

Forum: Ideas

The varying relationship between helping and individual quality

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Individuals of different quality often differ in their helping behavior, but sometimes it is the high-quality individuals who help most (e.g., human meat sharing, vigilance) and other times it is the low-quality individuals (e.g., reproductive queues, primate grooming). We argue that these differences depend on individual differences in the performance costs of actually helping, the opportunity costs from forsaking alternative activities, and the fitness benefits for engaging the help. If helping is more difficult for some individuals to do (quality-dependent help), it will usually be done by high-quality individuals, whereas help that all individuals could do equally well (quality-independent help) will be done by whoever pays lower opportunity costs. Our model makes novel predictions about many kinds of helping, allows us to categorize different types of helping by their relationship with individual quality, and is general enough to apply to many situations. Furthermore, it can be generalized to any other type of (nonhelping) behavior where there are individual differences in benefits, performance costs, or opportunity costs. *Key words:* altruism, biological markets, cooperation, costly signaling, generosity, mating, quality. [*Behav Ecol*]

INTRODUCTION

Animals within the same species can consistently differ in their tendency to help others (reviewed by Bergmüller et al. 2010). Some of this variation is predictable by variation in individual qualities like rank and body condition, but the direction of this effect can be different within the same species for different types of help. For example, low-ranking primates provide more grooming to high-ranking primates than vice versa (meta-analysis: Schino 2001), but high-ranking primates should provide more aid in agonistic interactions (Nöe and Sluijter 1995). Similarly, attractive males invest less in relationships, brood care, and experimental economics games than less attractive males do (Møller and Thornhill 1998; Gangestad and Simpson 2000; Takahashi et al. 2006; Zaatari and Trivers 2007), but other researchers argue that high-quality males use large-scale helping including the sharing of hunted meat to signal their quality to allies, mates, and competitors (Boone 1998; Gintis et al. 2001; Smith et al. 2003). Here we develop a model to resolve such conflicting predictions about who will provide more help—high- or low-quality individuals. Although the model is principally designed to explain variance in helping behavior, it is general enough to apply to other behaviors as well. As such, it helps extend existing models of individual differences, including signaling.

The payoff for helping depends on the costs and benefits, both of which can depend on the helper's quality in a few ways. Firstly, in some circumstances, the cost of performing a given behavior decreases with individual quality because

high-quality individuals can perform acts more efficiently or at less personal risk (lower "performance cost"). In such cases, helping is less costly for high-quality individuals, who may even use helping as a costly signal of quality because the low performance cost is less than any reputational benefits accrued (e.g., Boone 1998; Gintis et al. 2001; Lotem et al. 2003; Smith et al. 2003; Searcy and Nowicki 2005; Számadó 2011). Secondly, different individuals will experience different opportunity costs for helping because some individuals have better-paying alternative activities available to them that others do not have (Barclay 2010). For example, if quality is already perceivable from other cues, then high-quality individuals may refrain from helping because they could better invest their time and effort on direct mating effort rather than on brood care or earning a reputation for a willingness to help (Burley 1988; Møller and Thornhill 1998; Takahashi et al. 2006). As another example, satiated individuals experience lower opportunity costs from forgoing foraging than hungry individuals (Clutton-Brock et al. 1999, 2000). Thirdly, different individuals can experience different benefits for helping. For example, there are social rewards for helping others (e.g., reciprocity, partner choice, signaling a willingness to help), but some individuals may benefit more than others from these social rewards: they may be in a position of greater need or they may be less desirable in other domains, such that they benefit more from reciprocation or social recognition (e.g. Takahashi et al. 2006). Alternately, some individuals might receive a larger private benefit from performing an act that happens to also benefit others (Diekmann 1993; Nunn and Lewis 2001). These differential costs and benefits predict individual differences in helping.

The current model investigates differential costs and benefits by viewing helping behavior within a broader biological market where helping others is but one means of acquiring benefits and where there exists a trade-off between investing

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effort in helping versus elsewhere. We show that the type of help affects whether it will be performed by high- or low-quality individuals. Because “quality” is defined differently by different researchers and fields, our general model allows readers to define “quality” as is most appropriate in their system. This generality allows for more latitude to apply our model, provided that researchers are precise about how costs and benefits are affected by their own definition of quality in their system. Although we focus on helping behavior, many of the arguments will apply to any behavior.

