Altruism or Just Showing Off?

As the cheetah sees a gazelle standing silently in the wilderness, it slowly moves towards it. The cheetah suddenly springs up and initiates an active chase after the gazelle. The gazelle starts to run and then stots (running slowly initially and then jumping high). Is the gazelle trying to alert the other gazelles to the cheetah's presence, an act we call altruism, or trying to communicate to the cheetah to stop the fruitless chase, an anti-predator act? In other similar situations, some individuals of a species exhibit such an apparently altruistic behavior that has questioned many experts, may the motives be altruistic or selfish? In game theory, if individuals are in a state of self-interest, they would not be exhibiting such altruistic behavior if the reason is anything other than to increase the individual's utility. A "self-interested" individual is one who is just trying to maximize their own utility, not necessarily trying to harm others. The altruistic phenomenon that had become puzzling to many has been the topic of great interest for many researchers. Previously, there were three traditional models developed to explain this altruistic phenomenon and they occurred in the following order: group selection (GS), kin selection (KS) and reciprocal altruism (RA). Each of these models will be introduced and we will see how the "handicap principal" suggested by Amotz Zahavi has formed the basis of an alternative model to explain the altruistic behavior phenomenon; however, the strengths and limitations of all of these models will be presented.

The group selection claims the idea that an individual helps in a group if the benefit of the group exceeds the individual investment. Zahavi (1995) mentioned that group selection is not illogical but it has been shown to be vulnerable to social parasitism. By social parasites, he meant the individuals who do not invest in the group's welfare gain just as much as those who do invest in the group. This model is no longer adopted by most scientists. The model that was

later established was the model of kin selection. Zahavi (1995) suggested that the model of group selection claims the same concepts as the kin selection model with just one difference: helpers resort to their kin and relatives rather than to any group. However, according to Zahavi, they are both susceptible to social parasitism and are equally unstable. The kin selection model says that an individual helps his kin so that his/her gene frequencies will be maintained in a population. The next model adopted is reciprocal altruism. This model is about helping for reciprocation from the recipient sometime in the future. For higher animals such as monkeys and humans, we tend to have a punishment system for those who do not reciprocate so that reciprocation is highly adopted. Zahavi (1981) suggested a limitation to the model of reciprocal altruism that the mechanism to enforce reciprocation is costly to the individual who possesses it. So, would reciprocation be an adequate force that maintains the apparently altruistic phenomenon observed? The major cost is reciprocation enforcement. As evident by the group selection and kin selection models, selfish individuals who do not invest in punishing the social parasites gain more than those who do. Also, another downside to this model is that it does not explain cases where the act of the non-related altruist is never reciprocated. In the end, neither the kin selection nor reciprocal altruism models could explain helping at the nest by a non-related individual.

The alternative model to explain the "altruistic" behavior is based on the handicap principle. This principle is the idea that an individual is advertising his fitness by a costly display so that he gains direct benefits in the near future such as more mating or less pursuits by predators. This costly display may be any physical attribute possessed by or action done by an individual. In terms of the handicap principle, the act of altruism seen was interpreted as the "costly display". For example, the actor may be giving help to others just to gain social prestige

so that, when recognized, he/she may gain direct benefits. The support behind this idea is that only those individuals who are fit are able to afford these costly displays. So, it is sensible that these advertisements are "honest" and that others feel safe to believe them. In fact, it is credible that the cheetah in the opening story would avoid wasting energy in a fruitless chase after a healthy animal. Only those who are fit are able to grant its predator such an advantage. Also, Jared Diamond (cited in Wikipedia) has proposed that certain risky human behaviors such a bungee jumping may be expressions of instincts that have evolved through the operation of the handicap principle.

Ostreiher (2003) did a study on songbirds, the same subjects used by Zahavi (1995): Arabian babblers, *Turdoides squamiceps*. However, this experiment used mobbing and not the helping-at-the-nest behavior to investigate whether it is altruism or selfishness. Multiparticipant mobbing exhibited by these birds is when they crowd in large numbers around a predator, approaching and retreating alternately. This behavior includes calling loudly, raising and dropping their wings, and spreading and gathering their tails. Four important findings have been described in this paper that all supports the prey-predator communication hypothesis. The prey-predator hypothesis is also a hypothesis under the handicap principle described by Zahavi, 1977 and 1987 (cited by Ostreiher, 2003). It claims that a potential prey tries to convince its predator that it is not worth pursuing by exposing and attracting predator's attention. Briefly outlining, the first finding is that a single babbler's behavior is primarily anti-predator. When a single babbler was in a lonely situation, it was still exhibiting the mobbing behavior to both predators and foreign babblers. This shows that it could not be altruism, parental care or self-advertisement because no other babblers are around. The second finding is that the mobbing behavior intensity is influenced by the active presence of another babbler and not only as a

