat. Meat sharing generally occurs under pressure from beggars and at Gombe meat goes to the most persistent beggars. However, in some cases, males seem more willing to share with allies, kin or mates and are suggested to gain reciprocal benefits. Note that the ratings in Table S1 are for general (plant and insect) food acquisition. Ratings for hunting are given separately.

Within-group conflict: Alpha males sometimes break up disputes among other individuals and loser-support by the alpha male is common in captive groups. In general, adult males tend to break up fights between females. They probably gain from this behavior by protecting potential mates.

Between group interactions: At Tai, the alpha male was the leader in most intercommunity encounters. In the Ngogo community in Kibale forest, males that had greater mating success than expected for their rank participated in more patrols, and at Kanyawara low-ranking males were more likely to drop out of groups that traveled close to the periphery of the community range. At Gombe, the presence of certain males had a significant effect on the probability that a visit to the periphery turned into a patrol. These were not all alpha males and they were not necessarily impact hunters. Goodall noted that prime but not alpha males tended to lead patrols at Gombe and, notably, two alpha males tended to hang back during patrols. Given only moderate reproductive skew, most males are likely to benefit from range defense.

References: See [S14-18] for further information underlying our chimpanzee ratings.

Meerkats (*Suricata suricatta*). Meerkats are small carnivores belonging to the mongoose family (Herpestidae). They live in all parts of the Kalahari Desert in Botswana, in much of the Namib Desert in Namibia and southwestern Angola, and in South Africa. Clans are dominated by a pair of reproductive adults that generate the majority of the group's reproductive output. A meerkat clan often contains about 20 meerkats, but some "super-families" have 50 or more members. Meerkats live in large, underground burrow networks and are primarily insectivores. They also eat lizards, snakes, scorpions, spiders, plants, eggs and fungi. They have no excess body fat stores, so foraging for food is a daily need. They forage in a group with one "sentry" on guard watching for predators while the others search for food, and if it spots danger, it barks loudly or whistles. The alpha female gains her position via fighting. She dominates group reproduction by evicting females that attempt to reproduce. Group members regularly groom each other to strengthen social bonds. The alpha pair often scent-mark subordinates of the group to express their authority. Most meerkats in a group are all siblings or offspring of the alpha pair. Birth in general gives no status, at any stage of a meerkat's life. It comes with maturity and body size. Very occasionally subordinates will breed successfully and their pups

will be reared in mixed litters with the alpha's pups. When this happens, the alpha's pups will typically dominate the subordinates.

Movement: Groups spend most of their day foraging, and switch between burrows within their territory depending on food availability. Normally, this movement has no discernable leader, but they follow the rule of staying close together (often <1m) and are spread over a 20-50m line. However, the dominant female tends to lead the group out and back from foraging and she leads the group from the front when she 'wants' to move somewhere particular. The movements are based on by food discoveries and each group member stays close to others.

Food acquisition: Group members forage while moving together in tight bands. One member of each band will be on sentry duty. Nearly all their food is indivisible (i.e. small singly occurring prey items). All adults forage to feed themselves. Young follow an older member of the group who acts as the pup's tutor until young start foraging for food until they are about 1 month old. Young are provisioned by all group members in response to begging calls. Before this age, group members babysit the young and non-reproductive females often lactate to feed the alpha pair's young, while the alpha female is away. Pups are bought food by adult group members. More dominant animals will steal food or force subordinates away from a good foraging hole by growling and side-barging, but not that common.

Within-group conflict: The dominant female engages in the most conflict, attacking subordinates to assert her rank. As females get older, they become more aggressive towards subordinates. Dominant females will evict subordinates that grow too large. The result of the conflict is that virtually all subdominant females are evicted from the group as the mature.

