



A theory of leadership in human cooperative groups

Paul L. Hooper*, Hillard S. Kaplan, James L. Boone

Department of Anthropology, University of New Mexico, MSC01 1040, Albuquerque, NM 87131, USA

ARTICLE INFO

Article history:

Received 6 April 2009

Received in revised form

1 April 2010

Accepted 27 May 2010

Available online 2 June 2010

Keywords:

Hierarchy

Leadership

Collective action

Free-rider problem

Social complexity

ABSTRACT

Two types of models aim to account the origins of rank differentiation and social hierarchy in human societies. Conflict models suggest that the formation of social hierarchies is synonymous with the establishment of relationships of coercive social dominance and exploitation. Voluntary or 'integrative' models, on the other hand, suggest that rank differentiation – the differentiation of leader from follower, ruler from ruled, or state from subject – may sometimes be preferred over more egalitarian social arrangements as a solution to the challenges of life in social groups, such as conflict over resources, coordination failures, and free-riding in cooperative relationships. Little formal theoretical work, however, has established whether and under what conditions individuals would indeed prefer the establishment of more hierarchical relationships over more egalitarian alternatives. This paper provides an evolutionary game theoretical model for the acceptance of leadership in cooperative groups. We propose that the effort of a leader can reduce the likelihood that cooperation fails due to free-riding or coordination errors, and that under some circumstances, individuals would prefer to cooperate in a group under the supervision of a leader who receives a share of the group's productivity than to work in an unsupervised group. We suggest, in particular, that this becomes an optimal solution for individual decision makers when the number of group members required for collective action exceeds the maximum group size at which leaderless cooperation is viable.

© 2010 Elsevier Ltd. All rights reserved.

"All sons of Adam need, for the protection of their welfare in this world and the next, society, mutual aid, and mutual assistance: both to procure benefits and to ward off injuries. For this reason man is said to be civil by nature. Now when men group together there are some things they have to do to procure their welfare and some they have to avoid as being harmful, and they will be obedient to one who ordains those desirable objects and proscribes what is injurious."

Ibn Taymīya (1982 [c. 1300])

1. Introduction

Explaining variation in social and political organization across human and non-human animal societies is a major goal in biology and the social sciences (Clutton-Brock et al., 2009; Diamond, 1997; Johnson and Earle, 1987; van der Leeuw and Kohler, 2007; Wilson, 1975). Understanding why some societies are more hierarchically organized than others is a particularly important aim in this area. Another way to phrase this question is to ask: what evolutionary and behavioral processes lead con-specifics to

be more vertically differentiated by social rank in some circumstances, but not others? Within our own species, why is it that some human groups exhibit relatively egalitarian distributions of social power, while others exhibit more recognizable distinctions between dominant and subordinate, leader and follower, chief and commoner, king and subject, or ruler and ruled (Boehm, 2001; Earle, 1997; Kaplan et al., 2009)?

A well developed body of theory in biology and anthropology suggests that many, if not all, cases of rank differentiation between two individuals (or groups) are the result of the competition between the two, and the distinction by rank effectively codifies the higher-ranking individual's ability to realize his or her own interests at the expense of the lower-ranking individual. It is this logic that presumably underlies the formation of dominance hierarchies in most hierarchical animal societies. Such rank differences are expected to arise when some individuals have a significant advantage over others, resource patches are economically monopolizable by advantaged individuals, and the disadvantaged are unable to seek better alternatives elsewhere. Important theoretical work in this area includes models of economic defensibility (Boone, 1992; Brown, 1964; Dyson-Hudson and Smith, 1978; van Schaik, 1989), territorial circumscription (Carneiro, 1970; Kennett et al., 2009), and reproductive skew (Buston et al., 2007; Johnstone, 2000; Summers, 2005; Vehrencamp, 1983).

* Corresponding author. Tel.: +1 505 850 2869; fax: +1 505 277 0874.
E-mail address: phooper@unm.edu (P.L. Hooper).

An alternative body of thought in political philosophy and the social sciences, however, has suggested that greater differentiation by social rank may in some cases be preferred over more egalitarian arrangements by both higher- and lower-ranking individuals as a solution to the key challenges of life in social groups, such as conflict over resources, coordination failures, and free-riding in cooperative relationships (Flannery, 1972; Hobbes, 1964 [1651]; Johnson and Earle, 1987; March and Simon, 1958; Sanders and Price, 1968; Service, 1962; Steward, 1955; Weber, 1968). The existence of facultative, cooperation-facilitating leadership roles in otherwise egalitarian small-scale human societies – such as Amazonian poison-fishing leaders or Inuit whaling captains – supports this conjecture (Brown, 1991; Friesen, 1999; Johnson and Earle, 1987). Countless despots across history have themselves expounded such theories in an effort to legitimize their wealth and power, whatever its origin (Baines and Yoffee, 1998; Kramer, 1981). However, most modern versions of this idea – sometimes labeled as ‘integrative’ or ‘voluntaristic’ theories of hierarchy formation – have relied on informal, group functionalist, or group selection arguments, a fact which has hampered their acceptance by biologists and biologically oriented social scientists (see Diehl, 2000). With a few notable exceptions (e.g. Smith and Choi, 2007; Van Vugt, 2006; discussed in more detail below), there has been little formal analysis establishing whether, and under what conditions, self-interested individuals would prefer the establishment of more hierarchical relationships over more egalitarian alternatives (Table 1).

This paper aims to fill this theoretical void by fleshing out a formal individual-based theory for the acceptance of leadership in cooperative groups. Our argument is the following: in some social, economic, and ecological circumstances, there are gains to cooperating in groups of significant size. Incentives for individuals to shirk or free-ride on the cooperative contributions of others, or simply the difficulty of coordinating action among multiple actors, however, can prevent the realization of these gains. These problems tend to become more serious as group size increases. While genetic relatedness, reputation tracking, and norm enforcement by regular group members can attenuate these problems in small or medium-sized groups, these effects likewise

tend to diminish as the number of actors increases beyond certain limits (Boyd and Richerson, 1988; Dixit, 2004; Olson, 1965). We propose that the effort of a leader can reduce the likelihood that cooperation fails due to free-riding or coordination errors, and that under some circumstances, un-coerced group members would prefer to cooperate in a group under the supervision of a leader who receives a share of the group’s productivity than to work in an unsupervised group. We suggest, in particular, that this becomes an optimal solution for individual decision makers when the number of group members required for collective action exceeds the maximum group size at which leaderless cooperation is viable. The transition to cooperation under leadership should thus occur when the benefits from being able to successfully cooperate at larger scales exceed the costs of having a leader. This theory aims to contribute to our understanding of both the emergence of facultative leadership roles in small-scale human societies, as well as the emergence of more institutionalized functional hierarchies in larger-scale complex societies.

To examine the conditions under which enforcement by a leader can be a mutually preferred solution to the problem of cooperation in groups, we develop an evolutionary game theoretical model based on the public goods game in which the benefits of and scale required for cooperation are characteristics of the group’s ecological or economic niche. In Sections 2.1–2.3, we analyze the conditions under which collective action is sustainable without reinforcement, sustainable under mutual monitoring by group members, sustainable under reinforcement by a leader, or ultimately unsustainable. In the case that selection favors cooperation reinforced by leadership, in Section 2.4 we examine the expected division of benefits between leaders and followers, and the conditions that promote more or less egalitarian distributions of the spoils. We follow this with a discussion of related theoretical models, institutions of leadership in traditional human societies, and the complex interplay between leadership and social dominance in biological and anthropological theory.

2. A model for the evolution of collective action under leadership

2.1. The basic repeated public goods game

We begin with a model of a repeated public goods game, following the basic framework presented by McElreath and Boyd (2007, Section 4.5). Each generation, groups of size n are randomly formed from a very large population. Every round, each group member can cooperate by contributing to a public good, or defect and free-ride on the contributions of others. Those who contribute to the public good pay a private cost c and generate a public benefit b that is shared equally among all n group members. The probability that the group persists and continues to play the public goods game in the next round is w , meaning that groups play for an average of $1/(1-w)$ rounds. After play ends, agents reproduce according to their final payoff across all rounds and die.

In this setting, under what conditions could the strategy ‘always cooperate’ (conventionally labeled ALLC) out-compete the strategy ‘always defect’ (ALLD)? If there are x other cooperators in the group, the cooperator receives a payoff of

$$V(\text{ALLC}|x) = \frac{(x+1)b/n-c}{1-w}. \quad (1)$$

The defector, on the other hand, receives a payoff of

$$V(\text{ALLD}|x) = \frac{xb/n}{1-w}. \quad (2)$$

Table 1
Summary of variables used in the text.

Variable	Description
b	Benefit produced by contributing to the public good
c	Cost of contributing to the public good
n	Number of individuals in the group
w	Probability of interacting in a further round of play
s	Cost imposed on defectors (i.e. sanction or punishment)
\hat{s}	Cost imposed on non-taxpayers
c_m	Cost of monitoring one group member
c_s	Cost of punishing one defector
\hat{c}_s	Cost of punishing one non-taxpayer
t	Fraction of the benefits from cooperation appropriated by the leader (i.e. tax rate)
t_{egal}	Tax rate that yields equal payoffs to the leader and regular group members
V_0	Baseline fitness (added to each strategy’s payoff to calculate final fitness)
p	Fraction of pure cooperators in the acephalous population
q	Fraction of mutual monitors in the acephalous population
r	Fraction of reluctant cooperators in the acephalous population
$Q = 1 - (1-q)^{n-1}$	Likelihood that at least one other individual in the group is a mutual monitor
u	Fraction of pure cooperators in the hierarchical population
v	Fraction of willing taxpayers in the hierarchical population
y	Fraction of individuals willing to lead in the hierarchical population

Comparing these two expressions, the cooperator strategy can both invade and resist invasion by the defecting strategy as long as

$$b/n > c. \tag{3}$$

When this inequality is satisfied, contributing to the public good is simply self-interested, and the individual's marginal gain from contributing is positive regardless of other group members' contributions. This condition informs us that free unilateral contribution can only be sustained when its benefits are high relative to its costs and the group size is very small, which presents a major challenge to successful collective action in sizeable groups.

2.2. The public goods game under mutual monitoring and punishment

One potential solution to the problem of free-riding in collective action would be a conditional cooperator strategy analogous to the tit-for-tat reciprocator strategy in dyadic cooperation that 'punishes' non-cooperation with defection. This strategy, however, faces the problem that punishment cannot be directed solely toward defectors, and only garners higher payoffs than unconditional defection if all group members are conditional cooperators, which makes invasion nearly impossible except for very small group sizes (Boyd and Richerson, 1988; McElreath and Boyd, 2007).

