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H. Seno

Group size determined by fusion and fission

A mathematical modelling with inclusive fitness

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Abstract. We consider a mathematical model for the group size determination by the intra-reactions, self-growth, ostracism and fission within a group, and by the inter-reactions, immigration and fusion between two groups. In some group reactions, a conflict between two groups occurs about the reaction to change the group size. We construct a mathematical model to consider such conflict, taking into account the *inclusive fitness* of members in each group. In the conflict about the fusion between two groups, our analysis shows that the smaller group wants to fuse, while the larger does not. Also the criterion to resolve the conflict is discussed, and some numerical examples are given, too. It is concluded that, depending on the deviation in the total cost paid for the conflict by counterparts, the group reactions could result in a terminal group size different from that reached only by a sequence of outsider's immigrations into a group.

1. Introduction

Theoretical considerations for biological group formation have been attractive for many researchers in biology and mathematical biology [19,26,28]. As an interesting aggregation process related to biology, some mathematical models have been constructed and analyzed with an analogy of physical aggregation processes (see [5, 8,12–14] and their references). Apart from those models, some mathematical considerations based on individual fitness have been presented in a number of works. One of such well-known mathematical considerations is game theoretic modelling (for instance, [3,4]), of which some are related to foraging theory [7]. Another is modelling with dynamic programming [17,21,22]. For an example of such modelling analysis, the optimal hunting group size of lions was discussed [6,25], taking into account the physical condition of the hunter and the expected future energy gain.

In such frameworks of mathematical modelling, the relatedness among individuals has not been taken into account, although it is indicated by the theory of evolutionarily stable strategy (ESS) that the relatedness plays an important role in determining the group size [23,24]. For examples of such theoretical arguments,

H. Seno: Department of Mathematical and Life Sciences, Graduate School of Science, Hiroshima University, Higashi-hiroshima 739-8526, Japan. e-mail: seno@math.sci.hiroshima-u.ac.jp

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see Caraco and Wolf [6], and Packer *et al.* [25] who discussed the hunting group size of lions (for other examples in a different or more general context, see [9–11, 16,30,31]).

Assume that the mean fitness per individual within a group of n individuals is given as a function of n, $w(n)$, which increases for a range $1 \leq n < n_G$, and decreases for $n \geq n_G$. The size n_G maximizes the mean fitness $w(n)$ per individual inside the group, and was called *the optimal group size* [6,16,25,30]. The optimal group size n_G is derived as the ESS for an insider of the group. On the other hand, assuming that $w(n)$ falls below $w(1)$ when once the group size n exceeds a value n_S [i.e., $w(n) \geq w(1)$ for $n \leq n_S$, while $w(n) < w(1)$ for $n > n_S$], it is argued that the optimal group size n_G cannot be stable when solitary outsiders can freely join the group; solitary outsiders are expected to join the group as long as joining the group increases their own fitness, expanding the group size up to n_S, at which solitary outsiders no longer join the group and remain solitary, stopping group size growth by a sequence of solitary outsider's immigrations. Thus, n_S was called *the stable group size* by Sibly [29], and can be derived as the ESS for a solitary outsider against the group.

Both of the above-mentioned potential ESSs are based on the *direct fitness*, that is, on the fitness gained by each individual itself. However, the contribution of the *relatedness* to the determination of group size would be one of the main factors to be considered: a local population is considered where the mean degree of genetic relatedness within the population is r. If the relatedness coefficient r takes a non-zero value, i.e., if individuals have a significant relatedness, as is the case for many examples of group forming, the *inclusive fitness* (IF; see [15]) should be considered instead of the direct fitness. For example, Rodman [27] discussed groups of relatives and suggested that the group size to maximize each member's IF value exceeds the associated size to maximize the direct fitness (also see [1,2]).

In this paper, with mathematical modelling based on the principle to increase the IF, we discuss how the optimal group size is determined by the intra-reactions, ostracism and fisson, and by the inter-reactions, immigration and fusion between two groups. The aim of our analysis is not to consider how the change of group size would occur but to derive some theoretical results about the criterion to change the group size when it leads to an increase (or, at least, no decrease) of the IF of members in a group.

2. Fitness function *w*(*n*)

In this section, we describe the characteristic nature of the direct fitness function $w(n)$ considered in this paper, which gives the fitness value per individual within a group of n individuals. As in [16], we assume that the direct fitness function $w(n)$ has the following characteristics (see a numerical example in Fig. 1):

(i) There exists the unique group size n_G (> 1) such that

$$w(n) \leq w(n_G) \quad \text{for any } n.$$

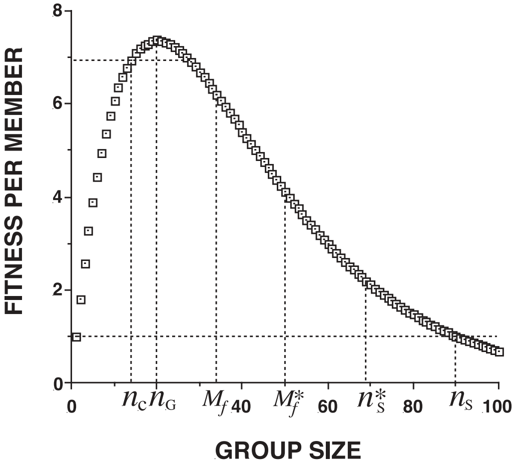

Fig. 1. A numerical example of the direct fitness function $w(n)$ which gives the expected fitness per member within a group of size n. As for those specific sizes indicated in figure, see text. $n_G = 20$, $n_S = 90$, and $n_c = 13$. In addition, $M_f = 34$, $n_S^* = m_f(1) + 1 = 69$, and $M_f^* = 50$ are for the case when $r = 0 \cdot 2$ with $k_{ji} = 1$ for any i and j.

(ii) $w(n)$ increases monotonically for $n \leq n_G$, whereas $w(n)$ decreases monotonically for $n > n_G$:

$$w(n) < w(n+1) \quad \text{for any} \quad n < n_G;$$
$$w(n) > w(n+1) \quad \text{for any} \quad n \geq n_G.$$

(iii) There exists the unique group size n_S such that

$$w(n) \geq w(1) \quad \text{for any} \quad n \leq n_S;$$
$$w(n) < w(1) \quad \text{for any} \quad n > n_S.$$

3. Fusion

3.1. Relative inclusive fitness

We define the *relative* IF value $\Phi_i(i+j)$ per member in the group $\mathbf{G}(i)$ of size i when the group fuses with another group $\mathbf{G}(j)$ of size j:

$$\Phi_i(i+j) := \Delta w(i+j, i) + r(i-1)\Delta w(i+j, i) + rj\Delta w(i+j, j), \quad (1)$$

where $\Delta w(i, j) = w(i) - w(j)$. $\Phi_i(i+j)$ gives the change of IF value for a member $\mathbf{g}$ in $\mathbf{G}(i)$ when $\mathbf{G}(i)$ fuses with $\mathbf{G}(j)$, relative to that when $\mathbf{G}(i)$ does not fuse and remains with size i. The first term of (1) means the contribution of $\mathbf{g}$'s own fitness, the second does that of the other members' fitness in the same group $\mathbf{G}(i)$, and the third does that of members' in the counter group $\mathbf{G}(j)$, weighted by the relatedness r. Let us remark that $\Phi_i(i) = 0$. Indeed, $\Phi_i(i)$ means the relative

IF value per member in $\mathbf{G}(i)$ when the size is kept i, so that the IF itself does not change.

Relatedness in this model is commonly given by r between members within the same group as well as between individuals belonging to different groups. This means that r corresponds to the relatedness averaged over the considered population including all groups. We further assume that the optimality for group size is governed only by the IF of an individual. If an individual could behave to afford the higher fitness to the closer related individuals, such a behavior would be favored by the natural selection. However, in our prototype model, we assume that such more informative behavior does not exist, whereas every individuals behave according to the mean relatedness given as a constant specified for the considered population. In addition, the behavioral choice by any member in the same group is assumed to be identical without any difference to maximize its IF value. As for a mathematically explicit introduction of qualitative difference between members in a group, for instance, see [18]. To introduce the difference of relatedness among individuals may be the next step of our modelling.

