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Levels of Selection in Synergy

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RESUMEN

La selección individual y la grupal se conciben usualmente como procesos evolutivos opuestos. Aunque ocasionalmente se reconocen casos de sinergia, su eventual importancia pasa más bien desapercibida. Sin embargo, la sinergia entre niveles es la explicación plausible para la evolución de colectivos como individuos de nivel superior en la jerarquía biológica, es decir, colectivos que se desenvuelven como unidades adaptativas, por ejemplo genomas y colonias de insectos sociales. La sinergia se basa en la supresión de la tendencia predecible de las unidades evolutivas a beneficiarse a expensas de otras unidades o del todo que contribuyen a construir. Ella explica plausiblemente la moralidad y la cooperación en humanos, cuyos grupos adquieren así el carácter de unidades adaptativas.

PALABRAS CLAVE: *selección grupal, selección individual, moralidad, altruismo vigilante, supresión del egoísmo, superorganismo, selección sinérgica.*

ABSTRACT

Individual and group selection are usually conceived as opposed evolutionary processes. Though cases of synergy are occasionally recognized, the evolutionary importance of synergy is largely ignored. However, synergy is the plausible explanation for the evolution of collectives as higher level individuals i.e., collectives acting as adaptive units, e.g., genomes and colonies of social insects. It rests on the suppression of the predictable tendency of evolutionary units to benefit at the expense of other units or of the wholes they contribute to build. It plausibly explains human cooperation and morality: the molding of human groups into adaptive units.

KEYWORDS: *group selection, individual selection, morality, policing-altruism, praise and blame, suppression of selfishness, super-organism, synergistic selection.*

I. BIAS TOWARDS CONFLICT

If selection operates at different levels, the evolution of traits that benefit groups but bring a disadvantage to individuals within groups is an open possibility. Such traits evolve when selection on groups overrides selection on individuals. The levels of selection conflict in this case. Surely, they need not conflict in every case and may occasionally operate in the same direction.

But in the case of altruism, multilevel selection theory assumes that conflict is unavoidable. This attitude is attributed to Darwin himself, who receives credit for fathering the insight that group selection overrides individual selection in the evolution of human morality [Ruse (1980); Richards (1987); Sober (1984), Wilson (1997); Sober and Wilson (1998); Gould (2002)].

Skeptics view group selection as a remote theoretical possibility. They dislike the thought that Darwin supported such a process in human evolution. Darwin spoke often ambiguously of selection of “communities” [Darwin ([1877] 1989)], meaning perhaps kin groups, and probably thinking of the breeders’ practice of selecting from kin as a successful proxy for individual selection [Darwin (1859), p. 237]. In chapter five of the *Descent of Man* he pointed to an individualistic explanation of morality in terms of what looked very much like reciprocal altruism one century ahead of Trivers [Trivers (1971)]. These facts are ammunition for those that remain unmoved by the well-known and apparently conclusive passages favoring group selection from that same chapter. Commenting on these passages, Williams argued that human social behavior does not require group selection to evolve, given the obvious advantages for an individual who “maximizes his friendships and minimizes his antagonisms” [Williams (1966), pp. 93f].

Both advocates and skeptics seem to agree on this point: group selection matters only when it overrides individual selection. It has occasionally been acknowledged, both abstractly [Wilson (1975)] and in relation to traits that are spiteful and benefit *groups* facing overexploitation [Wilson (1977); Gadgil (1975); Wade (1978)] that group selection can operate in synergy with individual selection. But regarding socially cooperative traits, recent discussions have often assumed that they are individually disadvantageous and that the levels of selection conflict in their evolution [Wynne-Edwards (1962); Maynard-Smith (1964), (1976); Williams (1966); Boorman & Levitt (1973), Wilson (1975), (1977)]. I here part ways with this orthodoxy and argue that, in regard to traits that benefit the group by being socially cooperative, individual and group selection can work together. Let me fleetingly point out that if the argument prospers, Darwin’s perceived ambiguity on the subject of human morality will turn out to be an artifact of contemporary bias. If we change our view of the relationship between levels of selection and admit the possibility of synergy for cooperative traits, Darwin’s advocacy of both individual and group selection for morality will no longer appear hesitant or inconsistent.

