



# Relationship between aggregation of rewards and the possibility of polymorphism in continuous snowdrift games



Koichi Ito <sup>a,\*</sup>, Hisashi Ohtsuki <sup>b</sup>, Atsushi Yamauchi <sup>a</sup>

<sup>a</sup> Center for Ecological Research, Kyoto University, Hirano 2-509-3, Otsu 520-2113, Japan

<sup>b</sup> Department of Evolutionary Studies of Biosystems, School of Advanced Sciences, The Graduate University for Advanced Studies (SOKENDAI), Shonan Village, Hayama, Kanagawa 240-0193, Japan

## HIGHLIGHTS

- In cooperation, individual investments are converted to reward for group mates.
- The conversion consists of aggregation process and functional conversion.
- Effects of aggregation process on evolution of cooperation are analyzed.
- It was shown that aggregation process determines a possibility of polymorphism.
- The analysis revealed necessary conditions for polymorphism of cooperation levels.

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## ABSTRACT

The existence of intra-population variations in cooperation level has often been reported by some empirical studies. Evolutionary conditions of polymorphism in cooperation have been investigated by using a framework of the continuous snowdrift game. However, our insights from this framework have been limited because of an assumption that the cooperative reward is a function of total amount of investments within an interacting group. In many cases, payoffs may actually depend on the interactions between the *effects* of such investments, such as members share the sum of beneficial effects that are individually produced from their own investments. Alternatively, payoffs may depend multiplicatively on investment, such as when investments are complementary. In the present paper, we investigated the influence of such difference on the evolution of cooperation with respect to three aspects of the aggregating process of individuals' contributions for reward, *i.e.* (i) additive or multiplicative, (ii) aggregation of either investments or effects, and (iii) promotion of advantage or suppression of disadvantage. We analytically show that the possibilities of the emergence of polymorphism are different depending on the type of aggregation process classified from these three aspects. Polymorphism of cooperation level never emerges unless the aggregation process is the aggregation of investment or the multiplicative aggregation of effect with suppression of disadvantage. Our results show the necessary condition for the emergence of polymorphic cooperation levels that are observed in various taxonomic groups.

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## 1. Introduction

Cooperative relationships have been widely observed in various taxonomic groups, involving bacteria, reptiles, mammals, and plants (Dugatkin, 1997; Sachs et al., 2004; Melis and Semmann, 2010; Raihani et al., 2012). Previous empirical studies about

cooperation have often reported the existence of intra-population variation in cooperation level. For example, yeasts cooperate with neighbouring cells by sharing their profit in the process of resource decomposition, in which morphs with different levels of enzyme production can coexist (Greig and Travisano, 2004). Animals or birds form groups and cooperate in being vigilant to approaching predators, but some individuals vary in their contributions to group vigilance (kangaroos, Carter et al., 2009; hyenas, Pangle and Holekamp, 2010). In plants, it has been reported that anti-herbivore defence by an individual plant often

\* Corresponding author. Tel.: +81 77 549 8240.

E-mail address: [hmito@outlook.com](mailto:hmito@outlook.com) (K. Ito).

reduces herbivory on its neighbouring ones (so-called “associational resistance”), but polymorphism of defence level is also observed in some cases (Agrawal et al., 2002; Hare and Elle, 2002).

In general, selfish individuals will obtain a higher payoff than cooperative ones because they receive the benefits of cooperation without paying cooperative costs. Therefore, explaining the reason why cooperative individuals can persist in the presence of selfish ones is a challenging and important subject in evolutionary ecology. In order to solve this problem, some mechanisms have been proposed, which include kin selection (Hamilton, 1964, 1972), future benefits (Clutton-Brock, 2002) and frequency dependent selection for the cooperative traits in the context of game theory (Maynard Smith, 1982). In particular, because game theory is a useful tool for describing the selection for the traits related to social interactions, game theory has been used for investigating the evolution of cooperation.

One important framework in game theory is the continuous snowdrift game, which is defined by Doebeli et al. (2004) as a game in which investment is a continuous variable and “investment incur costs to the donor and accrue benefits to both the donor and the recipient.” This differs from the more well-known continuous prisoner’s dilemma game in which the investment does not yield a reward directly to the investor (Killingback et al., 1999; Doebeli and Hauert, 2005). It should be noted that some studies of public goods game (Janssen and Goldstone, 2006; Deng and Chu, 2011; Chen et al., 2012) also satisfied the condition that was proposed by Doebeli et al. (2004), which can be categorized into continuous snowdrift game.