MODEL

We define “helping” as any behavior that benefits others, regardless of genetic relatedness or later benefits to self; those who disagree with this usage should substitute their own term for this broad class of behaviors. We let the inclusive fitness cost c for helping be a function of the amount of help performed h , the average population level of helping h' , and the performer's quality q . In mathematical terms, this becomes $c(h, h', q)$. We let b equal the inclusive fitness benefits that a helper receives when it performs a given level of helping h ; this inclusive fitness benefit (to the helper) will also be a function of the same 3 variables, that is $b(h, h', q)$, and can include reputational benefits (e.g., reciprocity, partner choice, costly signaling of physical quality, or willingness to help) or even any direct benefits from performing the act (e.g., share of a public good being provided). We make no assumptions about the shape of these curves. Because we are seeking qualitative predictions about helping and quality, we can address within-group competition by simply defining the fitness costs and benefits as being relative to whatever reference group is most appropriate (e.g., local vs. global competition, West et al. 2006). Combining costs and benefits, an individual's net fitness f is thus:

$$f = b(h, h', q) - c(h, h', q). \quad (1)$$

The optimal level of helping behavior for any given focal individual will be whatever maximizes this net fitness. What we seek to know is how the optimal level of helping $h = h^*$ will be affected by changes in the quality q of the focal individual ($\partial h^*/\partial q$), that is, we seek the optimal h for an individual of quality q within a population who all perform h' . Unless the optimal level of helping is either zero or the maximum possible help (“extremal” solutions), this optimum will be the point on the fitness curve where fitness does not change with changes in helping, that is, the point where:

$$\frac{df}{dh} = 0 \quad \text{at } h = h^*. \quad (2)$$

We make no assumptions about the shapes of $b(h, h', q)$ and $c(h, h', q)$. Instead, we use the implicit function theorem of multivariable calculus (Marsden and Tromba 1981), which gives a derivative to describe how the optimal helping h^* changes as q changes. This derivative is:

$$\frac{\partial h^*}{\partial q} = -\frac{\partial^2 f / \partial h \partial q}{\partial^2 f / \partial h^2} \quad \text{at } h = h^*. \quad (3)$$

The sign of the denominator on the right side of Equation 3 must be negative because h^* is a nonextremal fitness maximum by assumption (and the second derivatives of such fitness maxima are always negative). Thus, the sign of $\partial h^*/\partial q$, which is what we seek, will be the same as the sign of the numerator, $\partial^2 f / \partial h \partial q$ (due to the double negative). In other words, to determine whether the optimal helping h^* increases

or decreases with quality q , we need to know whether the per unit fitness effects of providing help ($\partial f / \partial h$) increase or decrease with q , that is, whether $\partial^2 f / \partial h \partial q$ is positive or negative. Thus, we can determine the direction of the relationship between h^* and q by computing the sign of $\partial^2 f / \partial h \partial q$, which, from Equation 1 equals:

$$\frac{\partial^2 b}{\partial h \partial q} - \frac{\partial^2 c}{\partial h \partial q} \quad \text{at } h = h^*. \quad (4)$$

The sign of Equation 4 will depend on how the marginal per unit benefits and costs of helping change with quality q (for an illustrative example, see Figure 1); these relationships will in turn depend on the species, the type of helping, and other specifics about the situation.

RESULTS

The relationship between quality and helping depends on how the costs and benefits vary with quality. We examine these separately.

Performance and opportunity costs

Suppose (initially) that the only cost of helping is a “performance cost” and that high-quality individuals are better able to bear this cost. Further suppose (for now) that the benefits of providing that help are independent of quality. In this case, the first term in Equation 4 becomes zero and $\partial^2 c / \partial h \partial q < 0$ because the marginal cost of helping is lower for high-quality individuals than it is for low-quality individuals (for an illustration, see Figure 1). Thus, in this case, Equation 4 must be positive in sign and high-quality individuals should provide more help.