I proceed as follows. After exploring several types of synergistic processes¹ and identifying cooperative traits that evolve through synergy, I argue that higher-level individuals or entities with super-organismic features are best explained through them. In the evolution of collectives acting as units, suppression of social selfishness (in the biological sense of behaviors that have a negative effect on the fitness of others) leads to synergy, for individual selection remains operative favoring suppressor traits over selfish ones. Hu-

man groups fit into this pattern: they are held together by moral norms, which serve the suppression of selfishness through praise and blame. Through praise and blame, reputation and punishment of norm violators become a public issue. This is the clue to synergy: in virtue of publicly controlled access to the benefits of social life, socially selfish individuals cannot achieve higher fitness than those that enhance unity at the *group* level. The last section briefly discusses a place for culture and concludes.

II. TYPES OF SYNERGY: A PROVISIONAL TAXONOMY

The controversial views of Wynne-Edwards confined the discussion of group selection to the evolution of individually disadvantageous traits, where individual and group selection conflict. When survival depends on reducing numbers in the population, individual selection will not favor traits that altruistically decrease, for the good of the group, fertility or feeding rates in their carriers. Models were developed to show that, despite their individual disadvantage, such traits can evolve in populations structured in groups with positive assortment of altruists. Several authors endorsed those models, but they observed that selfish and spiteful traits also benefit groups facing the challenge of overexploitation [Wilson (1977); Gadgil (1975); Wade (1978)]. Individual and group selection synergize in these cases. Wilson (1975) plotted the possible interactions between group and individual selection on four quadrants of relative fitness. He explicitly acknowledged synergy in the area to the right of the “ $f_d = f_r$ ” line and above the “ $f_d + (N-1)f_r = 0$ ” line – the Group Selection (GS) line (see fig. 1).

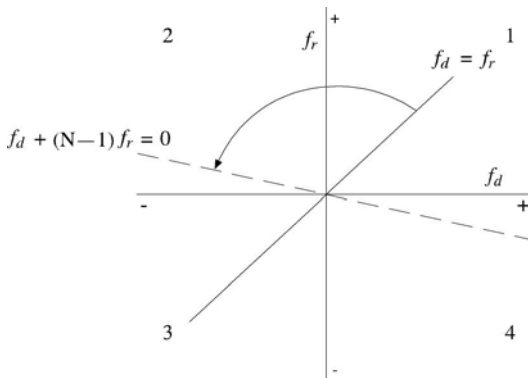


FIGURE 1. David Wilson’s (1975) 4 quadrants of relative fitness. Each point in the graph represents a new trait in a population. The X-axis gives its fitness-effects on donors (f_d); the Y-axis gives its fitness effect on receptors (f_r), in all possible combinations (+ or -). The solid line repre-

sents new traits that leave relative individual fitness unchanged; to its right, new traits are individually advantageous and are selected in *unstructured populations*. The dotted line represents traits that leave group-output unchanged. Points above it increase group-output; points below it decrease group-output. Both increase and decrease of group-output can be advantageous or disadvantageous, depending on the population challenge.

Note, however, that spiteful traits that benefit groups facing overexploitation are located *below* the dotted line: they increase group-fitness by decreasing group-output. For this reason, the legend to figure 1 proposes a re-interpretation of Wilson's graph: the line representing: $f_d + (N-1)f_r = 0$, – the GS line – shall be read as separating decrease (below) from increase (above) in group-output, not *fitness*. It is important to represent graphically increase and decrease in group-output. Group-fitness can be matched into both, depending on the circumstances. Populations are subject to two types of extinction threat: at high densities, they face extinction by overexploitation; at low densities, reaching a critical minimum size, they face the pressure of population bottlenecks [Gadgil (1975)]. Because of these two different selection pressures, group-fitness will be furthered sometimes by decrease and sometimes by increase in group-output. Therefore, synergistic selection happens for traits located both below and above the GS line, and to the right of the IS line (see fig. 2).