Between-group interactions: Meerkats frequently invade the territory of neighboring groups for food, especially during the dry season. Intruders can be from neighboring groups, newly formed groups or small bands of males prospecting for females. Conflicts start with displays (dust kicking, war dancing, puffing, vocalizations), and escalate to lethal aggression. Males lead the fights against prospecting males. Alpha males and females decide when to initiate and retreat from fights with other groups and leads the scent-marking. They will judge when to invade neighboring territories to attack and will lead the raiding group. The alpha-male typically leads the attack, always supported by the group. Males contribute more to defense, as females invest little in repelling male prospectors. Females fight intensely against other groups and participate in raids. The alphas gain more in terms of reproduction. However, all group members benefit in terms of survival.

References: See [S6, S19-21] for further information underlying our ratings for meerkats.

Plains zebra (*Equus quagga*). The plains zebra is the most common zebra, with a range spanning much of southern and eastern sub-Saharan Africa. It is a highly social species living in multi-level societies where the basic breeding unit is a stable hierarchical harems consisting of a single stallion and one to many females. Individuals come together to form herds of two to 100 harems. In addition, pairs of harems may create temporarily stable subgroups within a larger herd, allowing individuals to maintain social interactions with those in neighboring groups. Stallions form and expand their harems by abducting young mares from their natal harems. Therefore harem members are normally unrelated, which is highly unusual given that the social groups are so stable. Once mated, the mare becomes a permanent member of the new harem. Within the harem, ranks are fairly stable: new females rank lowest, a foal has the same rank as its mother and females that become unfit or weak drop in rank. The alpha female leads the group and mates first. The female members of a harem stays intact even if a new stallion takes over. Young females typically stay in their natal harem until another stallion abducts them. Young male zebras eventually leave and form bachelor groups. Stallions need to constantly defend their groups from other males, which often results in violent fights.

Group movement: Within a harem, an individual can initiate walking to a new location. This usually happens when the group is moving to a water source. Social rank within the hierarchy and whether the animal is lactating determines who initiates harem movement. Initiation predicts

travelling order and females respond to the initiation of movement. Lactation is the strongest predictor of whether the individual is initiating movement, followed by social rank.

Food acquisition: As zebras graze individually, there is no meaningful definition of leadership in feeding.

Within-group conflict: Zebra intervene in both affiliative and agonistic interactions within their herds. Males, especially high-ranking ones, intervene in conflicts at the highest rates. Male interventions are most common during courtship between mares and other males within their harems. Age and order of arrival in the reproductive group are most important in determining leadership. Young individuals also sometimes intervene on behalf of their mothers and vice versa. Mares intervene on behalf of other mares in response to harassment by males.

Between-group interactions: Herds, where several reproductive units associate, engage in the same activities and move around together. Temporary herds consisting of several hundred individuals are frequently observed in plains zebras. For females, foraging access when in herds or in single harems is equal, therefore they are indifferent. The benefit of herds for males is that they limit cuckoldry, by allowing male stallions which head a harem to keep bachelor males on the edge of the herd. It also provides protection from predators. Males pay a cost of being in a herd in terms of reduced time foraging. Breeding males have power in that they decide whether their harem joins and remains part of a herd. However, male power is limited in that if they push females around too much, they will be more likely to leave the harem.

References: See [S6, S22-24] for further information underlying our zebra ratings.

Spotted hyenas (*Crocuta crocuta*). Spotted hyenas are long-lived social carnivores that reside in complex female-dominated societies, called clans. Clans may contain 90 or more individuals that defend a common territory. Virtually all males permanently disperse from natal clans after puberty; females are philopatric. Clans contain one to several matrilines of adult females and their offspring, as well as multiple adult immigrant males. Natal females inherit their social ranks matrilineally, attaining a rank directly below that of their mothers; immigrant males queue for social status such that their rank is based on their tenure rather than their actions or qualities per se. Hyenas feed primarily on ungulates, most of which they hunt themselves.

