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A New Definition of Evolutionary Altruism*†

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진화론적 이타성의 표준적 정의는 그것을 구성하는 용어들에 있는 일상어적 잔재에서 유래하는 몇몇 심각한 결점이 있다. 이 논문에서 나는 혈연 이타성 이론, 호혜 이타성 이론 그리고 다-수준 선택 이론과 같은 주요 이타성 이론의 성과들에 입각하여 새로운 정의를 시도한다. 새로운 정의는 재생산의 간접성을 주요 종차로 삼는데, 그것은 재생산의 간접성이 이들 세 이론에서 공통적으로 제시되는 이타성 진화 기체의 핵심이기 때문이다. 새로운 정의는 직접-재생산 중심주의라는 다윈적 유산을 극복할 뿐 아니라, 선택과 진화에 새로운 접근로를 열어줄 수 있다고 기대된다. 그 새로운 접근로는 내가 이중-재생산 접근법이라고 부르는 것이다. 이타성의 진화를 위한 선택력을 직접적, 간접적, 그리고 환경적 요소로 삼분함으로써, 이 새로운 접근법은 개체주의와 다-수준 선택적 접근법에 대한 설득력 있는 대안이 될 수 있다.

【주요어】 생물학적 이타주의, 종차, 메타-형질, 간접성, 이중-재생산 접근법

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1. Introduction

One special feature of evolutionary biology seems to be the fact that it depend upon words from everyday life for their theoretical terminology much more than other precision sciences. Such words are capable of both revealing and obscuring important insights:

> On the one hand, we wish to understand how behaviors that we describe with familiar words evolved, and this effort is facilitated by using familiar words in evolutionary theory. On the other hand, familiar words usually have a variety of meanings that are surrounded by a dense atmosphere of values and associations. They lack the precision, uniformity, and neutrality that scientific terms are supposed to have (Wilson and Dugatkin 1992, 29).

The term 'altruism' in evolutionary biology is a good example of such words.[1] As Alexander Rosenberg points out, "the biological problem of altruism is vexed by a prior terminological controversy" (1992, 19).[2] But, the problem is, I think, not just terminological, it is conceptual, too. I believe that such controversy derives from the fact that definition of altruism is midway between everyday and scientific parlance. The remnant of everyday parlance, which is basically human-centric, disturbs

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[1] The word 'altruism' is known to have been coined first by French sociologist Auguste Comte in his Catechisme Positivisite. He coined it using a French word 'autre', which in turn derives from Latin word 'alter', 'other' in English, as an opposition to ethical 'egoism' (Wikipedia). 'Aaltruism' was first referenced in biology by Hamilton (1963). Yet the word became famous mostly due to Wilson (1975), in which he regards altruism as the "central theoretical problem of sociobiology" (p. 578).

[2] Kerr and Godfrey-Smith also point out the same problem; "the evolution of altruistic behavior has been a reliable source of controversy. Part of the controversy is a result of different definitions of the word" (2002a, 508).

objective and clear understanding of altruism. The motivation of this paper is simple: Let's redefine biological altruism more scientifically. In order to enter the discussion concerning altruism and get some insight, we may need to borrow words from daily life. However, once we reach a good point, we should kick away the ladder of everyday parlance.

It is known that the standard definition of biological altruism is paradoxical, because it cannot evolve by definition. Convincing theories such as kin selection theory, reciprocal altruism theory, and multi-level selection theory were suggested to solve this paradox and have been established successfully. If the paradox has been solved successfully, the original paradoxical definition of altruism should be redefined properly in such a way as to show "precision, uniformity, and neutrality" as much as possible. In this paper, first, I will summarize major shortcomings of the standard definition of biological altruism. Then, I suggest a new definition of biological altruism that is rigorous and free from everyday parlance. For it, I analyzed major theories of biological altruism, and suggest the *indirectness of reproduction* as the core differentia common to all of their definitions of altruism. Some advantages of the new definition will be presented also. Finally, I argue that the new definition will open a new approach to selection and evolution, what I call *the dual-reproduction approach.* In the argument, I will claim that by dividing the selective force for the evolution of altruism into direct, indirect, and environmental parts, the new approach can be a convincing alternative to both the individualist and multi-level selection approaches.

2. Conceptual problems of evolutionary

altruism

The problem of biological altruism is known to have a long history back to Darwin.[3] Two basic ideas came from Darwin's discussion on the problem. One is that altruism is the tendency or instinct to behave in such a way as to increase the fitness of the society or other members of the society at the cost of the fitness of the agent. The other idea is that the cost of an altruistic agent's fitness can be compensated by the flourishing of the communities with the greatest number of altruistic members. The first idea became the standard definition of evolutionary altruism, while the second idea became a key to solution to the problem of biological altruism.[4]

As is well known, since the standard notion of biological altruism is defined with fitness as one of its crucial intentions, it is quite different from everyday concept of the word.[5] In everyday parlance, an action

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3) Cf. Darwin (1859, 356-358), Rosenberg (1992), and Darwin (1871, 82-84, 87, 93).

4) Some of the examples of Darwinian definition of biological altruism are these; "any case where an animal behaves such a way as to promote the advantage of others of the species not its direct descendents at the expense of its own" (Hamilton 1963), altruistic behavior is defined as "behavior that benefits another organism, not closely related, while being apparently detrimental to the organism performing the behavior" (Trivers 1971), altruism is "self-destructive behavior performed for the benefit of others" (E. O. Wilson 1975), a behavior is altruistic "whenever the behavior increases the reproductive fitness of another at the expense of one's own reproductive fitness" (Rosenberg 1992), a behavior is altruistic "just in case it raises the expected reproductive success of an organism other than the agent, while diminishing the expected reproductive success of the agent (Kitcher 1993). "Individuals who increase the fitness of others at the expense of their own fitness are altruists, regardless of how, or even whether, they think or feel about the action" (Sober and Wilson 1998).

