Gains to cooperation drive the evolution of egalitarianism

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Abstract

There is wide variety in dominance hierarchies in both animal[1,2] and human societies[3–5], with major implications for health and well-being[6–8]. Understanding which conditions favour egalitarianism—a social setting characterized by low levels of aggression, muted hierarchies, and relatively equal distributions of resources and fitness outcomes—is thus of great theoretical and societal interest. Previous work has highlighted the role of low economic defensibility of resources[2,9,10], high costs of competition[11–13], levelling coalitions[14–17], and high gains to cooperation[5,18,19]. However, there is a lack of formal theoretical models that combine these conditions and generalize well across species and contexts. Here we provide a simple evolutionary model that incorporates economic defensibility, costs of competition and gains to cooperation, and shows for the first time that gains to cooperation alone can drive the evolution of egalitarianism. The model combines the well-known Hawk-Dove[20] and Prisoner's Dilemma games[21], which model dominance and cooperation, respectively. We show that when the gains to repeated cooperation are high relative to the benefits of hawkish social dominance, a 'Leveller' strategy—which punishes Hawks with non-cooperation—can evolve and drive Hawks out of the population. We find empirical support for the model among human foragers, in that groups with a greater reliance on hunting, which requires cooperation, are more likely to be egalitarian. We suspect that the model can also explain observed egalitarian outcomes in a number of other species relying on within-group cooperation [22,23 18,24]. Unlike previous theoretical models of egalitarianism[14–16] our model does not depend on coalitions or sophisticated cognitive abilities, and highlights a small number of ecological parameters to explain variation in dominance hierarchies and inequality across groups.

Results and Discussion

Our model is inspired by the life-ways of mobile hunter-gatherers, which are characterized by a high degree of interdependence in food production and reproduction, and an absence of overt hierarchies [4,5,17]. Mobile hunter-gatherers often face variable and unpredictable return rates, generating benefits to pooling risk among multiple independent foragers [25–27]. Foragers also often take advantage of economies of scale, where higher per-capita payoffs can be achieved through cooperative rather than solitary production [28–30]. We hypothesize that the importance of cooperation for success in hunter-gatherer societies is in fact essential for explaining their egalitarianism.

Egalitarianism [17,31–33] arises by the active suppression of dominance behaviour, ranging from shunning, ridicule and ostracism to collective punishment or execution [33,34]. While models have devoted substantial attention to egalitarian behaviour in the form of levelling coalitions [14–16], the roles of shunning and selective partner choice have received less attention. Mobile hunter-gatherers live in multi-level fission-fusion societies, with small foraging groups acting as units of cooperative production and resource-pooling [4,35]. In this context, when cooperation is essential to survival, would-be dominants can be shunned by 'voting with one's feet', i.e. by selectively interacting within groups or by switching between groups [31,33]. This reflects second-party punishment, which is common among hunter-gatherers [34,36], and does not require coalitions or collective action. Theory is needed to know what conditions favour egalitarianism that arises due to repeated dyadic interaction.

In this model, players play both Hawk-Dove (HD) and Prisoner's Dilemma (PD) games repeatedly across a number of rounds, and can condition their actions on their partner's past

behaviour in either game. Dominance behaviour is represented by playing Hawk in the HD, while shunning—represented by the Leveller strategy—is represented by defecting in the PD, which deprives Hawks of the gains to cooperation. Entering a cycle of mutual defection can be understood as a form of partner choice, as it effectively terminates the cooperative relationship [37] [38]. We interpret the extent of egalitarianism in the population in terms of the frequency of Doves (and equivalently, the absence of Hawks) in the population [20].

We provide both analytical solutions and simulations of the model. The analytical solutions show the conditions under which these new strategies can invade when rare. The simulations demonstrate the evolutionary plausibility of the model using replicator dynamics with deterministic mutation. The simulations illustrate the dynamic evolution of strategies, and highlight the effect of key ecological parameters on the evolution of egalitarianism through dyadic levelling.

To approach the joint game analytically, we utilize a framework for conditional strategies in repeated games in which the impulse to punish and receptivity to punishment are each coded as distinct traits that co-evolve under some conditions. The strategies are defined by a simple, mechanistic set of rules that determine an individual's behaviour conditional on their partner's past behaviour. Table 2 lists the eight binary strategy traits that define behaviour in the model; Table S1 lists all possible combinations of these binary strategy traits.

This framework allows modelling the co-evolution of the enforcement of and compliance to norms, without *a priori* assuming that a norm is already established in a population. This co-evolutionary force works in this model as long as selection can act on strategies that define behaviour toward infrequent strategy types. This is crucial for the evolution reluctant-but-savvy strategies (Conditional Hawk, Conditional Defector, and Acquiescent Hawk; described below) that are important precursors for pro-social conditional strategies (Conditional Dove, Conditional Cooperator, and Leveller). The simulation specifically assumes a small constant rate of mutation between strategy types. More generally, rare strategy types may also due to experiment, protest, or other sources of innovation.

We first derive a simple set of analytical constraints for the invasion of Leveller in the context of repeated cooperation and general hawkishness. We address the Iterated Hawk-Dove and Prisoner's Dilemma games in turn, then combine them to produce a set of predictions for the evolution of egalitarianism. The simulation illustrates the evolutionary dynamics and ecological patterns of egalitarian outcomes.

Table 1. Single-round payoffs to the row player in the HD and PD games.

