The Evolution of Giving, Sharing, and Lotteries

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A core feature of human societies is that people often transfer resources to others. Such transfers can be governed by several different mechanisms, such as gift giving, communal sharing, or lottery-type arrangements. We present a simple model of the circumstances under which each of these three forms of transfer would be expected to evolve through direct fitness benefits. We show that in general, individuals should favor transferring some of their resources to others when there is a fitness payoff to having social partners and/or where there are costs to keeping control of resources. Our model thus integrates models of cooperation through interdependence with tolerated theft models of sharing. We also show, by extending the HAWK-DOVE model of animal conflict, that communal sharing can be an adaptive strategy where returns to consumption are diminishing and lottery-type arrangements can be adaptive where returns to consumption are increasing. We relate these findings to the observed diversity in human resource-transfer processes and preferences and discuss limitations of the model.

Introduction

A core feature of human societies is that resources are not entirely consumed by the individuals who create or find them. Instead, resources are often transferred to others, including nonrelatives. Anthropologists have found that resource distribution processes can be governed in a small number of qualitatively distinct ways (Fiske 1991, 1992; Sahlins 1972). For example, one individual may maintain private ownership of the resource, asserting priority of access but deciding to transfer a certain fraction to someone else, as in gift giving. Alternatively, the resource may be communally shared, which means that it is available to all group members with no distinctions of ownership, bookkeeping, or restrictions of access.

Resources are usually communally shared within households (Elickson 2008; Fiske 1991), though communal sharing can sometimes have a wider scope, as in the sharing of large game resources in hunter-gatherer bands (Gurven 2004; Marshall 1961). There are additional types of transfer procedures. Layton (2000), for example, describes the dairy cooperatives that became widespread in France in the medieval period. On any particular day, one member would have the right to the milk of all of the cows belonging to association members. This is an example of a rotating credit association, a form of social institution whose occurrence is widespread, in which all participating individuals contribute and one of them takes all of the accumulated resource in any given time period (Arndt 1964). More generally, rotating credit associations belong to the class of what we will call lotteries. Lotteries differ from communal sharing in that in communal sharing, resources are pooled and access is given to everyone, whereas in lotteries, resources are pooled and one individual takes everything. That individual is chosen using some simple convention. On this definition, practices such as inheritance by unigeniture, whereby the whole of an inheritance is assigned to one individual using a birth-order convention, are examples of lotteries.

In this paper, we develop a theoretical model for the emergence of different types of resource transfers. Where redistributive arrangements such as communal sharing exist, they are psychologically and morally binding for those practicing them, and people do not necessarily justify their involvement in them in terms of individual advantage (Bell 1995). However, this does not mean that they have no utilitarian or adaptive value. If such arrangements have recurrently emerged under particular ecological conditions, it is likely that they actually benefit the individuals involved under just those conditions. Note that the level of analysis we are dealing with is the ultimate rather than the proximate (Scott-Phillips, Dickins, and West 2011; Tinbergen 1963). That is, we are concerned with establishing what kinds of resource-transfer arrangements maximize individuals’ expected payoffs (those payoffs being in some currency appropriately related to genetic fitness) under different ecological conditions. We are not here concerned with questions of proximate mechanisms, namely, how human individuals and social groups arrive at the resource-transfer arrangements that they do. We will touch briefly on questions of mechanism in “Discussion,” but the substance of our model is agnostic about how adaptive equilibria are in fact reached. This agnosticism about mechanisms is a common feature of behavioral ecological models (Scott-Phillips, Dickins, and West 2011).

Resource transfers are costly to the donor, at least in the short term, and beneficial to the recipient. Thus, as for any cooperative behavior, there are two ways they could be favored by natural selection; either there is, on average, some kind of
personal payback over the individual’s lifetime from being a donor, in which case the behavior is best described as mutual-benefit cooperation (West, Griffin, and Gardner 2007), or there is no such payback but the population is assorted or structured by relatedness, in which case the behavior is best described as biological altruism (Fletcher and Doebeli 2009; Hamilton 1964). We are considering here just the mutual-benefit case. That is, our model does not depend on relatedness between interaction partners but allows for there being direct benefits in terms of lifetime reproductive success from investing in others. The assumption that helping other individuals can be personally beneficial in the long run is shared by many influential models of the evolution of cooperation (Axelrod and Hamilton 1981; Clutton-Brock 2009; Kokko, Johnstone, and Clutton-Brock 2001; Trivers 1971; West, Griffin, and Gardner 2007). For some consideration of the likely impact of relatedness on the conclusions we reach, see “Discussion.”

The literature on mutual-benefit cooperation in humans has been somewhat dominated by the idea of reciprocity or variants of it (Axelrod and Hamilton 1981; Trivers 1971). The possibility of future reciprocation in the same currency is indeed one potential source of payback from helping another individual, but there are many others (Clutton-Brock 2009; Kokko, Johnstone, and Clutton-Brock 2001; Leimar and Hammerstein 2010; Tooby and Cosmides 1996; West, Griffin, and Gardner 2007). For example, the presence of another individual in the vicinity can dilute the risk of predation, allow larger game to be tackled than one could alone, furnish mating opportunities, provide information, make a division of labor possible, and so on. Such benefits of social living have been widely documented (Silk 2007; Silk et al. 2009). Cooperative behavior can also serve as a signal that others use in future partner choice (Roberts 1998; Smith, Bliege Bird, and Bird 2001), which once again provides a fitness payoff for cooperating. Many of these other cases differ from reciprocity as usually conceived in that the benefits arise simply from the recipients of cooperation pursuing their short-term self-interest, and so there are no problems of cheating and no requirement for enforcement (Clutton-Brock 2009; Connor 1995). Our model incorporates all of the ways in which one individual’s prospects are increased by improving the welfare of another individual into a single parameter, which, like Roberts (2005), we term the “degree of interdependence.”

Using this general framework, we consider the scenario where a member of a social group has obtained some fitness-enhancing resource. We ask, first, under what circumstances would he benefit from transferring it to others rather than keeping it for himself? Second, if he is to transfer some, what form of transfer procedure should he prefer? For example, he could maintain control of how the resource is allocated but donate a share of his choosing to others. However, this could be costly, because he would have to monitor and physically control the resource and potentially resolve conflicts with others who wish to consume more. Alternatively, he could enter a communal sharing arrangement, where he makes no attempt to monitor or control the fractions taken by himself versus others and thus avoids these costs. Finally, he and others could submit to some binding lottery-type arrangement and thereby get either none or all of the resource but avoid conflict.

In the next section (“Modeling Framework”), we describe our model, and in “Optimal Shares for Each Player,” we examine what fraction of a resource a person should want to consume for himself or herself and what fraction to transfer under varying ecological parameters but assuming that there is no cost to controlling how the resource gets allocated. This also allows us to explore the magnitude of the payoff for being in control of the allocation under different conditions (“Payoff for Controlling Allocation”). In “ESS Analysis,” we introduce the idea that controlling the allocation of a resource may be costly and that communal sharing and lottery arrangements may eliminate such costs. We then conduct an evolutionarily stable strategy (ESS) analysis, extending the HAWK-DOVE model of animal conflict (Maynard Smith and Price 1973) to examine under what circumstances policies such as communal sharing and lotteries can be evolutionarily stable. We conclude with a discussion of the implications and limitations of the model (“Discussion”).