5) The following figure shows the standard comparison between ordinary and biological senses of altruism (cf. Sober 1988, Rosenberg 1992):

would be called 'altruistic' only if it was done with the intention of helping others, and thus, 'altruism' and its associated words are defined on the basis of actor's motives as well as on the basis of effects. But in the biological sense, it is only the consequences of an action for reproductive fitness that determines whether the action counts as altruistic, no matter what the cause of the action would be. Because of the removal of the etiological or intentional element, "evolutionary altruism does not imply vernacular altruism, nor does vernacular altruism imply evolutionary altruism" and that "selfish actions can sometimes include motives that involve the welfare of others" (Sober 1988, 97, 78). However, there still remain some words with everyday parlance in the standard definition of biological altruism such as 'cost', 'benefit', 'sacrifice', 'advantage', 'expense', 'for', etc., which are basically human-centric. Behind these words, there also remains a human behavioralist element of give-and-take. The amalgamation of scientific and everyday parlance is, I think, the main source of the confusion and misunderstanding in the discussion of biological altruism.

Above all, there is the problem of "paradox of (biological) altruism."[6]

	Ordinary(vernacular) altruism	Evolutionary altruism
Definition	Benefit other at the cost of an agent	Increase other's fitness at the cost of an agent's fitness
Objects	Mainly higher animals including human beings	All organisms
Motivation	Mind(Intention, tendency, desire …) - essentially psychological	Traits or genes - essentially reproductive
Criterion of altruism	non-comparative	essentially comparative (=depending upon relative fitness)
Measure	Mental state of agents	Fitness calculation of behavior
Effects of behavior	Decrease of an agent's interest	Decrease of an agent's fitness
	Increase of other's interest	Increase of other's fitness

[6] I found the expression "the paradox of altruism" in Sesardic (1995).

Evolutionary altruism is a paradoxical pattern of behavior, because the definition of altruism itself does not seem to allow the trait or genes that cause the altruism to be selected and evolve. According to the standard definition, apparently "altruism is the very opposite of the survival of the fittest" (Sober and Wilson 1998, 19: their expression but not their idea), and so all solutions to the problem of evolutionary altruism "are designed to take the altruism out of altruism" (Trivers 1971, 35). From the standard definition of altruism came out the standard formulation of the problem of altruism: "How can altruism, which by definition reduces personal fitness, possibly evolve by natural selection?" (Wilson 1975, 3). In this regard, the standard definition should, I think, be used only temporary and heuristic ladder via which we can find a proper definition and explanation for the phenomenon of evolutionary altruism. Once the goal is successfully achieved, the heuristic ladder of everyday parlance should be thrown away. Since several convincing solutions to the problem of the paradox have been established successfully, it is the time for us to suggest a proper definition of biological altruism.

The paradoxical feature of the standard definition is, I think, one of the byproducts of its main flaw, viz., the fact that it does not have an appropriate 'specific difference (differentia)' which is necessary for the definition of crucial terms in science. The bold project of some sociobiologists to reduce ethics into biology is another byproduct of the flaw. The flaw can be confirmed by the fact that the standard definition of altruism is not only too broad but also too narrow. If an action is altruistic "when it increases the fitness of others and decreases the fitness of actors," any action that reduces an organism's fitness, including masochistic action such as "biting off one's leg," will count as altruistic (Gildenhuys 2003, 40). For such action can reduce the fitness of the agent and increase the fitness of its competitors. To count as altruistic, an action must do more than simply alter the relative fitness of the agent and its recipients. More generally, the standard definition does not exclude from its extension the behavior that increases the fitness of others at the cost of the fitness of an agent but is not selected. So, the standard definition of biological altruism is too broad. It is also pointed out that the ambiguity of 'fitness' is another source of the conceptual confusion of biological altruism. The meaning of fitness depends upon the conceptual frames we choose. Altruism in a local group may turn out to be selfishness in a global population. Also in these days we have several versions of fitness, such as classical fitness, inclusive fitness, and gene fitness (See Wilson and Dugatkin 1992). It seems to me that there must be some sort of meta-behavioral criterion or evolutionary force beyond the relative fitness.

On the other hand, it may be somewhat uneasy for our intuition to regard such a case as the decrease of virulence in the Myxoma virus (Lewontin 1970), the less successfulness of predators, or a special morphology of a mass of trees that is helpful for them to compete for light (Maynard Smith 2002) as altruism. Although they are certainly examples of biological altruism, it is not easy for our intuition to understand in what sense they are altruistic. In order for the concept of evolutionary altruism to cover various kinds of organisms ranging from trees and viruses to human beings, it should be defined with more general and rigorous words that are based upon some sort distinction between traits for behavior and a meta-trait for the traits.

There is one more flaw in the standard definition of biological altruism which, I think, would be more fundamental than the others. The Darwinian concept of biological altruism seems to be based upon an unjustifiably narrow scope of selection that may be called *direct-*

reproduction stand. I suspect that such narrowness is related with Darwinian point of view for evolution, viz., *from-the-selected,* which is comparable to *from-the-selector* (nature). From the view point of nature, what is important is not each individual organism but a certain trait that has been selected through that organism, and nature does not care who has it and how it is reproduced viz., directly by an organism itself or indirectly via other organisms. Selection can occur cross or over individuals as well as among individuals. Richard Dawkins calls such a Darwinian view point an "individual-centered stand" (1982, 6). Since Darwin considered evolution by direct reproduction as the only or at lease main mechanism of evolution, I like also call it a *direct reproduction-(centered) stand.*

These shortcomings of the standard definition of evolutionary altruism will become clearer through the analysis of main theories of biological altruism so far established. I will analyze the definitions of biological altruism in kin-selection theory, reciprocal altruism, and group selection theory in the next section, and make good use of the results as the basis for a new definition.