Picture populations as structured either into multigenerational [Maynard Smith (1964); (1976)] or trait groups [Wilson (1975); (1977)]. Suppose they experience either the pressure of overexploitation or the threat of extinction due to small numbers [Gadgil (1975)] and transmit these pressures down to its groups. Structured populations can effectively face any of the two threats either by self-serving or by altruistic traits. For example, the pressure for overexploitation can be met by cannibalism [Wade (1978)] on non-kin as resources decline; or, in a territorial species, by a trait that doubles the territorial demand for breeding, so that only half as much individuals enter the category of breeders [Gadgil (1975)]. *Bullies* with these traits gain in fitness by taking resources from others; and because they reduce group-output, they are also group selected; for groups without them will overexploit and decline and lose in the competition for proliferation. *Bullies* contrast with the traits mentioned by Wynne-Edwards, i.e., traits that protect the commons by depressing feeding or fertility rates in carriers, precisely because these are altruistic and bullies are not. Altruistic individuals decrease group-output by being *humble* and claiming less than others. Adapting Gadgil's terminology, bullies and humbles are *decadent* traits: they cope with the threat of overexploitation by reducing feeding or fertility rates either in themselves (humbles) or in others (bullies). The important difference between both is that *bullies* can be favored by selection at both levels, whereas *humbles* cannot.

Consider a trait favored by selection at both levels, but located above the GS line. Running speed, e.g., improves the ability of prey to escape predators. Traits like speed or height have been traditionally interpreted as

cases where the effect on group-output (i.e., fitness) is due to individual, not to group selection [Sober (1984)]. However, this interpretation is questionable. Speed is particularly important in gregarious species exposed to predation, where groups falling under a critical threshold go extinct. In a gregarious group, any individual's survival depends on the group's ability to avoid extinction. This ability depends on predation and recovery rates, which in turn depend on the frequency of fast individuals in the group. A single fast individual in a small group of slow individuals may avoid predation momentarily, but this hardly helps when every other group member has disappeared through predation. Though individual speed matters, it is not the fast individual alone, but the *group* with fast individuals that avoids extinction and determines whether speed is passed on to the next generation. The fitness of speed is an increasing function of both individual value and frequency. Therefore, the individual fitness value of speed is influenced by group level properties.

The examples of speed and cannibalism are usually interpreted as cases where increase in group fitness is only a *by-product* of increase in individual fitness [Okasha (2006)]. I think this is intuitively implausible for the examples mentioned. Take the case of speed. Unstructured populations are only under the regime of individual selection regarding speed. Individuals with the same speed will experience the same selection force. But in a population with group structure and the threat of small group extinction, two individuals with the same speed, i.e. a high value that gives them a good individual chance of surviving, will not have the same fitness across groups. Individual fitness in this case is strongly dependant on the differential survival of groups. The following table with fictional but realistic data illustrates the point.

| | HIGHEST SPEED (H) IN G_i (1 TO 10 SCALE) | FREQUENCY OF H IN G_i | H'S VIABILITY (v) INDEPENDENT OF SURVIVAL OF G_i | PROBABILITY OF SURVIVAL (g) OF G_i | H'S OVERALL VIABILITY (v.g) |
|-------------|--|-------------------------|--|--------------------------------------|-----------------------------|
| Group G_1 | 5 | 20% | .1 | .01 | .001 |
| Group G_2 | 5 | 80% | .1 | .01 | .001 |
| Group G_3 | 7 | 20% | .9 | .1 | .09 |
| Group G_4 | 7 | 80% | .9 | .8 | .72 |
| Group G_5 | 9 | 20% | 1 | .3 | .27 |
| Group G_6 | 9 | 80% | 1 | 1 | 1 |

TABLE 1: *Selection for running speed in a population structured into small groups.* Groups where the fastest individuals have a low value for speed (below predator speed) are likely to go extinct independently of their frequency in the group. Groups where the fastest individuals have a high value for speed survive depending on their frequency in the group. Groups with a high frequency have a good chance of surviving; but the chances are small for groups with a low frequency. Predator speed is held constant = 6.5.