A more promising route to self-supporting cooperation comes in the form of strategies that specifically target punishment at defectors (Boyd and Richerson, 1992; Boyd et al., 2003; McElreath and Boyd, 2007). Consider a mutual monitoring strategy (MM) that always cooperates and pays a cost c_m to monitor the contributions of each other group member each round. If any individuals in the group defect, the mutual monitor pays cost c_s to reduce the defector's payoff by s immediately following the round. These costs may be expected to vary as functions of the socioecology and technology of production or competition. The cost of monitoring, for example, should be lower when contributions are more openly observable and objectively measurable, or group members work simultaneously in the same location (Alchian and Demsetz, 1972).

We consider the evolution of mutual monitoring in the face of two competing strategies: pure cooperators (ALLC), who contribute to the public good but do not punish non-contributors; and reluctant cooperators (RC), who defect until they are punished, then (assuming the punishment is sufficiently severe) cooperate in every subsequent round.¹ Assuming that unconditional cooperation is unsustainable (i.e. condition (3) is not satisfied), under what conditions could mutual monitoring invade a population of reluctant cooperators?

On the first round, a monitor contributes to the public good, monitors all other group members' contributions, and punishes all those who defect. Thus, the monitor's first-round payoff in a group composed of $n - 1$ reluctant cooperators is

$$V_1(\text{MM}|\text{RC}) = b/n - c - (c_m + c_s)(n-1). \tag{4}$$

¹ Like Boyd and Richerson (1992) and McElreath and Boyd (2007), we set aside the unconditional defector strategy ALLD, for the reason that in any population in which punishment arises even occasionally, ALLD would continue to defect and suffer punishment in every round; as long as s is sufficiently large (condition (5)), this loss in fitness would eventually to ALLD's replacement by the more socially aware RC strategy. It is worth recognizing that mutual monitors attempting to invade a population in which there are still a significant number of unconditional defectors would face harsher invasion criteria, as the monitor's cost of punishing would have to be paid repeatedly and yield no benefit.

The payoff of each reluctant cooperator is reduced by s , which will be sufficient to discourage defection as long as the cost of being punished exceeds the net cost of contributing to the public good, or

$$s > c - b/n. \tag{5}$$

When the punishment is sufficiently severe, all group members will cooperate in all subsequent rounds. The final payoff to an invading monitor is then

$$V(\text{MM}|\text{RC}) = b/n - c - (c_m + c_s)(n-1) + \frac{w}{1-w} [b - c - c_m(n-1)]. \tag{6}$$

For the monitoring strategy to proliferate, its payoff must exceed the payoff of reluctant cooperators amidst their own type, or $V(\text{MM}|\text{RC}) > V(\text{RC}|\text{RC})$. As unmonitored reluctant cooperators incur no costs and confer no benefits, $V(\text{RC}|\text{RC})$ is simply zero. Monitors can thus invade as long as

$$b/n - c - (c_m + c_s)(n-1) + \frac{w}{1-w} [b - c - c_m(n-1)] > 0. \tag{7a}$$

Rearranging, this yields

$$b \left(\frac{1}{n} + \frac{w}{1-w} \right) > c_s(n-1) + \frac{1}{1-w} [c + c_m(n-1)]. \tag{7b}$$

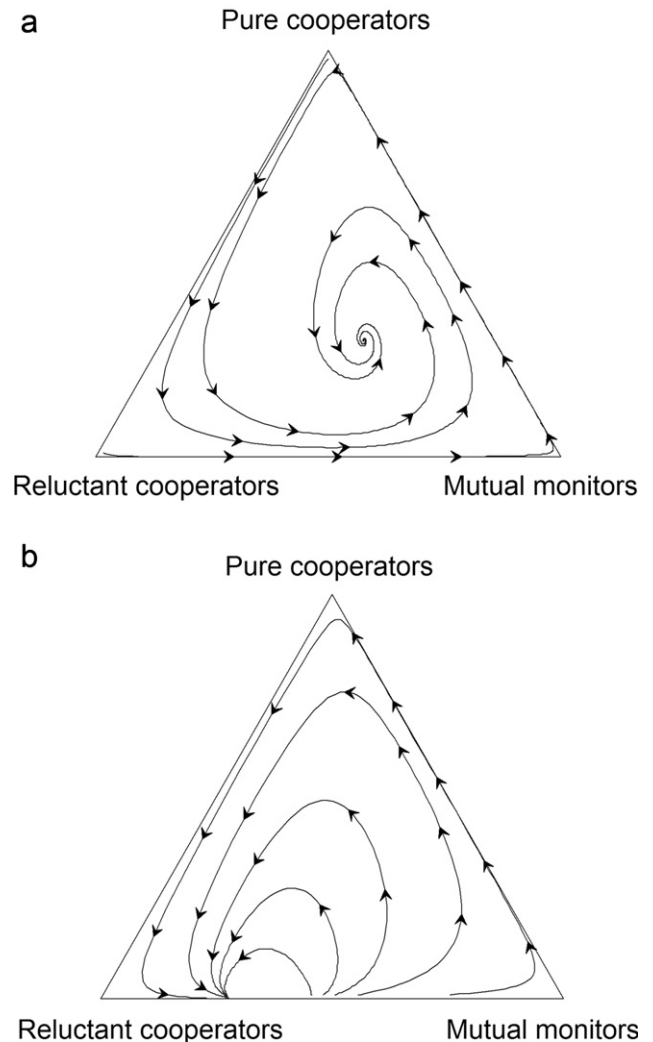


Fig. 1. The convergent dynamics of pure cooperators, mutual monitors, and reluctant cooperators in an acephalous population. In both panels $b=2$; $c=1$; $w=0.9$; $c_m=0.05$; $c_s=0.15$; $s=1.5$; and $V_0=10$. In panel (a) $n=3$; while in panel (b) $n=5$. (These plots were generated using the Baryplot R package provided in McElreath, 2008.)

This condition simply dictates that the long-term benefits of cooperation, monitoring, and punishment (left-hand side) must exceed their costs (right-hand side) for mutual monitors to invade a population of reluctant cooperators. Because an invading monitor must monitor and (in the first round) sanction all other members of the group, the invasion of mutual monitoring becomes more unlikely in larger groups, or when the costs of monitoring or sanctioning are high relative to the benefits of fellow group members' cooperation.

The conditions that allow mutual monitors to invade reluctant cooperators, however, do not guarantee a perfectly cooperative equilibrium (McElreath and Boyd, 2007). Specifically, mutual monitoring tends to be vulnerable to invasion by 2nd-order free-riders – such as pure cooperators, ALLC – who contribute to the public good but do not punish non-cooperators. Because pure

cooperators receive the benefits of collective action but avoid the costs of monitoring, they can actively invade a population of monitors as long as monitoring involves some non-zero cost (i.e. $c_m > 0$; if instead $c_m = 0$, ALLC receives the same payoff as MM in the absence of defection, and can thus drift passively into a population of MMs.)

In order to calculate the expected payoff to each strategy given a mix of strategies in the population, let p represents the fraction of pure cooperators, q the fraction of monitors, and r the fraction of reluctant cooperators, with $p + q + r = 1$. A monitor receives the benefits of cooperation produced by himself and the other MMs and ALLCs in all rounds, and those produced by reluctant cooperators in all but the first round; from this we subtract the cost of contributing and monitoring in all rounds, as well as the cost of punishing each reluctant cooperator in the first round. Thus

$$V(\text{MM}|p,q,r) = \frac{1}{1-w} [(1+(p+q+wr)(n-1))b/n - c - c_m(n-1)] - rc_s(n-1). \tag{8}$$

A pure cooperator similarly receives the benefits of cooperation produced by himself and the other MMs and ALLCs, and pays the cost of contributing in all rounds. A pure cooperator, however, will only benefit from the cooperation of reluctant cooperators if the group also contains a monitor to punish them. Let Q represent the probability that at least one other group member is a monitor, where $Q = 1 - (1-q)^{n-1}$. The expected payoff to a pure cooperator is thus

$$V(\text{ALLC}|p,q,r) = \frac{1}{1-w} [(1+(p+q+Qwr)(n-1))b/n - c]. \tag{9}$$

A reluctant cooperator receives the benefits of cooperation by MMs and ALLCs in all rounds, but he and his fellow reluctant cooperators will only contribute after the first round if at least one monitor is present. On average, punishment reduces the reluctant cooperator's payoff by s for each monitor in the group. Thus

$$V(\text{RC}|p,q,r) = \frac{1}{1-w} [(Qw+(p+q+Qwr)(n-1))b/n - Qwc] - sq(n-1) \tag{10}$$

(One should note that these payoffs are expected means across groups in a large, well-mixed population, and that individual payoffs will vary depending on specific group composition, especially when groups are small.)

The evolutionary dynamics of this system once mutual monitoring has invaded – addressed in more detail in the Online Appendix – can be summarized roughly as follows:

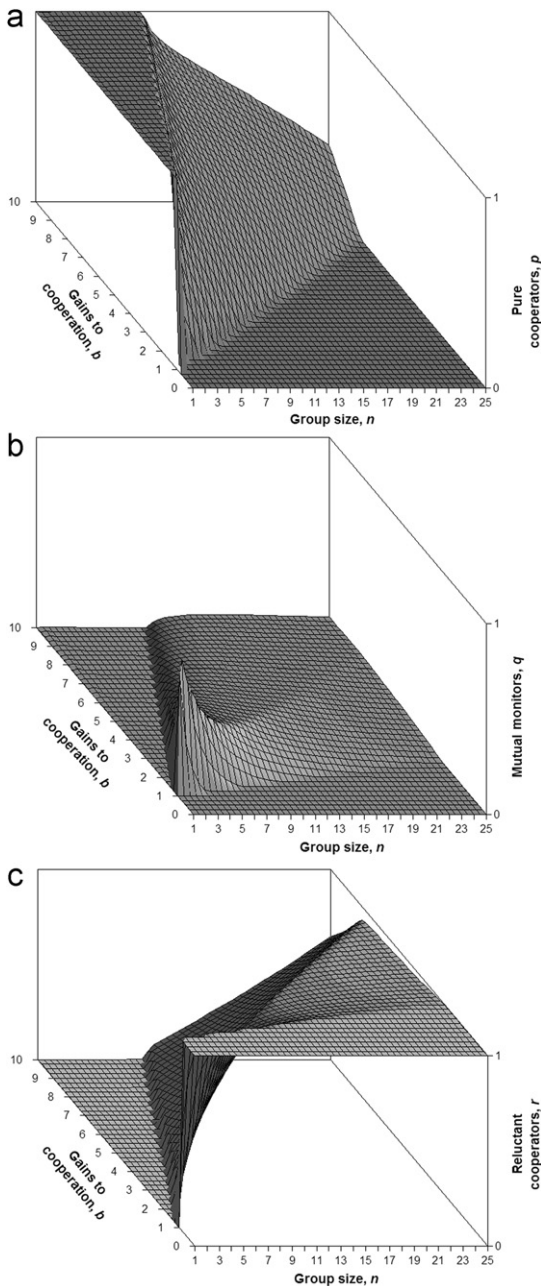


Fig. 2. Equilibrium frequencies of pure cooperators p , mutual monitors q , and reluctant cooperators r as functions of group size n and the gains to cooperation b in an acephalous population. $c = 1$; $w = 0.9$; $c_m = 0.05$; $c_s = 0.15$; $s = 1.5$; and $V_0 = 40$.