3. 'Altruism' in theories of altruism

The first solution to the problem of biological altruism is known to be the classical group selection theory suggested by Darwin. He argued that though altruistic individuals do worse than selfish ones in the same group, the groups of altruists out-compete groups of selfish organisms, then altruism can flourish. However, the classical group selection theory had been put aside a little bit from mainstream evolutionary biology since the 1960s, due mainly to G. C. Williams (1966)'s argument and John Maynard Smith (1964, 1976)'s proof against group selection. Alternative solution was suggested principally by W. D. Hamilton (1964). It is the "kin selection theory." Its basic idea is straightforward. A gene which codes for behavior that is costly to the individual who carries it, but benefits his genetic relatives will increase in frequency by natural selection, because the individual's relatives are likely to carry copies of the gene in question themselves. Altruism can evolve so long as the cost incurred by altruists is offset by a sufficient amount of benefit to sufficiently closely related relatives (Hamilton's Rule). He coined "inclusive fitness" to calculate the cost and benefit. It combines the organism's fitness with the fitness contribution (adjusted by some coefficient of relatedness) of each of its kin. "Not only will taking care of direct offspring be an adaptationally optimal strategy for individuals, but so will taking care of kin in proportion to their consanguinity" (Rosenberg 1992, 23; my emphasis). Hamilton's argument can be analyzed as follows:

1) Nature selects for the strategy that leaves the largest number of copies of the gene that codes for the strategy.
2) In the case of sexually reproducing organisms there are two such strategies:
    - A strategy that produces an organism's own offspring: Selfish traits are all traits whose selection and evolution is, by definition, possible only by direct reproduction of itself.
    - A strategy that produce kin's offspring instead of its own offspring. Altruistic traits: all traits whose selection and evolution is, by definition, possible only by the aid of indirect reproduction via kin.
3) The efficiency of each strategy is measured by an organism's individual fitness and inclusive fitness respectively
4) Inclusive fitness is the combination of the organism's individual

fitness and the fitness contribution to kin.
5) Accordingly nature will select for inclusive fitness.
6) If nature engages in kin selection by selecting for inclusive fitness, altruism may emerge as an adaptive strategy for an individual that is part of a group of kin.
7) Therefore, altruism can evolve.

Kin selection theory has been widely accepted among evolutionary biologists as the most plausible way of explaining the evolution of altruism from a Darwinian perspective (Okasha 2002, 139). The core of kin selection mechanism is the idea that an individual is often able to promote its own generic future indirectly via kin that carry copies of its genes. The idea opens the way to evolution by *indirect reproduction*7) and thus to dual-reproduction mechanism, which again opens the way to a new point of view for viewing selection and evolution that is different from the individual-centered stand. It is the view point of the selector, viz., nature. Nature has no reason to show general or inherent favoritism toward direct reproduction for the evolution of traits. In kin selection theory, what is selected is a certain trait and individuals that share the trait, which I call *the cross-individual stand*. Yet it is not a trait's or gene's point of view as Dawkins (1976) insists, because traits and genes cannot have eyes and thus points. Being entities that follow

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7) There is an article where the word 'indirectness' is intentionally used to explain biological altruism. Peter Gildenhuys insists as follows: "In Sober and Wilson's model, altruistic genes indirectly cause the replication of altruistic genes because by and large altruists are grouped with other altruists. … altruistic genes must replicate themselves indirectly by benefiting other altruist. Altruistic behaviors are ones that increase fitness indirectly, through benefiting other individuals within a population who share an altruistic disposition" (Guildenhuys 2003, 39, 40, 47; my italics). However, he did not go further. He did not use it to redefine altruism nor to suggest a new perspective.

biochemical mechanisms blindly, they are also a sort of 'the selected' like individuals and groups. The gene's point of view is in fact nothing but the nature's point of view.

If we use some words with everyday parlance, kin altruism would be defined roughly as follows:

> **Definition 1:** Kin altruism is a tendency of behavior caused by the trait (following the strategy) that promotes kin's reproductive future instead of one's own reproductive future

However, this definition is incomplete, for if the kin do not have the same trait that causes the same tendency, altruism cannot evolve. What is crucial in kin selection is not mere kinship or genetic relatedness itself but sharing the same altruistic trait. Terms like "promote," "future," and "instead" should be changed by other more rigorous words. Since the core of kin selection mechanism is the idea that the agent pursues indirect reproduction of the trait that is responsible for the altruism via kin, we can redefine altruism in kin selection more rigorously as follows:

> **Definition 2:** Kin altruism is a tendency of behavior caused by trait that reproduces themselves indirectly via kin that have the same trait.

The tendency of taking care of one's sisters (instead of one's own offspring) is altruism, for it is a tendency of behavior caused by the trait that reproduces themselves indirectly via sisters that might have the same trait. There is inevitable circularity in this definition, because the term "trait" is nested in the same term "trait." We cannot go further into the meaning of the "trait" to get more precise definition. The only meaning that is clear in the definition is that kin altruism is related with the indirectness of reproduction (replication) among kin. The trait responsible for altruism is not the sort of trait that causes various sorts of ordinary behavior, rather, it is a sort of meta-trait that causes only indirectness of reproduction. It doesn't care about what sort of behavior can do that job.

