Selective pressures for accurate altruism targeting: evidence from digital evolution for difficult-to-test aspects of inclusive fitness theory*

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Abstract

Kin selection theory predicts that evolution favors altruist genes that are more accurate in targeting altruism only to copies of themselves. We support this prediction by competing multiple altruist-targeting mechanisms that vary in accuracy in determining if a recipient carries a copy of the altruist gene. We compete altruism-targeting mechanisms that make energy donations based on (1) kinship (kin targeting), (2) genetic similarity at a level greater than expected for kin (similarity targeting), and (3) perfect knowledge of the presence of an altruist gene (Green Beard targeting). Natural selection favored the most accurate targeting mechanism available, once altruism *levels* were accounted for (Fig. 1). Our investigations also revealed that the Green Beard mechanism, originally invented as a hypothetical example of a perfectly accurate, cheater-proof system and subsequently discovered in nature, is in fact vulnerable to cheaters. Such cheaters prevent Green Beard targeting from outcompeting kin and similarity targeting (Fig. 1c). The reason is because Green Beard altruists donate to organisms that have Green Beards and make *at least one* Green Beard donation. There is thus an evolutionary pressure to donate only once, thereby qualifying to receive Green Beard donations while paying as little as possible. By increasing the number of donations necessary to *qualify* to receive Green Beard donations (T), we showed that organisms evolved to donate just above this threshold (Fig. 2). Green Beard targeting could only take advantage of its increased accuracy and outcompete kin and similarity targeting when we artificially set T to a high number, such as 100 (Fig. 1d). These results raise the question of how kin and similarity targeting differ from Green Beard targeting in being able to raise altruism levels despite the presence of cheaters. The answer is that they have built-in mechanisms that keep cheaters at bay (Fig. 3). We propose that Green Beard targeting can be augmented with a similar defense against cheaters if mutations that change the altruism level also change the marker (e.g., beard color), such that beard color reliably indicates the altruism level. This *Identical Beard Color* mechanism raises its altruism level automatically and outcompetes kin and similarity targeting due to better accuracy (Fig. 1e). Overall, our results confirm that natural selection favors altruist genes that are increasingly accurate in targeting altruism to only their copies. Our work also emphasizes that the concept of targeting accuracy must include both the presence of an altruist gene and the *level* of altruism it produces.

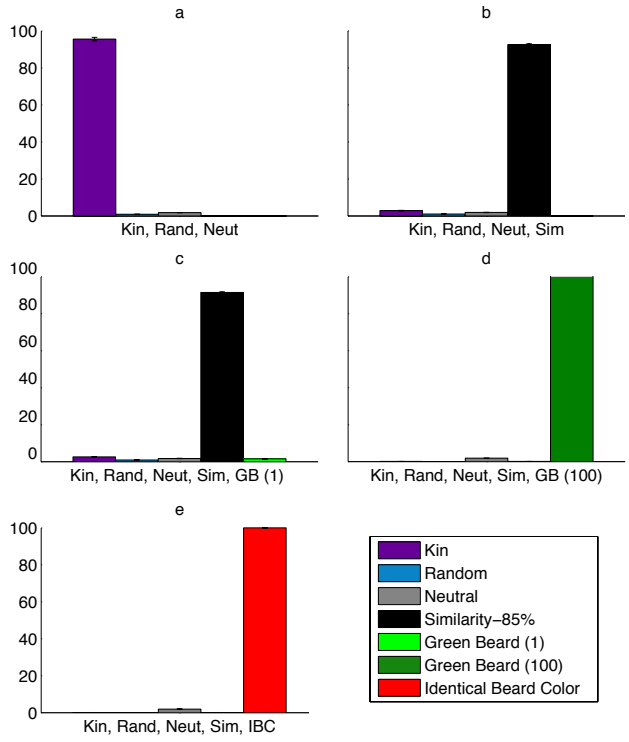

Figure 1: Evolved altruism levels for different targeting mechanisms. Plotted is the average number of donations made by last-generation organisms in 50 trials (+/- one standard error, often too small to distinguish). The maximum number of donations is capped at 100. (a) Targeting altruism based on kinship was selected for over two controls (targeting altruism at random, and a neutral instruction). (b) Targeting altruism based on high genetic similarity was favored over targeting based on kinship. (c) Selection did not favor targeting altruism via a Green Beard mechanism (with a threshold of 1) over kin and similarity targeting. (d) Selection favored a Green Beard mechanism with a threshold of 100 (the maximum number of donations allowed) over kin and similarity targeting. (e) Selection favors Identical Beard Color targeting over kin and similarity targeting.