3.2. Maximal fusion-acceptable group size

Now we define the *maximal fusion-acceptable group size* $m_f(i)$ for the group of size i by

$$m_f(i) := \max\{j \mid \Phi_i(i+k) \geq 0 \text{ for all } k \text{ with } 0 \leq k \leq j\}. \tag{2}$$

Hence, we have $\Phi_i\left(i + \left[m_f(i)+1\right]\right) < 0$. Group of size $m_f(i)$ is the largest group with which $\mathbf{G}(i)$ wants the fusion. Since $\Phi_i(i) = 0$ for any i, we find that $m_f(i) = 0$ if and only if $\Phi_i(i+1) < 0$. The group of such size i that $m_f(i) = 0$ does not want to fuse with any other group. As for $m_f(i)$, we can find the following:

Proposition 1. *The maximal fusion-acceptable group size $m_f(i)$ defined by (2) uniquely exists. For each $i < n_c$, $m_f(i)$ is non-increasing in terms of the relatedness r, for each $i > n_c$, non-decreasing, and $m_f(n_c) = n_c$, where*

$$n_c := \max\{j \mid w(k) \leq w(2k) \textit{ for all } k \leq j\}. \tag{3}$$

For any fixed relatedness r, $m_f(i)$ is non-increasing in terms of i.

The specific size n_c always exists well-defined as follows immediately from the characteristics of the fitness function w. Moreover, we can easily find that $1 < n_c < n_G$, since $w(1) < w(2)$ and $w(n_G) > w(2n_G)$.

In Appendix A, we prove the unique existence of $m_f(i)$ for each i, making use of the following specific sizes n_i and N_i:

$$n_i := \max\{j \mid w(k) \leq w(i+k) \text{ for all } k \text{ with } 0 \leq k \leq j\}; \tag{4}$$

$$N_i := \max\{j \mid w(i) \leq w(k) \text{ for all } k \text{ with } i \leq k \leq j\} \quad \text{for } i < n_G. \tag{5}$$

The uniqueness of N_i and n_i can be easily seen from the characteristics of the fitness function w. From the unimodality of w, $N_i \geq n_G$ and $i + n_i \geq n_G$. From the piecewise monotonicity of w, N_i and n_i are non-increasing in terms of i. Moreover, from definitions (4) and (5), $N_1 = n_S$, $N_{n_i} = i + n_i$, $N_{n_c} = 2n_c$, and $n_{n_c} = n_c$.

In Appendix B, we give the proof of the relation that $m_f(n_c) = n_c$, and some other mathematical characteristics of $m_f(i)$, which are useful for our analysis. The dependence of $m_f(i)$ on the relatedness r in Proposition 1 is proved in Appendix C, and the dependence on the group size i is proved in Appendix D.

As for the specific case of $i = 1$, Higashi and Yamamura [16] discussed the corresponding model and got the following result:

Proposition 2. *There exists a specific group size M_f defined by*

$$M_f := \min\left\{j \mid m_f(j) = 0\right\}, \tag{6}$$

such that $n_S \geq m_f(1) + 1 \geq M_f \geq n_G$. As the relatedness r gets larger, M_f becomes larger.

They called M_f (n_G^* in [16]) the *IF-optimal group size*, and $m_f(1) + 1$ (n_S^* in [16]) the *IF-stable group size*. M_f means the upper bound for the group size with which the group could make a fusion: Any group of size beyond or equal to M_f never wants to fuse with any other group, while every group of size below M_f wants to fuse with some group. Since Higashi and Yamamura [16] considered only the group size determined by a series of solitary outsider's immigrations into a group, M_f means the size with which the group does not accept any solitary outsider's immigration, and $m_f(1)$ means the maximal group size with which a solitary outsider wants to immigrate into the group. Thus, $m_f(1) + 1$ means the minimal group size with which a solitary outsider never wants to immigrate into the group. From the characteristics of w, we can easily find that $m_f(1) \geq n_G - 1$.

3.3. Conflict about the fusion

Next, we consider the existence of a conflict about the fusion between $\mathbf{G}(i)$ and $\mathbf{G}(j)$. If $m_f(j) < i$ when $\mathbf{G}(i)$ wants the fusion, the conflict about the fusion is likely to occur between these groups, because the condition $m_f(j) < i$ means that $\Phi_j(j + i) < 0$, so that $\mathbf{G}(j)$ does not want the fusion. Therefore, if there exists some i such that $m_f(m_f(i)) < i$, the conflict occurs for such a group $\mathbf{G}(i)$ at least when it encounters a group of size $m_f(i)$. This is because $\mathbf{G}(i)$ wants to fuse with the group $\mathbf{G}(m_f(i))$, while the condition $m_f(m_f(i)) < i$ means that

$$\Phi_i(i + m_f(i)) \geq 0 > \Phi_{m_f(i)}(m_f(i) + i), \tag{7}$$

so that $\mathbf{G}(m_f(i))$ does not want the fusion.

In contrast, if $m_f(j) \geq i$, the fusion can occur between them without conflict as far as $\mathbf{G}(i)$ wants the fusion, because the condition $m_f(j) \geq i$ means that $\Phi_j(i+j) \geq 0$, so that $\mathbf{G}(j)$ does wants the fusion, too. Moreover, if $m_f(m_f(i)) \geq i$, $\mathbf{G}(i)$ can make the fusion whenever it wants.

With mathematical arguments given in Appendix E, we obtain the following proposition and corollary about the occurrence of conflict:

Proposition 3. *In the group fusion, if the relatedness between two groups is 1 or if the larger group wants the fusion, so necessarily the smaller does. In contrast, if the relatedness between two groups is not 1, a conflict about the fusion could occur only when the group smaller than n_c wants the fusion, while the larger than n_c does not.*

Corollary 1. *Fusion always occurs between two groups of size below n_c, while it never occurs between two groups of size beyond n_c.*

3.4. Resolution of the conflict

To resolve a conflict, a compromise is necessary between those two groups in the conflict. Let us consider the conflict between $\mathbf{G}(i)$ and $\mathbf{G}(j)$ with $i < n_c < j$. From Proposition 3, $\mathbf{G}(i)$ wants to fuse with $\mathbf{G}(j)$, while $\mathbf{G}(j)$ does not with $\mathbf{G}(i)$.

Suppose that each member in $\mathbf{G}(i)$ has to pay a cost D_{ji} for the conflict on average over $\mathbf{G}(i)$, which in general depends on the group size i and the counter group size j. Thus, the group $\mathbf{G}(i)$ has to pay the total cost iD_{ji} to counter $\mathbf{G}(j)$ in the conflict. In the same way, $\mathbf{G}(j)$ has to pay the total cost jD_{ij} to reject the group $\mathbf{G}(i)$. For mathematical convenience, we define here the ratio k_{ji} of the total cost paid by $\mathbf{G}(j)$ to that by $\mathbf{G}(i)$ as follows:

$$k_{ji} := \frac{jD_{ij}}{iD_{ji}}. \tag{8}$$

Note that $k_{ij} = 1/k_{ji}$ from this definition.

Along the argument similar to that in [16], for the case that $\mathbf{G}(j)$ wins the conflict and succeeds in rejecting the fusion with $\mathbf{G}(i)$, the net increment of the IF value of each member in $\mathbf{G}(j)$, relative to the IF value when $\mathbf{G}(j)$ yielded to $\mathbf{G}(i)$ and let $\mathbf{G}(i)$ fuse with $\mathbf{G}(j)$, is given by

$$\Psi_j(j+i) := -\Phi_j(j+i) - D_{ij} - r(j-1)D_{ij} - riD_{ji} \tag{9}$$

$$= -\Phi_j(j+i) - \left[\frac{i}{j}\{1 + r(j-1)\}k_{ji} + ri\right]D_{ji}. \tag{10}$$

The first term of (9) means the increment of the IF value of each member in $\mathbf{G}(j)$, caused by keeping the group size j, relative to the IF value after the fusion. The second does the cost per member in $\mathbf{G}(j)$ about the conflict, and the third that of the other members in the same group $\mathbf{G}(j)$, weighted by relatedness r. The last term means the cost paid by members in the counter group $\mathbf{G}(i)$, weighted by the relatedness r.

In contrast, the net increment of the IF value of each member in $\mathbf{G}(i)$ for the case that $\mathbf{G}(i)$ wins the conflict and fuses with $\mathbf{G}(j)$, relative to the IF value when $\mathbf{G}(i)$ yielded to $\mathbf{G}(j)$ and gave up the fusion, is given by

$$\Psi_i(i+j) := \Phi_i(i+j) - D_{ji} - r(i-1)D_{ji} - rjD_{ij} \tag{11}$$

$$= \Phi_i(i+j) - \left\{1 + r(i-1) + rik_{ji}\right\}D_{ji}. \tag{12}$$

The first term of (11) means the increment of the IF value of each member in $\mathbf{G}(i)$, caused by the fusion with $\mathbf{G}(j)$. Terms from the second to the fourth have the meanings corresponding to those of (9).