Kin selection theory is applicable only to altruism among members of kin. There are other sorts of altruistic organisms that provide resources at their own expense to non-kin organisms. They are reciprocal altruism and genuine altruism. Following Frank (1988, 37), I use "genuine altruism" to represent altruism free from kinship and reciprocity. The term 'reciprocal altruism' was introduced as an explanation for non-kin altruism by Robert Trivers (1971). The basic idea is simple. If an organism's altruistic behavior is expected to be repaid by its recipient at least more than the cost in the future, it is adaptationally beneficial for the organism to act altruistically, and thus the tendency to act altruistically will be selected. It is more beneficial for both of us to let you scratch my itching back as a repay for my scratching your itching back than scratching each one's own itching back separately, given that we should live together for a long time. It is because scratching my own itching back is harder than scratching other's itching back. Trivers made a mathematical model to explain cooperative behaviors based on game theory. Trivers's model was developed into an evolutionary game model by Hamilton and Axelrod (1981). Their model showed that, under certain circumstances, the optimal strategy for an individual is "tit-for-tat (TFT)" strategy, which says cooperate in game one, and then in each subsequent game do what the other player did in the previous game. TFT was proven to be an optimal strategy for maximizing the individual's payoff and "an evolutionarily stable strategy" (ESS: Maynard Smith 1982), and shown to be applicable to a more complex situation where more than three participants are involved (Rapoport 1991).

What does altruism mean in reciprocal altruism? Quite different from kin altruism, reciprocal altruism is not altruism in proper. As Wilson and Dugatkin show, reciprocal altruism is rather cooperation, for both participants benefit from their behavior. "TFT is a strategy that sacrifices current-round opportunities to free-rider for future benefits from reciprocation by the other player" (Rosenberg 1992, 27). So, reciprocal altruism is a sort of "conditional altruism" (Sober 1993) or "a variety of Darwinian selfishness" (Sober 1988). The core mechanism of reciprocal altruism is that under certain circumstances, by promoting each other's reproductivity reciprocally, each individual can promote one's own reproductivity more optimally than when each one promote one's own reproductivity.

If we use some words with everyday parlance, reciprocal altruism would be defined roughly as follows:

> **Definition 3:** Reciprocal altruism is a tendency of behavior caused by the trait that promotes the other's reproductivity only when it also promotes one's own reproductivity no less than that.

Though partly, each one's altruistic trait is reproduced by each other's altruistic trait. Yet, since the final goal of cooperation is the optimization of one's own reproduction, reciprocal altruism is different from other altruism. Nevertheless, it is a sort of altruism, because each individual's reproduction is enabled by the other rather than by itself, more precisely, because the trait that causes cooperative behavior can be replicated indirectly via cooperative other's reproduction. However, this definition is also incomplete, for if the other(s) does not share the same trait that causes the same tendency, altruism can not evolve. The other's cooperative behavior might occur by chance or by some other reasons, such as culture. We can redefine reciprocal altruism more rigorously as follows:

> **Definition 4:** Reciprocal altruism is a tendency of behavior caused by the trait that reproduce themselves by mutual indirect-reproduction among crossed individuals that have the same trait.

There is the same sort of circularity in this definition, because term "trait" is nested in the same term.[8] For the same reason, we cannot go further to get more precise meaning. The only meaning that is clear in the definition is that reciprocal altruism is related with the mutual indirectness of reproduction. Again, the trait responsible for altruism is a sort of meta-trait that causes only indirectness of reproduction.

Let's turn to the group selection theory. "If group selection was an engine for controversy over the past 35 years, the subject of altruism was the fuel" (Kerr and Godfery-Smith 2002, 478). The debates between individual selectionists and group selectionists has dominated the discussions on altruism since early 1990's (e.g., a serious of debates concerning Kerr and Godfery-Smith 2002). At the heart of the debates, there has been Sober and Wilson (1998)'s new group selection model. The account they set off about how altruism evolves has shed a new light on understanding biological altruism.

A brief summary of their theory is this (Sober and Wilson 1998, 24-5; cf. Okasha 2000's summary). Imagine a population containing two types

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[8] A good evidence for the circulation is this: "Robert Trivers' concept of reciprocal *altruism* is founded on the idea that benefits to others at the expense of the self can be evolved if the actor is repaid by the recipient's *altruism* in the future" (Wilson and Dugatkin 1992, 32; my italics). Here, 'altruism' is nested in 'altruism'.

of organism, altruistic and selfish. For simplicity, reproduction is assumed to be asexual—the offspring of altruists are altruists, and similarly for selfish organisms. The population is subdivided into two groups. Group one contains mostly altruists with a few selfish; group two contains mostly selfish with a few altruists. Within each group, altruists are lower in fitness than their selfish counterparts by definition. An organism's fitness depends not only on whether it is altruistic or selfish, but also on which group it is in. The fitness of a group that contains a higher frequency of altruists is higher than that of the other group. If the parameters are chosen properly, "the differential fitness of groups (the force favoring the altruists) can be strong enough to counter the differential fitness of individuals within groups (the force favoring the selfish type)" (Sober and Wilson 1998, 26). Then, the global relative frequency of altruists will increase even though the local relative frequency will decline within each group in the second generation. In such a circumstance, if groups should breakup, merge into the global population, and then reform new groups periodically to prevent the selfish alleles spreading to fixation within each group, altruism can evolve.

As I mentioned, by 'genuine' I only mean the fact that the altruism is free from either kinship or reciprocity. The core mechanism of the evolution of genuine altruism seems to be that "the an individual disadvantage of behavioring altruistically is offset by the fact that altruists are grouped together, and thus tend to be the recipients of each others' help" (Okasha 2000, 139). However, being recipients of each others' help is not a necessary condition for genuine altruism to evolve. As we can see at the case of neuters of social insects and brain worms (Sober and Wilson 1998, 27-30), an altruistic individual's within-group fitness can be 0. So, kin and genuine altruism can evolve without being rewarded by other altruists, and therefore reciprocity is not necessary for kin or genuine altruism to evolve. What is crucial for genuine altruism to evolve is that sufficient number of other altruistic organisms (recipients of altruistic behavior) should be concentrated in certain groups periodically.9) The degree of being recipients of each others' help among altruists represents only the degree (force) of altruism. If we use some words with everyday parlance, genuine altruism would be defined roughly as follows:

> **Definition 5:** Genuine altruism is a tendency of behavior caused by the trait that promote the reproductivity of others within a group at the cost of one's own reproductivity.