consequence of the babbler's reaction to the predator. The intensity of the mobbing behavior increased with the number of assembled mobbers. The third finding is these birds were not taking risks in the presence of the predator which is inconsistent with the self-advertisement hypothesis because an animal must take risks to advertise itself. The fourth finding is that members of both sexes had similar motivations because no differences were found between the sexes. Both the prey-predator hypothesis and the self-advertisement hypothesis are claims under the handicap principle. But in this situation, it is in favor of prey-predator and not the self-advertisement hypothesis presented by Zahavi (1995). Also the fact that each babbler tries to compete with other babblers by increasing in mobbing intensity to convince the predator not to choose him supports the fact that mobbing is an 'audience effect' more for competition than for warning. This has been noted by Gyer et al. 1986; Gyger 1990; Evans & Meyer 1991, 1992; Marler & Evans 1996 (cited by Ostreiher, 2003). Although the traditional mechanisms were not investigated here to refute the self-advertisement hypothesis claim, this finding showed that not all apparent behaviors of altruism can be explained by the self-advertisement hypothesis.

Next, Covas R. et al (2006) did an experiment on social weaverbird *Philetairus socius* that gave evidence in support of one of the more traditional mechanisms of kin selection. This article supports the fact that altruism can evolve without advertising the fitness status of the actor. To determine the genetic benefits resulting from helping at the nest, they have explored the possible direct benefits that could be gained such as shared parentage (getting extra parentage from the other bird), extrapair fertilizations (direct reproduction) or egg-dumping (the practice of placing eggs in a nest built by another bird); indirect benefits such as increased production of nondescendant kin; or both. The direct benefits of reproduction can be determined by the measure of the relatedness of the nestlings to the helper by reliable molecular techniques

described in detail in the article. One of the major findings in this article is that helpers were more related to the nestlings (a bird too young to leave its nest) they were tending than to the other nestlings of other nests. This is illustrated in the Figure 1 below.

Figure 1
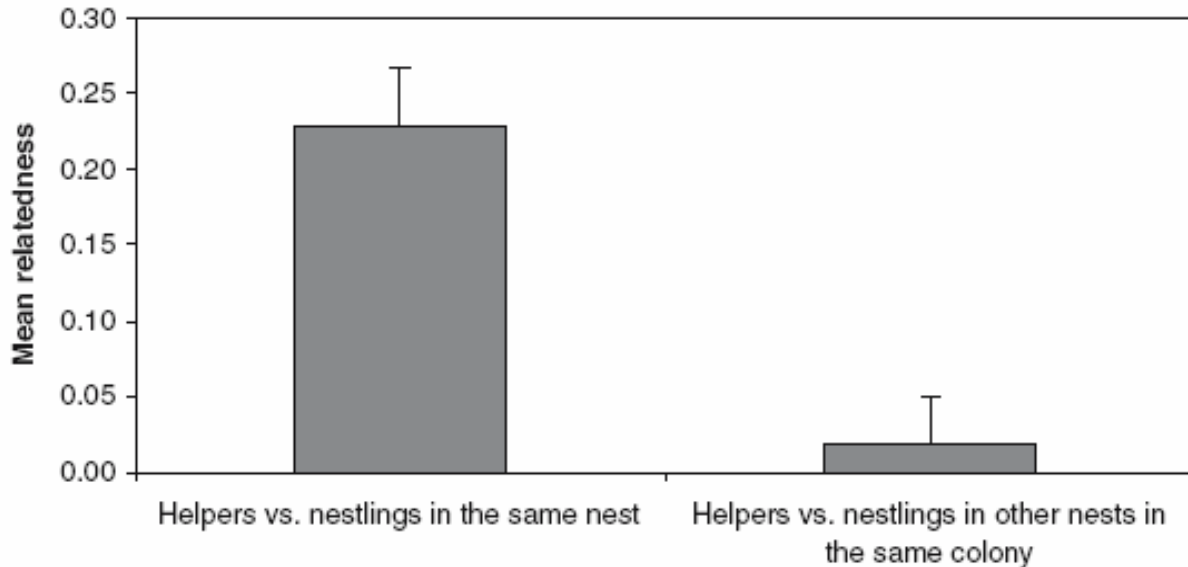
This graph shows that the mean-relatedness between adult helpers and the nestlings they were tending was higher than the relatedness between those same helpers and nestlings in other nests in the same colony. There is no supporting evidence for the direct benefit of extrapair parentage in this experiment but have been found in others done by Griffith et al. 2002, Legge and Cockburn 2000 (cited by Covas R. et al, 2006). The sociable weaver helpers do not appear to have access to reproduction suggesting that the important selective force behind cooperative breeding is not the direct benefits of immediate reproduction in this species. However, the indication of the active choice for associating with kin suggests that kin selection plays an important role in the maintenance of helping behavior in this species. Covas et al suggested that

there remain other unknown direct benefits, although non-reproductive, of remaining as a helper as well as female decisions.