As long as the conflict continues, relative IF values $\Psi_j(j+i)$ and $\Psi_i(i+j)$ eventually decline toward zero because the cumulative cost must be increasing monotonically in terms of the duration of conflict. At a moment, one of $\Psi_j(j+i)$ and $\Psi_i(i+j)$ must become zero while the other stays still positive. Then, from the viewpoint of the IF-optimal choice, the side with zero relative IF must yield to the other side with a positive relative IF, because the relative IF value of the former side would become negative if the conflict still continues. Therefore, it must be the moment of conflict resolution. If $\Psi_i(i+j)$ becomes zero while $\Psi_j(j+i)$ stays positive, then the fusion does not occur because $\mathbf{G}(i)$ gives it up. If $\Psi_j(j+i)$ becomes zero while $\Psi_i(i+j)$ stays positive, then the larger group $\mathbf{G}(j)$ must yield to the smaller $\mathbf{G}(i)$ and accept the fusion with it, increasing the group size by i.

From this argument, we define here the group size $m_f^*(j)$ *compromisingly acceptable* for $\mathbf{G}(j)$ in terms of the fusion. For each $n \le m_f^*(j)$, values of D_{nj} and D_{jn} must satisfy that $\Psi_j(j+n) = 0$ and $\Psi_n(n+j) \ge 0$ at the moment of the conflict resolution. For $n = m_f^*(j)$, values of D_{nj} and D_{jn} must satisfy that $\Psi_j(j+n) > 0$ and $\Psi_n(n+j) = 0$ at the moment of conflict resolution.

From (10) and (12), the condition that $\Psi_j(j+i) = 0$ or $\Psi_i(i+j) = 0$ gives the relationship of D_{ji} to the other parameters at the moment of conflict resolution. The obtained relationship can be used to cancel out D_{ji} in the non-negative condition, $\Psi_i(i+j) \ge 0$ or $\Psi_j(j+i) > 0$. In this way, we can lastly obtain the following result:

Proposition 4. *For the conflict resolution about the fusion between two groups of size i and j, the fusion compromisingly occurs if and only if the following $F(i,j)$ is non-negative:*

$$\begin{aligned} F(i,j) := &\big[\{1 + r(j-1)\}k_{ji} + rj\big]\, i\Phi_i(i+j) \\ &+ \big[1 + r(i-1) + rik_{ji}\big]\, j\Phi_j(j+i), \end{aligned} \tag{13}$$

where k_{ji} is a positive constant defined by (8) at the moment of conflict resolution.

Note that signs of $F(i,j)$ and $F(j,i)$ coincide, because $F(j,i) = k_{ij}F(i,j)$ with $k_{ij} = 1/k_{ji} > 0$. We remark that, when both $\Phi_i(i+j)$ and $\Phi_j(j+i)$ are non-negative, the sign of $F(i,j)$ is correspondingly non-negative for any value of k_{ji}. Hence, the occurrence of fusion determined by the sign of $F(i,j)$ in the above proposition includes also any consenting case without conflict.

From Proposition 4, we now get another definition of the group size $m_f^*(i)$ *compromisingly acceptable* for $\mathbf{G}(i)$: $F(i,j) \ge 0$ for all j with $1 \le j \le m_f^*(i)$ and $F(i, m_f^*(i)+1) < 0$. The existence of $m_f^*(i)$ for each i can be easily proved since $F(i,0) = 0$, $\Phi_i(i+j) < 0$ and $\Phi_j(i+j) < 0$ for suffciently large $j > n_{\mathrm{G}}$. From the definition of $m_f^*(j)$, when the fusion between $\mathbf{G}(i)$ and $\mathbf{G}(j)$ with $j \le m_f^*(i)$ compromisingly occurs, it is necessarily satisfied that $m_f^*(j) \ge i$. From Proposition 4, related to the existence of $m_f^*(i)$, some mathematical characteristics of

$m_f^*(i)$ can be obtained as shown in Appendix F. Moreover, the following corollary of Proposition 4 can be obtained (Appendix G):

Corollary 2. *As k_{ji} gets larger for any j, $m_f^*(i)$ becomes larger for $i < n_c$, and smaller for $i > n_c$.*

This corollary indicates that, as the total cost paid by the larger group for the conflict gets larger, the compromised fusion becomes more feasible, because m_f^* ({the larger group}) gets smaller.

Correspondingly to the specific group size M_f defined by (6), we can define

$$M_f^* := \min\left\{j \mid m_f^*(j) = 0\right\}, \tag{14}$$

which corresponds to n^* in [16]. Making use of the mathematical characteristics of $m_f^*(i)$ in Appendix F, the non-increasing monotonicity of $m_f(i)$ and n_i in terms of i, the definition of M_f given by (6), $n_{n_S-1} = 1$, and $n_{n_S} = 0$, we can easily find that $M_f \le M_f^* \le n_S$. Group of size beyond or equal to M_f^* never wants its fusion consentingly or compromisingly with any other group, while the group of size below M_f^* wants its fusion consentingly or compromisingly with some group.

We could obtain nothing general about the maximal group size composed by a fusion, that is, about the nature of $i + m_f^*(i)$. In this paper, it will be shown later by a numerical example that the size $i + m_f^*(i)$ can take its maximum for some $i > 1$: With the fusion, the group size can become larger than $n_S^* = 1 + m_f^*(1)$, that is, than the upper bound size determined by a series of solitary outsider's immigrations.

4. Fission

In this section, we consider the fission of a group $\mathbf{G}(n)$ of size n into two subgroups $\mathbf{g}(i)$ and $\mathbf{g}(n-i)$ of size i and $n-i$ respectively. As a specific case, we may consider a fission into $\mathbf{g}(1)$ and $\mathbf{g}(n-1)$, which can be called the *ostracism* for a member $\mathbf{g}(1)$.

According to the fission of a group $\mathbf{G}(n)$ into subgroups $\mathbf{g}(i)$ and $\mathbf{g}(n-i)$, the relative IF value per member in the subgroup $\mathbf{g}(i)$ can be given by

$$\begin{aligned}\Theta_n(i) &:= \Delta w(i,n) + r(i-1)\Delta w(i,n) + r(n-i)\Delta w(n-i,n)\\ &= -\Phi_i(i + [n-i]),\end{aligned} \tag{15}$$

where the function Φ is defined by (6). Only when both $\Theta_n(i)$ and $\Theta_n(n-i)$ are non-negative, the fission into subgroups $\mathbf{g}(i)$ and $\mathbf{g}(n-i)$ occurs without conflict between them. In contrast, if $\Theta_n(i) < 0 \le \Theta_n(n-i)$ or if $\Theta_n(i) \ge 0 > \Theta_n(n-i)$, a conflict about the fission occurs since one subgroup wants the fission and the other does not.

Making use of the characteristics of the IF function Φ analyzed in the previous section, from Proposition 3 and Corollary 1, we can obtain the followings:

Proposition 5. *If the relatedness among members in the group of size n is 1, the fission into two subgroups occurs whenever one of two subgroups wants the fission,* *while it never occurs whenever one does not want. If the relatedness is not 1, there could occur such a conflict about the fission that the smaller subgroup less than n_c does not want the fission while the larger than n_c wants.*

Corollary 3. *Group fission into two subgroups of size beyond n_c always occurs, while that into two subgroups of size below n_c never occurs.*

Thus, for any group of size not beyond n_c, any fission never occurs.

From the relation between Φ and Θ in (15), we remark that, according to the group fission, the maximal fusion-acceptable group size $m_f(i) + 1$ gives the minimal size of the counter subgroup against the subgroup of size i. In other words, the fission into two subgroups of size i and $n - i$ never occurs if $n < m_f(i) + 1$. Moreover, the specific group size M_f defined by (6) gives the lower bound for the group size with which a fission could occur: Any fission into two subgroups never occurs for the group of size not beyond M_f.

As for the resolution of the conflict about a fission, we can obtain the following result corresponding to Proposition 4:

Proposition 6. *For the conflict resolution about a fission into subgroups* $\mathbf{g}(i)$ *and* $\mathbf{g}(n - i)$*, the fission compromisingly occurs if and only if the following* $\Gamma(i; n)$ *is non-negative:*

$$\begin{aligned}\Gamma(i; n) := & \big[\{1 + r(n - i - 1)\}\kappa_{i;n} + r(n - i)\big]\, i\Theta_n(i) \\ & + \big[1 + r(i - 1) + ri\kappa_{i;n}\big]\,(n - i)\Theta_n(n - i),\end{aligned} \tag{16}$$

where $\kappa_{i;n}$ is a positive constant which denotes the ratio of the total cost paid by $\mathbf{g}(n - i)$ *to that by* $\mathbf{g}(i)$ *at the moment of conflict resolution:*

$$\kappa_{i;n} := \frac{(n - i)C_{n-i;n}}{iC_{i;n}}. \tag{17}$$

From (15), we used the following relation to derive this proposition:

$$\Gamma(i; n) = -\left. F(i, n - i)\right|_{k_{n-i,i}=\kappa_{i;n}}. \tag{18}$$

As a counterpart of $m_f^*(i)$, we can define the specific group size $m_d^*(n)$ that gives the maximal size of the larger subgroup fissioned from $\mathbf{G}(n)$. It is satisfied that $\Gamma(k; n) \geq 0$ for all k with $1 \leq k \leq m_d^*(n)$ and $\Gamma(m_d^*(n) + 1; n) < 0$. From Proposition 5, we find that $m_d^*(n) \geq n_c$.