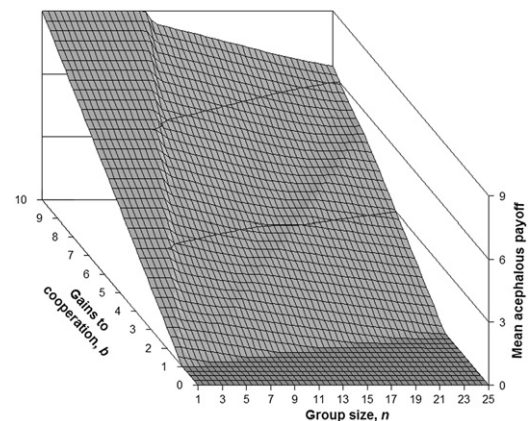


Fig. 3. Mean payoff per round to members of acephalous groups at equilibrium given the frequency of each strategy from Fig. 2.

- (a) Monitors are able to increase in the population when there are enough reluctant cooperators and few enough pure cooperators and monitors that monitoring yields a high differential benefit to individual monitors.
- (b) If monitoring is costly, pure cooperators gain an advantage over mutual monitors when there are few reluctant cooperators to defect, or at least enough willing monitors to neutralize the threat of their defection.
- (c) Reluctant cooperators, in turn, regain an advantage over pure cooperators when there are few enough monitors that defection is likely to go unpunished.

Fig. 1a illustrates these dynamics in a system that supports a stable mix of all three strategies at equilibrium, while Fig. 1b illustrates a case that supports only mutual monitors and reluctant cooperators at equilibrium.

The long-term outcome of the dynamics inherent in Eqs. (8)–(10) depends on the model's environmental parameters. Fig. 2 shows the equilibrium frequency of pure cooperators, mutual monitors, and reluctant cooperators as a function of group size and the gains to cooperation. The basic relationship is intuitive. Pure cooperators dominate when the gains to cooperation are high enough and group size is small enough that condition (3) holds. When unenforced cooperation becomes untenable due to increasing group size, mutual monitors and reluctant cooperators are able to enter the population and all three strategies co-exist at equilibrium (as in Fig. 1a). Past a certain threshold group size, however, the pure cooperator strategy becomes unsustainable, and the population is dominated by a mix of mutual monitors and reluctant cooperators (as in Fig. 1b); as group size continues to increase, the number of mutual monitors diminishes toward zero and defection dominates over cooperation. The decline in payoffs as cooperation and monitoring collapse due to increasing group size is shown in Fig. 3.

The results in Figs. 1–3 assume quite low costs of monitoring and sanctioning, which are fortuitous for the evolution of mutual monitoring. The range of group sizes that allow high levels of cooperation supported by mutual monitoring is further reduced with both higher costs of monitoring and sanctioning, and a lower probability of future interaction, as illustrated in Fig. 4b and c, respectively.² Intuitively, while the cost of inflicting punishment is often assumed to be significantly lower than the cost incurred by the punished individual (e.g. Boyd et al., 2003), high levels of costly punishment become unlikely when the cost of punishing is high. Fig. 4b represents the outcome under somewhat higher costs of monitoring and punishment, while Fig. A1 in the online appendix illustrates the effect of even greater costs.

2.3. The invasion of cooperation under leadership

Under the conditions that neither unconditional cooperation nor mutual monitoring can be maintained at a very high level, we consider a third possibility: cooperation reinforced by the effort of a leader who receives a share of group productivity. The following section examines the conditions under which a preference for hierarchical cooperation may invade a population dominated by non-cooperation.

Consider that each player may either be willing or unwilling to join a hierarchical group. Those who are unwilling to join

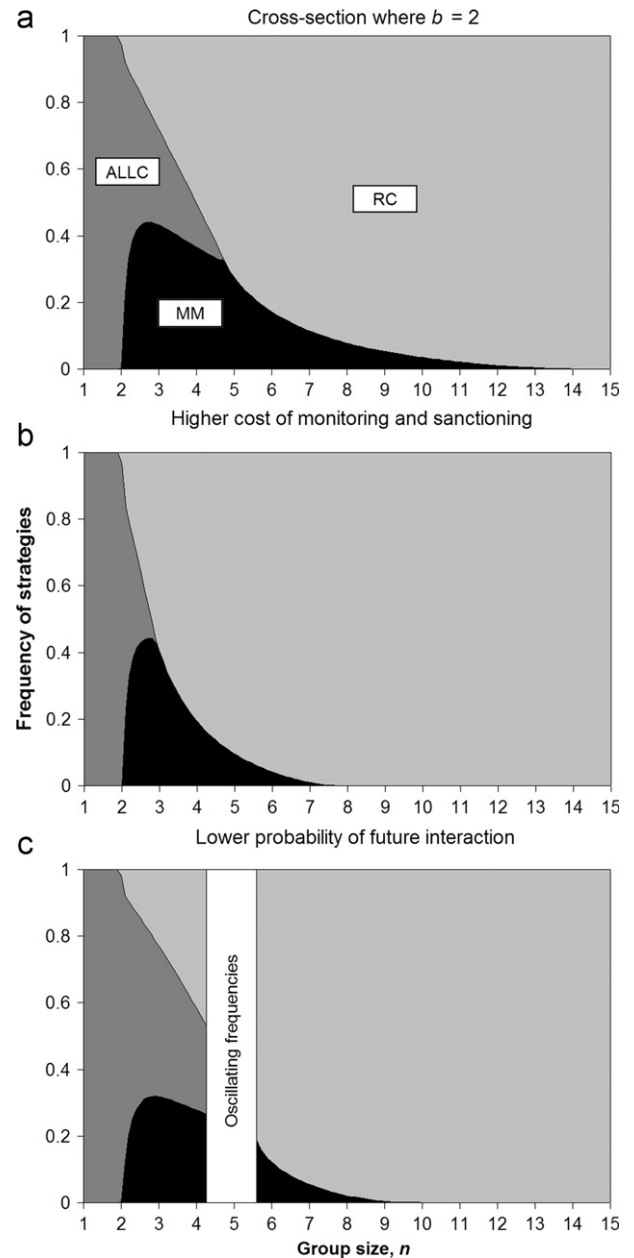


Fig. 4. Equilibrium frequencies of pure cooperators p (darker gray), mutual monitors q (black), and reluctant cooperators r (lighter gray) as functions of group size n in an acephalous population. The three frequencies are stacked and sum to one. (a) Baseline parameter values: $b=2$; $c=1$; $w=0.9$; $c_m=0.05$; $c_s=0.15$; $s=1.5$; and $V_0=40$. (b) Doubled costs of monitoring and sanctioning: $c_m=0.1$ and $c_s=0.3$. (Fig. A1 in the online appendix illustrates the effect of even greater costs, given $c_m=0.3$ and $c_s=0.6$). (c) Decreased probability of future interaction: $w=0.8$.

hierarchical groups continue to operate in leaderless or acephalous (“headless”) groups as one of the non-hierarchical types defined above (ALLC, MM, or RC). Those who are willing to join a hierarchical group may be either willing to lead (L) or unwilling to lead (UL). An individual who is willing to lead is willing to act as leader in a hierarchical group at a particular tax rate t , which is an evolvable attribute of each willing leader.

Each generation, individuals with hierarchical preferences are randomly sorted into groups composed of one leader and n normal group members. If any hierarchy-oriented group is formed that does not contain one individual who is willing to lead, group members simply play as non-hierarchical types as before.

² One may note that not all regions of the parameter space converge to single-point equilibria. Some converge on stable limit-cycles, in which the frequencies of the three strategies continually oscillate. Other parameter values produce unstable limit-cycles, which cause the system to spiral out to the extremes of the strategy space without converging. Fig. 4, for example, contains a region of intermediate group sizes in which the system does not converge to single-point equilibrium.

Within each hierarchical group, if there are multiple individuals who are willing to lead, we assume that the leader is determined by majority choice (or some similar mechanism) within the group. If group members are unrelated and the event of every individual voting for him or herself is disallowed, this process will result in the individual offering the lowest tax rate to be chosen as leader. Those who are willing to lead but are not chosen as leaders then act as regular hierarchical group members. (We assume here that the process of appointing a leader is costless, at least at the outset of the game; we consider the effect of costs to replace an appointed leader in Section 2.4 below.)

As before, regular members of hierarchical groups either contribute to the public good every round (a behavioral type which we will label H.ALLC), or free-ride each round until punished, then contribute thereafter (H.RC). Like mutual monitors, the leader pays a cost c_m to monitor each group member in each round and reduces the payoff of any defector by s at personal cost c_s .

If the leader has direct access to the public good, he or she may extract his or her fraction of benefits from the public good directly – increasing his or her payoff by tbx per round, if x is the number of contributors to the public good – and group members do not face the option of avoiding taxation. If, on the other hand, normal group members have direct control of their share of benefits of the public good, they may be tempted to not pay the leader's tax. We thus consider both a willing taxpayer strategy (H.T) that always pays the tax, and a reluctant taxpayer strategy (H.RT) that does not pay the tax until punished, then pays it in every subsequent round. If the temptation to evade taxes is indeed present in a population, we assume that the leader can additionally reduce the payoff of non-taxpayers by \hat{s} at a personal cost \hat{c}_s , and thereby motivate their payment of taxes in each subsequent round.

To clarify, each individual who is willing to join a hierarchical group is defined by three independent traits: they are either willing to lead (L) or unwilling to lead (UL); either a pure cooperater (H.ALLC) or a reluctant cooperater (H.RC); and either a taxpayer (H.T) or a reluctant taxpayer (H.RT). For notation, we concatenate the labels of regular group members using a period to delimit the dimensions; for example, H.RC.T represents a hierarchical reluctant cooperater taxpayer, while H.ALLC.RT represents a hierarchical pure cooperater reluctant taxpayer. Furthermore, when a strategy label appears as an argument in a payoff function, that payoff represents the payoff to that strategy when it actively played (not held latent); thus $V(L)$ represents the payoff to a willing leader who has actually been chosen as leader within his or her group, while $V(H.ALLC.T)$ represent the payoff to a hierarchical cooperating taxpayer who is indeed acting out that role as a regular hierarchical group member.