Hawk-Dove (HD)

	Dove	Hawk
Dove	$v/2$	0
Hawk	v	$v/2 - d/2$

Prisoner's Dilemma (PD)

	Cooperate	Defect
Cooperate	$b - c$	$-c$
Defect	b	0

Iterated Hawk-Dove

In the HD, strategies may either share or contest a resource of value v (see Table 1). Doves share the resource equally with other Doves and receive $v/2$. A Hawk paired with a Dove contests the resource and gain the full value of v, while the Dove gets nothing. A Hawk paired with another Hawk contests the resource, and gains the full value v when it wins, but incurs damage d when it loses. With equal probabilities of winning or losing, Hawks playing Hawks receive an average expected payoff of $v/2 - d/2$. Without repeated interaction, if $v<d$, the Hawk-Dove game converges to a mixed equilibrium with a frequency of Hawks equal to v/d. 1 If $v>d$, the population is fully dominated by Hawks.[20,39]

Table 2. Key model parameters and heritable strategy traits. See Table S1 for full list of 36 strategies given by all combinations of the eight binary strategy traits

Ecological Parameters		*Game*
v	Value of contested resource	HD
d	Cost of losing a contest	HD
b	Benefit of cooperation	PD
c	Cost of cooperation	PD
w	Probability of future interaction	HD + PD

Binary Strategy Traits		*Game*
1.	Dove/Hawk	HD
2.	Conditional Dove (yes/no)	HD
3.	Conditional Hawk (play Dove in response to Conditional Dove) (yes/no)	HD
4.	Cooperate/Defect	PD
5.	Conditional Cooperator (yes/no)	PD
6.	Conditional Defector (play Cooperate in response to Conditional Cooperator) (yes/no)	PD
7.	Leveller (yes/no)	HD + PD
8.	Acquiescent Hawk (play Dove in response to Leveller) (yes/no)	HD + PD

In the iterated HD, interactions are repeated with probability w. If w is high enough, the benefits of reducing aggression can allow the invasion of strategies that punish or otherwise discourage hawkishness, such as Conditional Dove, which plays Dove, but punishes hawkishness by playing Hawk. Conditional Dove in this iterated HD is similar in spirit, though not identical, to Retaliator, which arises in the one-shot HD.[20]

In some environments, rare Conditional Doves can cause selection for another binary strategy trait, Conditional Hawk, that is possessed by Hawks. Conditional Hawk allows Hawks to avoid damage from fighting (d) when paired with Conditional Dove by switching to playing Dove after being punished. In the current framework, Conditional Hawk and Conditional Dove can invade of population predominated by Unconditional Hawks (who always play Hawk) if the following three conditions are fulfilled.

1. The first condition is that the payoff to Conditional Hawks playing against Conditional Dove has to be greater than the payoff to Unconditional Hawks playing against Conditional Dove across rounds (otherwise Unconditional Hawk will remain the dominant strategy). If Conditional Hawks can do better than Unconditional Hawks against rare Conditional Doves (since they are otherwise identical) selection will favour the conditional behaviour.

In the first round, a Conditional Hawk paired with a Conditional Dove will play Hawk, and receive the full value of the contestable resource v. In the second round, which occurs with probability w, both will play Hawk and each on average receive $v/2 - d/2$. In the third and all subsequent rounds, which are weighted by the time-discounting expression $w^2/(1-w)$ [38], both switch to playing Dove and earn $v/2$. Thus, the expected payoff to Conditional Hawk against Conditional Dove is:

$$V_{\text{Conditional Hawk|Conditional Dove}} = \underbrace{v}_{\text{Round 1}} + \underbrace{w\left(\frac{v}{2} - \frac{d}{2}\right)}_{\text{Round 2}} + \underbrace{\frac{w^2}{(1-w)}\left(\frac{v}{2}\right)}_{\text{Rounds 3+}}$$

An unconditional Hawks playing against a Conditional Dove earns the same payoffs in the first two rounds, but in the third round earn v again, as Conditional Dove optimistically switches back to playing Dove, while Unconditional Hawk continues to play Hawk (see Methods). Both play Hawk in all subsequent rounds, as Conditional Dove returns to punishing the Unconditional Hawk. Thus, the expected payoff to Unconditional Hawk against Conditional Dove is:

$$V_{\text{Unconditional Hawk|Conditional Dove}} = \underbrace{v}_{\text{Round 1}} + \underbrace{w\left(\frac{v}{2} - \frac{d}{2}\right)}_{\text{Round 2}} + \underbrace{w^2 v}_{\text{Round 3}} + \underbrace{\frac{w^3}{(1-w)}\left(\frac{v}{2} - \frac{d}{2}\right)}_{\text{Rounds 4+}}$$

Setting $V_{\text{Conditional Hawk|Conditional Dove}} > V_{\text{Unconditional Hawk|Conditional Dove}}$ and simplifying yields the following constraint for the evolution of Conditional Hawk:

$$\frac{d}{(1-w)} > v \qquad \text{(Ineq. 1)}$$

2. The second condition for Conditional Dove to invade is that the payoffs to Conditional Dove against Conditional Hawk have to be greater than for Conditional Hawk playing against itself (otherwise selection will not favour Conditional Doves). In the first round, Conditional Dove will play Dove and earn nothing; in the second round both will play Hawk; and in the third and all subsequent rounds both will play Dove. Thus, the expected payoffs to Conditional Dove playing against Conditional Hawk are:

$$V_{\text{Conditional Dove|Conditional Hawk}} = \underbrace{0}_{\text{Round 1}} + \underbrace{w\left(\frac{v}{2} - \frac{d}{2}\right)}_{\text{Round 2}} + \underbrace{\frac{w^2}{(1-w)}\left(\frac{v}{2}\right)}_{\text{Rounds 3+}}$$

Meanwhile, Conditional Hawk playing against itself simply earns the expected payoffs of Hawks playing Hawks across all rounds:

$$V_{\text{Conditional Hawk|Conditional Hawk}} = \frac{1}{(1-w)}\left(\frac{v}{2} - \frac{d}{2}\right)$$

Setting $V_{\text{Conditional Dove|Conditional Hawk}} > V_{\text{Conditional Hawk | Conditional Hawk}}$ and simplifying yields the following constraint for the evolution of Conditional Dove:

$$d > v \qquad \text{(Ineq. 2)}$$

3. Lastly, the payoffs to Conditional Dove playing against itself have to be greater than to Conditional Hawks playing against Conditional Dove. Since Conditional Dove playing against itself is simply $\left(\frac{v}{2}\right)$ across all rounds, and the payoff to Conditional Hawks against Conditional Dove ($V_{\text{Conditional Hawk|Conditional Dove}}$) has been described above, this condition requires:

$$\frac{1}{(1-w)}\left(\frac{v}{2}\right) > v + w\left(\frac{v}{2} - \frac{d}{2}\right) + \frac{w^2}{(1-w)}\left(\frac{v}{2}\right)$$

This simplifies to:

$$wd > v \qquad \text{(Ineq. 3)}$$

Thus, the invasion of Conditional Dove requires that the future reduction in damage from contests, *wd*, exceeds the present value of the contestable resource, *v*. When *w* is low there is little scope for the invasion of Conditional Dove. As *w* and *d* increase, however, selection can favour the invasion of Conditional Dove and Conditional Hawk into a population predominated by Hawks.