In our considerations about the fission, we have not mentioned how the size of subgroup may be determined in the fission, or how each member belongs to one of subgroups. Our model is to consider theoretically the contribution of the group size to the change of the inclusive fitness of member, and hence we do not take into account the *process* of fusion or fission. It may be another theoretical problem to be considered.

5. Numerical example

In this section, making use of the fitness function $w(n)$ numerically given in Fig. 1, some properties of the group size determined especially by the group fusion are shown by numerical calculations.

For the numerical example of the fitness function $w(n)$ in Fig. 1, we have $n_G = 20$, $n_S = 90$, and $n_c = 13$. Critical sizes M_f, $n_S^* = m_f(1) + 1$, and M_f^* depend on the relatedness r and the parameter k_{ji}. As indicated in Fig. 1, $M_f = 34$, $n_S^* = m_f(1) + 1 = 69$, and $M_f^* = 50$ are for the case when $r = 0 \cdot 2$ with $k_{ji} = 1$ for any i and j. Indeed, for the case with $k_{ji} = 1$ for any i and j, we get the result about the r-dependence of critical sizes M_f, $n_S^* = m_f(1) + 1$, and M_f^* as shown in Fig. 2. Figure 2 shows that M_f^* takes its unique maximum at a specific range of relatedness r around 0·07. The terminal group size M_f^* is larger for an intermediate range of relatedness than for the other, so that the higher relatedness does not necessarily result in the larger group size. A similar result has been obtained by [16] according to the group size determined by a series of solitary outsider's immigrations.

5.1. Conflict about the fusion without cost deviation

In this section, we consider the case when $k_{ji} = 1$ for any i and j. Total costs paid by encountered groups in any conflict about the fusion are equal to each other. Conflict about the fusion occurs between encountered two groups of the gray and the black regions in Fig. 3. Groups of the gray region in Fig. 3 result in the compromised fusion, while those of the black region result in the rejection of the fusion. It can be seen from Figs. 3(a1, b1) that $m_f^*(i)$ located on the boundary between the gray and the black regions is non-increasing in terms of i. Moreover, from Figs. 3(a2,

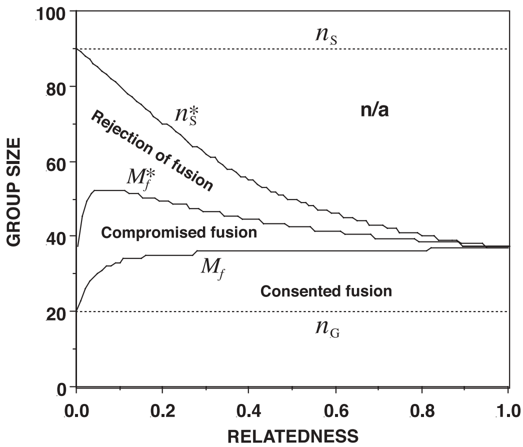

Fig. 2. Dependence of the critical sizes on the relatedness r, obtained numerically for the fitness function $w(n)$ given in Fig. 1 with $k_{ji} = 1$ for any i and j.

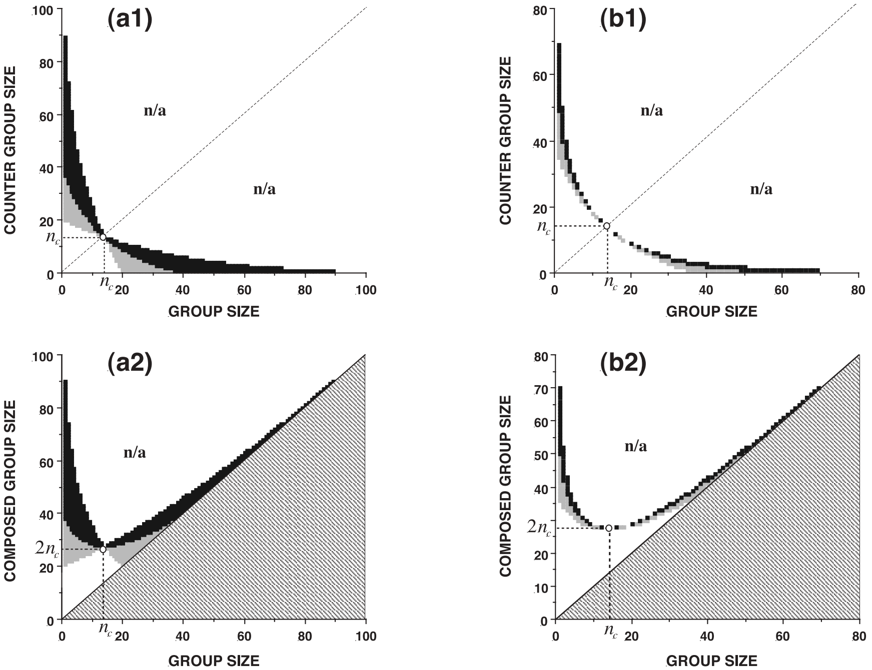

Fig. 3. Occurrence of the conflict about the fusion in case of $k_{ji} = 1$ for any i and j. (a) $r = 0$; (b) $r = 0{\cdot}2$. (a1) and (b1) are about sizes of encountered groups. (a2) and (b2) are about the group size composed by the fusion, so the hatched region is nonsense. The gray region is of the conflict to result in the compromised fusion, and the black region is of the conflict to result in the rejection of fusion. For the pair of group sizes below the gray and the black regions, the fusion occurs without conflict, while, beyond them, no group wants the fusion.

b2), the group size composed by the fusion takes its minimum at $i = n_{\rm c}$, and its maximum at $i = 1$ or $i = M_f^* - 1$. This holds for any relatedness r, as confirmed by some numerical calculations. Hence, we conclude that the maximal group size composed by the fusion is M_f^*. Further, we numerically find that $m_f^*(i)$ is larger for an intermediate value of the relatedness r as well as M_f^*.

By comparing (a) to (b) of Fig. 3, it is implied that the number of pairs of group sizes to cause the conflict about the fusion is non-increasing in terms of the relatedness r, and must be zero for $r = 1$. Indeed, this is numerically shown in case of $k_{ji} = 1$ for any i and j as indicated in Fig. 4(a). However, Fig. 4(a) shows also that the number of conflicts resulting in the compromised fusion is not necessarily non-increasing but increasing for a sufficiently small relatedness. In contrast, the percentage of the compromised fusions to the total conflicts appears to have a non-monotone variation in terms of the relatedness as shown in Fig. 4(b), although its overall tendency may be regarded as roughly increasing.

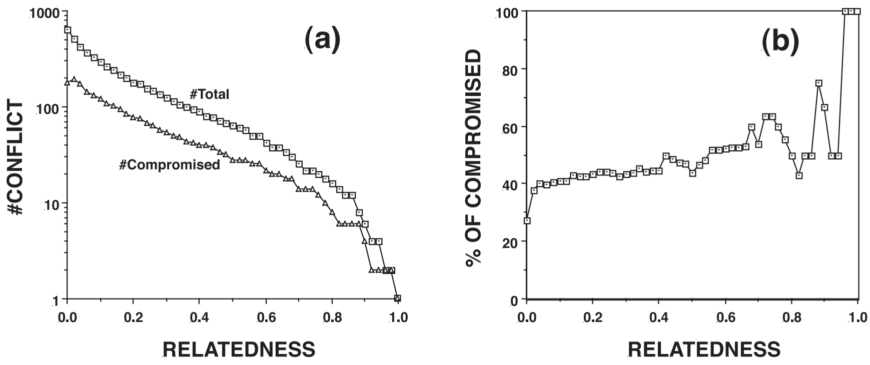

Fig. 4. (a) Dependence of the total number of pairs of group sizes to cause the conflict about the fusion, and that to cause the compromised fusion on the relatedness r. (b) Dependence of the percentage of the compromised fusion to the total conflict on the relatedness r. Numerical results with $k_{ji} = 1$ for any i and j.