However, suppose instead that the only cost of helping is an “opportunity cost” and that high-quality individuals experience this cost to a greater degree because they sacrifice opportunities for higher benefits in other fitness contexts whenever they help. For example, investing time and energy in helping

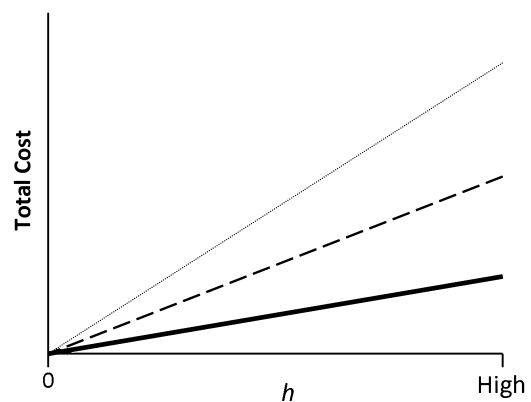


Figure 1

Illustrative linear example where total costs increase with the helping behavior ($\partial c / \partial h > 0$) for everyone but increase less steeply for those of high quality (solid line) than for those of medium quality (thick dashed line) and low quality (thin dotted line), that is the marginal cost per unit of help “decreases” with quality ($\partial^2 c / \partial h \partial q < 0$). Because of these lower marginal costs, high-quality individuals will tend to help more unless they also receive many fewer benefits (not graphed). If instead the marginal cost “increases” with quality ($\partial^2 c / \partial h \partial q > 0$), for example due to higher opportunity costs experienced by high-quality individuals, then the order of the lines would be reversed and low-quality individuals would tend to help more than the others.

others might cause high-quality individuals to lose more mating opportunities (Møller and Thornhill 1998; Gangestad and Simpson 2000) or opportunities for aggressive dominance behavior (Sell et al. 2009) than low-quality individuals would. Further suppose (for now) that the benefit of providing help is independent of quality. In this case, the first term in Equation 4 becomes zero and $\partial^2 c / \partial h \partial q > 0$ because the marginal cost of helping for high-quality individuals is greater than that for low-quality individuals. Thus, in this case, Equation 4 must be negative in sign and high-quality individuals should provide less help. If quality affects the performance costs and opportunity costs in opposite directions, then the sign of $\partial^2 c / \partial h \partial q$ depends upon the relative magnitudes of the performance costs and opportunity costs. For example, among subordinate *Polistes* wasps, high-ranking individuals may provide more effective brood care (slightly lower performance costs) but risk losing the opportunity to inherit a breeding position (much higher opportunity costs), such that the large difference in opportunity costs has more effect on who helps (Cant and Field 2001, 2005). As a human example, highly athletic individuals may be able to provide more effective volunteer help (e.g., at a food bank) but would give up more in terms of lost opportunities for sports or direct mating effort, and the latter effect would often be stronger.

We can explicitly model performance costs and opportunity costs in the marginal costs as follows. For simplicity, we will refer to these costs as p and m , respectively. If these costs are additive, then the total marginal cost (per unit of help) is $p + m$. In such a case, whether the total cost of helping will be higher for high- or low-quality individuals will simply depend on which is greater: the performance or opportunity cost. However, it is more likely that performance and opportunity costs are multiplicative: for example, if an act of helping takes 2 h (performance cost), and an alternative activity pays 4 fitness units per hour (opportunity cost), then the total cost of the helping is 8 fitness units. Thus, the total marginal cost of any given act of helping will usually be a product of the performance and opportunity costs, pm .

Following the product rule for derivatives, the derivative of this total marginal cost with respect to quality (for any given act of helping) is:

$$p \frac{\partial m}{\partial q} + m \frac{\partial p}{\partial q} \quad (5)$$

This derivative—and thus the sign of Equation 4—can be positive or negative depending on the magnitudes of the baseline performance and opportunity costs (p and m), as well as on quality-based individual differences in these costs ($\partial p / \partial q$ and $\partial m / \partial q$). To conceptualize these baselines and individual differences, we can use a graphing analogy by comparing them to the y -intercepts (i.e., the constants) and the slopes with respect to quality, respectively. All else being equal:

- When the “baseline” performance costs p are high in general, individual differences in opportunity costs ($\partial m / \partial q$) will have more impact on who helps. Whoever pays higher opportunity costs will be less likely to help as p increases because they will experience their high opportunity costs more. For example, if high-quality individuals pay the highest opportunity cost to help ($\partial m / \partial q > 0$), then increasing the overall difficulty of the task (p) will affect their net cost more than it will affect low-quality individuals, making the former less likely to help.
- When the “difference” in performance costs $\partial p / \partial q$ is high, high-quality individuals can help much more efficiently than low-quality individuals (e.g., costly signaling theory; Gintis et al. 2001) and should thus be more likely to help.