Modeling Framework

All mathematical derivations for the model are to be found in CA+ online supplement A, available as a PDF. Here, we confine ourselves to explaining the modeling assumptions and to presenting the qualitative patterns of the results. Our model concerns an idealized dyad in which two individuals, the focal and the partner, have to allocate the gains from a bout of production of a particular resource between them. We assume that consumption of the resource contributes positively to fitness by stipulating that the fitness payoff associated with consuming a fraction \( v \) of the resource is \( v^x \). The exponent \( x \) can be varied to capture the returns of different types of resources. If \( x \) is equal to 1, returns are linear. However, many resources will have diminishing returns to consumption. For example, eating 2,000 calories today over eating nothing dramatically increases survival, whereas eating 4,000 calories today over eating 2,000 makes much less difference. We capture this case by setting \( x \) to less than 1. By contrast, in the case of the French dairy farmers described above (Layton 2000), the milk of just a few cows could be used to make only a very small cheese, and because small cheeses did not survive the journey to market, they were essentially valueless. By contrast, a large cheese was robust enough to be transported and sold, which meant that the value of being able to make one large cheese was more than the sum of the values of several small ones of equal total mass. Under such circumstances, the returns to having more of the resource are increasing, which we capture by setting \( x \) greater than 1.
We also allow that having the partner alive and in proximity contributes positively to the focal’s fitness payoff by an amount \( s \). This positive effect could result, for example, from the dilution of predation risk, from improvement of per capita group productivity, or from the partner’s care for offspring of the focal, but our model is agnostic about the exact source of the benefit. We simply assume that there is some benefit to interacting with the partner, accruing either instantaneously or in the future, that is external to the consumption of the current resource to be allocated. The expected fitness for the focal associated with consuming a particular fraction of the resource thus reflects both the effect of his personal consumption and the viability of the partner. Because the partner gets to consume whatever the focal leaves, the focal faces a trade-off; as he increases his personal consumption, he simultaneously decreases his likelihood of having a viable social partner around. In supplement A, section 1, we show that under these conditions, the focal should allocate the next unit of the resource to the partner rather than consume it himself if \( sb > c \), where \( b \) is the benefit to the partner and \( c \) is the benefit foregone by the focal from consuming that unit (Roberts 2005). This makes intuitive sense, because \( sb \) is focal’s return on an improvement of \( b \) in the partner’s payoff, and for a behavior to be favored by selection, the overall fitness benefit must exceed the fitness cost. In what follows, we assume \( s \) to be symmetric between the two players and consider the range of values from no interdependence at all (\( s = 0 \)) to strong interdependence (\( s \) approaching 1, though note that values of \( s \) less than 0 and greater than 1 are logically possible and represent biologically plausible scenarios; we just do not explore them here).

### Optimal Shares for Each Player

Figure 1 shows the fitness payoff of obtaining different shares of the resource for different values of the returns function and level of interdependence. Where returns are linear and \( s \) is less than 1, the focal’s fitness is always increased by taking an extra fraction of the resource for himself (fig. 1, middle row). That is, unless further costs are introduced, the inequality \( sb > c \) is never satisfied with \( s < 1 \) for the linear-returns case, and resource transfer should not evolve. However, as the degree of interdependence becomes larger, the rate at which fitness increases with an increasing share of the resource becomes smaller. As \( s \) approaches 1, both players become indifferent to how the resource is allocated.

Where returns are diminishing and there is any degree of interdependence, the focal’s fitness is not maximized by taking everything. Instead, there comes a point where \( sb > c \) and it is more beneficial to use the next unit of resource to make a large increase in the partner’s fitness than to make a small increase in one’s own (fig. 1, top row). Thus, even given free and costless ability to control the allocation, the focal player should not take everything but instead take a fraction, which we designate \( \hat{p} \), for himself and leave \( 1 - \hat{p} \) to the partner. The value of \( \hat{p} \) depends on how steeply returns diminish and how strong the interdependence is (supplement A).

Where returns are accelerating and there is some degree of interdependence, the focal individual maximizes his fitness by taking everything but otherwise does better by taking nothing than by taking an intermediate proportion (fig. 1, bottom row). This is because having all the resource has much greater than twice the benefit of having half of it (and better than three times the benefit of consuming one-third, etc.).

### Payoff for Controlling Allocation

As returns move from accelerating to diminishing and interdependence becomes stronger, it makes increasingly little difference to a player’s fitness whether he manages to obtain his best possible allocation or the other player does so. Figure 2 illustrates this by showing the difference in payoff between completely and costlessly controlling the allocation, versus allowing the other player to completely control it, as a function of the degree of interdependence, for returns that diminish to various degrees. This difference sets a limit on the amount it would be worth paying to control the allocation of the resource versus letting the other player do so and thus suggests the kinds of circumstances under which attempting to maintain control of the resource may not be worthwhile.

### ESS Analysis

We conducted an ESS analysis by defining several different behavioral policies toward the resource allocation. Our analysis here enriches the model described thus far by considering costs of exerting control over the resource allocation. We include two costs, a cost of ownership (\( o \)) and a cost of conflict (\( c \)). The cost of ownership arises because claiming ownership entails taking possession, signaling the claim, and monitoring and physically controlling the resource. If one player pays the ownership cost and the other does not, then the “owner” allocates the resource, taking his preferred share for himself and leaving any remainder for the other. In the event that both players stake ownership claims, a conflict erupts, and the cost of conflict is the cost of resolving this one way or the other. This cost could include the risk of physical injury or simply attention, time, and energy spent in negotiating or contesting. If neither player pays the ownership cost, both players begin to consume the resource, and we assume that each will, on average, consume half. Because of interdependence, any costs paid by one player affect the other player’s fitness as well (scaled by \( s \)).

What strategies might a player adopt? While there are numerous logically possible strategies, the comparative empirical evidence shows that the resource distribution arrangements found across cultures are in fact drawn from a highly circumscribed set (Fiske 1991, 1992). Here, we focus on implementations of the three classes of strategy described at the beginning of “Introduction”: private ownership by an individual who asserts dominion over the resource, choosing his
preferred share first and then controlling the allocation to the other; communal sharing, where both players treat the resource as a common good that they freely consume without regard to who takes how much; and a lottery, whereby the whole resource is allocated to one player or the other by some convention. Thus, we define the following three strategies: (1) DOMINATE—always claims ownership; (2) SHARE—never claims ownership; and (3) LOTTERY—uses some freely available asymmetry to play either the DOMINATE strategy or the SHARE strategy (e.g., the older individual is the owner, or they take turns or flip a coin). As a consequence of this convention, LOTTERY employs the DOMINATE strategy half the time and the SHARE strategy the other half, and when two individuals playing LOTTERY meet, there are never any conflicts.

Note that these strategies also correspond to the HAWK, DOVE, and BOURGEOIS strategies, respectively, of the HAWK-DOVE model of animal conflict (Maynard Smith
Figure 2. Difference in payoff achieved by controlling the allocation of the resource versus allowing the other player to control it as a function of the degree of interdependence (s) for returns exponents varying from linear or accelerating (x ≥ 1) to sharply diminishing (x = 0.25).

1982; Maynard Smith and Price 1973). However, in our model, the value of controlling the resource arises endogenously from the interdependence and returns functions rather than being exogenous. Moreover, our cost of ownership o has no equivalent within the HAWK-DOVE framework. Our model reduces to HAWK-DOVE when s = 0 and o = 0. We assume that the probability of winning a conflict if one occurs is unrelated to whether the individual plays DOMINATE or LOTTERY.

Deriving the payoff function for each strategy playing against itself and against the other two strategies allows us to define the conditions for each strategy to invade every other. There are conditions under which each of the three strategies is a unique ESS, as well as a small region where either DOMINATE or SHARE is stable, and thus either could become fixed by chance (fig. 3; supplement A). Consider, for example, the second row, second column subplot of figure 3. Here the costs of ownership and conflict are set at 0.1 (i.e., one-tenth of the value of the resource). DOMINATE is stable where interdependence is low and returns are not too diminishing. With increasing interdependence, DOMINATE gives way to SHARE, where returns diminish sharply, and otherwise gives way to LOTTERY. The boundaries of the regions of stability are affected by changes in the costs. Increasing the cost of ownership increases the area of stability of SHARE relative to both other strategies, while increasing either cost (o or c) increases the region of stability of LOTTERY relative to DOMINATE. Where both costs are high enough relative to the value of the resource, DOMINATE can never invade, and the space is divided between LOTTERY and SHARE, with the boundary between them set by the interaction of interdependence and the returns exponent (fig. 3, bottom right subplot).