5.2. Conflict about the fusion with a cost deviation

Next, let us consider a case when $k_{ji} \neq 1$ and the total cost paid for the conflict depends on whether the group wants the fusion or not. We assume the following specific form of k_{ji}:

$$k_{ji} = h_\lambda(i, j) := \begin{cases} \lambda & \text{when } i > j; \\ 1 & \text{when } i = j; \\ 1/\lambda & \text{when } i < j, \end{cases} \tag{19}$$

where the parameter λ denotes the degree of the advantage of the larger group with regard to the total cost paid for the conflict about the fusion. The case when $k_{ji} = 1$ corresponds to that when $\lambda = 1$. Since we have shown in the previous section that the larger group does not want the fusion in the conflict, λ can be regarded as the degree of the advantage of the group which does not want the fusion in the conflict. As λ gets larger, the advantage of the larger group becomes greater. If $\lambda < 1$, then the smaller group in the conflict about the fusion has an advantage over the larger counter group with regard to the total cost paid for the conflict.

In Fig. 5, conflicting pairs of group sizes are indicated by the gray and the black regions for $\lambda = 2$ and $\lambda = 10$ respectively in case of $r = 0$. Since the occurrence of the conflict does not depend on k_{ji} but on the relatedness r, the total area of the gray and the black regions in Fig. 5(a) coincides with that in case of $\lambda = 1$ in Fig. 3(a). However, the gray region for the compromised fusion significantly depends on the value of λ.

As seen from Figs. 5(a1, b1), $m^*_f(i)$ located on the boundary between the gray and the black regions is non-increasing in terms of i as in Fig. 3 for $\lambda = 1$. In contrast, Figs. 5(a2, b2) indicate that the maximal group size composed by the fusion is not necessarily monotone in terms of i. Further, it is not necessarily equal to M^*_f. These results are different from those in case of $\lambda = 1$. Indeed, numerical results

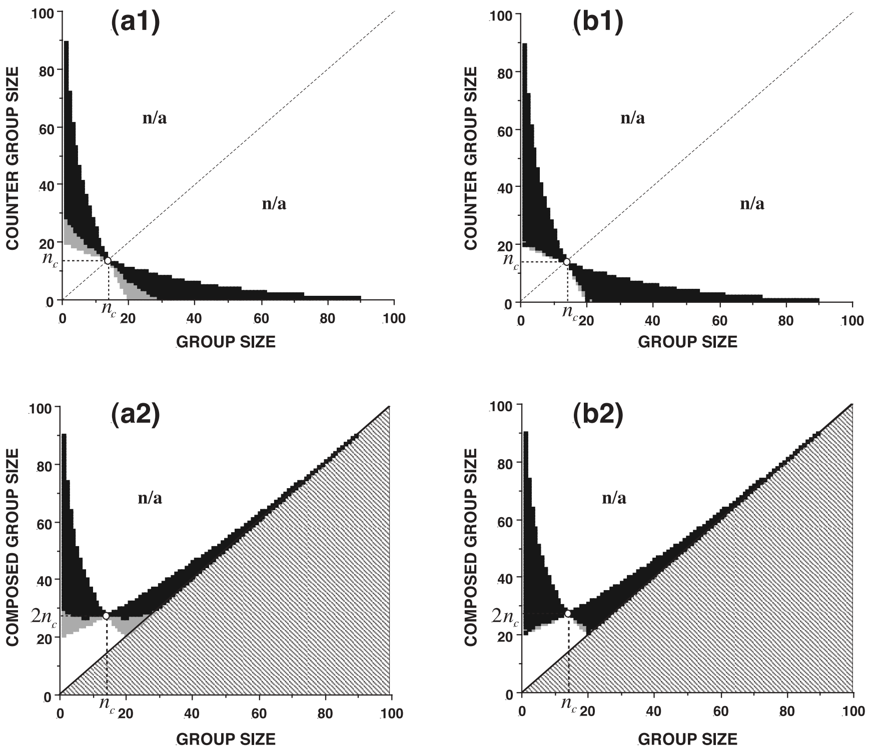

Fig. 5. Occurrence of the conflict about the fusion. In the case when $k_{ji} = h_\lambda(i, j)$ given by (19). Relatedness $r = 0$. (a) $\lambda = 2$; (b) $\lambda = 10$. Meanings of regions in these figures are the same as for Fig. 3.

shown in Fig. 6 clearly indicate that the maximal size is $2n_c$ for a sufficiently small relatedness r and a sufficiently large λ. Especially in case of $r = 0$, Fig. 6(b) shows the case when the maximal size composed by the fusion becomes $2n_c$ larger than M_f^* for sufficiently large λ. For r smaller than about 0·01 and λ larger than about 2, M_f^* can become smaller than $2n_c$ as indicated by the darkest region in Fig. 6(a).

Moreover, Fig. 6(a) shows that the maximal size composed by the fusion is not necessarily monotone in terms of the relatedness r, and takes its maximum for some r around 0·1. This is the same tendency as already mentioned for M_f^* in Fig. 2. Only for $\lambda \ll 1$ when the smaller group has a sufficiently great advantage over the larger counter group with regard to the total cost for the conflict about the fusion, the maximal size composed by the fusion is monotonically non-increasing in terms of the relatedness r, as indicated in Fig. 6(a). As for the λ-dependence, the maximal size composed by the fusion is non-increasing in terms of λ as seen in Fig. 6(a). Moreover, numerical calculations imply that $m_f^*(i)$ for each group size i is non-increasing in terms of λ, too.

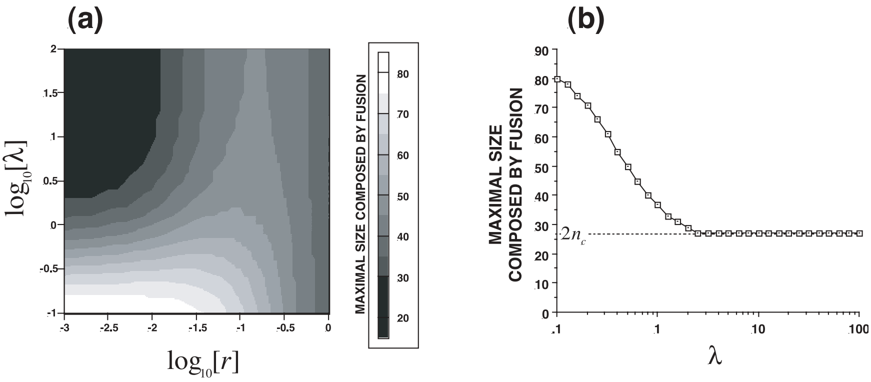

Fig. 6. Maximal group size composed by the fusion. (a) (r, λ)-dependence; (b) λ-dependence of the maximal size in case of the relatedness $r = 0$.

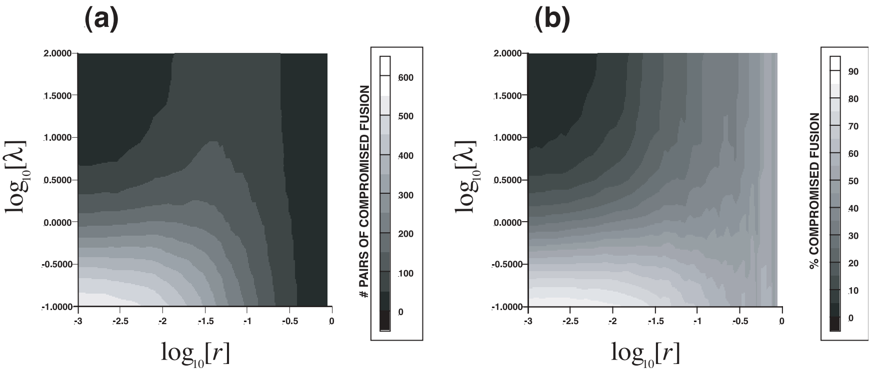

Fig. 7. (r, λ)-dependence of (a) the total number of pairs of group sizes which result in the compromised fusion; (b) the percentage of the compromised fusions to the total conflicts.

On the other hand, as shown in Fig. 7(a), the number of pairs of group sizes which result in the compromised fusion appears monotonically non-increasing in terms of the relatedness r for $\lambda \leq 1$, while it takes its maximum with an intermediate value of the relatedness r for $\lambda > 1$. As for the percentage of the compromised fusions to the total conflicts, the dependence on the relatedness r appears more complicated. Roughly saying from Fig. 7(b), it appears non-increasing in terms of r for $\lambda < 1$, while non-decreasing for $\lambda > 1$. This tendency clearly appears for some sufficiently small or sufficiently large λ, whereas it is ambiguous for some λ around 1.