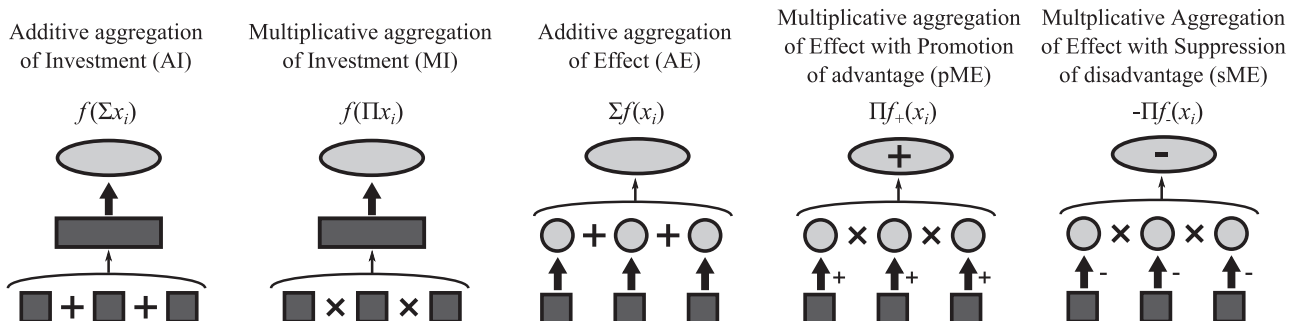
Previous studies have indicated that under some conditions the continuous snowdrift game can predict evolutionary branching, and therefore dimorphism of cooperation levels (Doebeli et al., 2004). Fluctuation in group size either stabilizes or destabilizes the dimorphism of cooperative levels depending on the shape of payoff function (Brännström et al., 2011), the existence of metapopulation structure relaxes the condition for the emergence of polymorphism (Parvinen, 2011), and a small population size prevents evolutionary branching (Wakano and Iwasa, 2013). Functional forms of reward and cost are also proposed as an important factor for the coexistence of polymorphic cooperation levels (Archetti and Scheuring, 2012). Doebeli et al. (2004) indicated that the concavity of both reward and cost functions is a necessary and sufficient condition for the occurrence of evolutionary branching.

These previous studies, however, generally have paid less attention to the process by which rewards result from investment. In the process of producing reward on cooperation, each individual provides ‘investment’ in order to obtain some advantageous ‘effect,’ the amount of which can be represented by a function of investment (e.g. an investment  $z$  produces an effect  $f(z)$ ). For

example, yeast produce enzymes in order to produce decomposition products, or in the group vigilance individuals consume time in vigilance in order to detect their predators. In cooperative interactions among multiple individuals, the contributions of neighbouring individuals are aggregated, and consequently each individual obtains a resultant effect as the reward of cooperation. We can consider some types of aggregation process depending on the mechanism of the aggregation.

First, we can consider two aggregation stages depending on whether the individuals’ contributions are aggregated at investments or at effects that is produced by such investment. These will only be equivalent if the aggregation is additive and the relationship between investment and effects are linear. However, this is likely to be unrealistic in most cases. For example, the amount of enzyme produced by yeast will not be linearly related to obtained decomposition, because the decomposition rate generally follows Michaelis-Menten kinetics (Zaks and Klibanov, 1985). The detail of the cooperation of yeast should be investigated by considering the chemical reaction-diffusion process (e.g. Borenstein et al., 2013; Scheuring, 2014). However, for generality of analysis, we summarize those processes into two simple equations, which are ineffective for quantitative predictions but effective for investigation of essential mechanisms in the considered system. One is that each individual produces enzyme  $z$ , and the total of this enzyme by all group mates,  $\Sigma z$ , is used to produce decomposed products  $f(\Sigma z)$ , in which aggregation occur before producing products. Alternatively, each individual invests energy  $z$  to produce decomposed products  $f(z)$ , the total of which,  $\Sigma f(z)$ , benefits the focal individual. In this case, the aggregation occurs after the producing products. We call the former “aggregation of investment” and the latter “aggregation of effect,” respectively throughout the paper.

The second issue is how the factors are associated, i.e., “additive aggregation” or “multiplicative aggregation” (e.g.  $\Sigma z$  or  $\Pi z$ ). An additive aggregation often applies to material benefits such as enzyme or decomposition products in yeast, but the multiplicative aggregation is also conceivable. Consider group vigilance: if individual bouts of vigilance overlap, the probability of spotting a predator is calculated by the product of the probabilities of a single individual not finding an enemy. This is also a greatly simplified situation, and the group vigilance should be investigated by considering behavioural process in detail (e.g. Proctor et al., 2001). However, this example shows that multiplicative benefit is more appropriate in some cases. Moreover, we can also consider the difference of reward type, i.e. the reward is obtained through whether promotion of advantage or suppression of disadvantage. In the cooperation in yeast, more investments promote the advantage by producing more decomposition products. Contrarily, in group vigilance, more investments suppress



**Fig. 1.** An image of the types of aggregation process of rewards obtained by considering the combination of three aspects. In the process of the cooperation, individuals’ contributions are aggregated on the stage of investments (boxes) or effects (circles), which eventually yields individual reward  $F$ . The plus and multiplication signs indicate the aggregation is additive and multiplicative, respectively. The difference that the reward type is promotion of advantage (arrows with plus signs) or suppression of disadvantage (arrows with minus signs) also makes difference in the multiplicative aggregation of effect, but in other cases it yields no difference (see main text in Model). Therefore, AI, MI, and AE are represented without distinction of the difference.

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