Mathematical Considerations on Establishment of Territory: How does Population Size of Ordered Individuals Influence on it?

順位構造をもつ個体群のサイズとなわばり形成の関係に関する数理的研究

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Sachiko YOSHIMURA

95251839

Department of Information and Computer Sciences, Faculty of Science
Nara Women's University
Kita-uoya-nishi-machi, Nara 630-8506
JAPAN

論文概要

なわばり形成と順位構造をもつ個体群のサイズとの関係に関する数理的研究

奈良女子大学理学部情報科学学科
95251839 吉村　佐知子

「一つの山には２匹のトラは棲むことができない」という中国のことわざがある。これは、”なわばり ”のことを表している。なわばりとは、「個体あるいは個体のグループが、明らかな防衛行動や誇示によって、多少とも排他的に含有する地域」(Wilson, 1975; Davies, 1978a) と定義されている。 なわばりに関する分類は、数多くあるが、あらゆる活動が行われる広いなわばり、交尾や求愛のためのなわばり、休息場所やかくれ場所としてのなわばり、そして非繁殖期の採餌なわばりなどがあげられる。本研究においては、採餌なわばりを取り扱う。採餌なわばりを持つ代表的な動物の一つにアユがあげられる。アユは、河川を遡上し、中、上流域で定住し、$1m^2$ あたり約 0.7 尾の割でなわばりを作ることは、宮地ほか (1952) の研究以来よく知られた事実である。ところが 1955 年には京都府北端の宇川で遡上数が格段に多く、$1m^2$ あたり約 5.4 尾の棲息数を数えた。この時には、多くの個体はなわばりを作らなかった。(川那部ほか, 1957)。つまり、アユは個体数密度に応じてなわばり制を発達させる。個体数密度が高くなり、なわばりを持たない個体が増えると、アユは、なわばりを持たなくなり、なわばり制が崩壊してしまう。なわばりを維持することは、その個体にとってはなわばり内の資源量をほぼ独占的に利用できるという利益がある反面、なわばりを侵入者から守るための時間やエネルギーの損失を伴う。なわばりを持たない個体の数が増え、なわばりを防衛するためになわばりアユが払うコストが増加した場合、もしも、それを維持することによって得られる期待獲得資源量がなわばりを放棄したときのそれよりも小さくなってしまえば、なわばり制が崩壊すると考えられる。このようにアユのなわばり行動は、純粋に個体にとっての損得から理解することもできると考えられる。

一般的に個体間には、質の違いが存在する。それは、例えば体の大きさなどである。この質の違いによって、集団内の個体の順位が決定する。本研究においては、それぞれの個体に順位が決まっている集団を考え、この集団内の個体が、なわばりを維持しない条件はどのようなものかについての数理的考察を行う。ここでは、それぞれの順位の個体がなわばりを持った場合となわばりを持たない場合、また、なわばりを持たない場合には、なわばりを攻撃する場合と攻撃しない場合、それぞれの期待獲得資源量を数理モデリングし、その大小関係を比較する。期待獲得資源量の多い方がその個体にとって、より適応的であると考える。

ただし、考える生息域内における可能ななわばりの総数には上限があると仮定する。したがって、順位の低い個体については、なわばりを持つ方がより適応的であっても、それが実現できるとは限らない。

なわばり外個体でなわばりに侵入しようとする個体は、単位時間あたり１つのなわばりに侵入しようとするものと仮定する。なわばり個体は同時に複数のなわ

ばり外個体から攻撃を受ける可能性がある。ここでは、なわばり個体同士、なわばり外個体同士の争いは考えていない。

なわばり個体が防御に成功した場合、侵入に失敗したなわばり外個体は、なわばり内の資源を獲得する事が出来ない。なわばり外個体が侵入に成功した場合には、当該なわばり外個体は、全て、なわばり内に侵入して、なわばり内の資源を獲得する。なわばり外個体がどのなわばりに侵入しようとするかは、ランダムであると仮定する。なわばり個体がなわばり外個体からなわばりを防御するのに必要なコストは、侵入してこようとするなわばり外個体の集団の順位の組み合わせとなわばり個体自身の順位に依存すると仮定する。また、なわばり外個体があるなわばりに侵入しようとしたときにかかるコストは、それぞれのなわばり外個体の順位と侵入しようとするなわばりのなわばり個体の順位に依存すると仮定する。さらに、同じなわばりに侵入しようとするなわばり外個体の集団の順位の組み合わせとなわばり個体の順位に依存して、侵入の成功確率は決まると仮定する。

なわばり個体は、必ずしもなわばり内の資源を全て獲得するとは限らない。一方、なわばり外個体は、生息域内でなわばり領域外の場所で資源を獲得する。なわばりに侵入しようとするかどうかに依らず、なわばり外個体の順位に依存して、なわばり領域外における獲得資源量が決まると仮定する。

全ての個体がなわばりを持たない状況において、各順位の個体について、自分のみがなわばりを持った場合と全くなわばりが存在しない場合の２つの場合における期待獲得資源量を比較し、全ての順位の個体についてなわばりを持たない方がより適応的であれば、なわばりの形成されない状況が安定である可能性がある。

そこで、まず、ある順位の個体のみがなわばりを持った場合に、なわばり外個体のうちどれだけが、なわばりに侵入しようとするのかに関する数理モデル解析を行い、その結果、なわばり個体の順位が高いほど、なわばりに侵入しようとするなわばり外個体の数は少なくなり、また、なわばりに侵入しようとするなわばり外個体の集団は、なわばり外個体のうち相対的に上位のもので構成されているということが導かれる。さらに、なわばり外個体の集団からなわばりを防御するために必要なコストは、なわばり個体の順位が低いほど、大きくなることも示されている。