Thus, to summarize, communal sharing or using a lottery can be favored over attempting to exert private control over the resource because the benefits of exerting control do not always exceed the costs. Increasing interdependence, the cost of ownership, or the cost of conflict reduces the payoff for exerting private control and makes it more likely that one of the other strategies will be superior. Other things being equal, communal sharing is superior to lottery mechanisms where returns diminish, and lottery mechanisms are superior to communal sharing where returns increase. Note that the zone
of stability of the DOMINATE strategy is not identical to the region where the focal’s optimal strategy is to keep all of the resource. The focal favors the partner having some of the resource whenever $x < 1$ and $z > 0$. Thus, there are regions within the parameter space where the focal should pay to keep control of the resource allocation (to be the “owner”) but yet give some of the resource away. These regions are characterized by diminishing returns and a level of interdependence that is not 0 (which would favor claiming ownership and keeping everything) but is not high enough to favor SHARE or LOTTERY. We can think of these regions as akin to gift giving or alms; the focal claims authority to take his

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**Figure 3.** Regions of the parameter space where each of the three strategies—DOMINATE, SHARE, and LOTTERY—is an evolutionarily stable strategy for different values of the cost of ownership, $o$, and the cost of conflict, $c$. 

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preferred share first but then chooses to improve the welfare of a dependent by giving him what is left over afterward.

Discussion

Our model provides a simple framework for understanding the evolution of resource transfers. People should favor transferring some of their resources under two sets of circumstances: (i) when there is a fitness payoff from having social partners and fitness returns to consumption are diminishing and (ii) when there is a cost to controlling the allocation of the resource that outweighs the benefit of having it all. The two sets of circumstances are not mutually exclusive, and their components interact, so that, for example, the existence of interdependence reduces the cost of controlling the allocation that it would be worth paying, as does the existence of diminishing returns. Scenario ii is familiar from tolerated theft models of hunter-gatherer sharing (Blurton Jones 1987; Winterhalder 1996). However, scenario i—where the focal could, at no cost, keep everything but actually does better by not doing so—is not found in tolerated theft models because they do not consider interdependence. Scenario i is potentially significant for understanding human cooperative motivation. People have often been shown to have other-regarding preferences when it comes to resource allocation, and these have been seen as difficult to explain using standard evolutionary reasoning (Fehr and Fischbacher 2003). However, this model shows that the existence of such preferences is readily explicable as long as the marginal benefits of resource consumption are often diminishing and there have recurrently been fitness benefits to be derived from having interaction partners.

As for our second question, that of what type of resource-transfer mechanism should be favored, our ESS analysis confirms that different resource-allocation arrangements are likely to be adaptive under different ecological conditions and for different resources. Where returns diminish and interdependence is substantial, each player prefers that both get some of the resource, and the incentive for controlling exactly how much is very small. Under these circumstances, communal sharing without distinction of ownership can be favored because it eliminates—for both players—the costs of staking an ownership claim. Thus, as Ellickson (2008) suggests, communal sharing may be favored because it eliminates transaction costs in highly interdependent social groups. Where returns are increasing and interdependence is substantial, each player prefers that one or the other of them gets all the resource, but it makes relatively little difference to them which one it is. Here, a lottery-type arrangement can be favored, where an arbitrary convention is used to assign all the resource to one person or the other without any conflict. Private control of the resource will emerge only where the costs of claiming ownership are small relative to the benefit, a benefit that is set by the combination of the returns exponent and the degree of interdependence. Thus, our model predicts that the allocation of resources should be sensitive to variation in social interdependence, the returns to consumption, and the costs of ownership and conflict.

These predictions seem intuitively plausible. Indeed, many familiar generalizations about the observed ethnographic diversity in human resource-allocation arrangements emerge quite naturally from the results of our simple model (table 1). Thus, this modeling framework has the potential to unify a large number of different ethnographic, sociological, and economic findings. In particular, it has the strength of showing how behaviors that seem on the surface to defy the predictions of models based on individual self-interest can in fact be favored by long-run self-interest once the transaction costs of claiming and defending property, and the positive externalities of social living, are taken into account. Depending on the four factors in our model, a person may prefer to share freely, to give away portions of the resources controlled, or allow himself to be bound by arbitrary social conventions that do not always produce results in his favor.

Our model has a number of features that should be noted. It describes a general case without specifying exactly how the social benefit s arises (whether predation dilution, foraging efficiency, complementary skills, signaling, etc.) or why reducing the transfer to the other player reduces the expected value of this benefit (which could be through the other player dying or dispersing or choosing different interaction partners). We feel that this generality is a strength rather than a weakness of the approach. There has been significant effort in recent years to construct general frameworks under which to unify the many different cases of cooperation in nature (Bshary and Bergmuller 2007; Buston and Balshine 2007; Fletcher and Doebeli 2009; Lehmann and Keller 2006; Roberts 2005; West, Griffin, and Gardner 2007), and exactly what the sources of social costs and benefits are in particular ecologies does not affect the general dynamics described here. Although we conceive of our model as dealing primarily with unenforced mutualisms, it is also relevant to enforced mutualisms. Although our model does not deal with how enforcement itself evolves (for recent approaches, see Boyd, Gintis, and Bowles 2010; El Mouden, West, and Gardner 2010; Frank 1995; Hruschka and Henrich 2006; Panchanathan and Boyd 2004), once enforcement mechanisms are widespread, then there is an expected payoff to the focal for a particular social partner continuing to prosper, and the basic structure of our model applies.

More significantly, our model is based on an idealized dyad, whereas many of the social phenomena we are interested in understanding involve interactions between multiple individuals. The multiperson situation has the potential to produce effects not seen in the dyadic one. For example, the difference in payoff between controlling the outcome and letting others have free access may be small when interdependence is high and there is one other player, but the cumulative payoff impact of providing free access to multiple other players, each of whom has slightly different interests to the focal and to each other, may be higher. On the other hand, the costs of
Table 1. Key generalizations from the ethnographic or psychological literature directly paralleled by results from the model

<table>
<thead>
<tr>
<th>Generalization</th>
<th>Example</th>
<th>Model result</th>
</tr>
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<tbody>
<tr>
<td>The more costly it is to exert ownership of a resource relative to its value, the more likely it is to be communally shared</td>
<td>Hunting or fishing territories are more often communal than small gardens or farms; in modern societies, highways are mostly provided communally, whereas electricity is metered</td>
<td>Increasing the cost of ownership reduces the ESS area for DOMINATE</td>
</tr>
<tr>
<td>The more returns to consumption of a resource diminish in a particular bout (e.g., because it comes in larger chunks), the more likely it is to be communally shared</td>
<td>Large-package animal products more often shared than vegetable foods (Gurven 2004); water resources often communal even when food is not</td>
<td>Decreasing $x$ increases the size of the ESS area for SHARE</td>
</tr>
<tr>
<td>The less steeply returns to consumption of the resource diminish, the more likely individuals are to use a lottery mechanism rather than share</td>
<td>Emergence of rotating credit associations for resources where a small amount has no benefit but a large amount does (Ardner 1964); unigeniture in inheritance where subdivision of farms would make them uneconomic</td>
<td>LOTTERY dominates SHARE where $x &gt; 1$</td>
</tr>
<tr>
<td>Mechanisms that make returns less diminishing lead to less widespread sharing</td>
<td>Sharing is widespread in hunter-gatherer societies with no storage and limited opportunity to pass on resources to offspring, whereas individual property rights are typical in pastoralist or agricultural societies, where resources can be passed on (Borgerhoff Mulder et al. 2009); market opportunities or storage technologies predicted to reduce scope of sharing</td>
<td>SHARE less likely to be stable as $x$ increases</td>
</tr>
<tr>
<td>The more shared interests individuals have above and beyond the current resource transaction, the more likely they are to communally share</td>
<td>Ubiquity of sharing in households (Ellickson 2008) or small groups with common interests (e.g., bands, military platoons; Fiske 1991; Sahlins 1972)</td>
<td>Other things being equal, increasing $s$ favors the SHARE strategy</td>
</tr>
<tr>
<td>The less individuals have interests in common outside of the current transaction, the greater the share of the resource they will try to take</td>
<td>Different levels of resource transfer between strangers and between friends or relatives (Berte 1988; Moore 2009)</td>
<td>Increasing $s$ decreases $\hat{p}$</td>
</tr>
<tr>
<td>The lower the costs of ownership and disputes are, the more private property rights are favored</td>
<td>States and other third-party enforcement mechanisms are conducive to private ownership</td>
<td>As the ownership and dispute costs decrease, the DOMINATE equilibrium area becomes larger</td>
</tr>
<tr>
<td>The more costly conflicts become or the higher the degree of shared interests are, the more likely sharing or dispute-avoiding conventions will evolve</td>
<td>Secular reduction in conflict; emergence of conflict-avoiding conventions when groups interact frequently</td>
<td>High values of the dispute cost are associated with large equilibrium areas of SHARE and LOTTERY</td>
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</tbody>
</table>