As described previously, the HD captures the effect of *economic defensibility* on the extent of contest behaviour, which depends on the benefits (*v*) and costs (*d*) of contests. All else equal, the conditions specified by inequalities (1-3) predict:

P1: Hawkishness increases (egalitarianism decreases) with the value of contestable resources (*v*).

P2: Hawkishness decreases (egalitarianism increases) with a higher cost of fighting (*d*).

When contests are costly (d>0), inequalities (1) and (3) also predict:

P3: Hawkishness decreases (egalitarianism increases) with a higher probability of future interaction (*w*).

Iterated Prisoner's Dilemma

In the Prisoner's Dilemma (PD), Cooperators pay a cost c to generate a benefit b for their partner. Defectors do not pay c, but receive a benefit b when paired with Cooperators, or nothing if they are paired with other Defectors (Table 1). With no repeated interaction (or other special conditions such as population structure or assortment), the Prisoner's Dilemma converges on mutual defection. In the Iterated PD, individuals continue to interact with probability w. Cooperators that cooperate unconditionally cannot invade because they will always be exploited by Defectors. Cooperative strategies that cooperate conditionally based on their partner's past behaviour, such as Tit-for-tat, can successfully establish cooperation under favourable conditions[21,42]. We consider the evolution of a strategy called Conditional Cooperator, which is similar to Tit-for-Tat in that it cooperates but punishes defectors by defecting.

For some parameter values, the presence of rare Conditional Cooperator strategies can select for a binary trait called Conditional Defector, which allows a Defector to switch to cooperating after having been punished by Conditional Cooperator. We assume that after punishing a Defector in round 2, a Conditional Cooperator optimistically returns to cooperating in round 3, at which point Conditional Defector and Conditional Cooperator lock into mutual cooperation (see Methods). A Conditional Cooperator paired with an Unconditional Defector, on the other hand, locks into mutual defection by round 4. Note that the only circumstance in which Conditional Defectors receive a different fitness from Unconditional Defectors is when they encounter rare Conditional Cooperators; Conditional Defectors and Unconditional Defectors playing each other are indistinguishable to selection. For Conditional Defector and Conditional Cooperator to invade a population of Unconditional Defectors, conditions 4, 5 and 6 must be fulfilled.

4. The payoffs to Conditional Defectors against Conditional Cooperator must be greater than the payoffs to Unconditional Defectors against Conditional Cooperator. Conditional Defectors earn b in the first round by defecting on Conditional Cooperator; Conditional Cooperate then defects and both earn 0 in round 2, after which both switch to cooperate and earn b-c for all subsequent rounds. Hence,

$$V_{\text{Conditional Defector|Conditional Cooperator}} = \underbrace{b}_{\text{Round 1}} + \underbrace{w\times 0}_{\text{Round 2}} + \underbrace{\frac{w^2}{(1-w)}(b-c)}_{\text{Rounds 3+}}$$

Meanwhile, Unconditional Defectors earn b on the first round, 0 on the second, and then b again as Conditional Cooperator optimistically returns to cooperating; since Unconditional Defectors do not respond, there is mutual defection for all subsequent rounds. Hence,

$$V_{\text{Don't-Conditional Defector|Conditional Cooperator}} = \underbrace{b}_{\text{Round 1}} + \underbrace{w\times 0}_{\text{Round 2}} + \underbrace{w^2 b}_{\text{Round 3}} + \underbrace{\frac{w^3}{(1-w)}\times 0}_{\text{Rounds 4+}}$$

Setting $V_{\text{Conditional Defector|Conditional Cooperator}} > V_{\text{Don't-Conditional Defector|Conditional Cooperator}}$ and simplifying yields:

$$wb > c \qquad \text{(Ineq. 4)}$$

5. For Conditional Cooperators to evolve, they must do better against Conditional Defectors than Conditional Defectors do against each other (which is simply mutual defection in all rounds, i.e. 0). Conditional Cooperator playing Conditional Defector pays the cost -c in the first round, receives 0 due to mutual defection in the second round, and cooperates successfully in all subsequent rounds. Thus:

$$V_{\text{Conditional Cooperator|Conditional Defector}} = \underbrace{-c}_{\text{Round 1}} + \underbrace{w\times 0}_{\text{Round 2}} + \underbrace{\frac{w^2}{(1-w)}(b-c)}_{\text{Rounds 3+}}$$

This is greater than $V_{\text{Conditional Defector|Conditional Defector}}$, i.e. 0, when:

$$\frac{w^2}{(1-w+w^2)}\, b > c\,. \qquad \text{(Ineq. 5)}$$

When w is near 1, the first-order approximation of this condition simplifies to $wb > c$, the same as Ineq. (4).

6. Finally, the payoff to Conditional Cooperator playing against itself has to be greater than the payoff to Conditional Defectors playing against Conditional Cooperator. The former is simply the gains to cooperation (b-c) in each round, whereas the latter is the same as $V_{\text{Conditional Cooperator|Conditional Defector}}$ above. This requires:

$$\frac{1}{(1-w)}\,(b-c) > b + w \times 0 + \frac{w^2}{(1-w)}\,(b-c)$$

This simplifies to:

$$\frac{w}{(1-w)}\, b > c \qquad \text{(Ineq. 6)}$$

In sum, inequalities (4-6) for the invasion of Conditional Cooperator require that the future benefits of cooperation exceed their current costs.

Combined Game

We link the iterated HD and PD, assuming both games are simultaneously played within the same pair in each round, and interaction repeats with probability w. We introduce two new strategy traits, Leveller—which cooperates, but punishes Hawk with Defect—and Acquiescent Hawk—which plays Hawk but plays Dove after being punished by Leveller (Table 2, Table S1). Leveller is like a Conditional Dove, in that it punishes Hawks, but does so with defection rather than hawkishness.