In contrast to traits typical for bullies, speed increases fitness in carriers not by taking from others, but by positively improving the carriers' fitness. Traits like these can be labeled *egoistic*, because carriers do not give to others, although they do not take from them either. They increase in frequency through individual selection; and since *groups* of *egoists* are good at avoiding extinction as explained above, egoism is group-advantageous when groups face an extinction threat due to small numbers. *Egoists* contrast with *bullies* as noted, but they contrast more specifically with a set of altruistic traits that produce public goods, such as traits for warning cries, for resource notification, or for environmental manipulation that makes nourishment available for all neighbors of the same species. These altruistic traits are also group-advantageous: groups with *providers* of public goods will out-compete groups without them. Again, adopting Gadgil's terminology, egoists and providers are *pioneer* traits: they cope with the threat of extinction due to small numbers by increasing group output.

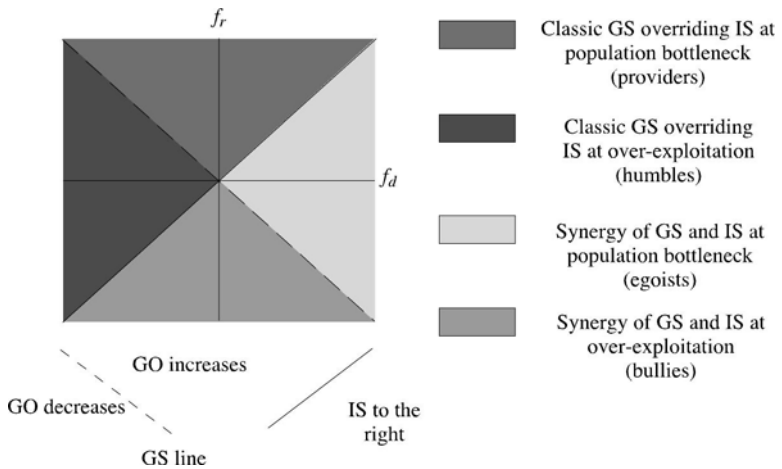


FIGURE 2. *Synergy and the 4 quadrants of relative fitness.* This graph takes into account that both increasing and decreasing group output (GO) can be beneficial for the group under different selection pressures. Areas of synergy are located both above (egoists) and below (bullies) the dotted (GS) line, and to the right of the IS line. The GS line has a -45° slope for ease of representation only

The partition into self-servers (*bullies* and *egoists*) and altruists (*humbles* and *providers*) is plotted by the individual selection (IS) line in figure 2. *Humbles* and *providers* are favored by classic group-selection overriding individual selection (located to the left of the IS line), whereas *egoists* and *bullies* instantiate currently (half)-acknowledged cases of synergy between individual and group selection (located to the right of the IS line). This partition cuts across the partition into decadents and pioneers, which is plotted by the GS line. *Decadents* decrease group output either through a self-serving or an altruistic strategy (*bullies* and *humbles* respectively); similarly, *pioneers* increase group output either through a self-serving (*egoists*) or an altruistic strategy (*providers*). Individual selection favors bullies and egoists and disfavors humbles and providers. When the latter characters are strongly altruistic (when their costs are greater than their benefits), they can only evolve through assortative grouping. Otherwise they disappear, for they indirectly create a new type: passive self-servers that do nothing, except receiving without reciprocating. These *free-riders* threaten to drive *humbles* and *providers* to extinction and force them to evolve protecting strategies that police