For the same reason as above, we can redefine genuine altruism rigorously as follows:

> **Definition 6:** Genuine altruism is a tendency of behavior caused by the trait that reproduce itself indirectly via others in a (non-kin) group that have the same trait.

There is the same sort of circulation in this definition.10) The only meaning of genuine altruism is that it is related with the indirectness of reproduction among a (non-kin) group. Again, the trait responsible for

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9) The fact that the secret of the evolution of altruism consists in "like should attract like" was hinted earlier by Hamilton (1963, 355). He said, "The only escape from this conclusion would be some kind of periodic reassortment of the tribes such that by chance or otherwise the altruists become re-concentrated in some of them."

10) Here is an example: "an altruistic trait is one that is deleterious to the individual possessing *it* but advantageous for the group in which *it* [the individual possessing *it*] occurs" (Sober 1993, 90; my italics). The term "altruistic trait" is nested in itself.

altruism is a sort of meta-trait that causes only indirectness of reproduction, too.

Through the analysis of the concept of biological altruism in the three main theories and the removal of terms with everyday parlance, we were able to figure out the proper definitions of three sorts of altruism. We found that the common differentia of the three sort of biological altruism is the indirectness of reproduction and selection. Any trait that can be reproduced and thus evolve only through other organism's reproductive activity is altruistic. In the next section, we will see some important significance of the new definition of biological altruism.

4. Some important significance of the new definition

According to the previous discussion, the directness and indirectness of reproduction and thus selection is the criteria of selfishness and altruism respectively. Selfish traits are traits whose selection and evolution is, by definition, possible only by direct reproduction of itself. Altruistic traits are traits whose selection and evolution is, by definition, possible only by indirect reproduction via other(s). The indirectness of reproduction is a principal differentia of the concept of biological altruism. Indirect reproduction favors the evolution of altruism, while direct reproduction favors the evolution of selfishness.11) Of course, altruistic traits can be reproduced directly. However, they cannot evolve

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11) Compare it to the idea that "Between-group selection favors the evolution of altruism; within-group selection favors the evolution of selfishness" (Sober and Wilson 1998, 33).

with direct reproduction alone, for altruistic traits are less fit than selfish ones on average. The selective force of altruism comes not from direct-reproductive force but from indirect-reproductive force.

As Sober and Wilson argue convincingly, genuine altruism is rather general sort of altruism. Kin is a kind of groups in which the interactors are relatives and reciprocally altruistic group is a kind of group in which they interact conditionally and repeatedly (1998, 110; Sober 1933, 116). Both kin and reciprocal altruism are special cases of genuine altruism. Therefore, biological altruism in general can be defined as follows:

> **Definition 7:** Biological altruism is a tendency of behavior (or a strategy of adaptation) of an organism caused by the trait that can reproduce itself indirectly via other organisms

Let's evaluate this new definition. Above all, being defined with purely evolutionary terms rigorously, it does not contain any paradox and is neither broad nor narrow. The trait that causes biting one's own leg cannot replicate itself via others, and thus cannot evolve. New definition excludes any tendency of behavior that is caused by the trait that cannot replicate itself indirectly from being altruism. Also, according to the new definition, there is no intuitive awkwardness in regarding the avirulence in the Myxoma virus, the less successfulness of predators, a special morphology of trees, etc., as examples of evolutionary altruism. Finally, the new definition is not based upon Darwinian "direct reproduction-centered stand" but upon "dual-reproduction stand." According to the latter, altruism is not a paradox or anomaly but a very natural phenomenon. So, the new definition of altruism is free from any shortcomings prevalent in the standard definition.

Compare the standard classification of behavior (Wilson and Dugatkin 1992, 30) with a new classification based upon the new definition. The former is as follows:

1) Altruism: decreasing self's fitness and increasing other's fitness
2) Cooperation: increasing both self's and other's fitnesses
3) Selfishness: increasing self's fitness and decreasing other's fitness
4) Spite: decrease both self's and other's fitnesses

And the new classification is as follows:

1) Altruism: pursuing indirect reproduction via others
2) Cooperation: pursuing indirect reproduction via others only when others pursue it, too.
3) Selfishness: pursuing direct reproduction only
4) Spite: pursuing neither direct nor indirect reproduction

The standard classification may be blurred depending upon the meaning of fitness, the frame of comparison, the point of time for measuring effects, etc. as well as upon the everyday parlance of some words (Wilson and Dugatkin 1992). The paradigm of direct-indirectness of reproduction gives us a simple, neutral, and clear criterion of the four sorts of behavior. It also gives us clearer intuition of different sorts of altruism by defining them only with indirectness of reproduction and interactors. Since, in the new definition, the degree of altruism depends most importantly upon the degree of indirect reproduction, at one extreme there is maximum altruism (= sacrifice) in which an agent pursues pure indirect reproduction with zero reciprocity from others. The brain worm is a good example. At the other extreme, there is minimum altruism (= cooperation), where an agent pursues conditional indirect reproduction with full reciprocity from others. Between the two extremes, there is a spectrum of various degrees of altruism. Kin altruism in social insects would be closer to the maximum altruism, but kin altruism in humans would be less than that.[12)]