6. Conclusion

We considered the group size determined by the intra-reactions (self-growth, ostracism and fission) and by the inter-reactions between two groups (immigration and fusion). It was shown that, in group reactions, a conflict between two groups could occur about the reaction, according to the increment of the *inclusive fitness* (IF) of members in each group. We discussed the conflict resolution, too. A numerical example explicitly showed some interesting natures of the size determined by such group reactions.

It is implied that there exists a certain critical group size, n_c in our model, at which the behavioral choice taken by the group in the conflict changes. The existence and the qualitative natures of the critical size n_c are determined by the qualitative characteristics of the direct fitness function $w(n)$. Since we assumed only the general qualitative characteristics of $w(n)$ in our mathematical model, those results in this paper would be applicable also for more concrete biological arguments.

The group size composed by the fusion may exceed the critical size n_c. When both of encountered groups have the size smaller than or larger than n_c, the conflict about the group reaction cannot occur. If every group in a community grows up its size and simultaneously comes to exceed the critical size, then any group does not want the fusion. Eventually, within such a community, the conflict about the fusion never occurs. However, even in such a case, the intra-group reactions, ostracism and fission, may occur, and the peace could not be necessarily maintained.

Our numerical example indicated that, in the case when the cost paid for the conflict significantly depends on whether the group wants the group reaction or not, the consequence of conflict would show some non-trivial features. The consequent group size can become larger by a group fusion than by a sequence of solitary's immigrations. This result implies that the group size dynamics could not be decomposed into only some reactions between a group and an individual. The group fusion (or fission) could not be necessarily treated as a series of solitary outsider's immigrations (or member's ostracisms).

Further, it was shown that the maximal group size composed by some group fusions takes its maximum for a relatively small positive relatedness. The larger relatedness does not necessarily result in the greater group size. Even though it might significantly depend on the characteristics of the direct fitness function, this result about the relatedness dependence of the maximal group size would hold for a wide family of direct fitness functions which satisfy the general assumptions in our modelling.

From Propositions 4 and 6, and from the k_{ji}-dependence of $m^*_f(i)$ in Corollary 2, we can prove that, for $\kappa_{i;n} \neq k_{n-i,i}$, it is likely that the fusion could occur between subgroups fissioned from a group: Even if the fission into $\mathbf{g}(i)$ and $\mathbf{g}(n-i)$ occurs, it is likely that the fusion between $\mathbf{g}(i)$ and $\mathbf{g}(n-i)$ could occur if the total cost paid by the larger group for the fusion is larger than that for the fission, relative to the total cost paid by the smaller group. Otherwise, the fusion between those fissioned subgroups does not occur. We may say the former fission *temporal* or *unstable*. From Corollaries 1 and 3, since the group fusion never occurs between two groups of size beyond n_c and so never does the group fission into two subgroups of size below n_c, such a temporal fission is likely to occur only into one subgroup of size not beyond n_c and the other of size not below n_c. However, we may consider that the actual fission would be never followed by such a fusion between two subgroups just after their fission. Indeed, the fusion between just fissioned two subgroups would be consumptive to lose some energy due to the conflict about the fission. It does not seem optimal as a behavioral choice, either.

It would be a natural extension of our modelling to consider the optimal behavioral choice taking into account future possible fusions and fissions. Such an optimal theory could be used to consider the maximization of the long term payoff. One way to incorporate such a structure to maximize the long term payoff with a sequence of behavioral choices would be a dynamic programming modelling [17,21,22]. It may be one of the next steps of our study for the theory of group size determination. In such a dynamic programming modelling, a criterion to estimate each single choice of behavior is necessary, so that we expect that the modelling and the results in this paper could contribute to such an advanced modelling.

Some statistical natures of group sizes within a community, for example, the frequency distribution or the rank-size relation, may be discussed through the theory of the optimal size with group reactions. It is expected that theoretical results including those in this paper will contribute to some understanding about the group size dynamics in nature.

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Appendix

A. Existence of $m_f(i)$

In this appendix, we prove the existence of $m_f(i)$. If it exists, the uniqueness is trivial from the definition in the main text. Since $\Phi_i(i) = 0$, we find that $m_f(i) = 0$ if and only if $\Phi_i(i+1) < 0$. Otherwise, $m_f(i) \geq 1$. Now, let us consider only the case when $\Phi_i(i+1) \geq 0$.

At first, let us consider

$$\Phi_i(i+i) = \{1 + r(i+i-1)\}\Delta w(2i, i). \tag{20}$$

We see that $\Phi_i(i+i) \geq 0$ only when the difference $\Delta w(2i, i) = w(2i) - w(i) > 0$. From the characteristics of w and the definition of n_c, $w(2i) < w(i)$ for any $i > n_c$, while $w(2i) \geq w(i)$ for any $i \leq n_c$. Thus, if $i \leq n_c$, then $\Phi_i(i+i) \geq 0$, and otherwise $\Phi_i(i+i) < 0$. This means that there exists the value defined as $m_f(i)$ less than i if $i > n_c$. So let us focus the case when $i \leq n_c$.

For $i \leq n_c$ and $j = N_i + k - i$ with $k \geq 1$,

$$\begin{aligned}\Phi_i(i + [N_i + k - i]) = \{1 + r(i-1)\}\Delta w(N_i + k, i) \\ + r(N_i + k - i)\Delta w(N_i + k, N_i + k - i). \end{aligned}\tag{21}$$

Since $i \leq n_c$ and $N_{n_c} = 2n_c \leq N_i$, we find that $i \leq N_i - i$. From the definition of N_i, $w(N_i+k) < w(i) \leq w(N_i)$. Therefore, $\Delta w(N_i+k, i) < 0$. If $N_i+k-i \leq N_i$, then also $\Delta w(N_i + k, N_i + k - i) < 0$, because $i \leq N_i - i < N_i + k - i$ and $w(N_i+k-i) \geq w(i) > w(N_i+1) > w(N_i+k)$ from the definition of N_i and the decreasing monotonicity of $w(n)$ for $n \geq n_G$. On the other hand, if $N_i+k-i > N_i$, then $w(N_i + k - i) > w(N_i + k)$ from the decreasing monotonicity of $w(n)$ for $n \geq n_G$ and the feature that $N_i > n_G$. This shows that $\Delta w(N_i + k, N_i + k - i)$ is negative again. Hence, the right side of (21) is negative for any $k \geq 1$. This means that $\Phi_i(i + j) < 0$ for any $j > N_i - i$ $(\geq i)$. Consequently there exists the value defined as $m_f(i)$ less than $N_i - i$ $(\geq i)$ when $i \leq n_c$. These arguments prove the existence of $m_f(i)$. □

B. Mathematical characteristics of $m_f(i)$

In this appendix, we prove some mathematical characteristics of $m_f(i)$, which appear useful for mathematical considerations about our model. At first, from definitions of N_i and n_i by (4) and (5), the following lemma can be easily obtained:

Lemma 1. *$n_c \leq n_i$ for $i < n_c$, while $n_i \leq n_c$ for $i > n_c$.*

Now we prove the following lemma about mathematical characteristics of $m_f(i)$:

Lemma 2. *$m_f(i)$ satisfies the following conditions:*

i) $n_i \leq m_f(i) < N_i - i$ for $i \leq n_c$;
ii) $N_i - i \leq m_f(i) \leq n_i$ for $i > n_c$ and $i < n_G$;
iii) $m_f(i) \leq n_i$ for $i \geq n_G$;
iv) $m_f(i)\big|_{r=1} \leq m_f(i) \leq m_f(i)\big|_{r=0}$ for $i \leq n_c$;
v) $m_f(i)\big|_{r=0} \leq m_f(i) \leq m_f(i)\big|_{r=1}$ for $i > n_c$;
vi) $m_f(n_c) = n_c$ independently of r.