| POPULATION CHALLENGE | TYPES MEETING CHALLENGE | SYNERGISTICALLY SELECTED TRAITS | |
|-----------------------|-------------------------|---|---|
| | | SELF-SERVING | ALTRUISM + POLICING |
| OVERPOPULATION | DECADENTS | <i>bullies</i> : increase own f by taking from others | <i>humbles</i> +policing: decrease own f and police group membership |
| POPULATION BOOTLENECK | PIONEERS | <i>egoists</i> : increase own f without taking from others | <i>providers</i> +policing: increase others' f at own cost and police group membership |

TABLE 2: Traits with different social effects are synergistically selected, given the appropriate population challenge, in structured populations.

social interaction [Wilson (1977); Nunney (1985)]; especially when *free-riders* evolve into *fakers* in order to deceive altruists into giving. *Fakers* are similar to *bullies* because they increase their fitness by taking from others: the latter by force, the former by trickery. Now, though strong altruists can spread through fortuitous positive assortment, in which case group selection overrides individual selection; they can also spread by evolving ways of controlling assortment, e.g. through policing. Since policing frustrates exploitation by *bullies* and *fakers*, and opens opportunities for mutually beneficial interactions, *policing-altruists* do better than non-altruists at the individual

level without losing their basic pro-social character. Positive assortment of altruists through policing is favored by individual selection; additionally, groups of *policing-altruists* beat groups of altruists where policing is absent. *Policing-altruists*, therefore, evolve through synergy – selection favors them at both levels. This picks up an early suggestion by David Wilson in relation to human societies: they flourish on traits that are both individually and group advantageous [Wilson (1977), p. 182], an idea that apparently disappeared from his later views [Sober & Wilson (1998), pp. 146f; Wilson & Wilson (2007)]. Synergistic selection, in sum, favors *bullies*, *egoists* and two sorts of *policing-altruists* under the appropriate population challenge (see table 2 above). Policing-altruism is a cooperative trait favored by synergistic selection.

III. SYNERGY, POLICING AND SUPER-ORGANISMS

Altruism can evolve when fortuitous assortative grouping occurs. But given that altruism creates benefits, natural selection will favor individual traits that propitiate selective assortment in order to prevent exploitation. Policing is a well-documented trait that controls assortative grouping, creates groups as adaptive units and is favored by both within- and between-group selection [Rosas (2008)]. Policing-altruism lies thus at the origin of super-organisms, or collectives acting as units sharing the same evolutionary fate. Egbert G. Leigh (1977) was among the first to point out an example of this phenomenon. He argued that the evolution of honest meiosis in genomes requires policing by individual genes to reconcile individual and group interests. Honest meiosis, which sustains the genome as an adaptive unit, must be actively defended within genomes, for these suffer under the effects of inner conflict. Distorter alleles cause meiotic drive and treacherously increase their probability of being transmitted down the generations. When they succeed, it is only at the expense of the fitness of the genome (the group), for segregation distorters usually cause inborn diseases. Leigh reasoned that extinction impinges particularly on species suffering the deleterious effects of segregation distorters. This higher-level process selects against their spread. But why are some species less affected by segregation distorters? The answer is that meiotic drive is *additionally* countered by *suppressor* genes [Hurst *et al.* (1996)]. When this happens, two selection processes at different levels and in synergy favor suppressor genes and honest meiosis: a process of individual selection between genes within a genome, and a process of group selection between genomes. Leigh wrote: “species are favored where selection *within populations* works more nearly for the good of the species” [Leigh (1977), p. 4543, italics added]. Higher level selection synergizes with lower level selection for the suppression of selfish genes.