The new definition implies a release from the restraint of the Darwinian legacy of "direct-reproduction stand" and takes the view point of the selector, i.e., nature. It asks us to stand at nature's point of view, for she does not show favoritism toward either direct or indirect production. From her point of view, what is important are each trait as well as the organisms that holds it. Nature does not care whether it is reproduced directly or indirectly. She cares only "Which one of the two ways of reproduction is higher than the other in terms of reproductive efficiency?" So, it is question begging as well as wrong to discriminate indirect reproduction from direct one and put favoritism toward one of them. Of course, generally speaking, direct reproduction may be safer and more successful than indirect reproduction, but indirect reproduction, though riskier, may offer bigger payoff. Nature will be the final decision maker about which one of the two is more effective. Considering the fact that altruism and cooperation exist widely in nature and that altruistic and cooperative organisms are rather more prosperous in many cases, there is no reason for us to put priority to direct reproduction. In this way, the new definition opens a new way for better understanding of evolution in general as well as biological

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12) If we use everyday parlance, things would be this: Since the degree of altruism of an agent may depend upon the degree of repay from other altruists. At one extreme, there is maximum altruism (sacrifices) where an agent benefits others at the cost of his own survival (and offspring) with zero reciprocity. At the other extreme, there is minimum altruism (cooperation) where an agent benefit other(s) as much as the recipient benefit (repay to) the agent with full reciprocity.

altruism.

Another potentially important characteristic of the new definition is that it offers a third approach to selection and evolution that may be an good alternative to both individualism and multi-level selection theory. According to the individualism, "individuals are the primary functional units" and group behavior is "just the product of interactions among individuals," and "groups are not functionally organized in their own right" (Sober and Wilson 1998, 10). G. C. William's classical version of individualism has developed into a refined version called "broad-sense of individualism" (Dugatkin and Reeve 1994, Sterelny 1996).13) According to this version, since an individual is the unit of survival and reproduction, selection occurs only in individuals, and the tentative elements such as genes and groups should be regarded as part of the individual's environment. Fitness is assigned only to individuals, and groups are regarded as part of the context that affects individual fitness. Any trait that has higher relative fitness than others will be selected and evolve through individuals that hold it.

According to Sober Wilson, there are multiple units of selection ranging from genes to groups, and each of the units often pulls in opposite directions with no single one being more fundamental than any of the others. Fitness is assigned to each of the levels, and selection occurs based upon the sum of all fitnesses. As we have seen in the previous section, altruism is selected when between-group fitness exceeds within-group fitness that operates against between-group fitness. All types of altruism can be explained by the dynamical relation between individual-level productivity (fitness) and group-level

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13) Kerr and Godfrey-Smith generalize the distinction of broad sense individualism and multi-level selection theory as the distinction between "the contextual and collective approach" respectively (2002).

productivity that operate opposite with each other (Sober and Wilson 1998, 55-100).

There is a broad agreement that individualist and multi-level selection approaches are mathematically and logically equivalent to each other. Mathematically, the two approaches are interchangeable, and each one has its own heuristic advantages (Dugatkin and Reeve 1994; Kerr and Godfrey-Smith 2002a, b; Sober and Wilson 1998; 2002).14) However, there is a somewhat serious controversy between the two approaches. It comes from the fact that while Sober and Wilson regard the group (structure) as an independent variable in selection and evolution of altruism, the individualists regard it only as a dependent variable to the individual.15) Sober and Wilson insist that individualists commit the averaging fallacy by claiming the "group selection does not exist *because* fitness can be assigned to genes or to traits of individuals by averaging over context" (2002, 531; their italics). By committing that fallacy, the individualists fail to disentangle "the different causal processes that lead to an evolutionary outcome" (2002, 531). For Sober and Wilson, the two approaches are not two different perspectives viewing one and the same evolutionary mechanism but two different evolutionary theories on one evolutionary mechanism. They insist that any perspective should agree that "altruism ··· requires a process of group selection to evolve" (Sober and Wilson 1998, 98).

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14) There is subtle difference between Dugatkin and Reeve and Kerr and Godfrey-Smith: Both of them agree to the idea that the two perspectives are interchangeable and that each view has its own set of heuristic advantages. Kerr and Godfrey-Smith add to it the idea that the two perspectives is usable in a cooperative manner like "gestalt-switches" (2002b, 479).

15) I suspect that behind this controversy there may be a metaphysical difference: Sober and Wilson ground their view on a realism, while the individualists ground their view on pragmatism. I will not pursue this issue here further.

In comparison, individualists claim that while the two approaches are two different perspectives for viewing the same evolutionary mechanism,[16] some key features of the problem of altruism are more readily seen from the individualist approach. For example, in the cases of kin altruism and reciprocal altruism, the individualist approach offers better view on both fitness structures and the definition of altruism and shows better heuristic power (Kerr and Godfrey-Smith 2002a). Another problem that is unfavorable to Sober and Wilson is the instability or arbitrariness of groups. As a level or unit of selection, the individual is well defined, clear, and distinct entity. "What makes organismic selection organismic, as opposed to genic or group selection, is that it is the organismic phenotype that directly interacts with environment and so is directly exposed to selection. That is, selection in such cases cannot 'see' the genes [and the groups], it 'sees' the organismic phenotype" (Brandon 1999, 167, my italics).[17] However, controversies surrounding groups haven't settled yet. The concept of 'group' hasn't been well defined and thus is far from being clear and distinct. Its meaning seems to be dependent upon contexts and perspectives as well as actual evolutionary processes (cf. R. A. Wilson 2003)

To make a long story short, while multi-level selection theory and individualism are mathematically equivalent approaches to each other,

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[16] "the group selection models are generated from a fitness-accounting scheme that merely produces an alternative picture of the same processes describes by the inclusive fitness models" (Reeve 2000, 66); "[while] trait groups that form superorganisms are vehicles, those that are mere trait groups, i.e., the vast majority of them, are not vehicles" (Sterelny 1996, 583).

