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Competitive helping increases with the size of biological markets and invades defection

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ABSTRACT

Cooperation between unrelated individuals remains a puzzle in evolutionary biology. Recent work indicates that partner choice can select for high levels of helping. More generally, helping can be seen as but one strategy used to compete for partners within a broader biological market, yet giving within such markets has received little mathematical investigation. In the present model, individuals help others to attract attention from them and thus receive a larger share of any help actively or passively provided by those others. The evolutionarily stable level of helping increases with the size of the biological market and the degree of partner choice. Furthermore, if individuals passively produce *some* no-cost help to partners, competitive helping can then invade populations of non-helpers because helpers directly benefit from increasing their access to potential partners. This framework of competitive helping demonstrates how high helping can be achieved and why different populations may differ in helping levels.

1. Introduction

Cooperation between unrelated individuals remains one of the big puzzles in evolutionary biology (e.g. Sachs et al., 2004; Vogel, 2004; Clutton-Brock, 2009; Pennisi, 2009). Despite much work on the Prisoner's Dilemma and various forms of reciprocity (for reviews, see: Axelrod, 1984; Brembs, 1996; Nowak and Sigmund, 2005), recent authors have questioned how many instances of cooperation match such payoff structures (Noë, 1990; Connor, 1995; Tooby and Cosmides, 1996; Silk, 1999; Clutton-Brock, 2009). Most importantly, many organisms do not equally accept all individuals as cooperative partners, but exercise choice as to whom they will associate with most (e.g. Peck, 1993; Noë and Hammerstein, 1994, 1995; Sherratt and Roberts, 1998; Barclay and Willer, 2007). Rather than being examined in isolation, costly forms of cooperation should be seen as one strategy within a broader context of social interactions that includes mutualistic partnerships with byproduct benefits, kinship, mating, and dominance contests. Because terminology varies widely between fields (e.g. "altruism" versus "cooperation" versus "helping"), I will use behavioral terms: "help" will broadly refer to any benefit (tangible or intangible) that one individual confers upon another intentionally or unintentionally, whether costly or free to the provider. I will refer to the costly provision of such help as "active" help (e.g. giving up resources), and the costless provision of help as "passive" help (e.g. unintentional byproducts and externalities). Those who disagree with such usage should substitute their preferred terms for costly and non-costly help.

1.1. From passive helping to active helping

Many, perhaps most, examples of "helping" involve mutualisms or byproduct benefits rather than costly provision of help to others (Sachs et al., 2004; Clutton-Brock, 2009). In such cases, individuals benefit others at no net cost to themselves when they follow their own best interests. For example, flocking, cooperative hunting, mobbing, and group defense are all activities where one's presence benefits others and the personal gain for joining can outweigh the cost of doing so. Other types of help are produced merely by spending time with individuals, such as when learned individuals function as "models" that others can learn from via infocopying (Tooby and Cosmides, 1996; Henrich and Gil-White, 2001), when some individuals produce food for their own benefit which can be scrounged (Barnard and Sibly, 1981; Vickery et al., 1991; Sherratt et al., 2009), or when individuals selfishly watch for or repel predators, violence, or harassment, and thus tend to provide environments free of such threats (Clutton-Brock, 2009). In interspecific mutualisms, one species' metabolic byproducts may benefit its symbiont (Sachs et al., 2004). Individuals benefit from associating with those who produce such "positive externalities", and those who are better at

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producing these externalities are expected to be more desirable as partners (Tooby and Cosmides, 1996).

In the context of this no-cost or passive help, one could also become a valuable partner by intentionally providing help directly to needy partners rather than doing so only incidentally (Seyfarth, 1977), and individuals vary in their ability to do so. It is obviously beneficial to interact with those who are willing to directly help partners, and ample research demonstrates that people prefer to associate with others who have demonstrated a tendency to give (e.g. Milinski et al., 2002; Barclay and Willer, 2007; Barclay, 2010). In order to attract attention from those who actively or passively help others, one may have to provide them with help in kind or in different currencies; this is the basis of reciprocity (Trivers, 1971). As such, active helping allows individuals to buy access to group members that they otherwise have no access to (Seyfarth, 1977; Henrich and Gil-White, 2001), or to buy more time or access to existing partners. Such active helping can include giving resources, coalitional support, or other forms of assistance that benefit the recipient more than they cost the provider. Active help can also be broadly construed to include other costly acts such as the granting of concessions (e.g. deference, tolerance of cuckoldry or theft) or increasing the production of what had previously been byproducts that others benefit from.

1.2. Biological markets: from active helping to competitive helping

When one individual gains access to additional partners or attention from such partners, this causes others to have less access and to receive less attention from those partners (Seyfarth, 1977). Thus, there is inherent competition over access to social partners, in what Noë and Hammerstein (1994, 1995) have termed a *biological market*. If all individuals can increase their value in this biological market by actively helping, then individuals who provide the most help will have access to the most (or the best) partners and/or more social attention from them. Thus, biological markets provide an incentive (conscious or not) for individuals to compete to give more than others in the biological market, and to send signals that imply such helping (Roberts, 1998). Such *competitive helping* (often called *competitive altruism*, Roberts, 1998) can occur whenever: (1) reputational benefits are a limited resource such that the best helpers receive more help than the next-best helpers; and (2) the benefit of receiving this additional help outweighs the cost of investing in additional helping. Competitive helping is more than "merely" trying to appear good; it occurs when individuals actively try to outdo each other by helping more than others (Barclay and Willer, 2007). Experimental evidence demonstrates that humans give more when competing over social partners than when such competition is absent (Barclay, 2004; Barclay and Willer, 2007; Chiang, 2010), and the increased status accruing to those who give money to others has also been interpreted as competitive helping (Hardy and Van Vugt, 2006).