At the organismic level, policing-altruism is exemplified by worker policing in honeybees: a trait by which workers kill eggs laid by other workers [Ratnieks and Visscher (1989)]. Egg-laying workers benefit as *egoists* and as *free riders*: they increase their reproductive output and cheat on collective colony work. Worker policing counteracts selfish designs and consolidates the colony as a super-organism. Existing data from social insects confirm that effective policing predicts better than relatedness high levels of worker altruism (sterility): in a plot of data for different species, the percentage of reproductive workers *increases* as relatedness increases, but the same percentage *decreases* as effective policing increases [Wenseleers and Ratnieks (2006)]. Selection for policing occurs both between and within colonies: between colonies, because policing increases colony (group) output; within-colonies, because in colonies headed by several queens or by one multiple-mated queen, workers are more related to the queen's sons than to the other worker's sons. This relatedness structure selects for aggression and policing against egg-laying workers. It is only through the eggs of egg-laying workers that non-policing genes can enter and increase in the colony. But their eggs are eliminated through policing. Therefore, policing genes increase in frequency within the colony through policing.

In general, whenever a biological entity (gene, organism, etc.) acts to benefit at the expense of its same-level partners and of the higher level collective (organism or group), its disposition to harm them in this way can be addressed as selfishness in a social sense. Policing is any trait designed to suppress selfishness in this social sense. It takes the group to an equilibrium state where selection favors the evolution of group-benefiting traits both at the individual and at the group level. Suppression of selfishness has recently been adopted by evolutionary biologist Steven Frank as a general evolutionary principle promoting cooperation across all levels of biological organization, including human groups and social institutions [Frank (2003)].

Human institutions manage to reconcile group and individual interests by emphasizing the role of policing and reputation. Prominent Darwinians have more or less explicitly appealed to these factors when suggesting that some institutions apparently produce both individual and group benefits. Alexander (1987), pp. 169f referred to this phenomenon when commenting on Fisher's views on the reproductive effects of heroism, and specially in relation to Darwin's views on praise and blame as a means to enforcing compliance with moral norms against defectors. The idea that reputation effects can reconcile individual and group benefit should be kept in mind when reading Darwin's brief comments on praise and blame in chapter 5 of *The Descent of Man*. A similar support for synergistic selection results from the view that signaling a good reputation can promote altruism through sexual selection [Zahavi (1975); Miller (2000)]. Reputation effects illustrate the synergy between levels, but this is veiled by the dominant practice of opposing them.

Current theory has yet to fully realize the importance of synergistic processes in the evolution of socially cooperative traits.

IV. MORALITY AND POLICING

I echoed above the traditional practice in evolutionary biology of denoting social traits by analogy to human character labels and matched the traits so labeled into different types of synergistic evolutionary processes. Whenever altruism in its several forms (humbles, providers) is coupled with character discrimination, leading either to policing or simply to choosiness, it will evolve through synergy instead of through group selection overriding individual selection. The analogy is illuminating in both directions, for in return it highlights the role of policing and reputation assessment in sustaining human morality. Evolutionary biologists are in a good position to appreciate this fact. George Williams addressed it when he raised the issue whether a trait for maximizing friendships and minimizing antagonisms is a group adaptation. Obviously, if an individual has the ability to build friendships with cooperators and confine its antagonism to defectors, he or she will benefit individually. Moreover, if individuals with this trait form cooperating groups, these groups will be fitter than those otherwise formed. Williams, however, adopted at that time an unnecessarily hard line by denying the apparent synergy of individual and group selection for this trait:

I wish to consider an apparent exception to the *rule that the natural selection of individuals cannot produce group-related adaptations*. This exception may be found in animals that live in stable social groups and have the intelligence and other mental qualities necessary to form a system of personal friendships and animosities that transcend the limits of family relationship [...]. Simply stated, *an individual* who maximizes his friendships and minimizes his antagonisms will have an *evolutionary advantage* [...]. There is theoretically no limit to the extent and complexity of *group-related behavior* that this factor could produce [...]. Ultimately, however, this would not be an *adaptation for group benefit*. It would be developed by the differential survival of individuals [...] [Williams (1966), pp. 93-94, italics added].