Group movement: Clans are structured by fission-fusion dynamics; individuals travel, rest and forage alone or in small subgroups that change membership roughly every hour. Individuals actively join subgroups containing preferred social and sexual partners. Adult females, especially high-ranking adult females are habitual leaders (lead more often than follow). High-ranking hyenas are more attractive social companions and more powerful social allies, but coercion is not used to promote followership (instead increased tolerance promotes followership). Although high-ranking adult female lead most often, particularly those female that are lactating, roles change regularly within these fission-fusion societies, and even low-ranking hyenas exhibit leadership at times.

Food acquisition: Although hyenas sometime hunt cooperatively, the average hunting group size is only 1.7 hyenas. Because high-ranking hyenas have priority of access to food, low-ranking individuals hunt at the highest rates and often do so alone to avoid within-group competition over kills.

Within-group conflict: All hyenas participate in within-group aggression, but high-ranking adult females engage in the highest rates of dyadic and coalitionary aggression, intervening in fights most often. High-ranking hyenas are most likely to win fights during within-group conflicts and have priority of access to key resources, including food and mates. Individuals that intervene on behalf of others also gain direct benefits from helping in coalitions.

Between-group interactions: Although most group mates join forces during between-group conflicts over territory boundaries, called clan wars, high-ranking adult females are most often at the front lines and disproportionally benefit from the outcomes of clan wars.

References: See [S25-28] for further information underlying our ratings for hyenas.

White-faced capuchins (*Cebus capucinus*). White-faced capuchins are long-lived primates that live in female philopatric groups. Males disperse, and although they can disperse singly, they generally transfer in the company of males from their previous group (related on average at the level of r=0.25). Males may co-transfer with the same male multiple times during their lives. Group size varies from 5-40, averaging 19 monkeys and exhibiting a female to male sex ratio of about 0.85. All-male groups form and can last for many months, but are not as permanent as multi-male multi-female groups. Relationships between neighboring social groups are hostile, and all males cooperate in defense of the group against potentially infanticidal intruder males from neighboring groups. Capuchins frequently form coalitions with members of all age-sex classes, for the purpose of feeding competition, rank acquisition, defense against predators, and defense against extra-group males. Capuchins are omnivores, eating primarily fruit and insects, but also eating some meat whenever they can obtain it.

Group movement: Most group members try to lead at least occasionally, but few are habitually followed. Results from different sites vary. At Lomas Barbudal, approximately half of all attempts to lead are by the alpha male, but other studies have a far more equal distribution of who attempts to lead. Success at leading group movement is highly distributed across group members, with females being very slightly more influential than males.

Food acquisition: Capuchins forage individually, though they do so while maintaining visual and auditory contact with other group members. Foragers do sometimes transfer food they have found and processed to other group members, but most of this takes the form of tolerated theft rather than active sharing.

Within-group conflict: Members of all age-sex classes participate in within-group aggression. Coalition formation is common, starting in infancy. Higher-ranking individuals meddle in others' conflicts more than lower-ranking individuals do, and they exhibit strong tendencies to support the higher-ranking opponent (unless the fight is between a male and a female, in which case they are more prone to supporting the lower-ranked female). However, the alpha male often ignores invitations to intervene. The alpha male and female are both extremely powerful and are rarely the targets of within-group aggression. Alpha males are highly effective at monopolizing reproduction, though inbreeding avoidance prevents them from breeding with their own daughters and granddaughters. Alpha males can maintain their positions for up to 17 years, though the mean length of an alpha male tenure is approximately one year. Attainment of the alpha position generally requires some physical conflict, but maintenance of that position is likely to be more dependent on effective management of allies.

Between-group interactions: Capuchins are highly xenophobic, and hence between-group interactions are hostile, sometimes resulting in death of males or infants. Females usually grab their infants and flee, while males stay and fight or display at one another. Alpha males participate more in these aggressive between-group interactions than subordinate males do, but all males participate at fairly high rates in these encounters. Currently available data suggest that males with a higher reproductive stake in the group (both in terms of future matings and defense of current offspring) participate at higher rates in group defense. Males are more likely to respond aggressively to threats from the neighbors if they see that someone else in the group is already responding aggressively.