Despite recent empirical work using a biological markets paradigm (e.g. Bshary and Schäffer, 2002; Barrett and Henzi, 2006; Barclay and Willer, 2007), there have been relatively few mathematical or computer-based theoretical studies investigating the effects of competition for partners on helping. Nesse (2007) investigated a Continuous Prisoner's Dilemma-like situation where partners could assort based on how much they give to partners, and he found "runaway social selection" for high giving. McNamara et al. (2008) showed that increased choosiness over partners leads to high levels of help given, and that choosiness and helping co-evolve. Johnstone and Bshary (2008) investigated systems with one population of potential exploiters and another population of potential victims, and found that market forces affect the victims' ability to leave exploitative partners, which in turn affects the amount of exploitation. The above models all assume partnerships in pairs and assume that each individual can only receive help from one potential partner at a time, whereas in many systems individuals can simultaneously receive help from multiple parties (e.g. Henrich and Gil-White, 2001). Models of partner competition by Ferrière and colleagues (Ferrière et al., 2002, 2007) do not specify this assumption of pairwise interactions, but do assume obligate and costly mutualisms among two different types or species (e.g. hosts and symbionts).

All of the above models – like most models of cooperation – investigate helping largely in isolation from other bases of partner choice, although they sometimes do draw some excellent parallels between cooperation and the literature on sexual selection (e.g. Noë and Hammerstein, 1994; Nesse, 2007). The current model differs from these previous investigations by investigating competitive helping within the larger context of general competition over social partners within a single type or single species. Thus, the present model is conceptually similar to assortative mating models or other such models where helping is used to increase one's access to desirable partners (e.g. Seyfarth, 1977; Schino, 2001; Gumert, 2007). Framing competitive helping within the broader context of partner selection has interesting implications regarding the amount of active helping displayed in different group sizes (see below) and by individuals of differing quality.

1.2.1. Competitive helping and market size

As group size increases, there are more potential partners that one could interact with (i.e. a larger market), and this can cause selection for higher helping, and any trait that might signal a tendency to help. This is analogous to competition between business firms: as the number of firms increases, they must "bid" for customers by offering better "deals". This can occur in biological markets just as in monetary markets. The pool of help produced by a group will increase as the group size increases, so bigger groups represent a bigger "prize" if one can attract a large share of that pool. Thus, larger biological markets are predicted to result in higher competitive helping. The effects of group size should be even greater when individuals assort based on quality because larger groups will have more individuals who resemble each other in quality, such that helping could be a strategy to give oneself an advantage in social competition with close competitors.

1.3. The current investigation

Here I present a model of competitive helping where individuals can use their active helping to attract the attention of others (and hence, any help that those others provide to their associates). This model resembles a foraging model where agents "forage" over the help that others provide. Agents can receive help from whoever attends to them, and they maximize their returns by attending to others in proportion to the amount of help produced by each ("matching law", e.g. Domjan and Burkhard, 1993). The model shows that such competitive helping: (a) is evolutionarily stable; (b) depends on the degree of partner choice; (c) increases with the number of competitors (i.e. the size of the biological market); and (d) can invade a population of nonhelpers as long as some passively provided help is present.

2. Methods

2.1. Conceptualization of the model and assumptions

Perhaps the best way to conceptualize the model is to first imagine a number of foraging animals distributing themselves among a number of food patches, or responding to different rates of reinforcement in an operant conditioning paradigm. In foraging paradigms, Ideal Free Distributions predict that animals maximize their food intake in the face of foraging competition by distributing themselves among food patches in proportion to the relative payoffs per patch (Milinski, 1979). Not all individuals attend to the best-producing patches because of competition over the resources produced, so it pays to do some foraging in less productive patches. Similarly, in operant conditioning paradigms, the Matching Law predicts that animals maximize their food intake by attending to different food dispensers in proportion to the relative rates of reinforcement at the different dispensers (for a review, see Williams, 1988; Domjan and Burkhard, 1993). If each of two food dispensers is capable of producing one reward every once in a while (a "variable interval schedule"), it pays to occasionally attend to the less productive dispenser in order to still have access to the rewards it produces (see Section 2.2.2 on deviations from Ideal Free Distributions and the Matching Law).

Now instead of imagining the food patches and dispensers as external resources, imagine that the animals themselves are the food patches or dispensers, such that the dispensers of help are *themselves* foraging over the help produced by others. The animals will distribute themselves among *each other* in proportion to how often each individual produces help. For example, an animal that can provide help on average twice a minute will receive twice as much attention from others as an animal that provides help once a minute. Unlike some models of Ideal Free Distributions, the present model assumes that individuals can invest fractions of their time in attending to specific targets rather than having each individual devote all its time to a specific partner; see Fig. 1 for examples. Time and attention are inherently limited resources, so when one individual attracts a larger share of attention by increasing its own production of help, it necessarily reduces the shares received by its competitors. Thus, the competition is implicit. Because I am modeling the effects of this sort of distribution rather than the process of how organisms distribution themselves, I assume for simplicity that the organisms are distributing themselves instantaneously and without cost (but see Section 2.2.2 for deviations from this).