However, if the trait: 1. benefits groups, 2. varies in frequency between groups, and 3. the variation causes groups to differentially proliferate or go extinct; then the trait is also a group adaptation. Williams accepts 1. So he would have to deny the conjunction of 2. and 3. However, evolutionary relevant competition between human groups that differ in the relevant respect is a plausible and commonly made assumption [Alexander (1987); Soltis *et al.* (1995); Sober and Wilson (1998)]. Moreover, its plausibility increases when taking into account that norms contribute to partition human populations into

groups with internal cohesion and boundaries sustained precisely through the influence of norms. This leads directly to synergistic selection. Synergistic selection promotes a full understanding of the emergence of higher-level individuality. For the capacity of a collective to act as an individual depends on defeating subversion from within by making group-advantageous traits also individually beneficial. Policing is the clue to the evolutionary process of synergy, where altruism no longer requires group selection overriding individual selection.

An evolutionary perspective encourages us to see policing and the active suppression of social selfishness as traits that are especially relevant for morality. Most evolutionary proposals have highlighted moralistic discrimination and aggression against defectors. This may be controversial among philosophers, but it is hardly an arbitrary stipulation. Praise and blame was, for example, Darwin's way of acknowledging reputation assessment and punishment as essential to the moral domain. Altruistic punishment is the contemporary version of the same attitude [Fehr and Gächter (2002)]. Even Trivers' reciprocal altruism [Trivers (1971)] contains it more or less explicitly. The common rationale underlying these proposals is the blending of a group-benefiting character with a trait labeled "policing". At any level of biological organization, it often happens that group-benefiting characters, i.e., traits that protect the commons or provide a public good, are such as to create total benefits that exceed the total costs (the two-person PD can be interpreted as a public goods game with $n=2$). But the returns are profitable for the individual only when the costs are distributed fairly, or nearly so, among beneficiaries. Except for the cases of mutualism among non-relatives, where benefits to others are side effects of benefits to self, and cases where parceling the good to be exchanged makes cheating difficult [Connor (1995); Clements and Stephens (1995); Dugatkin (2002); Stevens et al. (2005)], free riders and bullies make the evolution of cooperation through individual selection implausible. The evolution of cooperation depends then on the evolution of mechanisms that protect against those characters. The challenge is to avoid being tricked into carrying the burden of investment beyond what is individually profitable. The solution is to evolve "policing" traits, i.e., traits that protect individuals against exploitation and make moral behaviors individually advantageous within the group.

Let us assume that discrimination, choosiness and punishment of defectors are traits that achieve the required protection, as some evidence indicates [Alexander (1987); Boyd & Richerson (1992); Boehm (1999); Milinski et alii (2002), Panchanathan & Boyd (2003), (2004); Fehr and Gächter (2002); Fehr and Fischbacher (2004)]. Let us assume further that punishment of defectors avoids the second-order free-rider problem [Rosas (2008)]. If morality is thus rendered individually advantageous, the next step is to avoid thinking that group selection has thereby been rendered superfluous. Moral traits are, after

all, (mainly) traits for benefiting the group. Groups of altruists with such traits outcompete not only groups of egoists, but also groups of altruists who are vulnerable to free riders and bullies. What emerges is the synergy of group and individual selection. Altruists that practice praise and blame evolve through synergy. They police social interactions and control assortative grouping [Rosas (2008)]. The fitness consequences of such control are apparent. Control allows altruists to choose partners for cooperative ventures, rewarding moral characters by granting them access to cooperative benefits, and either publicly shunning or directly punishing socially selfish individuals. By controlling access to the benefits of cooperation, morality forces social selfishness into the lower fitness rank and tips the balance of individual selection towards compliers with moral norms.