Note. ESS = evolutionarily stable strategy.
preventing them access may be higher, too. How the dynamics of these forces would resolve is not straightforward to predict intuitively, and there may be important scaling effects on arrangements such as communal sharing as the number of individuals involved increases.

We acknowledge that the dyadic structure of our model is a limitation, but for a number of reasons, we see the value of first examining the dyadic case. Multimember social groups are to a considerable extent woven together by dyadic relationships, and dyadic allocation decisions of the kind our model describes are common in social life. Moreover, many of the conclusions of our model can be applied to larger group situations, at least as an approximation, by considering the individual who has obtained the resource as the focal and the rest of the group as the partner. Thus, the framework used here can be employed heuristically for thinking about the trade-off between allocation to private and public goods in group situations (a point made in Roberts 2005).

Another limitation is that we have not considered the effects of relatedness on optimal allocations. All of the shared interest in our model arises from increases in personal fitness from having a social partner; we do not consider the indirect fitness benefits if those partners are also related. Such effects have been extensively considered in reproductive skew models (Cant and Johnstone 1999; Johnstone 2000; Vehrencamp 1983), a class of models conceptually related to the current one, where dominant and subordinate individuals partition the reproductive output of the group between them. Though in general terms relatedness generates shared interest (Hamilton 1964) and thus might be expected to have similar effects to increasing our parameter, the consequences of increasing relatedness in reproductive skew models are not straightforward. Where fitness returns to personal reproduction are diminishing (e.g., because each successive offspring born to the same individual is less likely to survive to maturity), then increasing relatedness is predicted to lead to more evenly shared reproduction (Cant and Johnstone 1999; note that this is formally very similar to our prediction of more even resource allocation when is high and returns diminish). If returns are linear, dominants are predicted to take a larger share of reproduction if subordinates are related rather than unrelated (Cant 1998; Vehrencamp 1983) as long as the dominants are able to control the partition; if not, the predicted relationship is abolished or reversed (Reeve, Emlen, and Keller 1998). However, reproductive skew models specifically incorporate leaving the group and reproducing alone as a strategic option for the subordinate, and it is the fact that unrelated individuals require a larger incentive to stay that is driving these results. Our current model does not allow us to vary the attractiveness of the other player’s outside option or, equivalently, the incentive required to make them stay. This would be a useful elaboration, especially if coupled with incorporation of relatedness, because the availability of outside options is predicted to have different effects if groups are composed of nonkin rather than kin (Cant and Johnstone 2009).

These limitations noted, then, we feel that the modeling framework presented here has the potential to contribute to the development of more general theories of the functional basis of social arrangements. As noted in “Introduction,” our model predicts which equilibria human groups might be expected to reach for different types of situations but is agnostic about the mechanisms by which this actually occurs. However, prior research on resource allocation across cultures suggests that the observed behavioral strategies are underlaid by a set of universally available cognitive schemas (“relational models”), each of which is evoked by particular sets of situational and social cues and each of which engages particular moral motivations (Fiske 1991, 1992; Fiske and Haslam 2005; Rai and Fiske 2011). The cultural emergence of a particular resource-allocation convention results from the shared evolution of one of these schemas in a specific social and material context. These relational models are presumably the product of natural selection, and our model goes some way to explaining, at least for the communal sharing model, why it evolved and why it is evoked by the particular situational cues that it is.

Although our goal was to explain diversity in resource-transfer behaviors, our results might also be used to understand the psychology of dyadic relationships. In interactions with strangers, people often maximize their short-run self-interest. Among acquaintances, there may be transfer of resources, but each party keeps control and track of the amounts transferred. Among close friends and family, the flow of resources is governed by need, and explicit bookkeeping is considered inappropriate (Clark and Mills 1979; Rai and Fiske 2011; Silk 2003). Consider moving along the horizontal of increasing shared interest, where , , and in figure 3. At first, where , the focal should try to control the allocation and keep everything. Moving slightly to the right, so , the focal should still try to control the allocation, but if successful in doing so, the focal should give a minor fraction of the resource to the partner. Moving still farther to the right, we enter a region where the focal would do best simply to allow the partner free access and keep no account. Thus, our model predicts that as people build up shared interests, their relationships will change in ways that mirror the stranger-acquaintance-friend sequence.

References Cited


1 Allocations and Payoffs

As stated in the main paper, the primary fitness payoff to an individual is a function of the fraction of the resource consumed, $v$, and the returns to consumption, $x$. This payoff is given by:

$$\pi(v) = v^x$$

An individual also benefits secondarily from any increase in his partner’s fitness payoff, to an extent governed by the degree of interdependence, $s$. Given that the partner consumes whatever the focal individual does not $(1 - v)$, the total payoff for the focal player of any given allocation is:

$$\pi_{focal}(v) = v^x + s(1 - v)^x$$  \hspace{1cm} (1)

Since the partner obtains a fraction $1 - v$ of the resource, the partner’s payoff for a given allocation to the focal individual is:

$$\pi_{partner}(v) = (1 - v)^x + sv^x$$ \hspace{1cm} (2)

When should the focal player prefer to give an extra unit of the resource to the partner rather than keeping it for himself? This means asking when an allocation of $i$ units to the focal gives a better fitness payoff than an allocation of $j$ units, where $i < j$. This will be the case when:
\[ i^x + s(1 - i)^x > j^x + s(1 - j)^x \]

Rearranging:

\[ s[(1 - i)^x - (1 - j)^x] > j^x - i^x \]  \hspace{2cm} (3)

Since the benefit to the partner of an extra unit of resource is the increase in the partner’s personal payoff \((1 - i)^x - (1 - j)^x\), and the cost to the focal is the decrease in his personal payoff \(j^x - i^x\), we can rewrite Inequality (3) as \(sb > c\). This inequality states the general condition which must be satisfied for the focal to be selected to transfer a unit of resource to the partner if no other costs are present. It is intuitive, since \(sb\) represents the focal’s secondary payoff from a payoff of \(b\) to the partner, and thus the inequality amounts to the requirement that the focal’s secondary gain must exceed his primary loss if he is to benefit from transferring a unit of resource to the partner.

The fitness payoffs for the focal and the partner (from (1) and (2)) under different allocations of the resource, and different parameter settings, are plotted in figure 1 of the main paper. When returns are diminishing \((x < 1)\) and the two players have a stake in one another \((s > 0)\; \text{the subplot in the top row, second column, and the subplot in the top row, third column}) a player’s payoff reaches a maximum when he allocates less than all of the resource to himself \((0 < v < 1)\).