Assuming that enough individuals with hierarchical preferences have drifted into the population to form a group of $n+1$ players, and that at least one of these is willing to lead, under what conditions could hierarchical preferences invade a population dominated by reluctant cooperators? Let the fraction of hierarchical pure cooperators (H.ALLC) equal u and hierarchical reluctant cooperators (H.RC) equal $1-u$; let the fraction of hierarchical taxpayers (H.T) equal v and hierarchical reluctant taxpayers (H.RT) equal $1-v$. The leader offering the lowest tax rate t among those willing to lead in the group will then receive a first-round payoff of

$$V_1(L|u,v) = uvtbn - c_m n - (1-u)c_s n - (1-v)\hat{c}_s n. \quad (11)$$

If s and \hat{s} are sufficiently large to offset the benefits of defecting and refusing to pay the tax, group members will contribute and pay their taxes in each subsequent round. Because the benefits of contributing are diminished by taxation, the minimum punish-

ment s for reluctant cooperators must be higher in the leadership case than in the mutual monitoring case (condition (5)); thus

$$s > c - (1-t)b/n. \quad (12)$$

The minimum punishment \hat{s} for reluctant taxpayers must simply exceed the cost of the taxes themselves, which depends on both the tax rate and the magnitude of the public good produced. To guarantee full tax-paying when the potential gains to tax evasion are highest (namely, when all group members contribute to the public good) thus requires

$$\hat{s} > tb. \quad (13)$$

When the sanctions are sufficient to motivate both cooperation and tax-paying, the leader's final payoff across all rounds will be

$$V(L|u,v) = uvtbn - c_m n - (1-u)c_s n - (1-v)\hat{c}_s n + \frac{w}{1-w}(tb - c_m)n \quad (14)$$

The leader's payoff will exceed the mean payoff in a population dominated by acephalous reluctant cooperators when $V(L|u,v) > 0$, or

$$\left(uv + \frac{w}{1-w}\right)tb > \frac{1}{1-w}c_m + (1-u)c_s + (1-v)\hat{c}_s. \quad (15a)$$

Rearranging, this yields

$$t > \frac{c_m/(1-w) + (1-u)c_s + (1-v)\hat{c}_s}{[uv + w/(1-w)]b}. \quad (15b)$$

For the leader to have a payoff advantage over acephalous defectors, he or she must receive a fraction of group proceeds that is greater than the ratio of the costs of monitoring and sanctioning to the taxable benefits. In the most favorable circumstances for invasion, all hierarchical group members would be tax-paying pure cooperators, in which case this condition simplifies to

$$t > c_m/b. \quad (15c)$$

In the least favorable circumstances, where all cooperation and tax-paying must be enforced by punishment, the condition simplifies to

$$t > \frac{c_m + (1-w)(c_s + \hat{c}_s)}{wb}. \quad (15d)$$

Condition (15) assures that the chosen leader's willingness-to-lead trait will proliferate relative to acephalous defection. If other members of the hierarchical group are also willing to lead, whether their latent leadership trait proliferates as well depends on their payoff as regular group members.

The payoff to the regular members of a hierarchical group depends on their willingness to contribute to the public good, as well as their willingness to pay the leader's tax. The payoff functions for each of the four possible types are the following:

$$V(H.ALLC.T|u,v) = [1 + u(n-1)](1-t)b/n - c + \frac{w}{1-w}[(1-t)b - c]; \quad (16)$$

$$V(H.ALLC.RT|u,v) = [1 + u(n-1)]b/n - c - \hat{s} + \frac{w}{1-w}[(1-t)b - c]; \quad (17)$$

$$V(H.RC.T|u,v) = u(n-1)(1-t)b/n - s + \frac{w}{1-w}[(1-t)b - c]; \quad (18)$$

and

$$V(H.RC.RT|u,v) = u(n-1)b/n - s - \hat{s} + \frac{w}{1-w}[(1-t)b - c]. \quad (19)$$

The mean payoff of these strategies, weighted by their frequencies, is then

$$\bar{V}(H|u,v) = u(1-vt)b - uc - (1-u)s - (1-v)\hat{s} + \frac{w}{1-w}[(1-t)b - c]. \quad (20)$$

On average, the regular members of a hierarchical group will increase relative to acephalous defectors when $\bar{V}(H|u,v) > 0$, or

$$\left(u + \frac{w}{1-w}\right)(b-c) > \left(uv + \frac{w}{1-w}\right)tb + (1-u)s + (1-v)\hat{s}. \quad (21a)$$

This condition tells us that hierarchical group members will proliferate when then the net benefits of cooperation (left side) exceed the costs of taxation and punishment by a leader (right side). Isolating the tax term, this condition places a maximum on the tax rate such that

$$t < \frac{[u + w/(1-w)](b-c) - (1-u)s - (1-v)\hat{s}}{[uv + w/(1-w)]b}. \quad (21b)$$

In the less restrictive case that all members of the group contribute and pay the tax, this simplifies to

$$t < 1 - c/b. \quad (21c)$$

In the more restrictive case that all members are reluctant to both contribute and to pay the tax, the condition is instead

$$t < 1 - [c + (1/w - 1)(s + \hat{s})]/b. \quad (21d)$$

The restrictions that conditions (15) and (21) place on the tax rate of a hierarchical group invading a population of defectors are illustrated in Fig. 5. As the gains to cooperation increase, the range of viable invading tax rates expands. The range is more limited when group members are reluctant to cooperate or pay taxes, because both the productivity of the public good and the profitability of leadership are reduced. Increased costs of monitoring and sanctioning increase only the leader's minimum tax rate (condition (15); Fig. 5b). A decreased probability of future interaction shrinks the range of viable taxes only when some initial group members do not cooperate or pay taxes (conditions (15d) and (21d); Fig. 5c). Invasion is impossible at any tax rate for values of b less than or equal to $c + c_m$.

While conditions (15) and (21) specify the circumstances under which hierarchical preferences can invade a population of pure reluctant cooperators, leadership may also be capable of invading populations in which mutual monitoring only imperfectly stabilizes cooperation. This would require that the hierarchical group member and leader's payoffs exceed the mean payoff of acephalous group members given whatever mix of monitors, pure cooperators, and reluctant cooperators exists in the population at the time. Here we can specifically compare the success of hierarchical strategies against the equilibrium mix of acephalous strategies found in the preceding section and represented in Fig. 2.

Fig. 6 shows the expected equilibrium cooperative regime as a function of group size n and the gains to cooperation b . Free unilateral cooperation dominates where the gains to cooperation are very high and achievable in very small groups in accordance with condition (3). Where this condition is not fulfilled, however, some form of monitoring and punishment becomes necessary for successful collective action. As established in the preceding section, some amount of cooperation under mutual monitoring can be sustained where $b/n < c$, but this amount decreases steadily with increasing group size. As group size continues to increase, the system passes a threshold across which hierarchical strategies can earn higher mean payoffs than individuals in acephalous groups. Fig. 6 shows the location of this threshold assuming that hierarchical preferences will invade as long as a tax rate exists that gives both the leader and group members higher than the acephalous payoff, and that hierarchical group members are not initially reluctant to cooperate or pay taxes (i.e. $u = v = 1$; the alternative assumption that group members are reluctant shifts the threshold slightly to the right). Cooperation under leadership thus becomes the more profitable and competitive strategy when the gains to cooperation are too low or the group

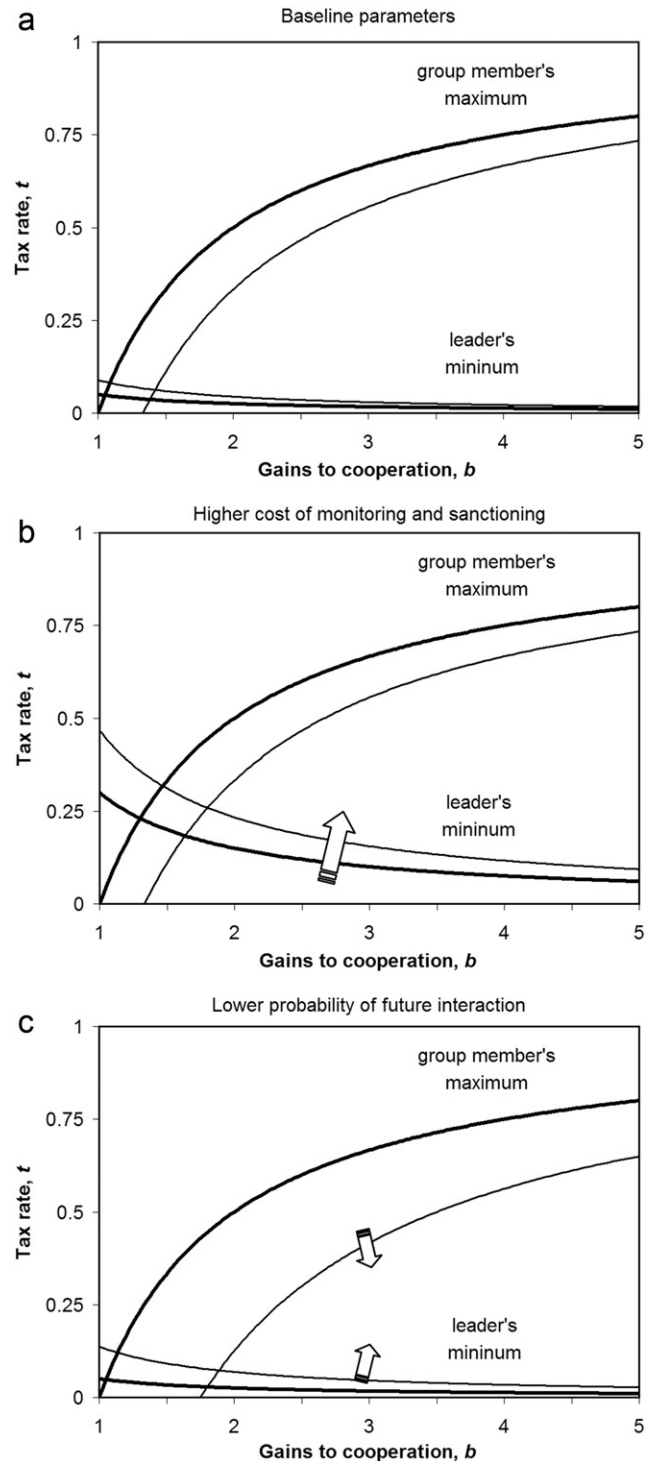


Fig. 5. The minimum and maximum tax rates allowable for the invasion of hierarchical types into a population dominated by defectors. The thicker black lines represent the limits when all invading group members are tax-paying cooperators, while the thinner black lines represent those when all invading group members are reluctant to both cooperate and pay taxes. These minimum and maximum values are given by conditions (15) and (21) in the text, respectively. (a) Baseline parameter values: $c = 1$; $c_m = 0.05$; $c_s = \hat{c}_s = 0.15$; $s = \hat{s} = 1.5$; and $w = 0.9$. (b) Higher costs of monitoring and sanctioning: $c_m = 0.3$ and $c_s = \hat{c}_s = 0.6$. (c) Lower probability of future interaction: $w = 0.8$. These constraints are unaffected by group size.

size is too large to allow dependable cooperation in acephalous groups.

