Altruism or Just Showing Off?

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Why would one perform a costly behavior if it does not benefit the actor himself but only the recipient? Four models are suggested to justify altruistic behaviour: group selection (GS), kin-selection (KS), reciprocal altruism (RA) and Zahavi's alternative model (Zahavi, 1995). Each model explains how altruistic behaviour can bring positive direct and/or indirect fitness/benefit to the actor.

GS model suggests that it is beneficial to invest in a group as this provides the individual with more in terms of general welfare than what they themselves invested in. GS model, however, is unstable because it is not immune to social parasites: A member of the group who invests nothing in their group receives as much utility as the rest of the members without the cost of helping.

GS model was later rejected by many scientists in the 60s and the alternative, KS model, was suggested. KS model has played a dominant role in understanding altruistic behaviour. In KS model, altruistic investments are justified by the beneficial effects on the fitness of the relatives, hence the increase in indirect fitness of the altruist. KS model suggest that more related an individual to its kin, the more help it offers.

Seychells warbler helpers *Acrocephalus sechellensis* do not work as hard when they raise half siblings than full siblings (Heinsohn and Legge, 1999). A decrease in parental care in males can be observed with low confidence in paternity. Other species such as Australian magpies *Gymnorhina tibicen* fail to help at all or help only if they have the incentive of direct paternity (Heinsohn and Legge, 1999). KS model, however, is as unstable as GS because if three brothers are walking and if one falls in the river, only one of them has to jump in to save the drowning brother. The third one does not have to risk himself but gains as much as the altruist (Zahavi, 1995). In addition, KS fails to explain why some helpers regularly aid nonrelatives. Covas, Dalecky, Caizergues and Dourelant believe that "kin associations might be a consequence of demographic viscosity rather than active choice" (Covas et al, 2006). Their experimental result shows that 50 % of the helpers were offspring or first order relatives of one and 43% were of both. There are however, 7% of them that are not related. KS model is appealing as an explanation because cooperative breeders and helpers often live as a family where the receivers of help are the close kin (Covas et al, 2006). Simple observation that suggests helping is common among the kin does not represent KS. According to Covas, Dalecky, Caizergues and Dourelant's experiment, the amount of help offered does not correlate with relatedness. KS model also fails to show a positive

correlation between the number of helpers and production of young (Heinsohn and Legge, 1999). In any case, the birds' promiscuity complicates the understanding of KS because the relatedness can only be assumed. Unless extrapair paternity or egg dumping is used, the assumed level of relatedness can be erroneous. KS is considered unstable as a model.

In RA model, the investment of the altruist is compensated for by the reciprocal investment of the other member. RA model is only stable when there is a mechanism that ensures the reciprocation. Punishment can only be seen in higher animals and therefore is a major problem in this model (Zahavi, 1995). A mathematical model reported by Nowak and Sigmund shows that cooperation can be established even when the actor knows that the recipient cannot return the favour (Ferriere, 1998). Nowak and Sigmund assume that any two organisms are unlikely to interact more than once. Elfstorm's experiment with rock pipits *Anthus petrosus* shows that neighbours return the favours when attacked by an intruder (Elfstorm, 1997). Pipits have stable territories and hold the central part of the territory even after the brood. When an intruder attacks a territory, the owner's neighbours cooperate and harass the intruder together without harassing each other. If the neighbour's help discourages the intruder, a successful and mutual defense system is established. Elfstorm's model

appears to support RA; however, [more] experiments are needed to find out whether neighbours reciprocate equal amounts of help" (Elfstorm, 1997).

On the other hand, Zahavi suggests in his alternative model that the "[altruist] gains from its investment by increasing its 'social prestige.' Helping may thus be considered as a simple selfish character" (Zahavi, 1995). For example, humans and highly social animals often help non-kin that may not return the favour (Bshary and Grutter, 2006). As a result, however, the altruists succeed in improving their social image, and hence individuals that witness the positive behaviour are more likely to help the altruists in the future. Bshary and Grutter provide an experimental evidence to support Zahavi's alternative model (Bshary and Grutter, 2006). A cleaner fish *labroids dimidiatus* may prefer consuming a host fish's mucous over eating ecotoparasites, and the host fish must make cleaners feed off the ecotoparasites to receive the cooperative service. A host fish, or a client, that has seen a cleaner fish cooperate would spend more time next to it than a cleaner fish with an "unknown cooperative level." Clients engage in image-scoring behaviour. To make such indirect reciprocity work, individuals must be watched and assigned "image scores" by their group members (Rerriere, 1998). White-winged choughs *Corcorax melanorhamphos* engage in a similar behavior; one to two year old helpers

have a tendency to cheat, if not being watched, when they are supposed to feed a nestling (Heinsohn and Legge, 1999). While chough helpers appear to be engaging in desired behaviour, if there is no witness at the nest, they consume the food they brought themselves. In addition to direct and indirect benefits, helpers also seek the additional benefit of being seen as a helper.

Zahavi's alternative model is the most stable of the four. The dominant KS model fails to show a positive correlation between the relatedness and the amount of help offered to the kin nor a positive correlation between the number of helpers and production of young (Heinsohn and Legge, 1999). "In addition to KS benefits, there is a range of other important direct benefits associated with group membership, which are often ignored" and one of the benefit is the "image score" (Covas et al, 2006). It appears that GS and KS are the consequences of demographic viscosity, not an active choice (Covas et al, 2006). On the other hand, RA is logical but fails to show that equal amounts of help are reciprocated (Elfstorm, 1997) "[Elfstorm's] alternative strategy is also strikingly similar to Zahavi's (1995) model 'altruism as a handicap' regarding the case of cooperation in groups of two" (Elfstorm, 1997). Scientists who use GS, KS or RA model often use Zahavi's model to support what their main models fail to explain rather than to criticize and

point out the instability of the alternative model (Elfstrom, 1997; Covas et al, 2006). On the other hand, the alternative model is often used to suggest the instability of the other three (Heinsohn and Legge, 1999; Rerriere, 1998; Zahavi, 1995; Zahavi, 2003). Zahavi's alternative model succeeds in filling the holes the other models couldn't and is the most stable model.

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