The final study done by Lotem et. al (2002) uses game theory models to show that the handicap principle holds from the fact that high-quality (high fitness) individuals are able to gain signaling benefits from altruistic acts that no longer depends on the probability of future reciprocation or punishment. The analysis in these models appears complex but they all converge to one main idea that when we make conventional reciprocity models more realistic by considering individual quality variation, Zahavi's handicap signaling principle becomes inevitable. Lotem et al (2002) modeled two cases: reciprocity without signaling (advertisement) and reciprocity with signaling.

For the reciprocity without signaling model, first a simple symmetric model similar to that of the prisoner's dilemma game was used. Three evolutionary game strategies (heritable behavior phenotypes) are considered: unconditional altruists (UAs), defectors (DEs) and conditional altruists (Tit-for-Tat (TfT) player). The UAs help individuals indiscriminately, DEs solicits and TfT players always help everyone unless it could classify a DE, whom will not be helped. The game matrix is illustrated in Figure 2.

Figure 2: Payoff matrix for the row player.

	UA	TfT	DE
UA	B-C	B-C	-C
TfT	B-C	B-C	-(1-r)C
DE	B	(1-r)B	0

B=accumulated benefit of receiving help over a lifetime.

C=the average lifelong costs of donating help.

r=the probability that an individual requesting help has been classified by the TfT player. So, 1-r is the probability that an individual requesting help is unclassified (0 < r <1).

The value of r depends on how well the TfT player's memory is and the probability of repeated

interactions with the same players. It has been shown that this system regardless of whether

C<B or C>B has a uniques ESS (evolutionary stable strategy), (DE, DE), ultimately resulting in

a population consisting of DEs only. A more realistic multitype model for heterogeneous

populations is then presented where the same matrix is being used except this time the

population is divided into two classes: low-quality individuals (L) and high-quality individuals

(H). The low-quality individuals have a higher cost of donating help (D) than the benefits they

get from reciprocation (D>B) and high-quality individuals have a net payoff (B>C). The

modified game is illustrated in figure 3 a complement from Lotem et al (2002).

Figure 3: multitype models

$$P_{HH} = (1-q)\begin{pmatrix} & UA_H & TfT_H & DE_H \\ B-C & B-C & -C \\ B-C & B-C & -(1-r)C \\ B & (1-r)B & 0 \end{pmatrix} \begin{matrix} UA_H \\ TfT_H \\ DE_H \end{matrix},$$

$$P_{LH} = (1-q)\begin{pmatrix} & UA_H & TfT_H & DE_H \\ B-D & B-D & -D \\ B-D & B-D & -(1-r)D \\ B & (1-r)B & 0 \end{pmatrix} \begin{matrix} UA_L \\ TfT_L \\ DE_L \end{matrix},$$

$$P_{HL} = q\begin{pmatrix} & UA_L & TfT_L & DE_L \\ B-C & B-C & -C \\ B-C & B-C & -(1-r)C \\ B & (1-r)B & 0 \end{pmatrix} \begin{matrix} UA_H \\ TfT_H \\ DE_H \end{matrix},$$

$$P_{LL} = q\begin{pmatrix} & UA_L & TfT_L & DE_L \\ B-D & B-D & -D \\ B-D & B-D & -(1-r)D \\ B & (1-r)B & 0 \end{pmatrix} \begin{matrix} UA_L \\ TfT_L \\ DE_L \end{matrix}$$

The P_{ij} shows the payoff for player i when it plays player j. D denotes the average accumulated

lifelong costs of altruism for low-quality individuals. So, in this system C<B<D. q is the

frequency of low-quality individuals in the population (0<q<1). The rest of the other population

consists of high-quality individuals and the frequency is denoted by 1-q. The above system

shows that if a high r is sufficiently maintained (ie r > C/B) and q is not too high (q<(rB-C)/r(B-

C)), a cooperative ESS profile can be achieved (TfT$_H$, DE$_L$). This seems logical because high-

quality individuals are able to afford to play TfT and low-quality individuals defect because their

limited "quality" requires a much higher cost for them to help.

Signaling benefits were introduced into this system and six ESS profiles and one

evolutionary stable set (ES set) were obtained. The game matrix is illustrated below. This

system assumes that every time an individual provides help, he is gaining some signaling benefit.

The signaling benefit is for example the recognition that he will get from other individuals as a

result of helping, the advertisement of his high-quality state.

Figure 4: multitype model with signaling benefits.

