

Group Selection to Fixation of an Altruistic Behavior in a
Population Divided into Breeding Isolates: A Model.

(Presented to the June 1976 Annual Meeting of the Animal
Behavior Society. University of Colorado, Boulder.)

F. T. Cloak. Jr.
1417 East Cook Street
Springfield, IL 62703

I want to show how truly altruistic behavior can evolve by means of natural selection. I don't mean kin selection, i.e. that an individual directs his altruistic behavior toward a kin-organism.

I certainly don't mean "reciprocal altruism" where one instruction, selfishly evolving, creates an environment where another instruction (the supposedly altruistic instruction) is selfishly adaptive -- "You altruistically scratch my back and altruistically won't punch you in the nose", and vice-versa. I called this "Environmentally Engendered Pseudo-Altruism" in another context.

I do mean that an altruist, a carrier of genetic or cultural instruction A, aids his conspecifics indiscriminately at some cost to his own genetic or cultural fitness. The altruistic act can be dramatic, such as risking one's life to rescue another from danger; or it can be ordinary, such as giving a peculiar call when a source of food is discovered. I'll use the latter for my example.

The fact that altruism is indiscriminate lets me make use of an altruism ratio. A certain number of altruistic acts -- it doesn't matter how many -- are, among them, determinants of non-occurrences of y altruists and of occurrences of z non-altruists; in other words, if those altruistic acts had not taken place, there would be z fewer organisms than there actually are, but there would be y more altruists than there actually are. So the altruism ratio AR is y/z , the number of altruists lost divided by the number of organisms gained; it's a cost/benefit ratio.

Now, can instruction A, for food-sharing, become universal in a population through natural selection? To do so, it must achieve and maintain a high frequency in groups of that population, through natural selection and not through drift.

(Aside) An altruistic cultural instruction may have an easier time than an altruistic genetic instruction achieving a fairly high frequency in a group, but its chances of maintaining that frequency over the long run are no better: Just as the cultural instruction may propagate through a group faster than selection can remove it, so may a countervailing cultural instruction to cheat. "Easy come, easy go."

I'm going to show first, how an instruction A for an altruistic act can achieve a high frequency and even become universal in at least one group in a population. Then I'll show how that universality will become typical of all groups and how "cheaters" will be eliminated.

First I must make my assumptions explicit. I make three kinds of assumptions:

Controlling assumptions, which have to be true if my version of altruism is to work;

Auxiliary assumptions, which spell out the controlling assumptions and have to be somewhere in the ball park; and

Simplifying assumptions, which need not be true but which help me to understand and calculate and explain the idea.

See Handout p.1

[FTC 2014: Handout p.1 reproduced as read on this page.]

Controlling Assumptions

The organisms occur in demes (breeding populations) divided into trait-groups that behave pretty much out of sight and sound of each other, following D. S. Wilson. Contra Wilson, however, the trait-groups are culturally and genetically pretty much isolated, also; i.e., there is little exchange of instructions across group boundaries. There is a maximum and minimum size for a group; if one becomes too big, it splits in two. This is contra Levins and others, who assume budding off from oversized groups. Budding is impossible here because if a group falls below a certain size it becomes moribund; i.e., it inevitably goes to size zero in a certain length of time.

Auxiliary Assumptions

Maximum Trait-group size = 30.

Minimum Trait-group size = ca. 6.

Altruism Ratio for Instruction A = 2/17

Simplifying Assumptions

The organisms are haploid. Altruism ratio is constant.

Overall numbers are limited by the food supply. The amount of food an individual gets is independent of the size of his group. Altruistic Instruction A is to share food.

Groups split exactly in half exactly at 30. Population is in equilibrium, initially, deaths equaling births. Groups rarely reach 30, rarely fall to 5. When a group acquires altruists, the change process (however slow) goes as follows: Gain 5 organisms, lose one altruist, gain 6 organisms, lose one altruist, gain 6 organisms, SPLIT. Group of 15 - proportionately for groups of other sizes.

Once the process begins, there is no further loss or gain of Instruction A through drift.

The controlling and auxiliary assumptions are consistent with what we know about primate groups, and not unreasonable for early hominid groups. They are, moreover, much less special and peculiar than those proposed by some other students of altruism and group selection; surely, therefore, they obtain in animal populations at many phylogenetic levels.