V. CONCLUSION: CULTURE, ALTRUISM AND THE SUPPRESSION OF SELFISHNESS

Moral behaviors are here depicted as biological adaptations. Couldn't they be acquired cultural practices instead? Cultural transmission could spread morality within the group: an individual can act morally, not from instinct, but by imitating successful and socially approved traits. Thus, individuals do not need biological pre-programming; sensitivity to praise and blame may lead them to behave morally. The only condition is that the group approves moral behavior.

However, we do not need to deal with culture and biology as rival or mutually exclusive explanations. Assume, as e.g. Darwin did, that the practice of approval/disapproval (praise and blame) is itself a biological adaptation, acquired by "primeval man at a very remote period". Castro and Toro (2004) have argued convincingly that this practice is required to enhance imitation and turn cultural transmission into an evolutionary successful trait. Apprentices can imitate all sorts of behaviors including maladaptive ones. Therefore, parental or social approval/disapproval is required to constrain the possible uses of imitation. Innate dispositions both for imitation and for approval/disapproval can be conceived as biological scaffolds that make cultural transmission possible and beneficial for individuals and groups.

However, a similar difficulty arises in regard to the uses of approval/disapproval. They are beneficial for individuals and groups when used to socially enforce norms that promote group welfare [Darwin (1877)], e.g., norms that prohibit free-rider behavior in social dilemma situations. But we often see that praise and blame also promote norms that deviate from the general good, in much the same way as an apprentice can imitate maladaptive behaviors. Food taboos are an example [Darwin (1877)]. Given praise and blame, and punishment, conformity to these norms is the rational and adaptive thing to do [Boyd & Richerson (1992)]. Therefore, it would be adaptive

to have a biological pre-programming for norms that prohibit free-rider behavior in the provisioning of genuine public goods, at least in some individuals. These can then shape the social environment to influence the behavior of others – a sort of niche construction. The instinctive demand for the good of the group will thus place a significant constraint on the uses of praise and blame; and a healthy one, for it will tie public opinion and social sanctioning to policing and suppressing selfishness in social dilemma situations.

Praise and blame are part of the biological scaffold for cultural transmission. When they promote norms that solve social dilemmas, they transform group-benefiting behavior into an individually advantageous trait. These norms are mechanisms adapted for suppressing, in self and in others, incentives for social selfishness (gaining benefits at the group's expense). They facilitate the spread of altruists through individual competition *within* a group. In turn, groups where free riding is suppressed will enjoy an advantage in competition, producing a notable group selection effect.

Traits that combine group-benefiting behaviors with the control of assortative grouping, and with the discrimination and punishment of defectors introduce an important novelty in the evolutionary taxonomy of social behaviors. They include traits for suppressing the effects of distorter alleles in unfair meiosis [Leigh (1977), Frank (2003)], for removing worker-laid eggs in honeybees (*Apis mellifera*) [Ratnieks and Visscher (1989)] and human morality [Rosas (2008)]. This category of altruism has been designed to eliminate subversion from within and enhance groups acting as adaptive units. It provides a basis for understanding super-organisms: instead of saying that individual selection has been suppressed within them [Wilson & Wilson (2007), pp. 339, 342], we are entitled to say that super-organisms emerge when individual selection positively favors, in synergy with group selection, combinations of altruism and policing. Attention to synergistic selection allows the following amendment to Wilson & Wilson's formulation of Darwin's original insight [Wilson & Wilson, (2007), pp. 335, 345]: "Policing-altruism beats selfishness both within and between groups".

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NOTES

¹ I use "synergistic processes" or "synergy" only to label a process where both individual and group selection favor group-benefiting traits, and in particular socially co-

operative traits. Peter Corning has called attention to the fact that most cases of cooperation in nature are not built on biological altruism, but on win-win interactions. He uses the term synergy to denote this type of interactions, which produce benefits for both individuals and groups [Corning (1997)]. Traits for these interactions coincide with weak altruistic traits in Wilson's (1979) sense.

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