To find the allocation which maximizes a player’s payoff when returns are diminishing \((x < 1)\), we differentiate Equation (1) with respect to the fraction allocated to him, which gives us:

\[ \frac{d\pi}{dv} = xv^{x-1} - sx(1 - v)^{x-1} \]

or:

\[ \frac{d\pi}{dv} = x \left( v^{x-1} - s(1 - v)^{x-1} \right) \]  \hspace{2cm} (4)

Equation (4) equals zero either when \(x = 0\) or when

\[ v^{x-1} - s(1 - v)^{x-1} = 0 \]  \hspace{2cm} (5)

Equation (5) can be rewritten as:

\[ s = \left( \frac{v}{1 - v} \right)^{x-1} \]

Solving for \(v\):
\[ s^{\frac{1}{x-1}} = \frac{v}{1 - v} \]

Resulting in:

\[ \hat{v} = \frac{s^{\frac{1}{x-1}}}{1 + s^{\frac{1}{x-1}}} \]  \hspace{1cm} (6)

Equation (6) is plotted in Supplementary Figure 1. \( \hat{v} \) represents the share of the resource that a player would optimally allocate to himself if he can completely and costlessly control the allocation. When returns are linear or accelerating \( (x \geq 1) \) or there is no interdependence \( (s = 0) \) a player prefers all of the resource for himself \( (\hat{v} = 1) \). When returns are diminishing \( (x < 1) \) and the two players have a stake in one another \( (s > 0) \) a player prefers less than all of the resource \( (\hat{v} < 1) \).

![Figure 1: Optimal share sought as a function of returns and interdependence. Numbers within the shaded regions depict the range of fractions of the resource a player would prefer to allocate to himself, \( \hat{v} \).](image)

With diminishing returns and interdependence, we can use the “optimal” allocation, given by Equation (6), to compute the payoff a player would gain if he...
controls the allocation, and the payoff he would gain if he concedes control of
the allocation to his partner. These payoffs are respectively given by:

$$\pi(\hat{v}) = \hat{v}^x + s(1 - \hat{v})^x$$  \hspace{1cm} (7)

and:

$$\pi(1 - \hat{v}) = (1 - \hat{v})^x + s\hat{v}^x$$  \hspace{1cm} (8)

The difference between (7) and (8), which we label $B_{own-cede}$, is given by:

$$B_{own-cede} = (1 - s)\hat{v}^x + (s - 1)(1 - \hat{v})^x$$

This can be rewritten as:

$$B_{own-cede} = (1 - s)\left(\hat{v}^x - (1 - \hat{v})^x\right)$$  \hspace{1cm} (9)

$B_{own-cede}$ represents the net benefit from controlling the resource over ceding
control to the other party (i.e., the payoff difference to a player between con-
trolling the resource completely or letting his partner control it). Equation (9)
is plotted in figure 2 of the main paper.

From Equation (9) we can see:

- The benefit of controlling the allocation decreases as interdependence in-
creases.
- The benefit of controlling the allocation increases as returns to consump-
tion increase.

2 Costs

We consider two types of cost: an ownership cost, $o$ and a conflict cost, $c$. The
ownership cost represents the cost of staking a claim to the allocation of the
resource, and monitoring whether this claim is being respected. The conflict cost
is contingent on the other player’s behaviour; if the other player also attempts
ownership, then a conflict erupts and it is costly for both players to settle it.
Note here the similarities and differences with Maynard Smith’s (1982) HAWK–
DOVE model. In that model, there is no cost of making an ownership claim
(no equivalent of our $o$). There is a cost of conflict $c$, but this is only paid
by the loser of the conflict, whereas our conflict cost is paid by both parties. This latter difference is unimportant. The consequential difference between our model and the \textit{HAWK–DOVE} model as regards costs is the introduction of $o$, and this model reduces to the \textit{HAWK–DOVE} model in the case where $s = 0, x = 1, \text{ and } o = 0$.

If the focal player pays the ownership cost $o$ and his partner does not, the focal player controls the allocation and takes $\hat{v}$ for himself, leaving $(1 - \hat{v})$ for the other. If neither player pays the ownership cost, both players begin to consume the resource, and we assume that each player will, on average, consume half of the resource. If both players pay the ownership cost, there is a conflict, which imposes a further cost $c$ on both players. The conflict is decided in favour of one player or the other with equal probability. Note that when costs are paid, they affect both the payoff of the player paying them, and the payoff of the other player, scaled by $s$.

These costs should be thought of as fractions of the maximum value of the resource. If a player consumes all of the resource, the payoff is 1, regardless of the returns on consumption. Thus, a value of $o = 0.1$ and $c = 0.2$ implies that the cost of claiming ownership of the resource is 10\% of the value of the resource and the cost of a conflict over the allocation is 20\% of the value of the resource.

## 3 Strategies and Interaction Payoffs

We consider three behavioural strategies.

- \textit{SHARE} does not attempt to control the resource allocation, and consequently never pays the ownership cost $o$. If the other player attempts to control the resource, an individual playing \textit{SHARE} cedes the resource and consumes the remainder left him, $(1 - \hat{v})$. When two \textit{SHARE}s meet, since neither claims ownership, they end up consuming half the resource each. The \textit{SHARE} captures the empirically-observed relational model of \textit{Communal Sharing}, in that \textit{SHARE}s neither attempt to own the resource, nor control the other party’s access it (Fiske, 1991).

- \textit{DOMINATE} attempts to control the resource allocation, always paying the ownership cost $o$. If the other player does not attempt to control the resource, an individual playing \textit{DOMINATE} consumes a fraction $\hat{v}$ of the resource, leaving $1 - \hat{v}$ to the other player. If the other player attempts to control the resource too, paying the ownership cost, a conflict erupts. In the event of a conflict, both players must expend the conflict cost, $c$. In half of these disputes, an individual playing \textit{DOMINATE} succeeds in controlling the allocation, garnering a fraction $\hat{v}$ of the resource for himself; in the other half, he loses control of the resource and consumes only $1 - \hat{v}$. This strategy represents the attempt to exert private property rights.
• LOTTERY plays either the SHARE strategy or the DOMINATE strategy with equal likelihood, using some freely available cue to decide which (for example, when arriving first, plays DOMINATE, and arriving second, plays SHARE). The consequence of this convention is that two individuals playing LOTTERY avoid any disputes and never have to pay the conflict cost c.

The DOMINATE and SHARE strategies considered in this model are analagous to HAWKS and DOVES in Maynard Smith’s (1982) canonical model of resource conflict, whilst the LOTTERY strategy is a homologue of the BOURGEOIS strategy, in that it uses an uncorrelated asymmetry as a convention to avoid disputes.

Supplementary Table 1 defines the payoffs for the row player for all possible interaction pairs.

Table 1: Interaction Payoffs

<table>
<thead>
<tr>
<th>Strategy</th>
<th>SHARE</th>
<th>DOMINATE</th>
<th>LOTTERY</th>
</tr>
</thead>
<tbody>
<tr>
<td>SHARE</td>
<td>$\pi_{S,S}$</td>
<td>$\pi_{S,D}$</td>
<td>$\pi_{S,L}$</td>
</tr>
<tr>
<td>DOMINATE</td>
<td>$\pi_{D,S}$</td>
<td>$\pi_{D,D}$</td>
<td>$\pi_{D,L}$</td>
</tr>
<tr>
<td>LOTTERY</td>
<td>$\pi_{L,S}$</td>
<td>$\pi_{L,D}$</td>
<td>$\pi_{L,L}$</td>
</tr>
</tbody>
</table>

We now derive each of the nine possible interaction payoffs listed in Supplementary Table 1.