Preferences for acephalous versus hierarchical groups also depend on the cost of monitoring and sanctioning. In contrast to

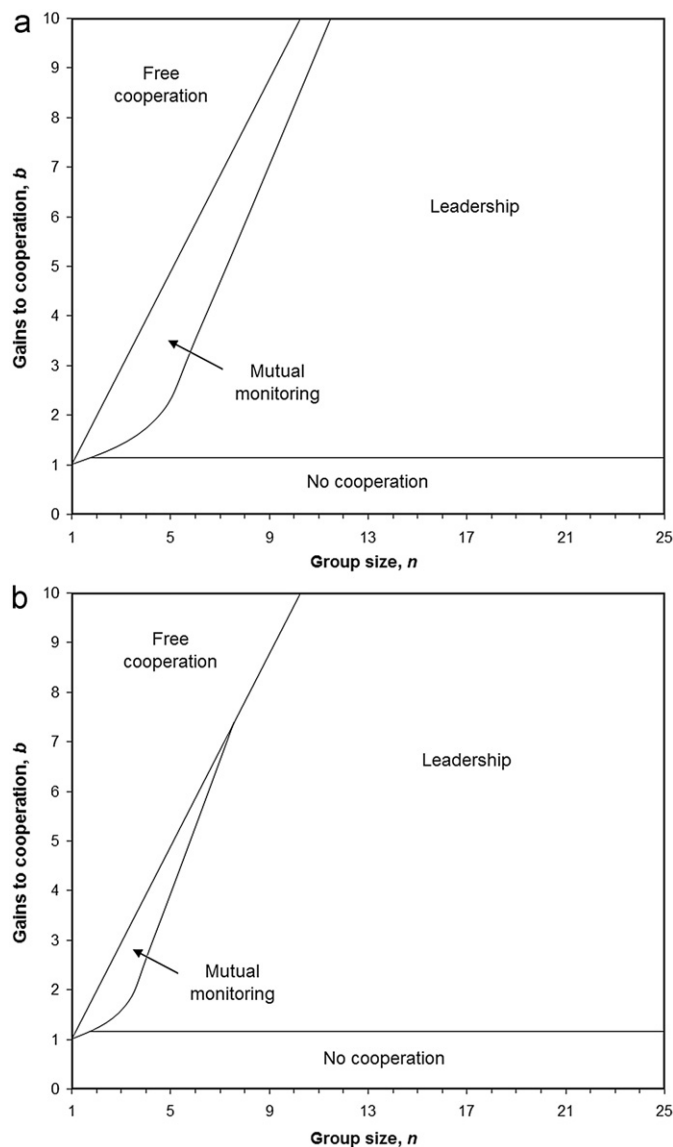


Fig. 6. Equilibrium cooperative regime as a function of group size and the gains to cooperation. (a) Baseline parameter values: $c=1$; $w=0.9$; $c_m=0.05$; $c_s=0.15$; $s=1.5$. (b) Doubled costs of monitoring and sanctioning: $c_m=0.1$ and $c_s=0.3$. (Fig. A2 in the online appendix illustrates the effect of even greater costs, given $c_m=0.3$ and $c_s=0.6$).

mutual monitoring's strong dependence on low monitoring costs, leadership remains quite robust to increased monitoring costs as long as the benefits produced from cooperation are sufficient to cover them. Fig. 6a represents the expected outcome under fairly low costs of monitoring and sanctioning, while Fig. 6b gives the outcome under somewhat higher costs; Fig. A2 in the online appendix illustrates the effect of even greater costs. As the cost of monitoring increases, the equilibrium level of cooperation under mutual monitoring declines quickly, and the transition from accephalous cooperation to cooperation under leadership occurs at lower values of b and n . It is notable that the current configuration does yield a difference in efficiency in the monitoring mechanism of mutual monitors versus leaders: specifically, when all group members monitor all other group members, the total cost of monitoring in the group is $n(n-1)c_m$, whereas when a leader monitors all group members, the cost is nc_m . This difference in efficiency, however, is not crucial to the model, and the results remain qualitatively similar even if the total costs of full monitoring in accephalous groups are made to scale linearly with

group size, as a result of the fact that the individual marginal benefit of monitoring one individual still declines steady with increasing group size.

2.4. The evolution of strategies and the negotiation of taxation within a hierarchical population

If hierarchical types can indeed proliferate in an accephalous population, the expected evolution of the hierarchical group member types amongst themselves is clear: as long as the sanctions are sufficiently strong (conditions (12) and (13)), tax-paying pure cooperators will always out-compete their more reluctant peers. For simplicity, then, we focus on the evolution of hierarchical populations dominated by tax-paying pure cooperators (i.e. where $u=v=1$) throughout the rest of the paper. The regular hierarchical group member's payoff in this case becomes

$$V(H) = \frac{1}{1-w} [(1-t)b-c]. \quad (22)$$

What then, of the evolution of the willingness to lead and the tax offers of potential leaders within the hierarchical population? At any time, there is some fraction of individuals in the hierarchical population who are willing to lead – say, y – and there is some distribution of tax levels offered by those who are willing to lead. We thus assume that in the random formation of groups, each group will contain on average $y(n+1)$ individuals willing to lead, and that these potential leaders offer tax levels that are randomly sampled from the distribution of tax levels in the population.

As stated earlier, in the absence of contrary interests, group members will choose the individual who is willing to lead at the lowest tax rate among from among all the $y(n+1)$ potential leaders in the group. Given full cooperation and tax-paying, this individual will receive

$$V(L) = \frac{1}{1-w} (tb - c_m)n \quad (23)$$

Those who would be willing to lead but do not because their offered tax level is rejected will receive the regular hierarchical group member's payoff (22).

Selection will act against the willingness-to-lead traits of chosen leaders who offer tax rates that give them less than the average payoff of the hierarchical population as a whole. The beneficiaries of this self-sacrifice will be those chosen leaders and unchosen potential leaders offering higher tax rates, as well as hierarchical group members who are unwilling to lead. If the hierarchical population begins with a distribution of potential tax offers that dips below the rate at which leaders receive at least as much as normal group members, selection will continue to drive the most generous leaders to extinction until the most generous are offering tax rates that yield payoffs at least as good as the regular hierarchical group member's payoff.

Once chosen leaders are earning even slightly more than regular group members, the willingness to lead will increase in the population, if it is not already widespread. Among those willing to lead, those who are actually chosen as leaders will increase relative to those offering higher tax rates who are not, and who are therefore receiving the regular hierarchical group member's payoff. Thus, selection will simultaneously work to prune the upper end of the distribution of tax offers.

Assuming that a willingness to lead at a particular tax level t_δ that gives the leader an advantage of δ above regular group members such that $V(L|t_\delta) = V(H|t_\delta) + \delta$ becomes dominant as the lowest tax level offered in the population, could a willingness to lead at a lower tax rate t_ε invade, where $V(L|t_\varepsilon) = V(H|t_\varepsilon) + \varepsilon$ and $0 < \varepsilon < \delta$? It can as long as a large enough fraction of individuals offering the higher tax level t_δ are out of work and earning the

(even lower) regular group member's payoff. With time, there should indeed be a significant number of unemployed potential leaders offering the current-lowest tax rate t_δ , because taxes have been selected downwards toward the level that results in an actual leadership payoff; thus the current-lowest tax rate should indeed be supplantable by one that is slightly lower but still at least slightly more than regular group members.

This process will cause the tax rate offered by potential leaders to converge on that which yields equal payoffs to group members and leaders, $V(L)=V(H)$, or

$$(1-t)b-c=(tb-c_m)n. \tag{24}$$

Isolated, this economically egalitarian tax rate is:

$$t_{\text{egal}} = \frac{b-c+c_m n}{b(n+1)}. \tag{25}$$

We expect the mean tax level offered in the population to converge on this value as greedier leaders are undercut (and out-reproduced) by more generous leaders. Substituting this tax rate back into either Eq. (22) or (23) yields both leader and group members a payoff of

$$V(L) = V(H) = \frac{1}{1-w} (b-c-c_m) \frac{n}{n+1}. \tag{26}$$

Fig. 7 shows the equilibrium egalitarian tax rate as a function of b , n , and c_m , while Fig. 8 shows the resulting payoff to leaders

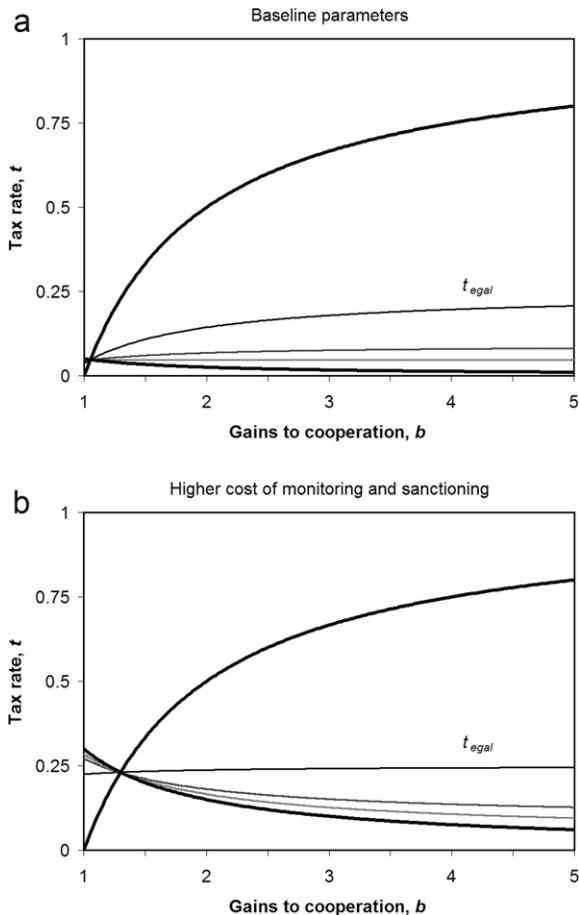


Fig. 7. The equilibrium egalitarian tax rate t_{egal} as a function of the gains to cooperation b and group size n . The egalitarian tax is represented by the thin black line for $n=3$, the dark gray line for $n=10$, and the light gray line for $n=20$. (a) Baseline cost of monitoring: $c_m=0.05$. (b) Higher cost of monitoring: $c_m=0.3$. The egalitarian tax rate is unaffected by changes in the cost of punishment or the probability of future interaction. The thick solid lines represent the same maximum and minimum tax rates as in Fig. 5.