The binary strategy trait Acquiescent Hawk is present or absent in each Hawk. Because selection can favour Acquiescent or Nonacquiescent Hawks, depending on the circumstance, Hawks are able to attend to the signal sent by Levellers or not, depending on the effects on their fitness. In the human hunter-gatherer context, Levellers would be those who punish would-be dominants by terminating a mutually beneficial relationship, such as reciprocal food sharing or cooperative hunting, and Acquiescent Hawks would be those who attempt dominance by default, but will resist the temptation to monopolize a resource to avoid punishment.

If the conditions for the establishment of cooperation by Conditional Cooperator—constraints (4-6)—are met, behaviour in the PD will converge on Conditional Cooperator, regardless of players' strategy in the HD. If there are no Hawks, there is no impetus for Leveller to evolve, but as long as some Hawkishness exists, Acquiescent Hawk and Leveller can invade under conditions 7, 8 and 9.

7. The payoff to Acquiescent Hawk playing against Leveller has to be greater than the payoff to Nonacquiescent Hawk playing against Leveller. Acquiescent Hawks (also playing Conditional Cooperator) facing Levellers earn the gains to cooperation (b-c) from the PD and v from the HD in the first round. In the second round, they still earn v from the HD, but are cheated in the PD (-c) since Leveller switches to defection. In the third and all subsequent rounds, both players play Dove and cooperate. Hence:

$$V_{\text{Acquiescent Hawk|Leveller}} = \underbrace{b-c+v}_{\text{Round 1}} + \underbrace{w\,(-c+v)}_{\text{Round 2}} + \underbrace{\frac{w^2}{(1-w)}\left(b-c+\frac{v}{2}\right)}_{\text{Rounds 3+}}$$

Nonacquiescent Hawks playing against Leveller earn the same payoffs as Acquiescent Hawks in the first two rounds, but continue to earn v from the HD in all subsequent rounds. The payoffs from the PD alternate between b (round 3) and $-c$ (round 4) as each player copies its partners

move on the previous round, before converging on mutual defection in round 5 and all subsequent rounds. Hence:

$$V_{\text{Nonacquiescent Hawk|Leveller}} = \underbrace{b - c + v}_{\text{Round 1}} + \underbrace{w\,(-c + v)}_{\text{Round 2}} + \underbrace{w^2(b + v)}_{\text{Round 3}} + \underbrace{w^3(-c + v)}_{\text{Round 4}} + \underbrace{\frac{w^4}{(1 - w)}(v)}_{\text{Rounds 5+}}$$

Setting $V_{\text{Acquiescent Hawk|Leveller}} > V_{\text{Nonacquiescent Hawk|Leveller}}$ and simplifying yields:

$$wb - (w^2 - w + 1)\,c > \frac{v}{2}$$

When w is near 1—which must be the case for either Conditional Cooperator or Leveller to evolve—the first-order approximation of this condition simplifies to:

$$w(b - c) > \frac{v}{2} \qquad \text{(Ineq. 7)}$$

8. The invasion of Leveller requires that the payoffs to Levellers playing against Acquiescent Hawks have to be greater than the payoffs to Acquiescent Hawks playing against each other. In the first round Leveller and Acquiescent Hawk cooperate and earn *b-c*, with Acquiescent Hawk gaining *v* in the HD. In the second round, Leveller defects in response to their partner's hawkishness, earning *b*, while the Acquiescent Hawk again gains *v*. In round 3 and all subsequent rounds, both cooperate and—due to the Hawk's acquiescence—share the resource equally. Hence,

$$V_{\text{Leveller|Acquiescent Hawk}} = \underbrace{b - c}_{\text{Round 1}} + \underbrace{wb}_{\text{Round 2}} + \underbrace{\frac{w^2}{(1 - w)}\left(b - c + \frac{v}{2}\right)}_{\text{Rounds 3+}}$$

Acquiescent Hawks playing against each other earn the gains to cooperation (b-c) and mutual hawkishness in all rounds:

$$V_{\text{Acquiescent Hawk|Acquiescent Hawk}} = \frac{1}{(1 - w)}\left(b - c + \frac{v}{2} - \frac{d}{2}\right)$$

Setting $V_{\text{Leveller|Acquiescent Hawk}} > V_{\text{Acquiescent Hawk|Acquiescent Hawk}}$ and simplifying yields:

$$wc + \frac{1}{(1-w)}\frac{d}{2} > \frac{v}{2}. \qquad \text{(Ineq. 8)}$$

9. Leveller playing against itself must earn a higher payoff than Acquiescent Hawk playing against Leveller (which has been described above). A pair of Levellers will cooperate (generating *b-c*) and share the resource equally (getting $\frac{v}{2}$) in all rounds. This condition is fulfilled when:

$$\frac{1}{(1-w)}\left(b - c + \frac{v}{2}\right) > b - c + v + w\,(-c + v) + \frac{w^2}{(1-w)}\left(b - c + \frac{v}{2}\right),$$

which simplifies to:

$$\frac{w}{(1-w)}\,b > \frac{v}{2}. \qquad \text{(Ineq. 9)}$$

All else equal, constraints (7) and (9) for the invasion of Acquiescent Hawk and Leveller predict:

P4: Hawkishness decreases, and egalitarianism increases, with higher net benefits of future cooperation.

Constraint (7) captures the key intuition for the evolution of levelling. Levelling requires that the future net benefits of cooperation, $w(b\text{-}c)$, exceed the benefits a Hawk receives from monopolizing the resource relative to Doves who share equally, $v/2$. This rule for the evolution of levelling, $w(b\text{-}c) > v/2$, shares structural affinity with Hamilton's Rule for the evolution of altruism ($br > c$)[40], the conditions for the evolution of Conditional Cooperator and Tit-for-Tat (constraint 4: $wb > c$), and the conditions for the evolution of Conditional Dove (constraint 3: $wd > v$). The social outcomes defined by constraints (1-9) that result from different values of *w*, *b*, and *v* are plotted in Fig. 1.