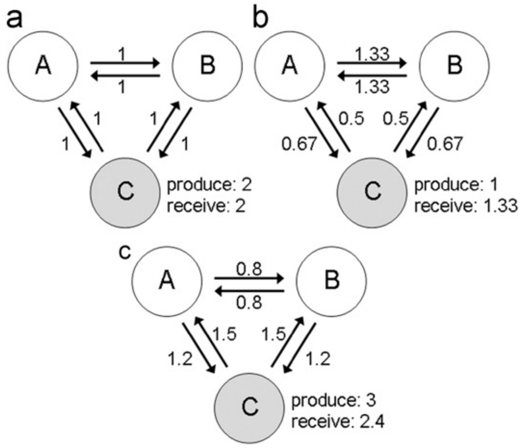

Fig. 1. Graph of a simple network ($N=3$) of competitive helping. Each individual receives a share of others' help in proportion to the help he/she provides, relative to what they provide for each other ("matching law"). (a) Imagine that all individuals provide 2 units of help. Taking *C*'s perspective, *C* will attend equally to *A* and *B* because they each provide 2. Similarly, because *C* also provides 2, *A* and *B* pay equal attention to *C* as to each other, so they all receive the same amounts of help (i.e. 2 total). (b) If *C* starts providing only 1 unit while the others provide 2, then from the perspective of either *A* or *B*, *C*'s help represents 1/3 of the total help available. *C* would thus receive 1/3 of *A* and *B*'s attention, and thus 1/3 of the help that *A* and *B* produce (i.e. 0.67 from each). This new total (1.33) is less than what *C* would have received by providing 2 units. (c) If instead *C* starts providing 3, then he/she now represents 3/5 of the help available to *A* and *B*, so *C* receives 3/5 of the help that A and B produce (i.e. 1.2 from each). This new total (2.4) is more than what *C* would have received by providing only 2. Whether this is worth the cost depends on the marginal fitness effects for receiving additional help.

Individuals divide their attention among other group members, and the help they produce is available for consumption by whomever they pay attention to. I assume that this help is targeted to single individuals rather than broadly distributed to all within proximity, and it is depletable, meaning that anything obtained by one individual benefits only that individual (i.e. help is a "rival good"). Although individuals can only give to one other individual at a time, they can receive from multiple individuals at the same time. As such, it is beneficial to receive large shares of social attention from multiple individuals, because one can then consume the help produced by multiple individuals; this is how helpers benefit from their helping. The model thus differs from other partner choice models because it does not assume that individuals form long-term partnerships with a single individual at a time and trade favours exclusively within that relationship (e.g. Nesse, 2007; Johnstone and Bshary, 2008; McNamara et al., 2008). Instead, organisms move around freely and frequently: they choose to attend to specific individuals in order to receive access to the help those individuals provide actively and passively, and one's own help is available to those to whom one attends in return. The more that one has to offer in the pool of potential partners, the more attention (and thus help) one receives from that pool. Once again, the current model examines the effects of these choices, not the processes of choosing.

This foraging framework (and its assumptions) is meant only as an illustration, not as a strict necessity. The most important point – and the only really crucial assumption – is that helpers will tend to receive a larger share of others' attention than will non-helpers, such that the amount of attention one receives is based (at least in part) on the amount of help one gives *relative to others* (see Appendix for justification). This increased attention increases the help available to helpers, which is what ultimately selects for helping.

2.2. The model

2.2.1. Proportional matching

I start by investigating only active help; Section 3.3 adds passive help. In the model, all individuals are of the same type. Each individual chooses to incur cost h ($h \geq 0$) to actively provide help at rate h (Table 1 lists all variables). Any mutant provides h_m, and this help is available to others according to the attention that the mutant pays to each of them. Everyone else actively produces h_p each, where h_p is the population level of helping. If there are N individuals in the biological market,[1] then from any rare mutant's perspective, the pool of help available to be competed over is $(N-1)h_p$. At any time, a mutant can be said to compete with $N-2$ individuals over the attention of each of the $N-1$ other members (i.e. it competes with everyone except the individual being competed for). Each individual receives help in proportion to the amount it produces (see Appendix A for justification). As such, the total amount of help received, r, by any mutant is

$$r=(N-1)h_p\frac{h_m}{h_m+(N-2)h_p} \tag{1}$$

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[1] Please note that N represents the number of potential partners who compete within a market, not the entire group size. The group size could actually be much bigger than the effective market size, given that some partner choices are constrained due to kinship (e.g. Hauser et al., 2009; Silk, 2009), age, sex, and proximity, and that competition over partners is sometimes only against members within the same category (e.g. competition among age-mates over coalitions with other age-mates).

Table 1
List of variables used in the model.