References: See [S29-35] for further information underlying our ratings for capuchins.

Small-Scale Human Societies

Ache. The Northern Ache are a nomadic foraging population that roamed the forested regions of North Eastern Paraguay until their permanent peaceful settlement by government agents and missionaries in the 1970s. Their subsistence economy was based on hunting mammals and extracting palm starch carbohydrate, along with fruit collection and exploitation of wild bee honey. Traditionally Ache lived in some 18 to 20 residential bands scattered over some 15,000 km2. Single residential bands contained about 35 individuals on average, but sometimes multiple bands would gather for a few weeks to participate in club-fighting rituals. There were no

named leadership positions (not even “headman”). Formal institutionalized leadership roles (chiefs) were introduced by missionaries immediately after peaceful contact, but here we describe the traditional forest leadership system.

Movement: During the post-contact period, we observed most adults participating in daily discussions about where and when to move, and the relative merits of alternatives. Both sexes sometimes take the lead in these discussions by advocating enthusiastically their particular preferences. However, informants report that in the pre-contact period there was usually a high status older man who “led” the band and decided when and where new camps would be relocated. Bands were often referred to by this man’s name (e.g., John’s band), and the same man was influential in other realms of decision making as well.

Food acquisition: Men and women often split up during the day and there were different leaders of both sexes for the different foraging subgroups. In decisions about which foods to exploit, where and how, both sexes could lead depending on the resource and relative expertise.

Within-group conflict: The Ache have no institutions or recognized leaders to resolve within-group disputes. Instead, older kin generally intervene on behalf of others. Ritualized club fights with rules to limit lethal outcomes also allowed males to confront other Ache men legitimately and attempt to resolve grievances.

Between-group interactions: Conflict between bands was ritualized, and only a few prominent men were involved in organizing and refereeing the multiband club-fight gatherings. Peaceful interactions between groups were mainly led by men, but when visiting close kin was the primary activity, women could also be "leaders" of the decision process.

References: See [S36, S37] for further information underlying our ratings for the Ache.

Cheyenne. The Cheyenne (self-designated *Tsistsistas*) are a Native American tribe of the northern and central Great Plains region. The features summarized here characterized Cheyenne society in the first half of the19th century, when they lived as nomadic equestrian bison-hunters and were still politically autonomous, though engaged in trade for Euro-American goods such as metal tools and firearms. At this time, the approximately four thousand Cheyenne had a rather elaborate system of institutionalized leadership. The tribal council of forty-four chiefs was drawn more or less equally from the ten constituent bands of the tribe; one member was chosen as head chief. Council chiefs were expected to be wise, generous, and free of personal animosities or interests, although some failed to live up to these standards. Other formal leaders included heads of the several warrior associations (war chiefs), senior priests in the ceremonial associations, and healers. Families varied in social prestige, which depended on a combination of material wealth (particularly in horses) and proper demeanor (including initiative, bravery in battle, and generosity), and leaders emerged primarily from these families, though ambitious individuals could rise from humble beginnings, and wealth could disappear overnight in an enemy raid. The ratings apply to tribal decisions, but note that the tribe dispersed into smaller units (bands, and sub-bands) for most of the annual cycle.

Movement: The entire tribe assembled annually for the summer months, and at this time decisions about movement and other domains was in the hands of the Council of Forty-Four. However, families and other sub-units could make their own decisions to travel to visit friends and relatives, engage in trade, and pursue other activities.

Food acquisition: During the tribal aggregation, bison hunting (the mainstay of the Cheyenne economy) was tightly regulated, as uncoordinated forays to hunt bison could scatter the herd and reduce the collective harvest. Those who disobeyed tribal rules about hunting could have their weapons and horses confiscated.