• The payoff for playing SHARE against another SHARE is the payoff for consuming half the resource, namely:

$$\pi_{S,S} = \pi(0.5) = 0.5^x + 0.5s^x$$

Rearranging:

$$\pi_{S,S} = \pi(0.5) = (1 + s)0.5^x$$

• When SHARE meets DOMINATE, the payoff is:

$$\pi_{S,D} = \pi(1 - \hat{v}) - s\hat{o}$$

• When SHARE meets LOTTERY, the LOTTERY attempts to control the resource half the time and otherwise doesn’t attempt control, resulting in the payoff:

$$\pi_{S,L} = 0.5\pi_{S,D} + 0.5\pi_{S,S}$$
• When DOMINATE meets SHARE, the payoff is:

\[ \pi_{D,S} = \pi(\hat{v}) - o \]

• When DOMINATE meets DOMINATE, there is always a dispute, with both players paying both the ownership cost, \( o \), and the conflict cost, \( c \). Each combatant will, on average, control the resource allocation half the time, resulting in the payoff:

\[ \pi_{D,D} = 0.5\left(\pi(\hat{v}) + \pi(1 - \hat{v})\right) - (1 + s)(o + c) \]

Substituting (7) and (8) into this expression, we have:

\[ \pi_{D,D} = 0.5\left(\hat{v}x + s(1 - \hat{v})x + (1 - \hat{v})x + s\hat{v}x\right) - (1 + s)(o + c) \]

This simplifies to:

\[ \pi_{D,D} = (1 + s)\left[0.5\left(\hat{v}x + (1 - \hat{v})x\right) - (o + c)\right] \]

• When DOMINATE meets LOTTERY, the LOTTERY attempts to control the resource half the time and cedes the control otherwise, resulting in the payoff:

\[ \pi_{D,L} = 0.5\pi_{D,D} + 0.5\pi_{D,S} \]

• When LOTTERY meets SHARE, the LOTTERY attempts to control the resource half the time and otherwise doesn’t attempt control, resulting in the payoff:

\[ \pi_{L,S} = 0.5\pi_{D,S} + 0.5\pi_{S,S} \]

• When LOTTERY meets DOMINATE, the LOTTERY attempts to control the resource half the time and cedes the control otherwise, resulting in the payoff:

\[ \pi_{L,D} = 0.5\pi_{D,D} + 0.5\pi_{S,D} \]

• When LOTTERY meets LOTTERY, we assume that the two individuals coordinate without conflict; during each turn, one player controls the resource and the other cedes control, resulting in the payoff:

\[ \pi_{L,L} = 0.5\pi_{D,S} + 0.5\pi_{S,D} \]
4 Evolutionary Dynamics

We can now calculate the evolutionary dynamics following Maynard Smith (1982). For each parametric combination, we want to find the evolutionarily stable strategies (ESSs). There are eight such possibilities:

1. No strategy is an ESS, resulting in a three-way polymorphism.
2. There is a polymorphic ESS between SHARE and DOMINATE.
3. There is a polymorphic ESS between SHARE and LOTTERY.
4. There is a polymorphic ESS between LOTTERY and DOMINATE.
5. SHARE is the only ESS.
6. DOMINATE is the only ESS.
7. LOTTERY is the only ESS.
8. Both SHARE and DOMINATE are ESSs.
9. Both SHARE and LOTTERY are ESSs.
10. Both DOMINATE and LOTTERY are ESSs.
11. All three strategies are ESSs.

Using the interaction payoffs listed in previous section, we derive the following results:

**If LOTTERY is an ESS, then neither SHARE nor DOMINATE are ESSs.** To see why, we find the conditions when LOTTERY is an ESS. In order for LOTTERY to be an ESS, LOTTERY must be an ESS against both SHARE and DOMINATE. We first find when LOTTERY is an ESS against SHARE.

\[
\begin{align*}
\pi_{L,L} &> \pi_{S,L} \\
0.5\pi_{D,S} + 0.5\pi_{S,D} &> 0.5\pi_{S,D} + 0.5\pi_{S,S} \\
\pi_{D,S} &> \pi_{S,S}
\end{align*}
\]

(10)

Next, we find when LOTTERY is an ESS against DOMINATE.

\[
\begin{align*}
\pi_{L,L} &> \pi_{D,L} \\
0.5\pi_{D,S} + 0.5\pi_{S,D} &> 0.5\pi_{D,D} + 0.5\pi_{D,S} \\
\pi_{S,D} &> \pi_{D,D}
\end{align*}
\]

(11)
From these two results, we can see that \textit{LOTTERY} is an ESS if \textit{DOMINATE} can invade a population of \textit{SHARE} \((10)\) and \textit{SHARE} can invade a population of \textit{DOMINATE} \((11)\). So, if \textit{LOTTERY} is an ESS, then neither \textit{SHARE} nor \textit{DOMINATE} are ESSs, eliminating possibilities 9, 10, and 11 from the list above.

We can also eliminate possibility 1 (i.e., no strategy is an ESS). For there to be no ESS, each strategy can invade a population of comprised of one of the other two strategies. With three strategies, there are six such inequalities which must be simultaneously satisfied. Inequalities \((10)\) and \((11)\) are two of these six. However, when \((10)\) and \((11)\) are satisfied, \textit{LOTTERY} is an ESS against both \textit{SHARE} and \textit{DOMINATE}.

\textit{SHARE} and \textit{LOTTERY} cannot be part of a polymorphic ESS. For both of the strategies to be part of a polymorphic ESS, each would have to be able to invade a population of the other. For \textit{SHARE} to invade a population of \textit{LOTTERY} requires:

\[
\begin{align*}
\pi_{S,L} & > \pi_{L,L} \\
0.5\pi_{S,D} + 0.5\pi_{S,S} & > 0.5\pi_{D,S} + 0.5\pi_{S,D} \\
\pi_{S,S} & > \pi_{D,S}
\end{align*}
\]  
(12)

And for \textit{LOTTERY} to invade a population of \textit{SHARE} requires:

\[
\begin{align*}
\pi_{L,S} & > \pi_{S,S} \\
0.5\pi_{D,S} + 0.5\pi_{S,S} & > \pi_{S,S} \\
\pi_{D,S} & > \pi_{S,S}
\end{align*}
\]  
(13)

Inequalities \((12)\) and \((13)\) cannot be simultaneously satisfied, so \textit{SHARE} and \textit{LOTTERY} cannot exist in a polymorphic ESS, thereby eliminating possibility 3 from the list above.

\textit{DOMINATE} and \textit{LOTTERY} cannot be part of a polymorphic ESS. For both of the strategies to be part of a polymorphic ESS, each would have to be able to invade a population of the other. For \textit{DOMINATE} to invade a population of \textit{LOTTERY} requires:

\[
\begin{align*}
\pi_{D,L} & > \pi_{L,L} \\
0.5\pi_{D,D} + 0.5\pi_{D,S} & > 0.5\pi_{D,S} + 0.5\pi_{S,D} \\
\pi_{D,D} & > \pi_{S,D}
\end{align*}
\]  
(14)
And for \textit{LOTTERY} to invade a population of \textit{DOMINATE} requires:

\[ \pi_{L,D} > \pi_{D,D} \]
\[ 0.5\pi_{D,D} + 0.5\pi_{S,D} > \pi_{D,D} \]
\[ \pi_{S,D} > \pi_{D,D} \]

Inequalities (14) and (15) cannot be simultaneously satisfied, so \textit{DOMINATE} and \textit{LOTTERY} cannot exist in a polymorphic ESS, thereby eliminating possibility 4 from the list above.

If \textit{SHARE} is an ESS against \textit{DOMINATE} (\(\pi_{S,S} > \pi_{D,S}\)), then \textit{SHARE} is also an ESS against \textit{LOTTERY} (\(\pi_{S,S} > \pi_{T,S}\)). This follows because \textit{LOTTERY} alternates between \textit{SHARE} and \textit{DOMINATE} when playing \textit{SHARE}. Thus, on half the interactions, a \textit{LOTTERY} will match the payoff of a \textit{SHARE}; on the other half, a \textit{LOTTERY} will have a lower payoff.