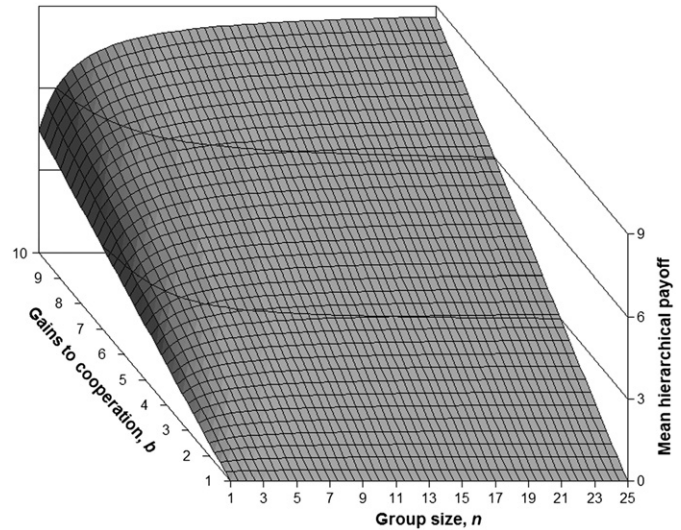


Fig. 8. Mean payoff per round to members of hierarchical groups at equilibrium under the egalitarian tax rate t_{egal} . The hierarchical payoff for some combinations of high b and low n falls below the mean acephalous payoff (Fig. 3), in which case acephalous cooperation is expected to dominate over hierarchical cooperation, as in the upper left region of Fig. 6.

and regular hierarchical group members at the egalitarian equilibrium. In contrast to acephalous cooperation's precipitous decline with group size, cooperation in hierarchical groups is remarkably robust even in very large groups. In fact, at this model's market equilibrium, leadership becomes cheaper in larger groups as the cost of the leader's compensation is split among a larger number of group members (although this would not necessarily be the case if the cost of monitoring one individual increased with group size).

The preceding analysis of tax evolution points to an important vulnerability of members of hierarchical groups: if leaders with reasonable offers are in short supply, those few who are willing to lead may extort extra resources from group members. We expect that generally, however – with some exceptions to be considered momentarily – selection favoring the willingness-to-lead at lower rates will be strong enough that generous potential leaders will not be in short supply. If we consider that a leader may be tempted to increase the tax rate after being appointed, they are limited by the willingness of other group members to take their position for the cheaper rate. (In the case that no other potential leader is available, group members could presumably be pushed to the maximum tax rate defined by condition (21c); past this point, group members would do better to disband and receive the non-cooperative payoff of zero.)

We consider four other conditions that might intervene to prevent leaders from receiving effectively the same net payoff as regularly group members:

- (a) If there is variance in the cost of monitoring across willing leaders, leaders facing especially low monitoring costs may set their tax rate just below the level of the next-best offer and pocket the difference as rent.
- (b) If leaders are capable of increasing the tax rate after appointment and group members must incur a cost to revolt or re-vote, leaders can demand an extra amount just under this cost without being ousted, even if there are willing replacement candidates.
- (c) Extra taxes can also be extracted if some other process increases the differential productivity of work under the current leader relative to what could be accomplished under

other potential candidates. If group members make investments in skills that are specific to their productivity under a particular leader, for example, these sunk costs would also be open to appropriation.

- (d) Finally, if there is not a tendency for candidates offering lower tax rates to be appointed leader, selection would not favor more generous leaders, and the regular group member's payoff could be reduced over time to just slightly more than the non-hierarchical alternative.

3. Discussion

3.1. Model summary and extensions

The present model demonstrates that the appointment of a supervising leader who receives a share of group productivity can be a robust and mutually preferred solution to the problem of free-riding in cooperative groups. As summarized in Table 2, this leadership regime becomes preferable to the alternatives of non-cooperation and leaderless cooperation when there are significant returns to scale, yet the size of the group demanded by the activity is too large for individuals to be motivated to either contribute to the public good or sanction free-riders on their own. The model also predicts that leadership will be preferable to leaderless cooperation when the cost of monitoring and sanctioning fellow group members is high enough that individuals would be unwilling to enforce cooperation on their own, but not so high that the gains from cooperation cannot cover the leader's enforcement costs. We show that under perfect competition between identical candidates for leadership, leaders are expected to receive approximately the same net payoff as regular group members. There is a greater possibility for inequality, however, when changing leaders is difficult or costly for group members, or a particular leader is able to enforce cooperation more efficiently than other potential candidates.

While this model takes the scale required for cooperation as an exogenous feature of the individual's socioecology, its basic results are likely to extend to situations in which the gains to cooperation are a variable function of group size, and individuals actively choose to join or leave groups based on both their size and organizational structure in order to maximize their returns from cooperation. We expect that in environments where the returns to scale diminish quickly, self-interested individuals will optimally form small groups in which unenforced cooperation and/or mutual monitoring are sufficiently stable to gain the benefits from cooperation, and the costs of leadership are unnecessary. When the potential benefits of cooperation reach the point of diminishing returns only at much larger scales, however, we expect that individuals who are willing to join large, hierarchically organized groups will out-compete those who are

only willing to join either large acephalous groups dominated by defectors, or smaller, more cooperative but less productive acephalous groups.

Additionally, while this model has concentrated on leaders' effort to solve the 1st-order free-rider problem, a leader might instead focus on solving the 2nd-order free-rider problem by increasing the incentives for regular group members to engage in mutual monitoring. This arrangement might be advantageous in some circumstances, for example, if regular group members face lower monitoring costs because they have better access to information about fellow group members' contributions, or if the equilibrium cost of leadership to group members is lower because the leader's effort necessary to enforce mutual monitoring is less than that necessary to enforce 1st-order cooperation itself. In this case, top-down hierarchical governance would act to reinforce, rather than replace, bottom-up community governance, making the system more robust to temporary failure at either level (Bowles and Gintis, 2002).

We should note that while the current model concentrates specifically on the question of when group members should be motivated to transition from a symmetrical to an asymmetrical division of the gross gains from cooperation, any sufficiently asymmetrical interest in reinforcing cooperation should prompt a kind of leadership effort similar to what we have represented here, whatever its cause (Dixit and Skeath, 1999; Tooby et al., 2006). Thus, if an individual enters the collective action game with a disproportionate interest in group productivity, they may also be willing to incur disproportionate costs of monitoring and sanctioning.

Finally, if collective action with or without mutual monitoring is somehow sustainable at high levels in large groups due to processes outside the scope of the current model, members of acephalous cooperative groups may sometimes be capable of holding out against the invasion of hierarchical types even when there are very high returns to scale. Other potential processes theoretically capable of reinforcing cooperation include: costly signaling (Boone, 1998; Gintis et al., 2001; Smith and Bliege Bird, 2000); group selection (Boyd et al., 2003; Gintis, 2000; Sober and Wilson, 1999); conformist cultural transmission (Henrich and Boyd, 2001); recursive punishment of non-punishers (Boyd and Richerson, 1992); optional participation (Hauert et al., 2007; Mathew and Boyd, 2009); and costless punishment of free-riders by withholding help in other cooperative domains (Panchanathan and Boyd, 2004). As the number of viable theoretical models aiming to explain large-scale human cooperation continues to grow, the answer will ultimately hinge on the empirics of cooperation in the real world.

3.2. Related models

Integrative "mutual benefit" theories for the origin of rank differentiation date back to the earliest law codes of Mesopotamia

Table 2
Conditions favoring the emergence of solitary, leaderless, and leaedered economies.

No cooperation	Cooperation without enforcement	Cooperation enforced through mutual monitoring	Cooperation enforced through leadership
Low gains to cooperation and/or High costs of monitoring and sanctioning	Very high gains to cooperation and Small group size	High gains to cooperation and Small to intermediate group size and Low costs of monitoring and sanctioning	Intermediate to high gains to cooperation and Intermediate to large group size and Low to intermediate costs of monitoring and sanctioning

(21st century B.C.: Kramer, 1981) and Vedic texts of India (8–7th centuries B.C.: Basham, 1967), and have since been expounded by a line of thinkers including Ibn Khaldūn, Thomas Hobbes, Max Weber, and Herbert Simon (Hobbes, 1964 [1651]; Ibn Khaldūn, 1967 [1377]; March and Simon, 1958; Weber, 1968). While formal benefit-cost models of voluntary hierarchy formation are still rare, the present models follow a number of important predecessors.

Work in game theory has established that designating a first-mover in coordination games can sometimes resolve coordination problems to all players' benefit (Dixit and Skeath, 1999; Lewis, 1969). In social psychology, Van Vugt and Kurzban have suggested that the adoption of leader and follower social strategies is equivalent to the adoption of alternative, complementary choices in pure and mixed-interest coordination games (Van Vugt, 2006; Van Vugt and Kurzban, 2007).

Economists will recognize that our model shares the basic logic of Alchian and Demsetz's (1972) theory of the firm. Alchian and Demsetz suggested that when there are gains to team production, yet individual team members are not sufficiently motivated to pay the cost of monitoring each others' behavior, shirking may be overcome by appointing a specialized monitor who receives title to the net earnings of the team. As a residual claimant on the team's productivity, the "team leader, manager, organizer, owner, or employer" has sufficient incentive to carry out the monitoring, while economies of scale ensure that team production under supervision remains the best option for employees, rather than solitary or unsupervised production. While their approach, in specifying the conditions under which different market- and firm-based relationships are likely to be favored, is also inherently ecological, we seek to extend the logic of leadership in team production to historical and ethnographic contexts outside modern capitalist economies. Dixit's model of contract enforcement by a profit-motivated 3rd party in the two-player prisoner's dilemma is also conceptually similar to the current approach, but does not capture the dynamics of cooperation in sizeable groups which are at the core of our model (Dixit, 2004, Chapter 4).

Our approach is most closely aligned with Smith and Choi's "managerial mutualism" agent-based simulation (Smith and Choi, 2007; see also Boone 1992). Like the model presented here, it is also based on a form of the public goods game. In the absence of a manager, cooperators both contribute to the public good and sanction defectors; when a manager is present, he or she pays the cost of sanctioning, while cooperators pay an exogenously fixed fee to the manager. The current model incorporates a number of features that are absent from or only implicit in Smith and Choi's simulation, including repeated interaction, 2nd-order free-riding in acephalous groups, tax evasion in hierarchical groups, and endogenous negotiation of the distribution of shares between managers and group members. Importantly, their model does not allow agents to choose to operate without a manager if one is already present, so does not directly address the formation of functional hierarchies based on mutual consent; rather, the invasion and stability of cooperation under management essentially requires that managers receive sufficiently high payoffs to proliferate in the population. The present model thus builds on their basic framework and more systematically analyzes the conditions and evolutionary dynamics leading to the acceptance and stability of supervised cooperation in groups.

Finally, this model shares some features with transactional reproductive skew (TRS) models (e.g. Buston et al., 2007; Vehrencamp, 1983), but differs in important ways. Here, reaping the gains to group production is represented as a collective action problem, and solutions to this problem constitute a central focus of the model, whereas in TRS models the benefits of group living

are produced by association alone. However, both types of models examine the equilibrium distribution of shares, and both depend on outside options. In 'concession' TRS models, the equilibrium division of shares forces the subordinate's payoff down to the payoff of his or her outside option (usually breeding solitarily); in 'restraint' TRS models, subordinates can claim greater shares of the surplus, but cannot push the dominant's payoff below his or her outside option (Buston et al., 2007; Johnstone, 2000). These same upper and lower bounds on taxation define the criteria for the invasion of hierarchical strategies in this model, where the outside option is defined by the payoff to non-hierarchical strategies.