[17] "Evolution ultimately occurs as a result of the differential reproductive success of individual organisms and the success (or lack thereof) of individuals in turn is caused by the various traits they possess." Except social insects, groups are not so stable nor distinct as individuals (R. A. Wilson 2003, 536).

the former is based upon the symmetry between the individual and group levels, and the latter is based upon the asymmetry between them.

If we adopt the new definition of biological altruism, we can obtain a new approach to selection and evolution, which may be called "dual-reproduction approach." It offers a new solution to the controversy between individualism and multi-level selection theory. First, the new approach solves the symmetry-asymmetry problem. On the one hand, the equivalence of direct and indirect reproduction in evolutionary processes favors the symmetry thesis of multi-level selection theory. Both of the dual-reproduction and multi-level approaches deny the uniqueness of individuals in evolutionary processes. They assign two sorts of fitness to the process of the evolution of altruism: Multi-level approach assigns within-group fitness and between-group fitness to the process, while dual-reproduction approach assigns direct-reproductive fitness and indirect-reproductive fitness. In this respect, multi-level approach seems to be closer to the causal reality than individualist approach. On the one hand, dual-reproduction approach coincides with individualism in the asymmetry thesis: While multi-level selection theory has the problem of instability of groups, dual-reproduction approach doesn't, for the latter adopts indirect reproduction instead group selection.

For this reason, although there may be no mathematical difference among the three approaches, dual reproduction approach has an important conceptual advantage. It can apply any sort of altruism in a unique and simple way. What we should do is to figure out direct and indirect reproductive elements in each evolutionary process instead of figuring out group structures with difficulty. This implies that there is asymmetry between "direct and indirect reproduction" and "within-group and between-group selection." Dual-reproduction approach shows that while individualist approach went too short, multi-level selection approach went a little bit too far in apprehending an evolutionary mechanism of altruism.

5. Group selection vs. indirect reproduction

One may doubt that the division of direct and indirect reproduction is a mere terminological trick of within-and among-groups selection.[18] In order to respond this doubt, we should answer the question "Whether the evolution of altruism is due to the property of group structure or others?" According to Sober and Wilson, a group is defined as "a set of individuals that influence each other's fitness with respect to a certain trait but not the fitness of those outside the group" (1998, 92). Any group that satisfies this criterion qualifies as a group in multi-level selection theory, regardless of how long it lasts or the specific manner in which groups compete with other groups (p. 92-3). Although it may be arguable whether this definition of groups is proper, we will concentrate our attention only on whether groups thus defined can be units of selection in the evolution of altruism. A key to the evolution of altruism in multi-level selection theory consists in a special structure of a population in which groups should breakup, merge into the global population and then reform new groups periodically. Groups should be biased in their proportion of altruists in such a way that altruists are concentrated sufficiently enough for the

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[18] More generally, "Is the new definition a terminological trick of Sober and Wilson's definition; altruism is "behavior that decreases relative fitness within groups, but increases the fitness of groups?" (1988, p. 99).

global relative frequency of altruists to increase over the decline of local relative frequency within each group in the next generation. If a sufficient number of other altruistic individuals in a group do not become the recipients of altruistic actions, altruism cannot evolve. Thus, four conditions are necessary for altruism to evolve:

a) Each altruist should have the ability to recognize other altruists in a population.[19]
b) Each altruist should have the disposition of "like attracts like."
c) Sufficient number of altruists should be concentrated in some of the groups (enough for the between-groups fitness to counter within-group fitness of altruists).
d) Groups should breakup and merge into the global population, and then new groups be reformed periodically.

While 'a)' and 'b)' are attributable to the property of individual organisms, 'c)' is attributable to that of groups, and d) is attributable to that of populations.[20] If any one of the conditions is not satisfied, altruism cannot be selected and evolve (cf. Sober and Wilson 1998, 33). Since the property that enables groups to undergo process 'd)' is

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19) The ability includes several possible alternatives as well, as we can see in this quotation: "it obviously makes no difference if altruists settle with altruists because they are related··· or because they recognize fellow altruists as such, or because of some pleiotropic effect of the gene on habitat preference" (Hamilton 1975, 337). So the ability to recognize is not essential.

20) Rosa (2007) claims that if the assortive grouping is deliberately produced by the same proximate mechanism that controls altruistic responses, 'c)' is attributable to individuals. And he suggests human society as an example. He argues that in such a case altruism is selected both at individual level and at the group level. 'c)' may be attributable to individuals as he claims. However, if it is the case, we don't need to appeal to groups for the explanation of the evolution of altruism any more, because such a case will turn out be the same as either reciprocal altruism or mere selfishness. Moreover, the process 'd)' would not be necessary any more.

attributable not groups themselves but the population to which the groups belong, the only condition that is possibly relatable to group selection will be 'c)'. Remember that in order for any level of organisms to be a unit of selection, it should show phenotypic variance, fitness variance, and heritability of traits relating to fitness (Darwinian conditions; Lewontin 1970). If groups are levels of selection, they should have such properties or the like. Sober and Wilson insist that their groups have such properties (1998). Their groups differ in terms of the composition of altruistic and selfish individuals and thus their fitness. If the composition is regarded as a sort of phenotype, there are phenotypic variance and fitness variance. And such a group property may be repeatedly formed throughout generations by some property of the population under certain environment. Their groups apparently satisfy Bandon (1990)'s conditions also.21) Be it may be, the fundamental question to be answered is "Do Sober and Wilson's groups really function as units of selection in the evolution of altruism?" or "Is there real competition among groups for the selection of altruistic traits?" I think, the answer is "No."