Variable	Definition
h_m	Level of active (costly) help by a rare mutant
h_p	Level of active (costly) help by each other population member
h^*	Equilibrium level of active help
N	Number of members in the biological market
m	Maximum possible fitness benefits from receiving help
x	A variable affecting the benefits curve (concavity vs. linearity of returns)
r	Total help received by the rare mutant
Z	Partner choice: degree to which individuals can choose partners based on the benefits for associating with them
W	Fitness payoff to the rare mutant in a population with active helping of h_p
k	Level of help passively provided at no cost (e.g. byproducts, externalities)
p	Proportion of attention invested in a mutant (see Appendix A)
A	Total help produced by the mutant (see Appendix A)
B	Total help produced by other population members (see Appendix A)

In Eq. (1), $(N-1)(h_p)$ represents the total help available to the mutant, i.e. the number of other group members times the amount produced by each. The fraction represents the proportion of each group member's help that the mutant receives, i.e. the amount produced by the mutant divided by the total amount produced by itself and all competitors (i.e. everyone except the other group member him/herself).

2.2.2. *Deviations from proportional matching*

Eq. (1) assumes that each individual receives help in perfect proportion to the relative amount of help it provides. In reality, perfectly proportional matching rarely occurs. Constraints such as movement time between patches, the cost of switching, imperfect information, and competitive interference will interfere with organisms' ability to choose the "best" options, and will thus result in deviations from Ideal Free Distributions (Kennedy and Gray, 1993) and from perfect matching (Williams, 1988; Domjan and Burkhard, 1993). To allow for deviations from perfectly proportional matching choices, I follow past research (e.g. Baum, 1979; Wearden and Burgess, 1982) in using an exponent z $(0 \leq z \leq \infty)$, where z is the degree of matching (i.e. degree to which one receives help in proportion to the relative amount of help one provides). With this new matching parameter, the total help received from all others becomes:

$$r=(N-1)h_p\frac{(h_m)^z}{(h_m)^z+(N-2)(h_p)^z} \tag{2}$$

When $z=0$, individuals cannot choose whom to associate with, such that all individuals receive equal attention and help from others regardless of how much they provide ("undermatching", Williams, 1988). When $z=1$, individuals can freely and perfectly choose partners based on how much help each produces, such that Eq. (2) simplifies to Eq. (1), i.e. all individuals receive help in proportion to the relative amounts that they give. When z equals infinity, it is a winner-take-all system (e.g. Frank and Cook, 1996) where the most generous individual receives all of the help produced by others ("overmatching", Williams, 1988). Although rare, the latter situation might occur if the help one confers upon partners is not depleted by others' use (e.g. "non-rival" public goods), such that it pays to attend most to whoever emits the most positive externalities regardless of who else associates with them and what anyone else produces.

2.2.3. *Adding diminishing marginal fitness benefits*

I assume that fitness increases as one receives more help, but the fitness benefits show diminishing marginal returns, i.e. after receiving much help, additional help received has little additional effect on fitness (e.g. Hauert et al., 2006; Johnstone and Bshary, 2008). Thus, I deviate from most models of cooperation by not having a constant cost/benefit ratio (e.g. $b/c=3$). Instead, I use the diminishing marginal returns function $mr/(mx+r)$ where m represents the asymptotic maximum benefit one would get if one received an infinite amount of help from others, and x $(0 \leq x \leq 1)$ is a scaling factor that affects the shape of the benefit function and represents how slowly the maximum benefit is achieved. Such a scaling factor x is difficult to grasp intuitively, so Fig. 2 illustrates the fitness effects of receiving help at different levels of x. At smaller values of x, the maximum fitness benefits are quickly achieved and additional help received has little additional fitness effect (a highly concave curve), as would be the case if organisms only need a small amount of help. At higher values of x, the fitness benefits are achieved more slowly but steadily (i.e. the marginal benefits remain more constant and linear). To further illustrate, take the example of helping others by providing opportunities for social learning (Henrich and Gil-White, 2001): x is low if you can learn something from someone by observing them do it once (i.e. full benefits achieved quickly, additional observation has no additional effect), whereas x is high if it takes many demonstrations – or active teaching – before one can learn the skill (i.e. full benefits achieved slowly, additional observation is still useful).

2.2.4. *Final fitness function*

The total fitness payoff, W, to any mutant is thus the fitness benefits minus the costs:

$$W=\frac{mr}{mx+r}-h_m \tag{3}$$

At an equilibrium, h^*, no individual can increase its fitness by changing its level of active helping. To find non-extremal values of h^*, we find the value of h_m for which the derivative of the fitness curve (with respect to h_m) equals zero when $h_m=h_p$. The derivative of this fitness function with respect to h_m is

$$\frac{dW}{dh}=\frac{m^2xz(N-2)(N-1)(h_m)^{z-1}(h_p)^{z+1}}{[(h_m)^z(h_p(N-1)+mx)+(mx(N-2)(h_p)^z)]^2}-1 \tag{4}$$