Once hierarchical types have invaded, differences in assumptions about the nature of the dominant/leader role lead to different equilibrium outcomes in this model versus transactional reproductive skew models. TRS models tend to assume that the player labeled as 'dominant' is irreplaceable or essential for the production of the surplus derived from group living (for example, because they control a high-quality resource patch); as a result, subordinates do not have the advantage of considering their payoff under another, more generous dominant, or as dominants themselves. In this model, where leadership is a service that may be provided by one among several potential candidates, the leadership market converges instead on a price of leadership that yields fairly equal payoffs to leaders and regular group members. To the extent that a leader does not have to be concerned with matching competing candidates' offers – either because revolt is impossible, or because he or she monopolizes some essential skill or resource – the negotiation of shares in our model converges on similar equilibria to those of concessional TRS models. Similarly, more egalitarian divisions become likely in TRS models if dominants are in competition for social partners (Reeve, 1998), or subordinates are able to consider becoming dominants elsewhere (Vehrencamp, 1983).

3.3. Leadership in the ethnographic and archeological record

Small-scale societies offer a number of clear examples of specialized coordinating, motivating, and enforcement roles of the type which we have highlighted here. As the theory predicts, leadership in these cases is associated with productive or competitive tasks which demand high levels of coordination and cooperation among a significant number of participants.

Among the marine hunters of Lamalera, Indonesia, for example, boat managers (*téna aleps*, literally "boat owners", although they do not actually own the boat) oversee sperm whale hunts undertaken by crews of eight to twelve men and supported by a number of craftsmen and other community members. The *téna alep* acts as a "coach or manager" who "serves as a nexus for the whaling operation, coordinating the three specialized and overlapping interest groups – crew members, corporate members, and craftsmen – that receive shares of the harvest." Intuitively, this leadership role is clearly absent in the case of smaller-scale hook-and-line and net fishing in the same community (Alvard and Nolin, 2002).

A similar role existed among the 19th-century Inuit of Northern Alaska in the context of hunting bowhead whales, weighing around 10,000 kg. Organized crews of seven to ten men operated under a formal crew chief, or *umialik*, who both directed the whale hunt itself and managed the redistribution of shares through the year following a successful kill (Alvard and Nolin, 2002; Friesen, 1999). In contrast, leadership in hunting was much more attenuated among the nearby Mackenzie Inuit of the Bering Strait, who used one-man kayaks to cooperatively drive pods of smaller beluga whales (~400 kg) into shallow

water where they could be speared. Individual hunters kept whatever animals they personally harpooned (Friesen, 1999). In this case, the coordination required to drive the belugas was likely less than that required to successfully manage a cooperative boat crew, while clear individual ownership over the returns eliminated the problems of free-riding and inequitable redistribution that are inherent in the case of the larger whales; both factors together may explain why there was a reduced demand for clear leadership in Mackenzie Inuit beluga hunts than in the larger whale hunts of the North Alaskan Inuit and Lamalera.

The need for collective action in raiding and warfare is likely to be a strong driver for the emergence of leadership roles. Between-group violence combines a number of factors that all strongly favor the emergence of pronounced leadership: it exhibits high potential gains to successful cooperation, large incentives to shirk, and – due to the dynamics of escalation between competing groups – often demands very significant group sizes (LeBlanc and Register, 2003). Indeed, leadership is clearly associated with warfare even at the smallest scales of human society: among the foraging societies in the Standard Cross-Cultural Sample (Murdock and White, 1980), 74% exhibit informal leadership during war, while 7% exhibit formal leadership; among those societies engaged in horticulture and shifting cultivation, 35% show informal leadership during war, and 55% exhibit formal leadership.³

The Mae Enga horticulturalists of highland New Guinea engaged in inter-clan warfare involving several hundred warriors. In times of war, the Mae Enga acknowledged fight leaders (“belly-stirrers”), who made tactical decisions, issued commands, and motivated warriors with both praise and insult. Big men, who occupied more formalized non-military roles, likewise provided “a constant flow of exhortations, praise, and insults intended to stimulate combatants to greater efforts.” These big men were also crucial in negotiating and enforcing settlements between competing clans, a task which might be impossible on an individual-to-individual basis, but which becomes manageable through the collective solidarity achieved through an individual’s elevation to leadership (Meggitt, 1977). The prominent chiefly roles of East African pastoralists, such as the Maasai, Turkana, and Samburu, may similarly be driven largely by endemic conflict between groups over cattle and grazing land; the greater inequality in wealth associated with herd-based economies, however, may be a conflating factor (Borgerhoff Mulder et al., 2009; Kaplan et al., 2009). LeBlanc and Register (2003) provide further evidence for the association between large-scale conflict and leadership across many subsistence types, from small-scale nomadic foragers to complex agrarian states.

The need to interact with – or struggle against – outside groups and governments may present many small-scale traditional groups with collective action problems that necessitate the development of more formalized political leadership in societies that were previously highly egalitarian. In our work with the Tsimane’ forager-horticulturalists of Bolivia, it is our impression that the role of village chief or “corrector” (*corregidor*) has arisen in the past three decades mainly in response to the need cohere at the village level in interactions with merchants, logging compa-

nies, NGOs, and government offices. The chief’s primary roles include enforcing attendance at community meetings – which most often address either relations with non-Tsimane’ or within-community grievances – and participation in community labor, such as maintaining the school or soccer field (both also recently introduced institutions) (Gurven et al., 2010; von Rueden et al., 2008). This shift toward more prominent political leadership in response to the need to interface with the outside world appears to be a common trend for many traditional groups, such as the Aché, Sirionó, and Toba of South America, and Mbuti and Okiek of Africa (Lee and Daly, 1999).

One influential approach to the development of early agrarian states was Wittfogel’s (1981 [1957]) theory of “oriental despotism”. Wittfogel argued that the organizational complexity of employing mass labor in the construction and maintenance of canals and dykes in large irrigation projects necessitated a strong, permanent, centralized management hierarchy, which found expression in early despotic states. When Earle (1978) reviewed the evidence for the necessity of centralized management in irrigation systems, however, he found that while irrigation systems are sometimes built by centralized, state-controlled organizations, very large-scale irrigation systems can often be constructed through a process of accretion, and then successfully maintained through the decentralized labor contributions of individual households. Of all the organizational problems associated with irrigation that he examined, Earle found that the problems of defense in warfare, the allocation of water rights, and the settlement of disputes were the only factors that seemed to actually necessitate a powerful central leader or manager. Sanders and Price underlined this point in their work on the early development of Mesoamerican civilization: “conflict [over water rights] stimulates the selective process in favor of centralized authority—the more severe the conflict, the greater the need for and probably evolution of centralized control” (Sanders and Price, 1968; cited in Earle, 1978). Webster (2005) has made a similar argument for the rise of centralized governance institutions in the Maya polity of Copán, focusing especially on management of land rights. We should caution, however, that a correlation between potential sources of social conflict and greater hierarchical differentiation cannot automatically be interpreted as evidence for a mutual-benefit scenario of hierarchy formation; in many cases, social dominants may simply be asserting their supremacy over subordinates as internal competition becomes more intense.

3.4. Cooperation-facilitating leadership and exploitive dominance

An important and open question in this field of research is how factors that drive bottom-up demand for leadership – such as high gains to large-scale cooperation and the potential for debilitating within-group conflict – and factors that promote exploitive social dominance – such as resource patchiness and differential accumulation of wealth – jointly determine sociopolitical outcomes. This question, which is key for understanding the organization of more complex chiefdoms and state-level societies, is theoretically and empirically challenging for at least four reasons:

- (a) The same factors often drive both leadership and exploitive dominance. Uneven distribution of high-quality agricultural land, for example, should promote both within-group social dominance as well as leadership in between-group warfare. Similarly, larger settlements both widen the resource base of dominants and require collective action to be carried out at larger scales. Intensification of land-based production can simultaneously necessitate greater levels of collective action

³ The SCCS includes societies chosen to be a representative sample of geographic regions and cultural clusters, and is available from Douglas White’s website: <http://eclectic.ss.uci.edu/~drwhite>. Foragers were classified based on the criteria in Marlowe (2003). The mating system of foragers in the standard cross-cultural sample. *Cross-Cultural Research* 37, 282–306. Horticulturalists and shifting cultivators were classified based on variable v833 ‘primary subsistence economy’. Results are reported for variable v902 ‘leadership during battle’.

and lead to steeper gradients in land productivity, and therefore greater returns to monopolization.

- (b) As implied, the effects of the factors promoting leadership on the one hand and promoting dominance on the other are likely to be interactive rather than strictly additive. High inequality in dominance-based social power, for example, could allow more powerful individuals to sanction group members at very low cost, and thereby stabilize leadership.
- (c) Exploitation and inequality may arise as a by-product of the demand for leadership. In terms of the present theory, imperfect competition between potential leaders or significant costs to emigrate away from exploitative leaders could drive the equilibrium tax level above the 'egalitarian' tax regime on which our analyses have focused. Even assuming perfect competition between potential leaders, differences in individuals' ability to monitor and sanction non-cooperators can also skew resources toward more skilled or efficient leaders (discussed in Section 2.4).
- (d) Leadership or management roles may also arise as by-products of basically exploitive social dominance. A despotic ruler who exacts tribute from his subjects, for example, should be motivated to perform services and apply pressures that increase the subjects' productive or competitive output—although perhaps at the expense of the subjects' own personal welfare.

While we suggest that the demand for leadership as a solution to the challenges of group living and collective action is indeed an important driver in human social evolution, given the clearly powerful role of dominance and exploitation, we expect it to explain only part of the variation in the extent of rank differentiation across human societies. Future models should aim to further integrate conflict-based and voluntary processes of social hierarchy formation, while future empirical work should focus on methods of estimating their relative importance across different socioecological contexts. At the minimum, the present paper has shown that voluntary hierarchies can be a stable outcome of individual decision making under certain conditions, and thereby makes progress in understanding the relationship between socioecology, cooperation, and hierarchy in human societies.