Conflict resolution: Like other equestrian Plains Indian tribes, Cheyenne engaged in chronic warfare with enemy tribes (and often the U.S. army). However, homicide within the tribe was a heinous crime, punished by collective ostracism. Other less serious conflict across kin groups or bands was adjudicated by the Council of Chiefs, but intra-band conflicts could be handled by

elders within the band. Both social disapproval and formal sanctions (whipping, confiscation of property, etc.) could be meted out, often by a warrior society on behalf of the Council.

Between-group interactions: Relations with outsiders were both friendly (trade, military alliances) and hostile. Again, the tribal Council of Chiefs claimed monopoly over decisions about external relations, though as the intensity of warfare increased in the late 19th Century the warrior societies began to challenge this monopoly.

References: See [S38-40] for further information underlying our ratings for the Cheyenne.

Inuit. Inuit as discussed here are the indigenous inhabitants of central and eastern arctic Canada (not the closely related peoples of arctic Alaska and Greenland with denser, more settled populations and more elaborate social and political institutions.) Populations are low density, and the traditional economy (which persisted until less than a century ago) required wide-ranging movement, with seasonal fission-fusion of social units. Inuit winter camps contained up to a hundred or more, and traditionally had a *de facto* leader, termed *isumatak* (literally, "one who thinks"); the position was based on experience and seniority, and leadership was by persuasion and charisma rather than by overt control. In the spiritual/ceremonial realm, leadership was exercised by the shaman (*angakuk*); he or she achieved this position by vision, often following severe illness, and validated it by magical feats and curing of illness; these abilities could sometimes be used coercively, to extract gifts or favors, to impose costly taboos, or to threaten magical harm. In the rare cases where the camp leader was also the shaman, much greater authority and control were exercised. Although polygyny was uncommon, male competition for mates was chronic, the best hunters (who were more likely to be leaders) sometimes had two wives, and overt wife-stealing (with resultant violence) was fairly common.

Movement and food acquisition: During the winter aggregation, decisions to move camp to find better hunting were decided by consensus, though the *isumatak* had considerable influence. However, territoriality was absent (at least within the regional population), and kinship ties widespread, so families were generally free to move to a different band if they did not like the local leadership. During late spring through early autumn, the band often dispersed into nuclear or extended family units, seeking scattered game and fish.

Conflict resolution: Most serious conflicts were resolved (or at least ameliorated) by movement of one party to the dispute to another camp. There was little effective leadership to force agreement or avoid bloodshed if things came to a head, and oral histories indicate homicide was not infrequent.

Between-group interactions: Most conflict between members of different bands was easily avoided by moving away. Organized raids were infrequent in the Inuit realm, and there were no war leaders. Trade, marital alliances, adoption, and temporary spousal exchange were frequently employed to cement alliances between members of different bands, but these decisions were made by individuals or families, not higher-level leaders.

References: See [S41-43] for further information underlying our ratings for the Inuit.

Kipsigis. The Kipsigis are a branch of the Kalenjin, an agropastoral Nilotic language speaking group who migrated into East Africa over 2000 years ago. While much affected by colonial developments during the 20th century, many of the community level institutions persist. There are two kinds of recognized leaders: a community/military leader (*Boyot ab kokwet/Kiruogindet neo*) and a prophet (*laibon*); the latter is a temporal institution adopted from the neighboring Maasai, and is not coded here due to its ephemeral role in Kipsigis daily life. We combined the coding of the *Boyot ab kokwet*, or equivalently the *Kiruogindet neo* (who had a very similar position but for a group of neighborhoods (*kokwetinwek*) rather than a single neighborhood (*kokwet*)). The ratings are based primarily on Peristiany's account from the 1930s; the *Boyot ab kokwet* position was relatively unchanged in the 1980s, although the *Kiruogindet neo* had largely disappeared during MBM's fieldwork period (1981-1990). Note that *Boyot* and *Kiruogindet neo* can be replaced, but typically the selection is through previous apprenticeship to the *Boyot ab kokwet* (as a *chemengesh*), such that once the former

chemengesh gets chosen to become *Boyot*, he is already proven and liked; so in practice the position is quite stable. The ratings for Kipsigis focus on the *kokwet* (community), but assume that the *Kuruogindet neo* happens to live in this otherwise typical *kokwet*.