For simplicity's sake, we'll examine different undersize groups of 15 organisms, some of whom are spontaneous A-carriers i.e. altruists. When (if) such a group reaches size 30, due to altruistic acts, it will have added 17 organisms and lost two altruists, so the number of altruists it will have at 30 can be calculated. See "Parent Group" column on table, p.2 of handout.

When a "parent" group of 30 then splits in half it may be that neither daughter group has as many altruists as the parent group had at 15; or one (or both) may have as many; or one may have more altruists than the parent group had at 15. The table indicates the probability of each of those outcomes for parent-group altruist counts (NA15) ranging from 2 to 15. Note the transitions in the "less" column at NA15 = 6 and especially at NA15 = 10.

At NA15=6, if NA30=10, prob. of "greater" becomes same order of magnitude as prob. of "less", At NA15=10, if NA30=19, prob. of "less" becomes zero. Frequency of altruists has nowhere to go but up.

Now I'm not arguing here that any particular trait-group will attain a high number of altruists; I'm only arguing that given time, some trait-group will do so. So what matters at any point is the highest altruist count going.

There are three good reasons why these probabilities are very conservative. One is that the altruism ratio of 2/17 is very high. Another is that a group-line may fall back at one fission and then come forward with doubled intensity. Suppose, for example, that in a group with NA15 = 7, so NA30 = 12, the worst thing possible happens: the altruists split evenly at fission, so each daughter group only has NA15 = 6, one less than the parent group had. That's a fall-back, but now there are two

groups with six altruists; the probability that they'll both fall back on the next go-around is only .1719, while the probability that at least one will increase back to 7 is roughly .3244.

Thirdly, perhaps the most important, instructions both genetic and cultural occur in family lines, because of the processes of their replication. If group fission occurs along family lines then we could expect a pronouncedly assortative distribution of instruction A, even dramatic leaps in the value of NA15 from the parent group to the best-endowed daughter group. From reading its abstract, I gather that a paper to be given by Chepko-Sade at these meetings this afternoon will support the hypothesis that group fission among rhesus, at least, does occur along family lines.

So it appears that a truly altruistic feature can evolve in a small group: Once drift provides 6 or 7 altruists in a group of 15, there is a substantial probability of the number reaching 11 in at least one descendent group, through natural selection. Once the number reaches 11, complete success is assured; the instruction will become universal in at least one group. Once the number in one group reaches 12 or so, even its less-endowed daughter will have at least 11 altruists, so its family line will spawn at least one all-altruist group. And so on, so more and more groups with more and more altruists arise.

But trait-groups with ever increasing frequencies of altruism cannot continue to grow and split, grow and split merely by (say) utilizing food resources more efficiently. The total number of organisms in the biotope can increase only to a point and then competition is sure to set in; groups with altruists in them continue to grow and split, but at a slower rate, and at the expense of groups lacking altruists. The amount of food an individual gets is now a positive function of the proportion of altruists in his trait-group. So groups without altruists cannot replace their numbers; they diminish in size and gradually die out, until there are no groups left without altruists. Then, similarly, groups with fewer altruists will be out-competed by groups with more altruists.

In time, only groups that are 100% altruistic can maintain themselves in the biotope; Instruction A is no longer facultative but is now obligatory for group survival, it has made itself indispensable.

What happened to the last of the only partly altruistic groups is exactly what happens, later on, to any group in which a mutant "cheater" appears. Within his group, the cheater outcompetes the other group members; he has more offspring than they, so the next generation has a higher percentage of cheaters, and so forth. But because it can't compete with other groups, his group diminishes in size over generations. Individual organisms may be born, lead satisfying lives, leave offspring, and die happy, but the group is slowly dying. Because group-death takes several organism-generations, no one may notice it. What appears obvious is that the altruism instruction A, in that group, is costly to its carriers -- which it is, in that group. But in the groups where its frequency is high, especially where it is universal, it benefits its carriers.

Or Does It? It benefits them, sure, since they can't propagate their genomes and cultural repertoires down through the generations without it. But it benefits them only because they are in competition with members of conspecific groups who also carry it at a very high frequency. In the long run, then, instruction A is beneficial to its carriers only in an environment which it has itself created. It has domesticated its carriers, and all the rest of their instructions, to its service, without giving them back anything they didn't have before (except numbers). In fact, it may well have made their lives worse.