Rather than focus on the details of this derivative, the important point is that it equals zero when $h_m=h_p$ at the equilibrium point:

$$h^*=\frac{[m^2xz(N-1)(N-2)]^{1/2}}{N-1}-mx \tag{5}$$

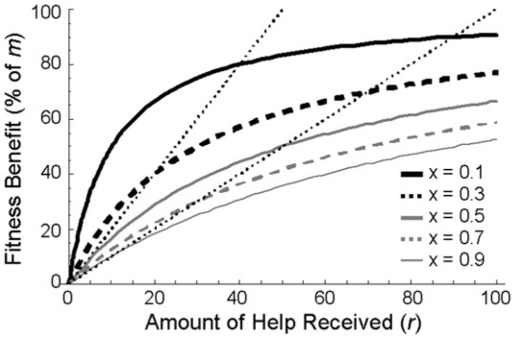

Fig. 2. Fitness gains as a function of the amount of help received (actively or passively), with the rate of diminishing marginal fitness returns determined by the parameter x. Under low x, the benefits curve is highly concave: it takes little help to receive high fitness benefits, but there is less advantage to receiving additional help (i.e. steeply diminishing marginal returns). Under high x, the benefits curve is more linear: the fitness gains are achieved more slowly but steadily (i.e. weakly diminishing marginal returns). At infinite r, all curves reach the asymptotic maximum fitness benefit m. For comparison, the two dotted diagonal lines represent traditional benefit to cost ratios of 2:1 and 1:1.

To show that h^* is indeed a fitness maximum, I note that the second derivative of the fitness function (with respect to h_m) is always negative whenever $N > 2$ and $z < 1$.[2] In other words, the equilibrium represents a local fitness maximum under many real conditions. The next sections examine the properties of this equilibrium.

At the endpoint $h_p = 0$, the derivative in Eq. (4) would negative, indicating that one's fitness would go down if one increased one's active helping, i.e. competitive helping cannot invade a population that has absolutely zero active and passive help. Section 3.3 will show that competitive helping can invade a population if passive help is present.

3. Results

3.1. Competitive helping increases with partner choice

The equilibrium (h^*) increases with the degree of matching z (Fig. 3): as z increases, the "winners" get increasingly disproportionate shares of others' attention and thus any help they provide, so it pays to invest more in such competition. When z approaches 0, individuals cannot choose partners, so it becomes no longer adaptive to actively help others because doing so does not attract attention.

3.2. Competitive helping increases with market size

As predicted, the equilibrium level of active helping (h^*) increases with the size of the biological market N whenever $N > 2$ (Fig. 4): as the number of potential partners gets bigger, there is larger pool of benefits to be competed over, and this drives active helping to higher and higher levels. The effect of each marginal increase in the market size depends on the shape of the benefits function (x), i.e. on the steepness of diminishing marginal returns.

3.2.1. Steeply diminishing marginal returns (low x)

At very low values of x, one need only receive a little help from others in order to get the maximum possible fitness effect (Fig. 2), i.e. the benefits curve is highly concave with quickly diminishing marginal returns. I previously (Section 2.2.3) gave the example to illustrate low x where learnable knowledge is easily acquired and implemented with very little observation of skillful individuals. As such, at very low values of x, h^* is not particularly high because one does not need to receive much help in order to experience the maximum fitness benefits, so there is little point in competing over additional help. Because of this, when x is low, increasing the market size N has a large positive effect on h^* in small markets but little additional effect on h^* after approximately $N=5$ (Fig. 4). In other words, in any system or species where receiving high amounts of help is no more beneficial than receiving moderate amounts, large and medium-sized groups will show approximately the same level of competitive helping.

3.2.2. Slowly diminishing marginal returns (high x)

Conversely, at high values of x, everyone experiences a smaller fitness benefit per unit of help received, but the per-unit benefits do not decline much even after receiving much help, i.e. the benefits curve is more linear with little or no diminishment of marginal returns. In the social learning example (Section 2.2.3), x is high if it takes many instances of observation (or active teaching) to effectively learn knowledge from others, as is typical with many socially acquired human skills. Correspondingly, when x is high, increasing the market size causes gradual (rather than steep) increases in h^*. In fact, h^* continues to increase with increasing market size even when $N > 20$. For example, if $x=0.9$, h^* is twice as high when $N=100$ than when $N=20$ (for parameters $k=1$ and $m=100$), and when $x=0.928$ there is no stable level of active helping at all until the market size is $N > 20$. In other words, in any group or species where receiving high amounts of help is much more beneficial than receiving moderate amounts, large groups will show more competitive helping than medium-sized groups.

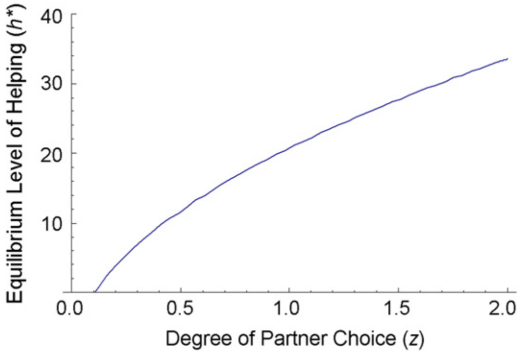

Fig. 3. The evolutionarily stable level of active help (h^*) increases as partner choice (z) increases, i.e. when the best helpers get an increasingly disproportionate share of others' attention. Parameters displayed are $m=100$, $x=0.3$, $k=1$, $N=10$.