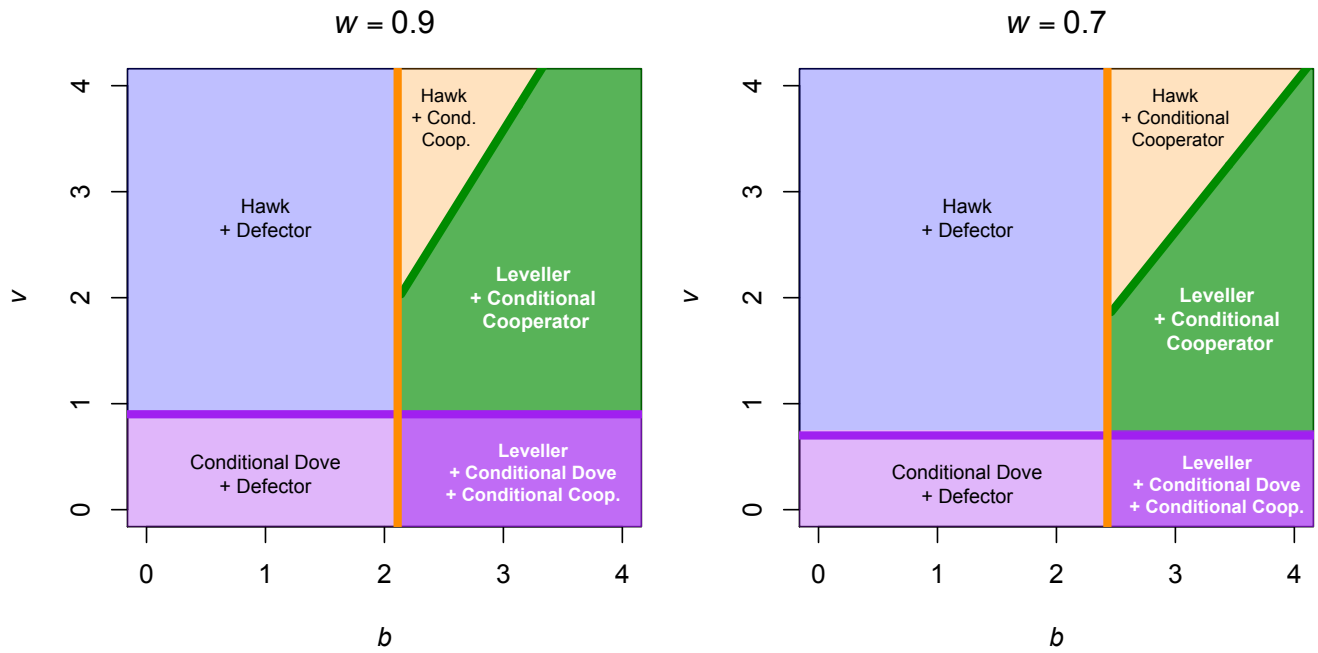

Figure 1. When can Leveller invade? Left-hand panel: Values of *b* and *v* that favour the invasion of Leveller given a relatively high probability of future interaction, $w = 0.9$, and $d = c = 1$. In the blue region of low *b* and high *v*, none of the constraints (1-9) are met, and hawkish defectors dominate. Conditional Dove is able to invade below the purple line (constraint 3). In the light purple region of low *b* and low *v*, Conditional Dove can invade, but Conditional Cooperator cannot. The invasion of cooperative strategies (Conditional Cooperator and Leveller) requires that the future benefits of cooperation outweigh its costs, i.e. that b is right of the orange line (constraint 6). In the orange region of intermediate *b* and high *v*, Conditional Cooperator can invade, but Hawks still dominate the population. The invasion of Leveller additionally requires that the future benefits of cooperation are high relative to the benefits of hawkishness, i.e that *b* is below and to the right of the green line (constraint 7). In the dark purple region where all three constraints are met, either Conditional Doves or Levellers or both strategies can invade and supress hawkishness. Right-hand panel: Conditions for the invasion of Leveller when the probability of future interaction is relatively lower, $w = 0.7$, and $d = c = 1$. With a lower probability of repetition, the region favouring the invasion of Leveller contracts, and hawkish, non-cooperative strategies dominate except for very high *b* and low *v*.

Simulations

The evolutionary dynamics of this model can be simulated using standard replicator dynamics with constant mutation rates (see Methods). Figs. 2 and 3 show the result of these simulations assuming that initial populations are 100% hawkish, defecting, and non-compliant, and that other strategies can arise through mutation. Whether newly introduced strategies become common in the population depends on selection, which in turn depends on the value of the ecological parameters for a given run.