Movement and food acquisition: There are no clear leaders in these domains, with household heads (always men) making decisions about where to take cattle, when to make trips to markets, and where to cultivate, on both daily and annual basis. A household head can enforce his wishes over his wives and children, but women have considerable control over distributions of food within their polygynously-married unit. The influence of the household head as a leader is based on achieved characteristics (respect, influence and personal characteristics), although gender of course is ascribed. It appears that Kipsigis household heads make decisions primarily to benefit their households, although men do make movement decisions to benefit their "reserve herds".

Conflict resolution: The *boyot ab kokwet* (mediator judge) needs public approval in influencing and even adjudicating the outcome of conflicts. He is typically seen as the mouthpiece of the *kapkiruok* (elders council) and has no private individual authority. He is also the main executor, but in many instances he calls a committee of elders (*Kapkiruok*) to help adjudicate. These elders councils have very little power to force anyone into anything. He appears to have been largely selected by the previous *Boyot* as an apprentice, on basis of respect, age, good apprenticeship, wealth, wives, domineering personality, and colorful speech. Benefits are unclear; the only payment he receives for his services is the hind leg of a sacrificed goat or bull.

Between-group interactions: Generally the *Boyot* and *Kiruogindet* have the same powers about taking *kokwet* to war as solving internal conflicts. The only difference is that the *Kiruogindet* has more power in this domain.

References: See [S44-45] for further information underlying our ratings for the Kipsigis.

Nootka. The Nootka (*Nuu-chah-nulth*) occupy the deeply indented outer coastline of Vancouver Island, Canada. Traditionally, each local group of several hundred people was politically autonomous, and consisted of a core group of title holders ("nobles"), commoners, and slaves, in an approximate ratio of 20:60:20. Titles were inherited patrilineally or transferred through marriage, and conferred control over material property (wealth goods, prime fishing sites), privileges (from whale hunting to ceremonial roles), and intangible wealth in the form of songs, spirit allies, and such. Each local group had a senior chief, as well as close relatives, who held other political offices (speaker, war chief, etc.) and specific titles or rights. The chief was the ultimate decision-maker regarding organization of communal efforts in subsistence, house-building, food storage, trade, and inter-group relations (both peaceful, as in potlatch feasts, and in raiding for booty, slaves, or revenge). Generally, only nobles owned slaves, who were war captives or children thereof. Female slaves were concubines of their owners. Polygyny was common among the wealthy (i.e., the highest-ranking nobles) who could afford bride-price, and sought marriage alliances with title-holders in other groups.

Movement and food acquisition: Nootka settlement focused on the winter village, with it cedar longhouses, totem poles, and stores of food. But movement to summer fishing camps, as well as shorter forays for other resources and trade, were essential. The chief ultimately coordinated the complex logistics underpinning the Nootka economy, but could rarely force commoners to comply (slaves, of course, were ordered without compunction). Commoners often had relatives in multiple local groups, and could move between them; indeed, title-holders competed to attract industrious or skilled commoners, as they provided crucial labor in both subsistence and in wealth production (e.g., carvings and other goods).

Conflict resolution: Nobles had life-or-death power over slaves and some coercive power over commoners (e.g., by ordering slaves to punish disobedient commoners, or expelling them from the local group). However, specialists disagree about the degree of power chiefs had over freemen in their group.