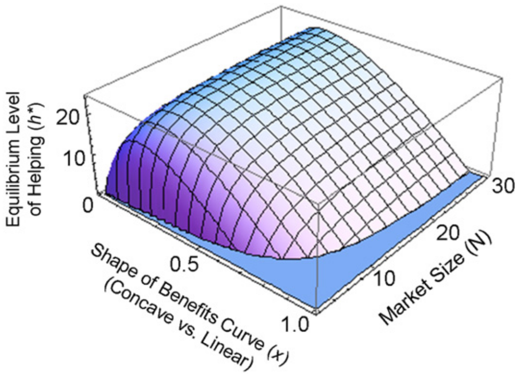

Fig. 4. The evolutionary stable level of active helping (h^*) increases with increasing group size (N) and decreases when the benefits curve is more linear than concave, i.e. when it takes much help to reach the maximum fitness benefit (high x). Increasing the group size beyond $\sim N=5$ has little additional effect when x is low but continues to have an effect when x is high. The shaded area at bottom represents zero active helping at equilibrium. Parameters displayed are $m=100$ and $k=1$.

3.2.3. Intermediate values of x

Competitive helping is highest at low-intermediate levels of x. At very low levels of x, individuals do not need much help from others and thus do not benefit from competing over more; at very high x, the benefits of receiving each unit of help are too low to justify the cost of competition. Intermediate levels of x represent a balance between these two forces. Increasing the market size has a modest effect at such levels.

3.3. Invading all-defect

Many models of cooperation have an equilibrium with zero active help, and the frequency of helpers must exceed some

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[2] In rare cases where $z > 1$, the second derivative is negative if $h_m^z(z+1)[mx+(N-1)(h_p+k)] > h_p^z mx(N-2)(z-1)$, which is true unless z, N, m, and x are all very large.

critical threshold before helping can take over (e.g. Axelrod, 1984; Panchanathan and Boyd, 2004; Hauert et al., 2006). Any complete model of cooperation must explain how this critical threshold is reached. If all help is costly to provide and no one provides any even by mistake, then competitive helping cannot invade because there are no benefits to attracting attention from others (see Section 2.2.4).

However, if some help is provided at no net cost (e.g. mutualistic help or help that also benefits the provider), then it can be beneficial to provide costly help even if no one else in the population does. In the presence of costless passive help, paying to help others is directly beneficial to oneself, as it increases the total attention one receives from others, which increases one's share of any help they passively provide. One competitive helper in a population of defectors would do better by helping others than by not helping, because doing so would increase its "market value" and give it access to benefits that it otherwise would not be able to attract (e.g. attention and passive help from more individuals or higher quality individuals). This logic holds as long as individuals associate more with those who provide the most benefits for association, which is a reasonable assumption and is supported by work on operant conditioning (e.g. Domjan and Burkhard, 1993). This does not require pre-existing cognitive adaptations for preferring active helpers, merely a low-level learning rule for preferring those who provide the highest net benefits for associating with them, which could function whether such help is provided actively or passively.

To model this, let us assume that each individual can sometimes produce help at no cost to itself, and this happens at the rate k, such that each population member provides a total of h_p+k and a rare mutant provides a total of h_m+k. For purposes of simplicity and model tractability, I assume for now that this passive (costless) help has similar properties to active (costly) help, namely that it is conferred upon specific individuals rather than broadly distributed equally to everyone in the whole population (e.g. only conferred upon those in immediate proximity, see Sherratt et al., 2009), and that active and passive help are additive (e.g. costly help that involves increasing the production of goods that are normally byproducts). The present model is also symmetrical in that it assumes that all individuals confer the same amount of passive help and that they differ only in the help they actively provide. However, these assumptions are made only to increase the model's tractability and are not necessary for competitive helping to invade: all that is necessary for the basic logic of this model to work is that those who provide more help overall will tend to receive a larger share of the available costly and/or non-costly help provided by others in the population.[3] As long as that one core assumption is met, the marginal advantage of receiving more passive help can potentially outweigh the cost incurred to attract others' attention. For example, in mobile populations where passive help is conferred only upon immediate neighbors, active helpers would spend a higher-than-average proportion of their time surrounded (on all sides) by others, and thus would receive a higher-than-average share of passive benefits (from all directions). Any additional assumptions about the passive help (e.g. additive with active help, degree to which it disperses spatially) will only affect the quantitative predictions of the model, and will not affect the qualitative prediction that a rare active helper can benefit from receiving a larger share of the passive help provided by others. Future models will examine deviations from the non-core assumptions, such as asymmetries in individual quality and ability to provide.

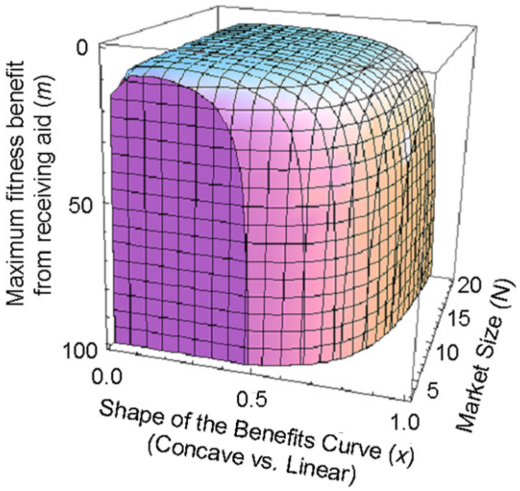

Fig. 5. Conditions under which competitive helping can invade a population of non-helpers: the solid area represents conditions where a rare mutant's fitness would increase if it slightly increased its active helping above the population state of zero active help. Parameters displayed are $k=1$ and $z=1$.