- When the “baseline” opportunity costs m are high in general, individual differences in performance costs ($\partial p / \partial q$) will have more impact, such that only high-quality individuals are likely to provide the help efficiently enough (i.e., low enough performance cost) to make it worth the total cost.
- When the difference in opportunity costs $\partial m / \partial q$ is high, those paying higher opportunity costs are much more likely to refrain from helping and instead invest in whatever higher payoff alternative activities are available. For example, if high-quality males could invest in mating effort instead of helping, then they will help less (Møller and Thornhill 1998; Gangestad and Simpson 2000; Barclay 2010); if high-quality individuals forage much better than low-quality individuals and are more likely to be sated, then the former will help more (Clutton-Brock et al. 1999, 2000).

Whether helping is positively or negatively related to quality will depend on the magnitude of these 4 effects. This model supports the intuition that when one type of individual (high or low quality) pays higher performance or opportunity costs, that type of individual is less likely to help. A less intuitive finding of this model is that baseline opportunity costs accentuate the effects of individual differences in performance cost and vice versa. In practical terms, this means that increasing everyone’s “outside options” equally will result in individuals with low performance costs doing proportionally more of the observed helping (though the overall helping will be lower). Conversely, increasing the overall difficulty of helping will result in proportionally more of the helping being done by those with low opportunity costs.

Differences in marginal benefits for helping

It is also possible that the marginal benefits for providing help depend on one’s quality (Diekmann 1993; Nunn and Lewis 2001). If so, this can change the sign of Equation 4 and thus the predicted relationship between helping and quality. For example, low-quality individuals might reap higher per unit fitness benefits per unit of reputation earned (i.e., $\partial^2 b / \partial h \partial q < 0$), for example if they are in a greater position of need. Alternately, high-quality individuals might reap more benefits than do low-quality individuals per unit of help they provide (i.e., $\partial^2 b / \partial h \partial q > 0$) because the combination of high quality and good reputation interact synergistically to make them exceptionally desirable partners or because they receive a higher share of a public good provided (Nunn and Lewis 2001).

Integrating differences in costs and benefits

Table 1 summarizes how differences in benefits, performance costs, and opportunity costs will affect whether high-quality individuals help more than low-quality individuals (or vice versa). If the costs and benefits of helping both increase with quality (or both decrease), this will reduce the relationship between helping and quality, with the net direction depending on whether it is the costs or benefits that are most affected by quality. Because we made no assumptions about the detailed shapes of the cost and benefit curves, this model has broad general applicability.

DISCUSSION

Individual quality has much different effects on helping behavior depending on how it influences costs, so it is useful to distinguish between “quality-independent help” that can be performed equally well by anyone and is thus more influenced by opportunity costs and “quality-dependent help” that is sufficiently difficult or costly to perform such that only those of high competence or resources can afford the performance

Table 1
Costs and benefits that affect whether high-quality individuals help more than low-quality individuals or vice versa

Type of cost or benefit	Who experiences the cost less or the benefit more?	Who will help more? (all else being equal)	Example	Sample references
Performance costs (examples include various types of help)	High-quality individuals	High-quality individuals	Sharing of difficult-to-acquire resources (e.g., hunted meat or prey, monetary donations)	Smith et al. (2003), Bliege Bird et al. (2001), Boone (1998), Zahavi A and Zahavi A (1997), Harbaugh (1998), Strathern (1979), Goldman (1937), and Cant and Field (2005)
	Low-quality individuals	Low-quality individuals	High-risk aid (e.g., conflict intervention, predator defense, dangerous emergency rescue)	Seyfarth (1977), Rhine and Westlund et al. (2006)
	High-quality individuals	High-quality individuals	Effectiveness or efficiency increases with skill (e.g., political support, intense physical help, knowledge transfer)	Erdle et al. (1992) and Nöe and Sluijter (1995)
Opportunity costs (examples include alternative activities that will affect opportunity costs)	Low-quality individuals	Low-quality individuals	Situation rare/unlikely	None predicted
	High-quality individuals	High-quality individuals	Foraging with a satiation point	Clutton-Brock et al. (1999, 2000) and Wright et al. (2001)
	Low-quality individuals	Low-quality individuals	Additional mating opportunities available (e.g., polygyny)	Burley (1988), Møller and Thornhill (1998), and Gangestad and Simpson (2000)
	High-quality individuals	High-quality individuals	Foraging without a satiation point	Cant and Field (2001, 2005)
Benefits of helping (examples include situational factors that affect who benefits more from helping)	High-quality individuals	High-quality individuals	Opportunity to occupy a breeding position in a reproductive queue	
	Low-quality individuals	Low-quality individuals	Synergistic interaction between quality and reputation for helping (e.g., democratically choosing leaders)	Van Vugt and Ahuja (2011)
	High-quality individuals	High-quality individuals	Higher need for a public good or collective resource that disproportionately benefits high-quality individuals (e.g., greater shares of a collective resource, threats that target high-quality individuals)	Killing and Milinski (1992) and Silk et al. (2004)
	Low-quality individuals	Low-quality individuals	Formation of coalitions	Nöe and Sluijter (1995), Mesterton-Gibbons and Sherratt (2007), and Benenson et al. (2009)
	High-quality individuals	High-quality individuals	Higher need for reciprocation	
	Low-quality individuals	Low-quality individuals	Higher need for a public good that disproportionately benefits low-quality (e.g., vigilance depending on spatial position within a group)	Yaber and Herrera (1994)