$\psi(x,y)$ denotes the ratio of benefits to the conditional altruists to the benefits for unconditional

altruists. Thus, $\psi(x,y) = E_{TfT}/E_{UA}$. S denotes the additive signaling benefits. The six ESS

solutions and one ES set solution are outlined below:

ESS profile ($\oplus$ denotes a mixed solution)	payoff constraints	ESS is attained for:
1. (UA_H, DE_L)	$C < S < D$	all r and q
2. $(UA_H, TfT_L \oplus DE_L)$	$C < S < D$	$r > \rho,\ q > \theta_3$
3. (TfT_H, DE_L)	$S < C$	$r > C/B,\ q < \theta_2$
4. (DE_H, DE_L)	$S < C$	all r and q
5. $(TfT_H, TfT_L \oplus DE_L)$	$S < C$	$r > \rho,\ q > \theta_1$
6. $(TfT_H \oplus DE_H, DE_L)$	$S < C$	all r, and $q < \theta_2$
7. ES set: (UA_H, UA_L)	$S > D,$	

where

$$\rho = \frac{D - S}{B}\ ;\ \theta_1 = \frac{r - \rho}{r(1 - \rho)}\ ;\ \theta_2 = \frac{rB - C + S}{r(B - C + S)}\ ;\ \theta_3 = \frac{\rho}{r}.$$

Just to explain a few important ESS that make intuitive sense, we could see that when C<S (the

signaling benefit is greater than the cost of helping), the individual is able to make a net profit

just by the signaling benefit alone even without reciprocity. This is seen in the first ESS where

unconditional altruism is stable and is independent of constraints of reciprocity parameters (r and

q). We could also see that all of the cooperative ESS (nos. 1-3, 5 and 6) has a high-quality

individual tied to the unconditional altruistic behavior and the low-quality individuals tied to the

defecting behavior which shows that quality is correlated with altruism. An individual who tries

to cheat (one of low-quality who tries to signal high) will have a fitness loss because S<D (the

signaling benefit is much lower than the cost of making the signal). So, it makes sense for a low-

quality individual not to cheat. However, the only non-cooperative ESS (no.4) has both the high

and low quality player giving no help, (DE$_H$, DE$_L$). This makes sense because there would be no

net loss if they do not make the expenditure of helping but this is rarely seen. To make the first

ESS meaningful, the fraction of low-quality individuals in the population, q, have to be greater

than zero, otherwise the condition C<S<D would not hold true. This is explanatory in the

definition of D, where it could not exist without the presence of low-quality individuals. If everyone is of high-quality, then helping would be adaptive in the whole population. If this happens then the ES set holds true (no. 7) in that everyone helps unconditionally when S>D. However, quality would no longer correlate positively with helping because everyone is the same as everyone else. So, this helping quality would not be used as an "indicator" and will then be selected against because the signal becomes cheap. The system would then collapse. In nature, the altruistic behaviors could be explained by this signaling theory, and the signal benefits are the force that maintains this altruistic interaction.

In conclusion, every model has its own logic and is good for explaining the altruistic behavior in different situations. But every model has its own drawbacks because they may not be considering all factors nor be used in every context. However, the self-advertisement hypothesis of the handicap principle can be applied to the most diverse contexts. For example, in the study done by Covas R. et al, the wearbirds were showing kin selection in the context where there is choice given. However, it doesn't explain situations where a bird is helping a non-relative or another group. In these cases, the reciprocal altruism model or the self-advertisement hypothesis of the handicap model works best. Still, the reciprocal altruism model cannot explain helping behaviors that were not seen to be reciprocated. The upper hand of the handicap principle is that it can be used to explain altruistic behaviors in situations that can not be explained by any of the other three models. One of the strengths of the handicap principle is that it was modeled using game theories and was found to contain many evolutionary stable strategies. This is a strong support for the stability of this principle. I could relate more with the handicap principle because I believe in the fact that individuals are self-interested and that self-advertisement from a high-quality individual is a good way to maximize there own utility.

References:

http://en.wikipedia.org/wiki/Handicap_principle

Covas, R. et al. (2006). Kin Associations and Direct vs Indirect Fitness Benefits in Colonial

Cooperatively Breeding Sociable Weavers Philetairus socius. *Behav. Eco.l Sociobiol.*,

60, 323-331.

Lotem, A., Fishman, M.A., and Stone, L. (2002). From Reciprocity to Unconditional Altruism

through Signaling Benefits. *Biological Sciences*, 270, 199-205.

Ostreicher, R. (2003). Is Mobbing Altruistic or Selfish Behavior? *Animal Behavior*, 66,145-

149.

Zahavi, A. (1995). Altruism as a Handicap: the Limitations of Kin Selection and Reciprocity.

Journal of Avian Biology, 26,1-4.