Updating Eqs. (2), (4), and (5) to include the provision of non-costly help results in the following equations:

$$r=(N-1)(h_p+k)\frac{(h_m+k)^z}{(h_m+k)^z+(N-2)(h_p+k)^z} \tag{6}$$

$$\frac{dW}{dh}=\frac{m^2xz[N(N-3)+2](h_m+k)^{z-1}(h_p+k)^{z+1}}{[(mx+(N-1)(h_p+k))(h_m+k)^z+(mx(N-2)(h_p+k)^z)]^2}-1 \tag{7}$$

$$h^*=\frac{[m^2xz(N(N-3)+2)]^{1/2}}{N-1}-k-mx \tag{8}$$

h^* is a fitness maximum because the second derivative of the fitness function (with respect to h_m) is always negative whenever $N>2$ and $z<1$.[4] To mathematically demonstrate the invasion of competitive helping, I test whether fitness increases with increasing active help even when there is no helping in the population, i.e. I test whether the slope of the fitness function (with respect to h_m) is positive when h_m and h_p are zero. Following Eq. (7), this is true when:

$$\frac{(N-2)m^2xz}{(N-1)(k+mx)^2}>1 \tag{9}$$

Fig. 5 shows the conditions under which this inequality is satisfied and competitive helping can invade. Competitive helping is more likely to invade when the maximum fitness benefits from receiving help (m) are high, when group size (N) is large, and when partner choice (z) is high. At higher levels of x, the benefits of help are achieved much more slowly, and this inhibits the ability of competitive helping to invade because the marginal fitness effects of extra help received are not worth the cost required to get it.

Some passively-provided help (k) is necessary to get active helping off the ground: without such costless help, a rare giver would have nothing to gain from the increased attention from defectors. However, as long as there is *some* passively produced or

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[3] The literature on pseudo-reciprocity (e.g. Connor, 1986, 1995) also assumes that costly help can be used to increase the byproduct benefits that one receives from partners, but the mechanism is slightly different: pseudo-reciprocity involves helping others so that they are capable of producing more byproduct benefits for oneself, whereas in the present model an organism who actively helps others is more successful at competing over the existing pool of byproduct benefits produced by population members.

[4] In rare cases where $z>1$, the second derivative is negative when $(h_m+k)^z(z+1)[mx+(N-1)(h_p+k)]>(h_p+k)^z mx(N-2)(z-1)$, which is true unless z, N, m, and x are all very large.

mutualistic help ($k>0$), higher rates of passively produced help will surprisingly *decrease* the ability of competitive helping to invade, presumably because one has to spend more on active helping in order to attract an appreciably greater amount of help from others.

This analysis shows that competitive helping can invade a population of all-defectors because competitive helpers receive a larger share of any help passively provided by their neighbors, and this can outweigh the cost of unreciprocated giving. Thus, competitive helping can be beneficial as long as there are some mutualistic benefits for associating with others and if individuals can choose with whom to associate. Once active helping starts to invade, this increases the benefits of attracting good partners, and the passively produced help becomes no longer necessary.

4. Discussion

The present model shows the benefits of using active helping as a means of competing with others to buy access to more or better quality partners or more help from those partners (e.g. Seyfarth, 1977; Roberts, 1998). With this type of competitive helping, the "dilemma" of costly helping disappears because each individual follows his/her self-interest: he/she invests in attracting partners and attends to those who confer benefits upon others. This competitive helping can even invade a population of defectors so long as (some) individuals produce some non-costly help or positive externalities to others; such externalities can include mutualistic benefits, byproduct benefits, or lower levels of manipulation, and these are believed to be common among non-humans (Tooby and Cosmides, 1996; Clutton-Brock, 2009). Once competitive helping establishes a foothold, such passive help is no longer necessary. This process of competitive helping can create a positive feedback loop causing an escalation of helping in a "runaway" process until very high levels of giving are reached (Nesse, 2007; McNamara et al., 2008). Such an escalation could occur over evolutionary time, or via learning within an organism's lifetime as group members react to the available payoffs. This escalation ceases only when the marginal cost of providing additional active help is greater than the marginal benefits one would experience from receiving additional help.

Because competitive helping can invade a population of defectors, it may be an early stage in the evolution of reciprocity. Individuals will actively provide help to attract desirable partners, and since active help is desirable in its own right, everyone will also seek to associate with those who give help and avoid those who do not give; they will also actively help the helpers in order to attract them. This process would result in partners actively helping each other, and other aspects of reciprocity like punishment of defections would then arise whenever freedom of partner choice is imperfect (e.g. when mobility between partners is not immediate or involves costs), or when punishment and similar forms of partner control become more effective or more cost efficient than switching partners. It remains to be seen whether individuals switch from partner choice to partner control depending on the relative costs of each. Wilson and Daly (1998) show that human males use coercive control in romantic relationships to prevent high-value partners from exercising the free choice to leave, so similar effects may be seen in non-romantic cooperative relationships.