Let's see their own model in *Unto Others* p. 23-26. Group1(G1) and Group2(G2) have different compositions of altruistic and selfish individuals, and thus different group fitness. Group selection models "are concerned with the spread of an individual phenotype in a group-structured population, and hence define group fitness as average individual fitness" (Okasha 2005, 1020). And Group fitness is the mean

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21) "when there is no variance in group fitness, or when the variance in group fitness dose not depend on group structure (for example, group differential reproduction is independent of the relative frequency of altruists in the group, but dependent on shelter availability in the physical environment), a process of selection between group cannot occur" (Brandon 1990, 98-116).

fitness of individuals within a group, i.e., the expected number of offspring within that group, relative to the mean fitness of another group (Shavit 2005). Fitness of G1 or G2 is calculated as the sum of average fitness of altruists and that of selfish individuals in each group. In order to argue for group selection, there should be competition between G1 and G2 for altruism, and again, for the competition to come into being, the relative fitness of G1 and G2 should be compared with each other.[22)]

However, things are somewhat different from what Sober and Wilson argue, because there is no such thing as "fitness of G1" or "fitness of G2" in their model. Of course, one may calculate each of them as "mere the arithmetical sum of the fitnesses of the individuals that compose it [the group]" (Maynard Smith 2002, 526), but the problem is that the fitnesses of G1 and G2 thus calculated are not used for the selection of altruism. Only average fitness of all altruists and that of selfish individuals in each group are counted in the fitness calculation for the selection of altruism (Guildenhuys 2003). The force that enables the evolution of altruism is not the fitness of each group as a whole but the fitness of altruists as a whole within each group. The fact that the fitness of each group as a whole is not counted for the selection of altruism in their model means that selection for altruism in the *group* level does not occur! One may claim that there is selection for altruism in the subgroup level. But subgroups do not meet Sober and Wilson's definition of groups. There might be selection among populations, if

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22) Robert Wilson points out the same problem: "Group productivity is parameterized solely in terms of the individual composition of groups and then used to define the particular contributions of individuals to overall group productivity. ··· it does not allow one to represent circumstances in which groups play a more agent-like role in natural selection (R. A. Wilson, 2003, 543).

they satisfy the above four conditions. Yet, the selection may occur not for altruism but for a certain group-level property for the evolution of altruism. In this regard, I agree with Guildenhuys (2003)'s claim:

> "··· Sober and Wilson's model is a model of population selection after all, but not a model of group selection for altruism. Instead their model can be construed as a model showing how a population-level property of biased subgroup formation can be selected for when as least some members of the population are altruists. ··· [They] have simply confused the importance of a group-level property for the evolution of altruism with the group selection for altruism (Gildenhuys 2003, 46-7).

Although Guildenhuys makes a mistake in mixing up 'c)' to 'd)', the intuition that the group property of biased subgroup formation itself is not a criterion of the selection for altruism is basically correct.

The dual-reproduction approach divides fitness into direct and indirect reproductive elements. The direct reproductive element may correspond to Sober and Wilson's within-group fitness. But the indirect reproductive element does not correspond to between-group fitness. Between-group fitness is divided into an indirect reproductive part (a total fitness given to all altruists within each group) and an environmental part (a total fitness given to all selfish individuals within each group). So, the new approach represents the causal mechanism in the evolution of altruism more nicely than multi-level selection theory on the one hand, it is free from the controversial entities of groups more appropriately than individualism on the other hand. What a nice Hegelian Aufheben!

One may also ask, "Is direct and indirect reproduction a mere terminological substitute for individual and kin parts of inclusive fitness?" If the altruism in question is merely kin altruism, the answer would be "Mathematically 'Yes', but conceptually 'No'." While kin selection theory is an individualist theory based upon the view point of *the selected* (genes and individuals), the new approach is, so to speak, an inter-individualist theory based upon the view point of *the selector*. Besides, kin altruism is only a special case of genuine (i.e., general) altruism, thus the fitness structure of the two theories are different from each other. In kin selection theory, there is no room for the environmental element of fitness.

5. Conclusion

In this paper, I tried to suggest a new definition of biological altruism that is rigorous and free from everyday parlance. For it, I analyzed major theories of biological altruism and found that indirectness of reproduction is a core differentia common to all sorts of biological altruism. The new definition thus formulated is this: Biological altruism is a tendency of behavior (or a strategy of adaptation) of an organism caused by the trait that can reproduce itself indirectly via other organisms. The new definition has several advantages. It doesn't have any paradox, it is neither too narrow nor too broad, it is free from the restrain of Darwinian legacy viz., "a direct-reproduction stand," and thus it is grounded upon the view point of the selector rather than the selected.

The new definition opens the way to a new approach to selection and evolution, what I call, "dual-reproduction approach." By dividing the selective force for the evolution of altruism into direct, indirect, and environmental parts, the new approach shows the possibility of being a convincing alternative to both individualist and multi-level selection approaches. Besides, the new approach is expected to shed a new light on the problem of the unit of selection.

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A New Definition of Evolutionary Altruism

Sang Mo Jung

The standard definition of evolutionary altruism has several shortcomings mainly due to the remnant of everyday parlance in its terminology. I try to suggest a new definition based upon the results of the main solutions to the problem of biological altruism, viz., kin section, reciprocal altruism, and multi-level selection theories. The new definition takes the indirectness of reproduction as a principal differentia, for it is the core of the evolutionary mechanism of altruism common to all these theories. The new definition can not only overcome the Darwinian legacy of *the direct-reproduction stand* but also open the way to a new approach to selection and evolution that I call *the dual-reproduction approach.* I argue that, by dividing the selective force for the evolution of altruism into direct, indirect, and environmental parts, the new approach can be a convincing alternative to both individualist and multi-level selection approaches.

[Key Words] altruism, differentia, meta-trait, indirectness, dual-reproduction approach