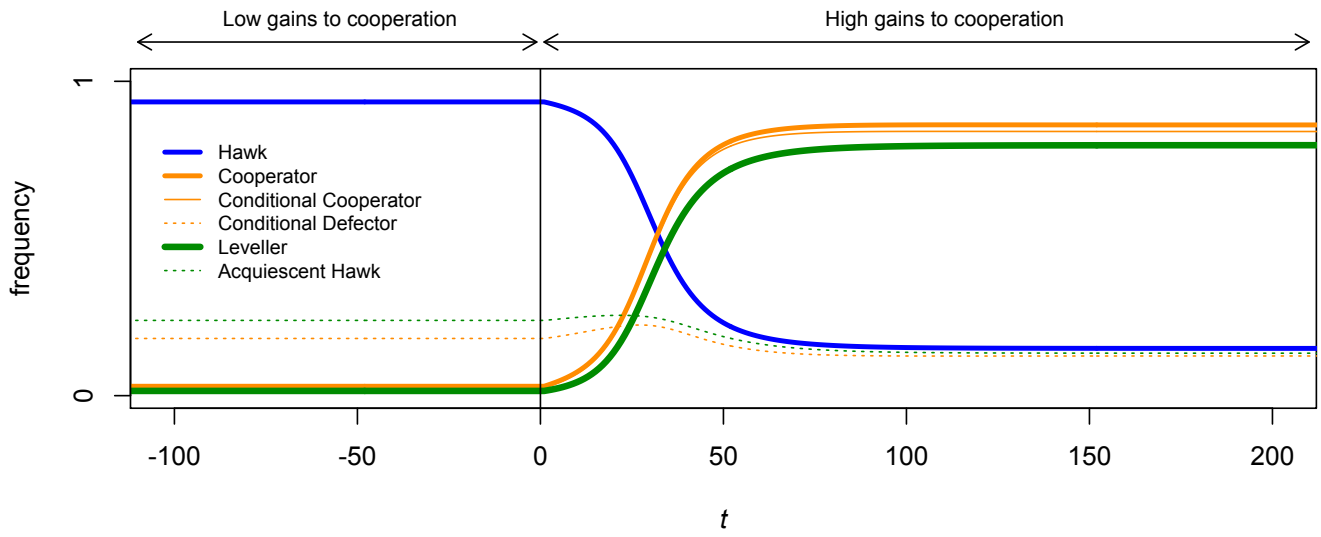

Fig 2. Increased gains to cooperation allow the evolution of egalitarianism through levelling. The plot shows the evolution of strategies before and after an ecological shift from lower to higher benefits of cooperation (from $b = 1$ to $b = 2$). Before the ecological shift, Hawks and Defectors dominate the population. After the shift, more compliant strategies (Conditional Defectors and Acquiescent Hawks) become more common among Defecting Hawks, while Conditional Cooperators and Levellers become predominant overall. Other parameters are held fixed at $v = 1$, $c = d = 1$, $w = 0.9$ and $m = 0.01$.

Fig 2 shows **P4** play out through historical time following an increase in the gains to cooperation, from $b = 1$ to $b = 2$. Before the shift—to the left of the solid vertical line—the population rests at a stable equilibrium of virtually all Hawks and Defectors. Compliant strategies are able to invade by mutation and exist at low frequencies. Following the shift, Compliant strategies first increase in frequency, which eventually allows Cooperate, Conditional Cooperator, and Leveller to invade and establish themselves as the core of the population. At the new equilibrium, the population exhibits higher levels of cooperation, lower frequency of contests, and more equal sharing of resources due entirely to an increase in the net benefits of cooperation and second-party punishment, i.e. the invasion of Leveller.

Fig. 3 shows how the long-run outcomes of the simulation vary in response to the ecological parameters b and v. Holding all other parameters constant, if b is sufficiently high for the evolution of reciprocal cooperation (Conditional Cooperator), Leveller co-evolves with Conditional Cooperator and drives down the equilibrium frequency of Hawks in the population. As v increases, the value of b necessary for the evolution of Leveller is greater. The value $w = 0.9$ implies 10 interactions on average, which is not unreasonably high for long-lived species with relatively stable groups, such as humans and other primates.

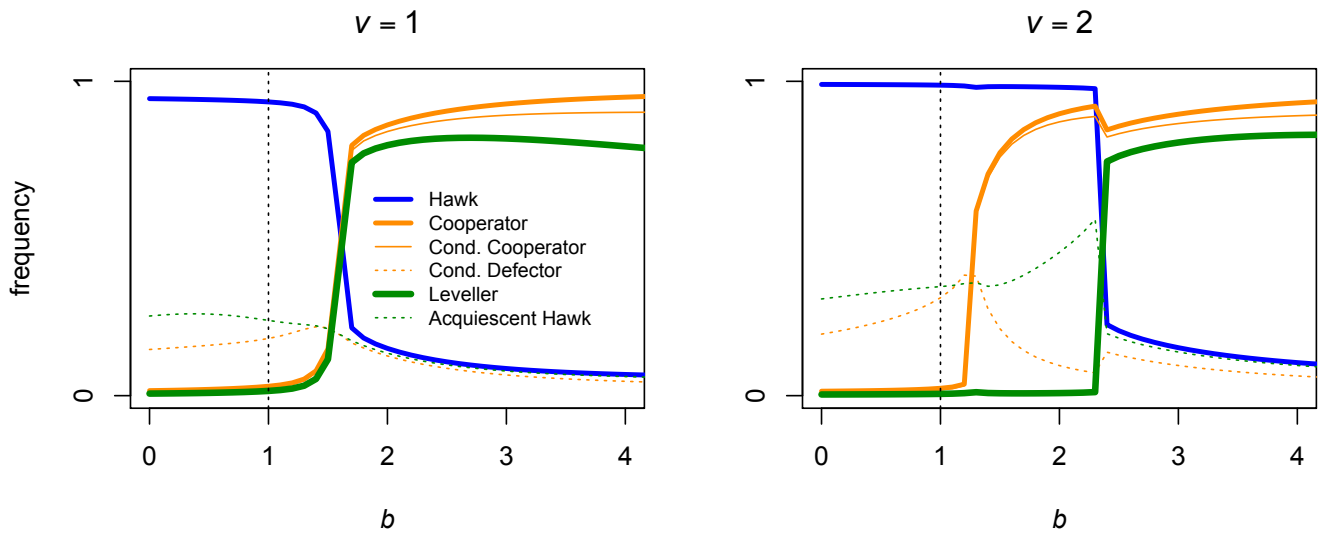

Fig 3. Simulated long-run outcomes as a function of *b*, the gains to cooperation, and *v*, the value of contestable resources after 100,000 iterations. (a) Lower value of contestable resource, $v = 1$. (b) Higher value of contestable resource, $v = 2$. Other parameters are held fixed at $c = d = 1$, $w = 0.9$ and $m = 0.01$.

Empirical Test Among Human Foragers

Given its small number of parameters and the generality of its logic, our model should extend to a wide range of empirical contexts. To test its predictions we draw on Binford's[41] database of human foragers to model the probability of egalitarianism operationalized as the *absence of class stratification* (see Methods). *Gains to cooperation* (**P4**) are represented in terms of the percentage of the diet derived from hunting. This is because the high variance in hunting return rates yield high benefits to reciprocal food sharing, and economies of scale favour cooperative production[29,42]. We include controls for *economic defensibility* (**P1**)—proxied by the presence of horses, food storage, and formal ownership of resources—as well as total population size and geographic region. The results of this analysis (Table 3) show strong support for the central prediction **P4** that benefits to cooperation significantly drive egalitarianism: an increase in the reliance on hunting by one standard deviation is associated with a 2.7-fold increase in the probability of egalitarianism. Fig. 4 plots the predicted probability of a population exhibiting egalitarianism as a function of dependence on hunting under conditions of low economic defensibility (horses, storage, and ownership = 0, i.e. absent), mean defensibility (horses, storage, and ownership = mean of sample), and high defensibility (horses, storage, and ownership = 1, i.e. present). At low defensibility, this measure of egalitarianism is already at ceiling levels and there is little scope for hunting to have an effect. (Note that at the intercept, logistic(19.9) = 1; this is likely due to the fact that the response variable, stratification, does not capture the continuous range of variation in egalitarianism among groups for whom stratification = 0). At intermediate and high defensibility, however, hunting significantly predicts egalitarianism.