If \textit{DOMINATE} is an ESS against \textit{SHARE} (\(\pi_{D,D} > \pi_{S,D}\)), then \textit{DOMINATE} is also an ESS against \textit{LOTTERY} (\(\pi_{D,D} > \pi_{T,D}\)). This follows because \textit{LOTTERY} alternates between \textit{SHARE} and \textit{DOMINATE} when playing \textit{DOMINATE}. Thus, on half the interactions, a \textit{LOTTERY} will match the payoff of a \textit{DOMINATE}; on the other half, a \textit{LOTTERY} will have a lower payoff.

The preceding analyses pare down the list of possible evolutionary outcomes to:

- There is a polymorphic ESS between \textit{SHARE} and \textit{DOMINATE}.
- \textit{SHARE} is the only ESS.
- \textit{DOMINATE} is the only ESS.
- \textit{LOTTERY} is the only ESS.
- Both \textit{SHARE} and \textit{DOMINATE} are ESSs.

Before we find the conditions for these evolutionary outcomes, we examine the \textit{SHARE–DOMINATE} polymorphic ESS more closely.

What is the distribution of \textit{SHARE} and \textit{DOMINATE} at the polymorphic ESS? Let \(\hat{\rho}\) be the fraction of \textit{DOMINATE} at the polymorphic ESS. At this polymorphic ESS, the payoff of \textit{SHARE} and \textit{DOMINATE} will be the
same, an individual will interact with a partner playing the DOMINATE with probability $\hat{p}$, and interact with a partner playing the SHARE with probability $1 - \hat{p}$:

$$\hat{p}\pi_{D,D} + (1 - \hat{p})\pi_{D,S} = \hat{p}\pi_{S,D} + (1 - \hat{p})\pi_{S,S}$$

Solving for $\hat{p}$:

$$\hat{p} = \frac{\pi_{S,S} - \pi_{D,S}}{\pi_{D,D} - \pi_{S,D} - \pi_{D,S} + \pi_{S,S}}$$  \hspace{1cm} (16)$$

**Can LOTTERY invade this polymorphic ESS?** Inequalities (10) and (11) show us that LOTTERY is an ESS whenever SHARE can invade DOMINATE and vice versa (i.e., when there is a polymorphic ESS between the two strategies). Suppose that the population is at the SHARE–DOMINATE polymorphic ESS. We can ask whether LOTTERY can invade. For this to happen, the payoff of a mutant LOTTERY must be higher than the payoff of the residents, comprised of a mix of SHARE and DOMINATE. At the polymorphic equilibrium, the payoff of SHARE and DOMINATE will be same, so we can compare the payoff of a mutant LOTTERY with the payoff of either the SHARE or DOMINATE strategies. Here, we compare the payoff of a mutant LOTTERY against a SHARE:

$$\hat{p}\pi_{L,D} + (1 - \hat{p})\pi_{L,S} > \hat{p}\pi_{S,D} + (1 - \hat{p})\pi_{S,S}$$

Solving for $\hat{p}$:

$$\hat{p} > \frac{\pi_{S,S} - \pi_{D,S}}{\pi_{D,D} - \pi_{S,D} - \pi_{D,S} + \pi_{S,S}}$$ \hspace{1cm} (17)$$

From Equation (16), we see that the right-hand side of Inequality (17) is equal to $\hat{p}$. Making this substitution, Inequality (17) becomes $\hat{p} > \hat{p}$, a condition which cannot be satisfied; LOTTERY cannot invade a population of SHARE and DOMINATE.

In fact, the payoff of a LOTTERY is the same as the payoff of residents of a SHARE–DOMINATE equilibrium. The same situation occurs with the BOURGEOIS strategy against a population of HAWKS and DOVES (Maynard Smith, 1982). In order to transition from the SHARE–DOMINATE polymorphic ESS to the LOTTERY ESS, some kind of assortment is required, like kin-biased interaction, which increases the probability of mutant LOTTERIES interacting
with one another above chance. With such assortment, selection will result in the LOTTERY ESS.

To prove this, we introduce a new model parameter, $r$, meant to represent non-random assortment, which could be generated through kin-biased interactions, for example. Again, we let $\hat{p}$ represent the frequency of DOMINATE at the polymorphic equilibrium between DOMINATE and SHARE. When considering rare mutants playing LOTTERY, the frequency of LOTTERY is approximately zero and so the frequency of SHARE will be approximately $1 - \hat{p}$.

As the overall frequency of LOTTERY is close to zero, the average payoff of DOMINATE and SHARE will be dominated by interactions with others playing DOMINATE and SHARE. As such, we can assign the probability of either a DOMINATE or SHARE interacting with a LOTTERY to be approximately zero. Additionally, we can assign the probability of LOTTERY interacting with another LOTTERY above and beyond $r$, the non-random assortment parameter, to be approximately zero.

With these assumptions, we can define the probabilities of forming different types of pairs. We denote these probabilities with $Pr(i|j)$ which represents the probability of interacting with a partner playing strategy $i$ given the focal individual plays strategy $j$.

$$
\begin{align*}
Pr(D|D) &= r + (1-r)\hat{p} \\
Pr(S|D) &= (1-r)(1-\hat{p}) \\
Pr(L|D) &\approx 0
\end{align*}
$$

$$
\begin{align*}
Pr(D|S) &= (1-r)\hat{p} \\
Pr(S|S) &= r + (1-r)(1-\hat{p}) \\
Pr(L|S) &\approx 0
\end{align*}
$$

$$
\begin{align*}
Pr(D|L) &= (1-r)\hat{p} \\
Pr(S|L) &= (1-r)(1-\hat{p}) \\
Pr(L|L) &\approx r
\end{align*}
$$

(18)

In order to derive the equilibrium distribution of DOMINATE and SHARE, we find when their expected payoffs are equal:

$$
Pr(D|D)\pi_{D,D} + Pr(S|D)\pi_{D,S} = Pr(D|S)\pi_{S,D} + Pr(S|S)\pi_{S,S}
$$

Substituting the interaction probabilities into (18), and solving for $\hat{p}$, we have:
\[ \hat{p} = \frac{\pi_{S,S} - (1-r)\pi_{D,S} - r\pi_{D,D}}{(1-r)(\pi_{D,D} - \pi_{D,S} - \pi_{S,D} + \pi_{S,S})} \]  

(19)

Note, when \( r = 0 \), Equation (19) reduces to Equation (16).

Next, to determine whether \( \text{LOTTERY} \) can invade with non-random assortment, we find when the payoff of a mutant playing \( \text{LOTTERY} \) is higher than the payoff of a resident. (Note, at the polymorphic equilibrium, the payoff of \( \text{SHARE} \) and \( \text{DOMINATE} \) will be same, so we can compare the payoff of a mutant \( \text{LOTTERY} \) with the payoff of either the \( \text{SHARE} \) or \( \text{DOMINATE} \) strategies. Here, we compare the payoff of a mutant \( \text{LOTTERY} \) against a \( \text{SHARE} \).)

\[ Pr(D|L)\pi_{L,D} + Pr(S|L)\pi_{L,S} + Pr(L|L)\pi_{L,L} > Pr(D|S)\pi_{S,D} + Pr(S|S)\pi_{S,S} \]

Substituting in the interaction probabilities from (18), and solving for \( \hat{p} \), we have:

\[ \hat{p} > \frac{\pi_{S,S}(1 + r) - \pi_{D,S} - r\pi_{S,D}}{(1 - r)(\pi_{D,D} - \pi_{D,S} - \pi_{S,D} + \pi_{S,S})} \]  

(20)

Note, when \( r = 0 \), Inequality (20) reduces to Inequality (17).