Between-group interactions: War was endemic (as elsewhere on the Northwest Coast), and trade also was highly developed. Chiefs attempted to channel trade ties their way, via intermarriage and other alliances with nobles in other groups, but this was far from a monopoly.

References: See [S46-49] for further information underlying our ratings for the Nootka.

Pimbwe. The Pimbwe are organized as a petty chiefdom lying in the Rukwa valley of western Tanzania. They speak a Bantu language, closely related to Fipa, a neighboring ethnic group with a much stronger chieftainship (defined by Willis as a State) on the top of the Ufipa Plateau. The Pimbwe numbered 20-30,000 in the early 20th century (the "ethnographic present" adopted here). They were at this time ruled by a chief (*Mwene*) in association with his mother, known as the queen-mother (*Wacisongwa*). The chieftaincy was inherited matrilineally, but was highly contested. The country was divided into administrative districts (*ivikandawa*), each of which was under the authority of a sub-chief called *Mwene Nkandawa*. The villagers then elected village chiefs or headmen (*Basengi*), and nominations were supposed to be confirmed by the *Mwene*. The Chief did not have an elaborate court; elders and advisors (*mgawe*) were supposed to keep them in check and help with the affairs of state.

Movement: Primary decisions about where to live, where to visit, where to market acquired resources, etc. are made at individual as much as household level, given instability of marriage and household membership. Movement decisions may be followed by juveniles or a friend, but can be made by almost any adult; thus power seems very limited. Individuals making movements are assumed to be doing it to benefit themselves, so benefits are equalized.

Food acquisition: Primary decisions about subsistence (foraging and farming) are made at individual level, but with some coordination at the household level (with respect to farming), unlike movement. Household heads can make decisions about farming and foraging, but they cannot enforce compliance. Although decisions can be made by almost any adult, there is some gender predominance (e.g., for hunting and fishing).

Conflict resolution: The chief (*Mwene*) largely monopolizes power in this and the next domain, but does delegate some decisions to the sub-chief (*Mwene Nkandawa*) and the village headmen (*Basengi*). Although many of the 25 chiefs documented historically used their position to exert supreme power, they were also bitterly opposed by rival chiefly lineages, sub-lineages or cadet lineages. Chiefs also have an array of advisors (*mgawe*), executives, subchiefs (at village level), poison tasters, and ritual experts below them. Matrilineal inheritance (to current chief's sister's son). Benefits included rights to all harvests, ivory, and stolen weapons; some chiefs renowned for stealing wives.

Between-group interactions: Similar to within-group conflict resolution, but more concentrated decision-making and greater power, particularly during warfare.

References: Ratings are based on the description in Seel et al. [S50], for a hypothetical village where householders make decisions about food and movement, but the Chief and Subchief happen to reside.

Shoshone. Shoshone (self-designated *Numa*) are indigenous inhabitants of the central Great Basin of North America. We focus on the Western Shoshone, whose homeland covers what is now eastern Nevada and western Utah, and on conditions at early contact (mid-19th century) as derived from traveler's accounts as well as ethnographic research with older informants in the 1930s, supplemented by archaeology. Leadership was almost always situational, focused on coordinating communal hunts (rabbit and antelope drives) and ceremonial gatherings; criteria for leaders included sex (male), age (senior but active), and recognized ability or knowledge. In a few areas with higher resource (and population) density and less fluid movement, more defined leadership (village headmen) were found. In some cases, the headman "was also antelope shaman, festival director, 'talker' at festivals, or rabbit-hunt leader" [S51, p148]. Coercive leadership was completely absent; a leader "was followed as long as he was considered to be a 'good' leader. If he ceased to be such he lost his following" [S52, p66].

Movement and food acquisition: Western Shoshone population density was very low, annual ranges extensive, and family groups moved over large areas freely, associating with kin or unrelated families opportunistically. The primary role of a camp leader was to serve as a clearing house for information on ephemeral resource concentrations, and to coordinate movement to winter camps in the piñon pine groves.