4.1. *Variation in helping across populations*

The model predicts increased competitive helping when there are more individuals to compete with and compete over, i.e. larger social markets. All else being equal, the effective size of such markets will be greater when: (1) group size is larger; (2) fewer partners are "pre-chosen", which otherwise would occur when there is reliance on kinship or other fixed factors such as sex, age, or early association; and (3) individuals have greater ability to move between partners (a.k.a. "relational mobility", Schug et al., 2009). Cultural or individual variation in these factors could thus underlie some of the observed individual and cultural variation in helping (e.g. Henrich et al., 2005), and is an important topic for future investigation. Relative to many other animals, humans have larger group size (i.e. high N), less reliance on kin or other such "pre-chosen" coalition partners (i.e. higher z), high potential gains from help (i.e. high m), and high reliance on socially acquired information with long acquisition time (i.e. high x). As such, competitive helping may also be a factor in the high rates of helping in humans.

4.2. *Future directions and conclusions*

This model demonstrates that within a biological market, competitive helping can invade and be evolutionarily stable, and the equilibrium level of helping increases with greater partner choice and market size. In this model, all individuals are of one type and simultaneously compete with and compete over all other individuals. However, it can be extended to two different types, such that it applies specifically to mating interactions or interspecific mutualisms such as ants and acacia trees or roots and their microbial symbionts (Noë, 2001; Sachs et al., 2004). This will be a topic for future investigation. The current model also assumes that all individuals are equally effective at producing passive and active help, and that all help is linearly additive and has similar properties; future research will investigate deviations from these assumptions. Because competitive helping is one strategy within a biological marketplace (Noë and Hammerstein, 1994, 1995), it may occur in any system where individuals can choose how much to associate with different individuals and can adjust how good a "deal" they offer to those associates.

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Appendix A. Model of proportional matching

The following is a justification of why each individual receives help in proportion to the amount of help it produces (Eq. (1) in main text).

Much research in operant conditioning shows that animals respond to different sources of food or other reinforcement (A and B) at rates which are approximately proportional to the relative rates of reinforcement (i.e. frequency of food availability). Moreover, responding in this fashion maximizes one's intake (for reviews, see Williams, 1988; Domjan and Burkhard, 1993). This is known as the Matching Law. In its strictest form, the Matching Law is shown by the formula $R_A/(R_A+R_B)=r_A/(r_A+r_B)$, where R_A and R_B are the rates of responding to A and B and r_A and r_B are the rates of reinforcement. Most formulae on the Matching Law use two response options, A and B (for a review, see Williams, 1988), so here I generalize these formulae to multiple options.

From the formula of Baum (1981; see also Johnstone and Bshary, 2008), any individual X receives a rate of return for attending to individual Y in proportion to $1/(t+E)$, where t is the time it takes Y to provide help and E is the time in between when that help is available and when X next attends to Y in order to receive the help. I analyze this from the perspective of any given focal individual deciding how to invest attention between one mutant who produces help at the rate A and the $(N-2)$ other group members who produce help at the rate B (in Eq. (1), $A=h_m$ and $B=h_p$).

To determine the time t to produce resources, Baum (1981) takes the inverse of the rates of production. Thus, in the present model, it takes the mutant $1/A$ amount of time to produce one unit of help, and the other group members $1/B$. To determine the amount of time E before the focal individual next attends to the mutant or any given other population member, I follow Baum (1981) in letting p be the proportion of time that the focal individual spends attending to the mutant, which leaves $[(1-p)/(N-2)]$ as the proportion of time that it attends to each of the other $N-2$ population members (i.e. other than itself and the mutant). Thus, any focal individual will take $1/p$ amount of time before it next attends to the mutant, and $1/[(1-p)/(N-2)]$ time before it next attends to any given other population member.

Following Baum (1981), the rate of return for attending to the mutant is thus proportional to:

$$\frac{1}{(1/A)+(1/p)} \tag{A.1}$$

The rate of return for attending to each other population member is thus proportional to:

$$\frac{1}{(1/B)+1/[(1-p)/(N-2)]} \tag{A.2}$$

Given that there are $N-2$ other population members, the overall rate of return is:

$$\frac{1}{(1/A)+(1/p)}+(N-2)\frac{1}{(1/B)+1/[(1-p)/(N-2)]} \tag{A.3}$$

To find the optimal investment of attention, call it p^*, we take the derivative of Eq. (A.3) with respect to p, and find the value of p where this derivative equals zero. Thus

$$p* = \frac{A}{A+(N-2)B} \tag{A.4}$$

Since $A=h_m$ and $B=h_p$, this produces the proportional matching seen in Eq. (1) from the main text (in Eq. (6), $A=h_m+k$ and $B=h_p+k$). As such, those who produce more help will receive more attention from others, and thus also receive more opportunities to get a share of the help produced by those others. When individual X attends more to individual Y, it increases its availability to Y, which increases the rate at which its help is available to Y. This in turn gives Y an incentive to attend more to X because it experiences a higher rate of reinforcement for doing so. Competition over a given partner simply reduces the rate of return available from that partner. The equilibrium investment of attention is the point at which no individual can increase its rate of return by switching how much time it invests in each other group member.

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