The moral of all this is that only an instruction benefits necessarily from altruistic behavior; its carriers and/or their groups benefit only incidentally -- as a means to the instruction's benefit -- if at all.

Another thing to notice is that the altruistic instruction A has altered its environment, by adding organisms to it, in a very directional way. One might say that it has degraded the environment so that these organisms can't live there anymore without it. Now any new instruction that acts contrary to the

altruistic outcome of instruction A's action will be hard put to get established. On the other hand, any novel instruction that cooperates with A to further elaborate, reinforce, buffer, supplement or protect it will be most likely to succeed. Thus are trends, and complicated exploitative systems of instructions, established.

SUMMARY

I've shown that a genetic or cultural instruction for indiscriminately altruistic behavior will propagate to universality in an environment where partially isolated trait-groups grow through altruism and then divide more-or-less equally.

I've also suggested that the real unit of evolution, cultural as well as genetic, is neither the individual organism nor the group, but is, rather, the elementary self-replicating instruction.

Note (2014): The numbers on page 2 of the following handout were swotted up by the use of a Texas Instruments Scientific Calculator I bought in the early seventies. Someone at the conference kindly informed me that I was using a Hypergeometric Probability Function. - FTC

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Once the process begins, there is no further loss or gain of Instruction A through drift.

PARENT GROUP

"BEST" DAUGHTER GROUP

NA15 = number of altruists in group of 15 organisms. After ?? altruistic acts, this becomes NA30 = number of altruists in group of 30.

Group of 30 organisms then divides into two groups of 15, daughter groups of original group of 15. Numbers below indicate the probability that the higher NA15 of the two, relative to the NA15 of the parent group, will be

NA15	NA30 calcula- ted	NA30 assigned	less	the same	greater
2	0	0	1.0000	---	---
3	2.62	2	1.0000	---	---
		3	.7759	.2241	---
4	4.90	5	.6705	.2874	.04215
5	7.18	7	.6102	.3098	.08004
6	9.47	9	.5730	.3184	.1086
		10	.3001	.4578	.2451
7	11.75	12	.2896	.4468	.2636
8	14.03	14	.2848	.4430	.2722
9	16.31	16	.2848	.4430	.2722
10	18.59	18	.2896	.4468	.2636
		19	---	.5503	.4497
11	20.87	21	---	.5730	.4270
12	23.16	23	---	.6120	.3898
13	25.44	25	---	.6705	.3295
		26	---	.4023	.5977
14	27.72	28	---	.5172	.4828
15	30.00	30	---	1.0000	---

done

I want to show ^{how} ~~that~~ truly altruistic behavior can evolve by means of natural selection. I don't mean ~~de jure~~ ^{an} kin selection, i.e. that individual directs his altruistic behavior toward a kin-organism, although the mechanism I propose probably involves de facto kin selection.

I certainly don't mean "reciprocal altruism" which ~~means that~~ ^{where} one instruction, selfishly evolving, creates an environment where another instruction (the supposed; y altruistic instruction) is selfishly adaptive -- "You altruistically scratch my back and I altruistically won't punch you in the nose", and vice-versa. I called this "Environmentally Engendered Pseudo-Altruism" in another context.

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~~As a handy device, I'll~~ [^] make use of an altruism ratio. A certain number of altruistic acts -- it doesn't matter how many -- are, among them, determinants of non-occurrences of y altruists and ^{of} occurrences of z non-altruists; in other words, if those altruistic acts had not taken place, there would be z fewer organisms than there actually are, ~~###~~ but there would be y more altruists than

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The controlling and auxiliary assumptions are consistent with what we know about primate groups and not unreasonable for early ~~human groups~~ hominid groups. (5)

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The table indicates the probability of each ~~###~~ of these outcomes for parent-

group altruist counts, ranging from 2 to 15. Note the transitions in the "less" column at $NA_{15} = 6$ and at $NA_{15} = 10$. ^(NA_{15})
^{especially} At $NA_{15} = 6$, if $NA_{30} = 10$, prob. of "greater" becomes same order of magnitude as prob. of "less". At $NA_{15} = 10$, if $NA_{30} = 14$, prob. of "less" becomes zero. Frequency of

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Once drift provides 6 or 7 altruists in a group of 15, there is a substantial probability of the number reaching ¹¹ ~~10~~ in at least one descendent group, through

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