Table 3. Bayesian multi-level logistic regression estimating the probability of egalitarianism (defined as a lack of class stratification) across human foragers. Mean and 95% confidence intervals are on the logit scale. OR = Odd's ratio, i.e. the change in probability of egalitarianism with a change of 1 standard deviation in the predictor

Variable	Prediction	Mean	2.5%	97.5%	OR
Intercept	.	19.89	13.23	27.01	.
Horses	**P1** (-)	-3.09	-5.52	-0.6	0.05
Storage	**P1** (-)	-5.18	-8.22	-2.36	0.01
Ownership	**P1** (-)	-2.97	-4.33	-1.63	0.05
Hunting	**P4** (+)	0.99	0.38	1.68	2.7
ln(Population)	.	-0.91	-1.44	-0.41	0.4
sd(Region random effect)	.	6.51	1.03	14.44	.

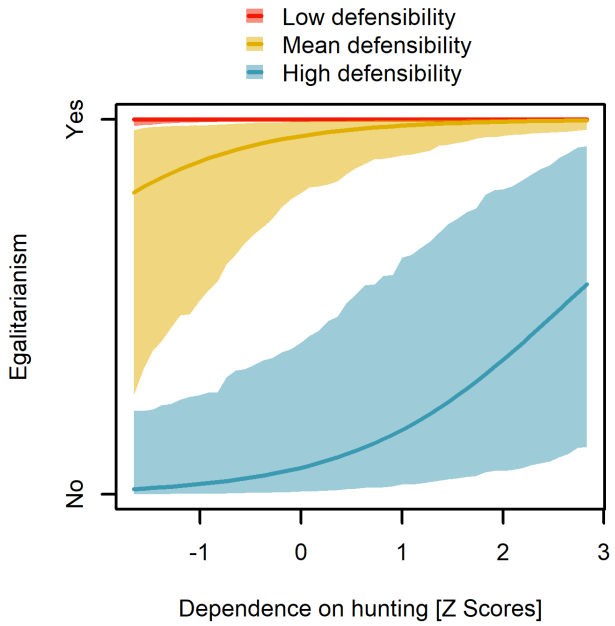

Fig. 4: Predicted probability of egalitarianism as a function of dependence on hunting, at different levels of economic defensibility of key resources (see text and Table 3 for details).

Conclusions and Future Directions

Our model provides a first proof of principle that gains to cooperation can lead to egalitarianism because withholding cooperation can be an effective means of punishing dominance behaviour. These results are bolstered by data from other species where a greater reliance on cooperation increases affiliation between dominants and subordinates and may reduce inequality in fitness outcomes[18,23,24]. At first glance, our model seems discordant with the phenomenon of cooperative breeding, which requires high levels of cooperation but is often associated with strong despotism and high reproductive skew[43]. In these contexts, inclusive fitness benefits, lack of dispersal options, and the high economic defensibility may explain why subordinates accept despotic dominants. If subordinates are allowed to choose completely freely among dominants in classic models of reproductive skew, egalitarianism does ensue[44,45]. Such partner switching may be key egalitarianism among human populations[46], and is equivalent to the refusal to cooperate (i.e. the Leveller strategy) in our model.

Our model could be extended in several ways. We did not consider errors in play (outside of mutation), invasion by any number of conceivable new mutants, or formal partner choice based

on the partner's previous behaviour with self or others; such extensions took decades to explore for the iterated PD and HD individually [20,37–39,47–53]. In future work, the model could also incorporate the formation of levelling coalitions[14–16] that further reduce the gains to dominance, or top-down coalitions that re-enforce the status quo and increase the benefits to hawkishness. Our model also does not treat the effect of stable individual differences in fighting ability or productivity[54], which could affect the relative bargaining power of individuals in the model[44]. As such, the model provides a basic framework on which greater theoretical intricacy and empirical realism can be built.

Our model suggests the importance of the following measures for empirical study: the benefits and costs of dyadic cooperation; the likelihood of future interaction; the direct benefits and costs of competitive behaviour; and the indirect costs of competitive behaviour due to retaliation and exclusion. It is our hope that rigorous empirical study and formal modelling of the hypotheses discussed here—*gains to cooperation*, *costs of competition*, *economic defensibility*, and *coalition formation*—will allow us to explain and predict variation in real-world egalitarian behaviour and social structure.

Materials and Methods

Model and Simulation Details

The simulation results are generated by numerically simulating the replicator dynamics and mutation of each strategy for a given set of parameter values using the R Language for Statistical Computing[55] as summarized in the following steps. The code for the simulation can be downloaded as a supplementary file.

Step 1. Set parameter values

Set the numerical values of the exogenous parameters v, d, b, c, and w.

Step 2. Calculate fitness

Given the parameter values, calculate the expected fitness of each strategy i when paired with each other strategy j (including i) across rounds, denoted $V_{i|j}$. Including Conditional Dove and Conditional Hawk, there are 36 unique strategies, defined in Table S1. (For simplicity, the simulations used to produce Figures 2 and 3 did not consider these two strategy traits, resulting in 14 unique strategies.) This results in a 36 × 36 payoff matrix with numerical values for $V_{i|j}$ in each cell. In combination, the strategy traits of i and j uniquely determine the behaviour and payoffs of each agent in rounds 1, 2, 3, 4, 5, and all subsequent rounds. For tractability, a number of simplifying assumptions are made regarding conditional interaction between two agents i and j across rounds.