When these factors work in opposite directions (e.g., if high-quality individuals face lower performance costs but higher opportunity costs), the net prediction depends on which effect is stronger.

costs of being magnanimous ($\partial^2 c / \partial h \partial q < 0$). To our knowledge, this paper is the first to make this distinction; in fact, little work has explicitly compared opportunity costs and performance costs beyond a small mention (e.g., Dugatkin and Godin 1992; Bergstrom and Lachmann 1998; Amsler 2010). Barring large differences in the benefit functions, quality-dependent help should be performed more by high-quality individuals who can afford to do so. If quality individuals are the only ones who can afford to perform quality-dependent help, they may also use it to signal their quality (Gintis et al. 2001; Smith et al. 2003). Conversely, quality-independent help will depend on who pays lower opportunity costs, such as low-quality partners helping others to compensate for a lack of other desirable qualities in a reciprocal relationship or biological market (Barclay 2010).

Who pays a higher opportunity cost for helping: high- or low-quality individuals? This depends on the alternative behaviors available to each (e.g., feeding, mating effort) and whether there is a satiation point where an individual no longer benefits from engaging in the alternate behavior (e.g., eating when one's belly is full). If high-quality individuals are sated sooner, then they pay a lower opportunity cost for helping. For example, good foragers are more likely to have eaten their fill, so it costs them less to switch from foraging to brood care or sentinel behavior (Clutton-Brock et al. 1999, 2000). If instead the high-quality individuals could perform a high-benefit behavior with no easily reached satiation point (e.g., males using mating effort to attract additional mates), then high-quality individuals would pay a higher opportunity cost for giving up that activity to help others, so all else equal they should help less. Thus, one would predict that the relationship between individual quality and helping behavior will depend on the type of outside options and the presence of a satiation point in those options, and this will differ across species and situations. Consistent with this prediction, Møller and Thornhill (1998) found that more attractive male birds provided less parental investment than unattractive males in species with high extra-pair paternity (i.e., no satiation point on mating effort, therefore high opportunity costs for helping), whereas the reverse was true in species with low extra-pair paternity (i.e., additional mating effort no longer pays off, therefore low opportunity costs for helping). We look forward to investigations of such satiation points in other studies of helping and individual quality.

Our model tracks "fitness" costs and benefits—not some proxy like survival alone—and individuals who have nothing to lose (e.g., zero chance of reproduction) experience less of a fitness cost for their actions (Daly and Wilson 1988; Cant and Field 2001). For such individuals, even small inclusive fitness benefits could be sufficient to select for helping. For example, this principle is generally accepted as a factor in the evolution of cooperative breeding because ecological constraints reduce options for independent breeding (e.g., Keller and Reeve 1994; Bergmüller et al. 2007). This point about measuring fitness costs must be remembered when testing our model.

Because costs and benefits differ between individuals and over time, helping should be a facultative strategy that is tailored to the performance cost of the helping and also to one's changing outside options and alternative means of accruing fitness. It is even possible that some of the heritable variation in helpful behavior (Krueger et al. 2001) will be related to heritable variation in quality-related traits (e.g., attractiveness), and this relationship will differ for quality-dependent and quality-independent help. This distinction between quality-dependent help and quality-independent help can resolve discrepant findings and theories about who will help and also demonstrates that different types of helping should be treated differently.

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