If we now substitute the equilibrium fraction of \( \text{DOMINATE} \), derived in Equation (19), for \( \hat{p} \) in the left-hand side of Inequality (20), we have:

\[ \frac{\pi_{S,S} - (1-r)\pi_{D,S} - r\pi_{D,D}}{(1-r)(\pi_{D,D} - \pi_{D,S} - \pi_{S,D} + \pi_{S,S})} > \frac{\pi_{S,S}(1 + r) - \pi_{D,S} - r\pi_{S,D}}{(1 - r)(\pi_{D,D} - \pi_{D,S} - \pi_{S,D} + \pi_{S,S})} \]

With some algebra and substitutions, this reduces to:

\[ c > 0.5\hat{x} - 0.5\left(\hat{v}\hat{x} - (1-\hat{v})\hat{x}\right) \]  

(21)

With linear returns (\( x = 1 \)), a self-interested individual would prefer all of the resource for himself (\( \hat{v} = 1 \)). Making these substitutions, condition (21) becomes \( c > 0 \). This means that, with \textit{any} amount of assortment (\( r > 0 \)), \( \text{LOTTERY} \) will invade a mix of \( \text{SHARE} \) and \( \text{DOMINATE} \) if there is \textit{any} cost to resource conflict.
With accelerating returns \((x > 1)\), a self-interested individual would again prefer all of the resource for himself \(\hat{v} = 1\). Substituting in these values, condition (21) becomes:

\[
c > 0.5^{x} - 0.5
\]

When returns accelerate \((x > 1)\), the required cost of conflict is negative \((c < 0)\). So, with accelerating returns, LOTTERY will always invade a mix of SHARE and DOMINATE, whatever the cost of conflict.

With diminishing returns \((x < 1)\), the invasibility of LOTTERY is more complicated. Condition (21) is plotted below in Supplementary Figure 2, showing the minimum conflict cost \((c)\) for LOTTERY to invade an equilibrium mix of DOMINATE and SHARE as a function of interdependence \((s)\) and returns \((x)\). As interdependence increases from zero to one, this minimum cost rapidly diminishes to zero. The threshold conflict cost reaches a maximum at returns intermediate between zero and one. So, when interdependence is near zero and the returns exponent is around 0.4, the minimum conflict cost reaches its maximum around 0.2 or 20% of the value of the resource if consumed completely by one person.

When the conflict cost is below the threshold value (i.e., Condition (21) is not satisfied), LOTTERY has the same payoff as residents of the mixed equilibrium; LOTTERY can only increase in frequency through drift, and when the frequency of LOTTERY is sufficiently high, selection will drive the population to the LOTTERY ESS. When the conflict cost is above the threshold, LOTTERY will invade and go to fixation when there is any non-random assortment \((r > 0)\).

We now return to finding the conditions for the remaining evolutionary outcomes.

**When is DOMINATE an ESS?** As previously shown, when DOMINATE is an ESS over SHARE, DOMINATE is also an ESS over LOTTERY. The condition for DOMINATE to be an ESS over SHARE is given below.

\[
\pi_{D,D} > \pi_{S,D}
\]

\[
0.5\left(\pi(\hat{v}) + \pi(1 - \hat{v})\right) - (1 + s)(o + c) > \pi(1 - \hat{v}) - so
\]

\[
0.5\left(\pi(\hat{v}) - \pi(1 - \hat{v})\right) > o + c(1 + s)
\]

\[0.5B_{own-cede} > o + c(1 + s) \quad (22)\]
Conflict cost must be around 1% of the resource value.
Conflict cost must be between 5% and 10% of the resource value.
Conflict cost must be greater than 20% of the resource value.

Figure 2: Minimum conflict cost for LOTTERY to invade an equilibrium mix of DOMINATE and SHARE as a function of interdependence (s) and returns exponent (x).

**When is SHARE an ESS?** As previously shown, when SHARE is an ESS over DOMINATE, SHARE is also an ESS over LOTTERY.

\[
\begin{align*}
\pi_{S,S} &> \pi_{D,S} \\
\pi(0.5) &> \pi(\hat{v}) - o \\
\pi(\hat{v}) - \pi(0.5) &< o
\end{align*}
\]

We re-label \(\pi(\hat{v}) - \pi(0.5)\) as \(B_{\text{own-share}}\), which represents the payoff difference between owning the resource (hence, controlling the allocation) and sharing it. (Note that this is not the same as \(B_{\text{own-cede}}\), which is the payoff difference between owning the resource and the other player owning it). This results in:

\[
B_{\text{own-share}} < o
\]  \hspace{1cm} (23)
That is, \textit{SHARE} is an ESS when the difference between controlling the allocation of the resource and sharing it ($B_{\text{own-share}}$) is less than the cost of making an ownership claim, an intuitive result. Notice, the conflict cost doesn’t enter into Inequality (23). In Maynard Smith’s (1982) model, this kind of outcome (i.e., an evolutionarily stable population of \textit{DOVES}) is not possible, since that model had no necessary cost of making an ownership claim. In the current model, \textit{SHARE} does increasingly well as $o$ becomes larger, and also as $B_{\text{own-share}}$ becomes smaller, which it does as interdependence increases and/or returns become more steeply diminishing.

\textbf{When is there a polymorphic ESS between \textit{SHARE} and \textit{DOMINATE}? Or, when is \textit{LOTTERY} an ESS?} As previously shown, both of these outcomes happen under the same conditions.

In order for \textit{SHARE} and \textit{DOMINATE} to be a polymorphic ESS, each strategy must be able to invade a population of the other.

There is a polymorphic ESS between \textit{SHARE} and \textit{DOMINATE} when \textit{SHARE} can invade a population of \textit{DOMINATE} and \textit{DOMINATE} can invade a population \textit{SHARE}. This situation occurs when neither Inequality (22) nor Inequality (23) are satisfied.

\begin{equation}
B_{\text{own-share}} > o > 0.5B_{\text{own-cede}} - c(1 + s)
\end{equation}

\textbf{When are both \textit{SHARE} and \textit{DOMINATE} ESSs?} This occurs when both Inequalities (22) and (23) are satisfied.

\begin{equation}
0.5B_{\text{own-cede}} - c(1 + s) > o > B_{\text{own-share}}
\end{equation}

This is an interesting case, which does not occur in Maynard Smith’s \textit{HAWK–DOVE} model. When condition (25) is satisfied, either \textit{SHARE} or \textit{DOMINATE} can be an ESS. The evolutionary outcome will be determined by path dependence; resource allocation can be based on domination or sharing. Note, even though either strategy can be an ESS, a population playing \textit{SHARE} will always have higher average payoffs than a population playing \textit{DOMINATE}. If there is any type of selection process which favors the equilibrium with the higher average payoff, allocations based on sharing should be more common than allocations based on domination.

Putting Conditions (22), (23), (24), and (25) together, Supplementary Table 2 shows when each of the four evolutionary outcomes result.
Table 2: Evolutionary Outcomes

<table>
<thead>
<tr>
<th></th>
<th>(0.5B_{own-cede} &gt; o + c(1 + s))</th>
<th>(0.5B_{own-cede} &lt; o + c(1 + s))</th>
</tr>
</thead>
<tbody>
<tr>
<td>(B_{own-share} &lt; o)</td>
<td>DOMINATE and SHARE ESS</td>
<td>SHARE ESS</td>
</tr>
<tr>
<td>(B_{own-share} &gt; o)</td>
<td>DOMINATE ESS</td>
<td>LOTTERY ESS</td>
</tr>
</tbody>
</table>

The definitions of the parameters in Supplementary Table 2 are given below:

- \(B_{own-cede} = \pi(\hat{v}) - \pi(1 - \hat{v})\). \(B_{own-cede}\) represents the difference in payoff between controlling the allocation of the resource \(\pi(\hat{v})\) and ceding control of the allocation to the other player \(\pi(1 - \hat{v})\).

- \(B_{own-share} = \pi(\hat{v}) - \pi(0.5)\). \(B_{own-share}\) represents the difference in payoff between controlling the allocation of the resource \(\pi(\hat{v})\) and sharing the resource equally with the other player \(\pi(0.5)\).

- \(o\) represents the cost of claiming ownership of the resource.

- \(c\) represents the cost of a conflict, when both players claim ownership of the resource.

- \(s\) represents interdependence, the benefit that each player derives from having the other in the interaction environment.

The evolutionarily stable outcomes are plotted for a range of parameter values in figure 3 of the main paper.

References