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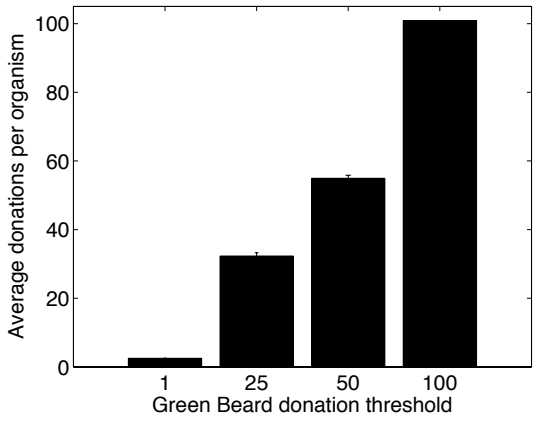

Figure 2: Evolved altruism levels for different Green Beard thresholds. Plotted is the average number of donations made per organism for different threshold values (T) of the donate-threshold-gb instruction (averaged from the final populations of 50 trials per treatment +/- one standard error, often too small to distinguish). Organisms evolved to perform enough donations to surpass the threshold and thus qualify to receive altruism, but did not perform substantially more than T donations.

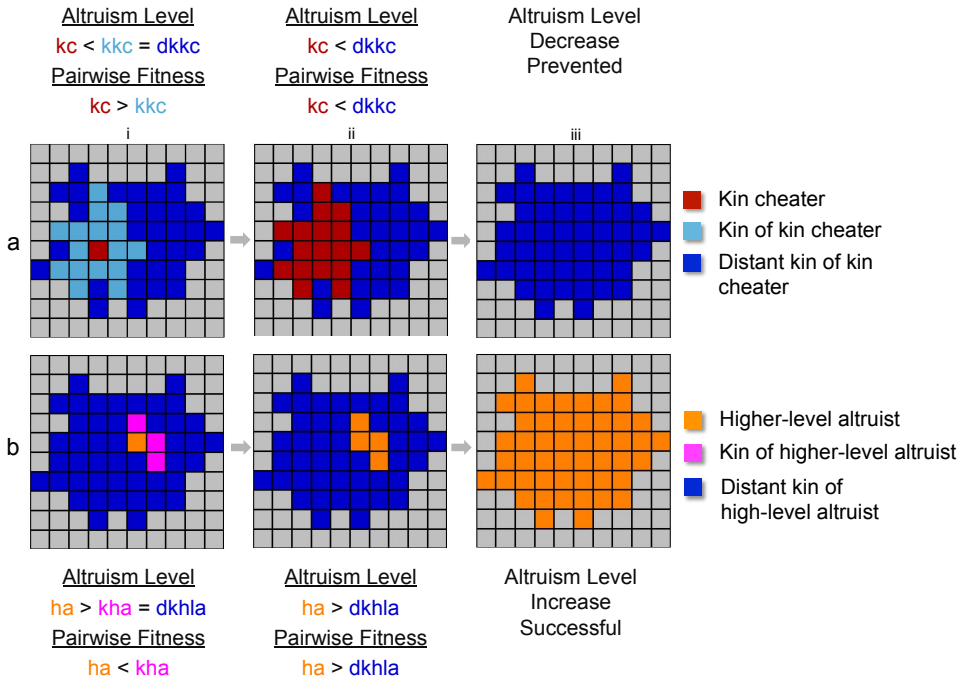

Figure 3: How kin and similarity targeting can evolve persistently high altruism levels. A thought experiment illustration showing how (a) kin-based altruism naturally thwarts kin-cheaters and (b) enables enduring increases in altruism levels. (a-i) Consider a group of related organisms that are altruistic to each other (blue and light-blue). One organism may mutate to be less altruistic, becoming a kin-cheater (red), but since only its closest relatives (light-blue) will consider it kin, only they will be altruistic toward it. (a-ii) The kin-cheater will tend to supplant its kin because it receives more donations from them than it gives. (a-iii) Once the kin-cheater has replaced those that considered it kin, the kin-cheater is left receiving donations only from other kin-cheaters. This group (red) will have a lower altruism level than their distant kin (blue) and will come to be replaced by them. (b-i) Now consider an organism (orange) that mutates to have a higher level of altruism than its ancestors (blue). Initially, it will be selected against because it gives more donations to those that it considers kin (pink) than it receives from them. (b-ii) If the less-altruistic kin of the higher-level altruist are killed off by drift, then the higher-level altruist and its offspring (orange) will have a competitive advantage over their distant ancestors (blue). (b-iii) While chance is required to start the process, once it has occurred there will be selection for the higher level of altruism. There are additional factors that complicate all of these fitness comparisons, but for clarity we have sketched these scenarios only in broad strokes.