Proof of i). The upper bound for $m_f(i)$, that is, $m_f(i) \leq N_i - i$ can be proved directly from the proof for the (unique) existence of $m_f(i)$, given in Appendix A. So let us focus the lower bound for $m_f(i)$. When $i \leq n_c \leq n_i$ from Lemma 1, we find that $\Phi_i(i + j) \geq 0$ for any $j \leq n_i$. This is because, from the definition of n_i and the increasing monotonicity of w, $w(i + j) \geq w(j) \geq w(i)$ when $i \leq j \leq n_i$, and $w(i + j) \geq w(i) \geq w(j)$ when $j < i \leq n_i$. As a result, $m_f(i) \geq n_i$. □

Proof of ii) and iii). When $i > n_c$ and $j = n_i + k$ with $k \geq 1$,

$$\Phi_i(i + [n_i + k]) = \{1 + r(i - 1)\}\Delta w(i + [n_i + k], i) + r(n_i + k)\Delta w(i + [n_i + k], n_i + k). \quad (22)$$

From the definition of n_i, we can find that $w(i + n_i + 1) < w(n_i) \leq w(i + n_i)$. Since $i+n_i > n_G$, $w(i+n_i+k) \leq w(i+n_i+1)$ for $k \geq 1$. In addition, for $i < n_G$, from Lemma 1, $n_i \leq n_c$ when $i > n_c$, and $i + n_i = N_{n_i} \geq N_i > n_G$ from the non-increasing nature of N_i in terms of i. Hence we find that $w(n_i+i) < w(i)$. For $i \geq n_G$, the decreasing monotonicity of w leads to the inequality $w(i + n_i + k) <$

$w(i)$. This argument shows that $\Delta w(i + [n_i + k], i) < 0$, subsequently the first term of the right side of (22) is negative.

In the same way, from the piecewise monotonicity of w, if $n_i + k > n_G$, then $w(i + n_i + k) \leq w(n_i + k)$. If $n_i \leq n_i + k \leq n_G$, then $w(n_i) \leq w(n_i + k)$. Since $w(i + n_i + k) \leq w(n_i)$ for $k \geq 1$, we lastly find that $\Delta w(i + [n_i + k], n_i + k) < 0$. Thus, the right side of (22) is negative for any $k \geq 1$. Therefore, $m_f(i) \leq n_i$.

Next, when $n_c < i < n_G$ and $j = N_i - i - k + 1$ $(1 \leq k \leq N_i - i)$,

$$\begin{aligned}\Phi_i(i + [N_i - i + k + 1]) = \{1 + r(i - 1)\}&\Delta w(N_i - k + 1, i)\\ &+r(N_i - k - i + 1)\\ &\times\Delta w(N_i - k + 1, N_i - i - k + 1).\end{aligned} \quad (23)$$

Since $1 \leq k \leq N_i - i$, we find that $i + 1 \leq N_i - k + 1 \leq N_i$. Thus, from the definition of N_i, $w(N_i - k + 1) \geq w(i)$. Since $i > n_c$ and $N_{n_c} = 2n_c$, and since N_i is non-increasing in terms of i, we find that $2i \geq N_i$, that is, $N_i - i \leq i$. Besides, from the previous arguments, $1 \leq N_i - k - i + 1 \leq N_i - i$. Hence, from the increasing monotonicity of w, $w(N_i - i - k + 1) \leq w(i)$. Therefore, the right side of (23) is non-negative for any k. This means that $m_f(i) \geq N_i - i$. □

Proof of iv) and v). From (1), we can obtain the following equation:

$$\Phi_i(i + j) = (1 - r)\,[\Phi_i(i + j)]_{r=0} + r\,[\Phi_i(i + j)]_{r=1}\,. \quad (24)$$

Since $0 \leq r \leq 1$, this means that

$$[\Phi_i(i + j)]_{r=0} \leq \Phi_i(i + j) \leq [\Phi_i(i + j)]_{r=1}$$

or

$$[\Phi_i(i + j)]_{r=0} \geq \Phi_i(i + j) \geq [\Phi_i(i + j)]_{r=1}\,.$$

Thus, from the definition, $m_f(i)$ exists between $m_f(i)\big|_{r=1}$ and $m_f(i)\big|_{r=0}$.

Next, since

$$[\Phi_i(i + j)]_{r=0} = w(i + j) - w(i), \quad (25)$$

it is easily found from the definition of N_i that $m_f(i)\big|_{r=0} = N_i - i$ for $i < n_G$. Besides, from the characteristics of w, $[\Phi_i(i + j)]_{r=0} < 0$ for any $i \geq n_G$. From i) and ii), this argument proves iv) and v). □

Proof of vi). Since $N_{n_c} - n_c = n_c$ and $n_{n_c} = n_c$, from i), we find that $m_f(i) \to n_c$ as $i \to n_c$. From the definition, n_c is determined only by the nature of w, independently of r. □

C. r-dependence of $m_f(i)$

Relations iv) and v) of Lemma 2 in Appendix B mean that, for $m_f(i)$ with $0 < r < 1$,

$$\big[\Phi_i(i + m_f(i))\big]_{r=1} < \big[\Phi_i(i + m_f(i))\big]_{r=0} \quad \text{for } i \leq n_c;$$
$$\big[\Phi_i(i + m_f(i))\big]_{r=0} < \big[\Phi_i(i + m_f(i))\big]_{r=1} \quad \text{for } i > n_c.$$

Thus, from (24) in Appendix B, as r becomes larger, $\Phi_i(i + j)$ gets smaller for $i \leq n_c$ and larger for $i > n_c$. This means that, in terms of r, $m_f(i)$ is non-increasing for $i \leq n_c$ and non-decreasing for $i > n_c$. □

D. i-dependence of $m_f(i)$

At first, as mentioned for (25) in Appendix B, $m_f(i)\big|_{r=0} = N_i - i$ for $i < n_G$. Since N_i is non-increasing in terms of i, $m_f(i)\big|_{r=0}$ is decreasing for $i < n_G$. Moreover, from (25), $m_f(i)\big|_{r=0} = 0$ for $i \geq n_G$. This argument shows that $m_f(i)\big|_{r=0}$ is non-increasing in terms of i.

On the other hand, in order to consider the i-dependence of $m_f(i)\big|_{r=1}$ for a fixed relatedness r, let us see the following relation:

$$\Phi_i(i+j) - \Phi_j(i+j) = -(1-r)\{w(i) - w(j)\} \tag{26}$$

as easily obtained from the definition of Φ. In case of $r = 1$, the above relation leads to the equation

$$[\Phi_i(i+j)]_{r=1} = \left[\Phi_j(i+j)\right]_{r=1}. \tag{27}$$

The relation (27) especially indicates that the signs of both sides of (27) coincides with each other: When the sign is negative, it means that, if $m_f(i)\big|_{r=1} < j$, then $m_f(i)\big|_{r=1} < i$ and vice versa for two groups of size i and j. In contrast, when the sign is non-negative, it means that, if $m_f(i)\big|_{r=1} \geq j$, then $m_f(j)\big|_{r=1} \geq i$ and vice versa.

Now, suppose that there exists some group size i such that $m_f(i)\big|_{r=1} < m_f(i+1)\big|_{r=1}$. Then, there must exist a group size j such that $m_f(i)\big|_{r=1} < j \leq m_f(i+1)\big|_{r=1}$. The first inequality gives the relation $m_f(j)\big|_{r=1} < i$, while the second does $m_f(j)\big|_{r=1} \geq i+1$. This is contradictory. Consequently, there cannot exist any group size i such that $m_f(i)\big|_{r=1} < m_f(i+1)\big|_{r=1}$. This proves that $m_f(i)\big|_{r=1}$ is non-increasing in terms of i.

Since both $m_f(i)\big|_{r=0}$ and $m_f(i)\big|_{r=1}$ are non-increasing in terms of i, and since $m_f(i)$ corresponds to the sign change of the function Φ, if the right side of (24) in Appendix B for $i = p$ with a fixed r changes its sign at $j = q$, then that for $i = p+1$ changes its sign at j not beyond q. This means that $m_f(i)$ is non-increasing in terms of i with any fixed relatedness r. □

E. Proof of Proposition 3 and Corollary 1

To prove Proposition 3 and Corollary 1, we use the following lemmas:

Lemma 3. *If $w(i) \leq w(j)$, then $\Phi_i(i+j) \geq \Phi_j(i+j)$. The equality holds only when $r = 1$ or $w(i) = w(j)$.*

Lemma 4. *$w(m_f(i)) \geq w(i)$ for $i \leq n_c$, and $w(m_f(i)) < w(i)$ for $i > n_c$.*

From the relation (26) in Appendix D, the proof of Lemma 3 is clear. So we give here only the proof of Lemma 4. From Lemmas 1 and 2 in Appendix B, when $i < n_c$, it is satisfied that $i < n_c \leq n_i \leq m_f(i) < N_i$. From the definition (4) of N_i, $w(j) \geq w(i)$ for any $j \leq N_i$. Thus, $w(m_f(i)) \geq w(i)$. When $i > n_c$, it is satisfied that $m_f(i) \leq n_i \leq n_c < i$. Hence, from the increasing monotonicity of w, $w(m_f(i)) \leq w(n_i)$. The definition of n_i gives the following inequality: $w(n_i) \leq w(i+n_i)$. If $i \leq n_G$, then, from the increasing monotonicity of w, $w(n_i) < w(i)$. If $i > n_G$, then, from the decreasing monotonicity of w, $w(i) > w(i+n_i)$. Lastly, $w(n_i) < w(i)$ for $i > n_i$. Therefore, $w(m_f(i)) < w(i)$. □

Proof of Proposition 3 and Corollary 1. Lemmas 3 and 4 show that, if $r \neq 1$,

$$\Phi_i(i+m_f(i)) \geq \Phi_{m_f(i)}(m_f(i)+i) \quad \text{for any } i < n_c;$$
$$0 \leq \Phi_i(i+m_f(i)) < \Phi_{m_f(i)}(m_f(i)+i) \quad \text{for any } i > n_c.$$

Therefore, $m_f(m_f(i)) < i$ for some $i < n_c \leq m_f(i)$, while $m_f(m_f(i)) \geq i$ for any $i > n_c \geq m_f(i)$. This means the following: Between two groups of size i and j such that $i < n_c < j$, if the larger group of size j *wants the fusion*, the smaller of size i does. In the conflict about the fusion, the smaller of size i *wants the fusion* and the larger of size j does not.