Conflict resolution: Very little information exists on this domain for Shoshone. The inference is that conflicts were handled by avoidance (movement to other camps) and intercession of elder kin if necessary.

Between-group interactions: Because of extensive movement (see above), ethnolinguistic boundaries were almost nonexistent, and group membership was fluid and transitory. In most areas, warfare was scarce or absent, so military leaders were unknown until historic times led to conflict with Euro-American settlers.

References: See [S51-54] for further information underlying our ratings for the Shoshone.

Tsimane'. The Tsimane' are a group of forager-horticulturalists native to the Beni department of lowland Bolivia. The subsistence economy is based primarily on hunting, fishing, collecting, and swidden horticulture. The size of Tsimane' villages range from a few dozen to a few hundred individuals. Within villages, most individuals reside in multi-generational residential clusters composed of a number of nuclear families, often closely related. Families change residence within or between villages relatively at a relatively high frequency, often in response to major life transitions, local opportunities, or conflict. The present codes are intended to reflect the realities of leadership among the Tsimane' prior to the existence of political institutions that developed in the 1980s under the guidance of North American missionaries, which are known from ethnographic accounts and the living and written memory of Tsimane' adults.

Tsimane' leadership roles in the past apparently arose occasionally and facultatively, but were informal and less prominent (muted) in comparison to those of more complex neighboring groups, such as the Baure, Cayuvava, and Mojos. Members of Tsimane' residential clusters often recognized one individual as *ayo'*, who played a predominant role in decision-making and coordination within and between clusters. The term *baba* was employed for village leaders, who played a similar role at larger scales of integration. The positions were most commonly held by older adult men and (less frequently) women, with younger leaders arising in cases of exceptional charisma or acuity.

Under the guidance of North American missionaries in the 1980s, a governing council named the *Gran Consejo Tsimane'* was formed together with the offices of president and a variety of council members. Around the same time and under the same direction, community leaders called *corregidores* began to be appointed by a consensus process within each village; *corregidores* tend to hold office for a period of months or years, until they step down or consensus shifts to favor another community member. While a *corregidor* sometimes finds himself in a position to benefit from interactions with the outside world, many community members and past *corregidores* report avoiding the post due to its perceived burden.

Movement: Daily decisions regarding travel for productive, social, and other purposes were often decided spontaneously on an individual basis. An adult group member, including an *ayo'*, would also sometimes coordinate activities, particularly those requiring significant collective action, such as poison fishing events or some forms of horticultural labor. Children often accompanied parents for safety and to contribute help, but were also free to pursue their own independent activities under many circumstances. On longer time scales, decisions regarding where to live, for how long, were typically reached by adult consensus, with the potential for relatively stronger input from more influential family and cluster members, including the *ayo'*.

Food acquisition: As described above, food production decisions were undertaken in an essentially self-organized manner, with the possibility of top-down coordination by more influential adult family members. Poison fishing events—including the preparation of the poison and weirs, and harvest of fish—were often initiated and coordinated by one or several leading

adults. Burning new horticultural fields and harvesting were often undertaken collectively at the instigation of motivated individuals.

Within-group conflict resolution: An *ayo'*, *baba* or another prominent community member would sometimes play a role in mediating disputes within villages, and in deciding and realizing sanctions (punishment) against acts of wrong-doing recognized by the community.

Between-group interactions: Tsimane' oral histories recall the leadership of adult men in historical conflicts with the neighboring Moseten in the 19th and 20th centuries. Community leaders—the *babas* of the past and *corregidores* of the present—also played important roles in communicating and negotiating with outsiders, including river merchants, loggers, ranchers, highland colonists, NGOs, missionaries, and researchers. Exploitation by Spanish-speaking river merchants is reported to be the original proximate reason for the creation of the role of *corregidor*.

References: See [S55-60] for further information underlying our ratings for the Tsimane'.

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