1. In the first round, an agent plays Cooperate only if it has Cooperator = 1, and plays Dove only if it has Dove = 1.
2. After the first round, i can condition its behaviour in each round on j's behaviour in the previous round, and vice versa.
3. When an agent i with Cooperator=1 and Conditional Cooperator = 1 interacts with an agent j with Cooperator = 0, i will cooperate while j will defect in round 1. In round 2, i will defect in response to j's defection in round 1 and communicate an admonishment, "I am defecting because you defected." An agent with Conditional Dove = 1 or Leveller = 1 similarly communicates that its conditional Hawkishness/Defection is due to its partner playing Hawk in the first round.

4. When an agent *i* with Conditional Cooperator = 1 admonishes agent *j* with defection in round 2, whether *j* begins to cooperate in round 3 depends on whether *j* believes the admonishment, i.e. whether *j* has Conditional Defector = 1. If Conditional Defector = 1, *j* will begin cooperating in round 3 and all subsequent rounds. If Conditional Defector = 0, *j* will continue to defect in round 3 and all subsequent rounds. Similarly, an agent admonished by a Conditional Dove or Leveller will only begin playing Dove in round 3 if it has Conditional Hawk = 1 or Acquiescent Hawk = 1, respectively; otherwise it will ignore the admonishment and continue to play Hawk. Evolution can thus favour the willingness to attend to the punisher's admonishment or not depending on the parameter values.
5. An agent *i* with Conditional Cooperator = 1 that has admonished *j* in round 2 acts optimistically and returns to playing Cooperate in round 3. If *j* continues to play Defect in round 3, *i* will return to playing Defect in round 4 and all subsequent rounds. Similarly, an agent *i* with Conditional Dove or Leveller = 1 that admonished *j* playing Hawk in round 2 will optimistically play Dove or Cooperate in round 3, but return to playing Hawk or Defect if *j* continues to play Hawk.
6. Strategies with Conditional Cooperator, Conditional Dove, or Leveller = 1 do not play Hawk or Defect in response to being admonished with defection or hawkishness. In other words, admonishment does not trigger conditional strategies in the same way as defection or hawkishness that is not accompanied by an admonishment.
7. Only strategies with Cooperator = 1 can have Conditional Cooperator = 1 or Leveller = 1, while only strategies with Dove = 1 can have Conditional Dove = 1. In other words, only Cooperators can conditionally punish others with defection, while only Doves can conditionally punish others with hawkishness.
8. Only strategies with Cooperator = 0 can have Conditional Defector = 1, while only strategies with Dove = 0 can have Conditional Hawk = 1 or Acquiescent Hawk = 1. In other words, compliance in response to admonishment is irrelevant for those who already begin by cooperating or playing Dove.

Step 3. Simulate replicator dynamics

Set the starting frequencies of each strategy, which sum to 1. As a conservative starting point, it is assumed that hawkish, defecting, non-compliant strategies represent 100% of the population. Given the frequency of strategy *i* at time *t*, $F(i)_t$ the frequency at time *t*+1 is calculated as:

$$F(i)_{t+1} = F(i)_t \frac{\sum_j F(j)_t \left(V_{i|j} + V_0\right)}{\sum_j F(j)_t \sum_k F(k)_t \left(V_{j|k} + V_0\right)} + M(i)$$

The term V_0 represents baseline fitness outside the context of the game, which controls the force of selection, prevents negative overall fitness values, and is set by default to 10. The mutation term $M(i)$ represents the change in the frequency of *i* due to random mutations. Mutations are crucial to the simulation for two reasons. First, given an initial population of 100% hawkish defectors, mutation is the only way that new strategies enter the population. Second rare mutants exert weak selection pressures on compliant strategies that are essential for the invasion of conditional strategies such as Leveller. With a fixed mutation rate *m* (0.01 by default) and an equal probability of mutating into each of *n* distinct strategies, the net change in frequency of strategy *i* due to mutation is:

$$M(i) = \sum_j \frac{mF(j)_t}{n} - mF(i)_t$$

Step 4: Extract results

To produce the results in Fig. 2, starting from a fully Hawk-Defector initial population, replicator dynamics were iterated for 10,000 time steps with $b = 1$. After 10,000 iterations, the value of b was shifted from 1 to 2, after which the replicator dynamics were continued for an additional 10,000 time steps. Fig. 2 plots the strategy frequencies from time steps 9,900 through 10,200, with $t = 0$ marking the ecological shift occurring at 10,000 iterations. Fig. 3 plots the long-run strategy frequencies after 100,000 time steps.

Empirical Test

We analyse data drawn from Binford's forager database[41], a global database of hunter-gatherers including 339 populations freely available at http://capone.mtsu.edu/eaeff/downloads/mycloud/DEf01f.Rdata with accompanying documentation at http://intersci.ss.uci.edu/wiki/txt/LRBcodebook.txt. Egalitarianism was coded as a binary trait defined by the absence of class distinctions (egalitarian if 'class' = 1, non-egalitarian otherwise), resulting in 222 egalitarian and 115 non-egalitarian societies. Predictors of egalitarianism include several proxies for defensible resources, which are expected to decrease egalitarianism (**P1**): the presence of horses (present if 'huntfil2' = 2, absent otherwise), food storage, (present if 'store' ≥ 2, absent otherwise), and private ownership (present if 'owners' ≥ 2, absent otherwise). The predictor that proxies gains to cooperation, expected to increase egalitarianism (**P4**), was reliance on hunting (mean=33.1%, SD=20.1), which was subsequently transformed into Z scores. The model also controls for log population size, which was centered on 0, and for geographic region by including a region-level random effect ('wlocation'). The total dataset includes 337 groups from 67 regions.

We fit this as a binomial model with a logistic link function using a Bayesian approach implemented in the MCMCglmm package [56] in R 3.4.2. [55]. The model used slice sampling and weakly informative priors (fixed effects: Gaussian, mean = 0, SD = 100; random effect: half-cauchy, location = 0, scale = 10; residual variance: 1)[57]. Markov chains were run for 1e6 iterations with a burn-in of 1e5 and samples taken from every 250th iteration. Convergence of the Markov chains was assessed visually by inspecting trace plots and effective sample sizes, and formally by calculating the Gelman-Rubin diagnostic (all 1). The code for running this analysis can be downloaded as a supplementary file.

Author contributions

P. L. H. and H. S. K. conceived of the research. P. L. H. designed and analysed the model. P. L. H. and A. V. J. analysed the empirical data and wrote the paper.

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