Let us consider the fusion between two groups of size i and j such that $i \leq j < n_c$. From Lemmas 1 and 2 in Appendix B, since $n_c \leq m_f(i)$ and $n_c \leq m_f(j)$ so that $j < m_f(i)$ and $i < m_f(j)$, the fusion occurs without any conflict. On the other hand, in case of two groups of size i and j such that $n_c < i \leq j$, from Lemmas 3 and 4, since $n_c \geq m_f(i)$ and $n_c \geq m_f(j)$ so that $j > m_f(i)$ and $i > m_f(j)$, both two groups do not want the fusion. In the case when $i < j \leq n_c$ or $n_c \leq i < j$, the same argument can be applied. Therefore, taking into account viii) of Lemma 2 in Appendix B, it is lastly proved that the conflict could occur only between two groups of size i and j such that $i < n_c < j$.

If the relatedness $r = 1$, Lemma 3 indicates that $\Phi_i(i+j) = \Phi_j(i+j)$ for any i and j, so that $\Phi_i(i+m_f(i)) = \Phi_{m_f(i)}(m_f(i)+i)$ for any i. This means that $m_f(m_f(i)) = i$ for any i. Hence, whenever one group wants the fusion, so does the other. Consequently, when $r = 1$, the conflict about the fusion never occurs. When $w(i) = w(j)$, $\Phi_i(i+j) = \Phi_j(i+j)$. Thus, the conflict cannot occur, either. These arguments prove Proposition 3 and Corollary 1. □

F. Mathematical characteristics of $m^*_f(i)$

In this appendix, we prove the following lemma related to the existence of $m^*_f(i)$:

Lemma 5.

$$n_i \leq m^*_f(i) \leq m_f(i) \textit{ for } i < n_c;$$
$$m_f(i) \leq m^*_f(i) \leq n_i \textit{ for } i > n_c;$$
$$m^*_f(n_c) = n_c.$$

Let us begin with the conflict about the fusion between two groups of size i and j such that $i < n_c < j$. From Proposition 3, since the smaller group *wants the fusion* while the larger *does not*, the compromised fusion can be realized by the larger group's yielding to the smaller and accepting the fusion. Otherwise, the smaller group yields to the larger and gives up the fusion. The former resolution of conflict means that the maximal group size compromisingly acceptable for the larger group is greater than the selfishly acceptable size: $m^*_f(j) \geq m_f(j)$. On the other hand, the latter means that the maximal group size compromisingly acceptable for the smaller group is less than the selfishly acceptable one: $m^*_f(i) \leq m_f(i)$. In the case when $i = n_c$, since $m_f(n_c) = n_c$ (Lemma 2 in Appendix B), we find that $m^*_f(n_c) = m_f(n_c) = n_c$.

Next, we prove that $n_i \leq m^*_f(i)$ for $i < n_c$ and that $m^*_f(i) \leq n_i$ for $i \geq n_c$. For a group of size $i < n_c$, we find that $i < n_c \leq n_i \leq m_f(i)$ from Lemmas 1 and 2 in Appendix B. Thus, $\Phi_i(i+n) \geq 0$ for any $n \leq n_i$. Now, consider the relative IF value $\Phi_n(i+n)$ for $n \leq n_i$. From the definition of n_i, we find that $\Delta w(i+n, n)$ is non-negative for any $n \leq n_i$. From i) of Lemma 2 in Appendix B, we find that $i < i+n \leq i+n_i \leq N_i$. Hence, $w(i+n) \geq w(i)$ from the definition of N_i. Lastly, $\Phi_n(n+i) \geq 0$ for any $n \leq n_i$. Since both $\Phi_i(i+n)$ and $\Phi_n(n+i)$ are non-negative for any $n \leq n_i$, we find that $F(i, j) \geq 0$ for any $j \leq n_i$, so that $n_c \leq n_i \leq m^*_f(i)$.

In case of $i \geq n_c$, from the definition of n_i and the characteristics of w, we find that $w(i+n) < w(n)$ for any $n \geq n_i + 1$. Since $i \geq n_i$ from Lemma 1 in Appendix B, $i + n > i + n_i = N_{n_i} \geq N_i$ for $i < n_G$. Thus, from the definition of n_i, $w(i+n) < w(i)$ for $i \leq n_G$. For $i > n_G$, the decreasing monotonicity of w leads to the inequality $w(i+n) < w(i)$. Therefore, $\Phi_n(i+n)$ is negative for any $n \geq n_i + 1$, and simultaneously $\Phi_i(i+n) < 0$. This means that $F(i, j) < 0$ for any $j > n_i$, so that $m^*_f(i) \leq n_i \leq n_c$.

Since $n_{n_c} = n_c$ and $m_f(n_c) = n_c$ (Lemma 2 in Appendix B), we can find that $m^*_f(n_c) = n_c$. □

G. Proof of Corollary 2

Let define the following function $\Xi(i, j)$ independent of both k_{ij} and k_{ji}:

$$\Xi(i, j) := rj\left[\Phi_i(i+j) + \Phi_j(i+j)\right] + (1-r)\Phi_i(i+j). \tag{28}$$

Then, $F(i, j)$ defined by (13) can be expressed as

$$F(i, j) = i\,\Xi(i, j)k_{ji} + j\,\Xi(j, i). \tag{29}$$

When $j \leq m^*_f(i)$, we have $F(i, j) \geq 0$ from Proposition 4. At first, in the case when $i < n_c < j \leq m^*_f(i)$, we know that $m^*_f(i) \leq m_f(i)$ from Lemma 1 in Appendix B and Lemma 5 in Appendix F. Hence, $j \leq m_f(i)$ and thus $\Phi_i(i+j) \geq 0$. Now, if $\Phi_j(i+j) \geq 0$, then $\Xi(i, j) \geq 0$. In contrast, when $\Phi_j(i+j) < 0$, consider the following inequality:

$$\Xi(i, j) \geq rj\left[\Phi_i(i+j) + \Phi_j(i+j)\right]. \tag{30}$$

If $\Xi(i, j) < 0$, the right side of (30) is negative, so eventually $\Xi(j, i) < 0$. This implies that $F(i, j) < 0$. Since this is contradictory to $F(i, j) \geq 0$, it is concluded that $\Xi(i, j) \geq 0$. Hence, in the case when $i < n_c < j \leq m^*_f(i)$, $F(i, j)$ is non-decreasing as k_{ji} gets larger. This means that $m^*_f(i)$ in this case is non-decreasing as k_{ji} gets larger.

Next, let us consider the case when $m_f^*(i) < n_c < i$. In this case, from Lemma 1 in Appendix B and Lemma 5 in Appendix F, it is assured that $m_f(i) \leq m_f^*(i) < n_c < i$. Since we are interested in the case of the conflict about the fusion, let us consider only the case when $m_f(i) < j$, so that $m_f(i) < j \leq m_f^*(i) < n_c < i$. In this case, we have $\Phi_i(i+j) < 0$. If $\Phi_j(i+j) \leq 0$ in this case, we obtain a contradictory result such that $F(i, j) < 0$. Hence, $\Phi_j(i + j) > 0$. Let us now turn to $F(j, i)$. Along the same line of argument, it can be shown that $\Xi(j, i) \geq 0$, so that $F(j, i)$ is non-decreasing as k_{ij} gets larger. Since $k_{ij} = 1/k_{ji}$, $F(j, i)$ is non-increasing as k_{ji} gets larger. Since $F(j, i)$ has the same sign as $F(i, j)$, this result shows that $m_f^*(i)$ is non-increasing as k_{ji} gets larger when $m_f(i) < j \leq m_f^*(i) < n_c < i$. □

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