Acknowledgments

This work benefited from input from Samuel Bowles, Eric Alden Smith, Ugo Pagani, Kenneth Sokoloff, Robert Allen, Suresh Naidu, Robert Boyd, Peter Turchin, Arthur Robson, Matthew McIntyre, Oskar Burger, and Ann Caldwell Hooper; three anonymous reviewers gave thoughtful feedback that improved the model and manuscript in multiple ways. It was supported by the Santa Fe Institute through the Behavioral Sciences Program and the Complex Systems Summer School (NSF Grant no. 0200500: "A Broad Research Program in the Sciences of Complexity"), and the Howard Hughes Medical Institute through the Program in Interdisciplinary Biological and Biomedical Sciences at the University of New Mexico.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtbi.2010.05.034

References

- Alchian, A.A., Demsetz, H., 1972. Production, information costs, and economic organization. *American Economic Review* 62, 777–795.
- Alvard, M.S., Nolin, D.A., 2002. Rousseau's whale hunt? Coordination among big-game hunters. *Current Anthropology* 43, 533–559.
- Baines, J., Yoffee, N., 1998. Order, legitimacy, and wealth in ancient Egypt and Mesopotamia. In: Feinman, G.M., Marcus, J. (Eds.), *Archaic States*. SAR Press, Santa Fe, pp. 199–260.
- Basham, A.L., 1967. *The Wonder that was India*. Macmillan, London.
- Boehm, C., 2001. *Hierarchy in the Forest: The Evolution of Egalitarian Behavior*. Harvard University Press, Cambridge.
- Boone, J.L., 1992. Competition, conflict, and the development of social hierarchies. In: Smith, E.A., Winterhalder, B. (Eds.), *Evolutionary Ecology and Human Behavior*. Aldine de Gruyter, Hawthorne, NY, pp. 301–337.
- Boone, J.L., 1998. The evolution of magnanimity: when is it better to give than to receive? *Human Nature* 9, 1–21.
- Borgerhoff Mulder, M., Bowles, S., Hertz, T., Bell, A., Beise, J., Clark, G., Fazzio, I., Gurven, M., Hill, K., Hooper, P.L., Irons, W., Kaplan, H., Leonetti, D., Low, B., Marlowe, F., McElreath, R., Naidu, S., Nolin, D., Piraino, P., Quinlan, R., Schniter, E., Sear, R., Shenk, M., Smith, E.A., von Rueden, C., Wiessner, P., 2009. Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. *Science* 326, 682–688.
- Bowles, S., Gintis, H., 2002. Social capital and community governance. *The Economic Journal* 112, 419–436.
- Boyd, R., Richerson, P.J., 1988. The evolution of reciprocity in sizeable groups. *Journal of Theoretical Biology* 132, 337–356.
- Boyd, R., Richerson, P.J., 1992. Punishment allows the evolution of cooperation (or anything else) in sizeable groups. *Ethology and Sociobiology* 13, 171–195.
- Boyd, R., Gintis, H., Bowles, S., Richerson, P.J., 2003. The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences* 100, 3531–3535.
- Brown, D.E., 1991. *Human Universals*. McGraw-Hill, New York.
- Brown, J.L., 1964. The evolution of diversity in avian territorial systems. *Wilson Bulletin* 76, 160–169.
- Buston, P.M., Reeve, H.K., Cant, M.A., Vehrencamp, S.L., Emlen, S.T., 2007. Reproductive skew and the evolution of group dissolution tactics: a synthesis of concession and restraint models. *Animal Behaviour* 74, 1643–1654.
- Carneiro, R.L., 1970. A theory of the origin of the state. *Science* 169, 733–738.
- Clutton-Brock, T., West, S., Ratnieks, F., Foley, R., 2009. The evolution of society. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* 364, 3127–3133.
- Diamond, J., 1997. *Guns, Germs, and Steel: The Fates of Human Societies*. Norton, New York.
- Diehl, M.W., 2000. Some thoughts on the study of hierarchies. In: Diehl, M.W. (Ed.), *Hierarchies in Action: Cui Bono?*. Center for Archeological Investigations Carbondale, pp. 11–30.
- Dixit, A.K., 2004. *Lawlessness and Economics: Alternative Modes of Governance*. Princeton University Press, Princeton.
- Dixit, A.K., Skeath, S., 1999. *Games of Strategy*. W.W. Norton & Company, New York.
- Dyson-Hudson, R., Smith, E.A., 1978. Human territoriality: an ecological reassessment. *American Anthropologist* 80, 21–41.
- Earle, T.K., 1978. Economic and Social Organization of a Complex Chiefdom. Museum of Anthropology, University of Michigan.
- Earle, T.K., 1997. *How Chiefs come to Power: The Political Economy in Prehistory*. Stanford University Press, Stanford.
- Flannery, K., 1972. Cultural evolution of civilizations. *Annual Review of Ecology and Systematics* 3, 399–426.
- Friesen, T.M., 1999. Resource structure, scalar stress, and the development of Inuit social organization. *World Archaeology* 31, 21–37.
- Gintis, H., 2000. Strong reciprocity and human sociality. *Journal of Theoretical Biology* 206, 169–179.
- Gintis, H., Smith, E.A., Bowles, S., 2001. Costly signaling and cooperation. *Journal of Theoretical Biology* 213, 103–119.
- Gurven, M., Borgerhoff Mulder, M., Hooper, P.L., Kaplan, H., Quinlan, R., Sear, R., Schniter, E., von Rueden, C., Bowles, S., Hertz, T., Bell, A., 2010. Domestication alone does not lead to inequality: intergenerational wealth transmission among horticulturalists. *Current Anthropology* 51, 49–64.
- Hauert, C., Traulsen, A., Brandt, H., Nowak, M.A., Sigmund, K., 2007. Via freedom to coercion: the emergence of costly punishment. *Science* 316, 1905–1907.
- Henrich, J., Boyd, R., 2001. Why people punish defectors—weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical Biology* 208, 79–89.
- Hobbes, T., 1964. [1651], *Leviathan*. Washington Square Press, New York.
- Ibn Khaldūn, 1967. [1377]. *The Muqaddimah: An Introduction to History*. Princeton University Press, Princeton.
- Ibn Taymiya, 1982. *Public Duties in Islam*. The Institution of the Hisba, The Islamic Foundation, Leicester.
- Johnson, A.W., Earle, T., 1987. *The Evolution of Human Societies: From Foraging Group to Agrarian State*. Stanford University Press, Stanford.
- Johnstone, R.A., 2000. Models of reproductive skew: a review and synthesis. *Ethology* 106, 5–26.
- Kaplan, H.S., Hooper, P.L., Gurven, M., 2009. The evolution and ecological roots of human social organization. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* 364, 3289–3299.
- Kennett, D.J., Winterhalder, B., Bartruff, J., Erlandson, J.M., 2009. An ecological model for the emergence of institutionalized social hierarchies on California's Northern Channel Islands. In: Shennan, S. (Ed.), *Pattern and Process in Cultural Evolution*. University of California Press, Berkeley.

- Kramer, S.N., 1981. *History Begins at Sumer*. University of Pennsylvania Press, Philadelphia.
- LeBlanc, S.A., Register, K.E., 2003. *Constant Battles: Why we Fight*. St. Martin's Griffin, New York.
- Lee, R.B., Daly, R. (Eds.), 1999. *The Cambridge Encyclopedia of Hunters and Gatherers*. Cambridge University Press, Cambridge.
- Lewis, D., 1969. *Convention: A Philosophical Study*. Harvard University Press, Cambridge.
- March, J., Simon, H., 1958. *Organizations*. Wiley, New York.
- Marlowe, F.W., 2003. The mating system of foragers in the standard cross-cultural sample. *Cross-Cultural Research* 37, 282–306.
- Mathew, S., Boyd, R., 2009. When does optional participation allow the evolution of cooperation? *Proceedings of the Royal Society B* 276 1167–1174.
- McElreath, R., 2008. Baryplot R package.
- McElreath, R., Boyd, R., 2007. *Mathematical Models of Social Evolution: A Guide for the Perplexed*. University of Chicago Press, Chicago.
- Meggitt, M., 1977. *Blood is their Argument: Warfare among the Mae Enga Tribesmen of the New Guinea Highlands*. Mayfield, Mountain View, CA.
- Murdock, G.P., White, D.R., 1980. Standard cross-cultural sample. In: Barry, H., Schlegel, A. (Eds.), *Cross-Cultural Samples and Codes*. University of Pittsburgh Press, Pittsburgh, pp. 3–43.
- Olson, M., 1965. *The Logic of Collective Action: Public Goods and the Theory of Groups*. Harvard University Press, Cambridge.
- Panchanathan, K., Boyd, R., 2004. Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature* 432, 499–502.
- Reeve, H.K., 1998. Game theory, reproductive skew and nepotism. In: Dugatkin, L., Reeve, H.K. (Eds.), *Game Theory and Animal Behaviour*. Oxford University Press, Oxford, pp. 118–145.
- Sanders, W.T., Price, B., 1968. *Mesoamerica: The Evolution of a Civilization*. Random House, New York.
- Service, E., 1962. *Primitive Social Organization: An Evolutionary Perspective*. Random House, New York.
- Smith, E.A., Bliege Bird, R., 2000. Turtle hunting and tombstone opening: public generosity as costly signaling. *Evolution and Human Behavior* 21, 245–261.
- Smith, E.A., Choi, J.K., 2007. The emergence of inequality in small-scale societies: simple scenarios and agent-based simulations. In: van der Leeuw, S., Kohler, T. (Eds.), *The Model-Based Archaeology of Socio-Natural Systems*. SAR Press, Santa Fe.
- Sober, E., Wilson, D.S., 1999. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Harvard University Press, Cambridge.
- Steward, J.H., 1955. *The Theory of Culture Change: The Methodology of Multilinear Evolution*. University of Illinois Press, Urbana.
- Summers, K., 2005. The evolutionary ecology of despotism. *Evolution and Human Behavior* 26, 106–135.
- Tooby, J., Cosmides, L., Price, M.E., 2006. Cognitive adaptations for *n*-person exchange: the evolutionary roots of organizational behavior. *Managerial and Decision Economics* 27, 103–129.
- van der Leeuw, S., Kohler, T. (Eds.), 2007. *The Model-Based Archaeology of Socio-Natural Systems*. SAR Press, Santa Fe.
- van Schaik, C.P., 1989. The ecology of social relationships among female primates. In: Standen, V., Fley, R.A. (Eds.), *Comparative Socioecology: The Behavioral Ecology of Humans and Other Mammals*. Blackwell, Oxford, pp. 195–218.
- Van Vugt, M., 2006. Evolutionary origins of leadership and followership. *Personality and Social Psychology Review* 10, 354–371.
- Van Vugt, M., Kurzban, R.K., 2007. Cognitive and social adaptations for leadership and followership: evolutionary game theory and group dynamics. In: Forgas, J. (Ed.), *The Evolution of the Social Mind: Evolutionary Psychology and Social Cognition*. Psychology Press, New York, pp. 229–243.
- Vehrencamp, S.L., 1983. A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour* 31, 667–682.
- von Rueden, C., Gurven, M., Kaplan, H.S., 2008. The multiple dimensions of male social status in an Amazonian society. *Evolution and Human Behavior* 29, 402–415.
- Weber, M., 1968. *Economy and Society: An Outline of Interpretive Sociology*. Bedminster Press, New York.
- Webster, D., 2005. Political ecology, political economy, and the culture history of resource management at Copán. In: Andrews, E.W., Fash, W.L. (Eds.), *Copán: The History of an Ancient Maya Kingdom*. SAR Press, Santa Fe, pp. 33–72.
- Wilson, E.O., 1975. *Sociobiology: The New Synthesis*. Belknap Press, Cambridge.
- Wittfogel, K., 1981. [1957]. *Oriental Despotism: A Comparative Study of Total Power*. Vintage Books, New York.