なわばり内で獲得する資源量からなわばりを防御するためのコストを引いた分が、なわばり個体が獲得すると期待できる正味の資源量である。個体群内に唯一のなわばりが存在する場合についてのなわばり個体の正味の期待獲得資源量に関する数理モデルを解析した結果、本文中の Proposition 1 の条件が満たされる時、全ての個体がなわばりを持たない状況からは、なわばりが全く形成されないことが導かれる。

Proposition 1 による結果に基づいて以下のような議論を展開できる。なわばり個体の順位の低下に伴う、なわばり内での期待獲得資源量の減少が、全ての個体がなわばりを持たない場合に当該個体によって獲得されると期待される資源量の減少よりも急激な場合、第１位の個体に関する条件 (30) のみでなわばり形成の有無が判断できる。なわばり内での期待獲得資源量と、全ての個体がなわばりを持たないときのなわばり外での期待獲得資源量は、共に、順位が下がるに伴って減少するが、常に正の値である。前者から後者を引いた値が順位に関する増加関数であり、ある値に漸近する場合には、第１位の個体がなわばりを防御するために必要なコストよりもその漸近値の方が小さければ、Proposition 1 の条件が満たされるのでなわばりは形成されない。

また、なわばりが存在する安定な状態が実現しない条件を数理的に考察し、

Proposition 2 の結果が得られた。個体郡内の個体間の質の違いが小さいときには、k_1^{tr} は、1位の質が低くなるのに伴い、相対的に小さくなるが、$P_1(\{N\})f_{1,N}-d_{1,N}$ は1位と N 位の差が小さくなるので逆に大きくなる可能性がある。$k_N^{out}(\Xi_N)$ は集団サイズが大きいときにはより多くの個体と共に生息域内の資源量を分けなければならないので小さくなる。例えば集団の大きさが十分に大きいときには、質の違いが小さくなると考えることができる。なぜなら、その場合、順位の最も高い個体でさえ、十分な資源量を獲得できるとは期待できないからである。よって、N が十分に大きい時、Proposition 2 の条件が満たされる可能性が高くなる可能性があるだろう。また、集団のサイズが十分に小さい場合にも、質の違いが小さくなると考えることができるかもしれない。なぜなら、その場合には、順位の最も低い個体でさえも、ある程度十分な資源を獲得すると期待できるからである。この時には、$P_1(\{N\})f_{1,N}-d_{1,N}$ は1位と N 位の差が小さくなるので大きくなる。$k_N^{out}(\Xi_N)$ は集団サイズが小さいときには、大きくなる。よって集団の大きさが十分に小さい場合にも、Proposition 2 の条件が満たされる可能性が高くなる可能性があるだろう。

全ての個体が同等であり、個体間に順位が存在しない場合のなわばりの存在性について、侵入成功確率やコストに対して具体的な関数形を仮定して、数値計算も用いて解析を試みた。解析の結果、個体の適応的な行動選択についての3つの平衡状態が存在することが示された。1つ目は、Fig. 2 で示したような状況である。なわばり外個体の割合がある閾値よりも小さい場合には、平衡状態において、許される最大数 n_{max} 以下のなわばりが存在し、全ての個体が適応的な行動選択をしている状態が実現する。なわばり外個体の割合がある閾値よりも大きい場合には、平衡状態において、なわばりは存在しない。2つ目は、Fig. 3 で示したような状況である。なわばり外個体の割合が、ある閾値以下の場合、なわばりは許される最大数 n_{max} 個できる。なわばりの数には上限があるので、なわばりを持つことが出来ない個体が存在すると考えられる。なわばり外個体の割合がその閾値より大きい場合には、個体群内になわばりがない状態が平衡状態となる。3つ目は、Fig. 4 で示したような状況である。任意のなわばり外個体の割合に対して、行動の適応的な選択の後の平衡状態においては、個体群内になわばりは存在しない。

さらに、Fig. 5 は、集団の大きさが十分に大きいとき、または十分に小さいとき、上記の3つ目の場合が実現する可能性が高くなることを示している。これは、Proposition 2 の結果に関する考察に相当する内容である。また、n_{max} は、可能ななわばり数の上限であり、考える生息域の質が良いほど、この上限数が、増加すると考えられる。さらに、Fig. 5 より、十分小さな n_{max} について、つまり、生息域の質が悪い場合については、平衡状態において、なわばりが成立しにくいことが示唆されている。

本論文の結論の一つ、集団のサイズが大きいときには、なわばりが形成されにくい可能性があるという結論は、アユの場合の、個体数密度が高くなる場合に、なわばりが崩壊してしまうという観察事実に対応していると考えられる。

1 Assumption and Modeling

1.1 Environment and Population Structure

Territory is defined as any defended area. *Territorial* individual tries to defend its territorial area against every *non-territorial* invaders. We consider a closed population of size N. We assume that each individual of the population could choose its behaviour to have its own territory or alternatively to remain as an outsider without any territory, that is, as a non-territorial. The behavioral choice of each individual is assumed to depend on the amount of resource is expected to be gained by the chosen behaviour.

We assume some difference in quality among individuals, for example, in terms of the body size. Such qualitative difference determines the relative *rank* of each individual in the considered population. We define the set Ω_n of ranks of n territorial individuals as follows:

$$\Omega_n = \{\omega_i |\ i = 1, 2, \ldots, n;\ \omega_i < \omega_j \ \text{ for } \ i < j\},$$

where ω_i is the rank of territorial individual which has the i th rank relative in the territorial subpopulation. Similarly, we define the set Γ_l of ranks of l non-territorial individuals as follows:

$$\Gamma_l = \{\gamma_i |\ i = 1, 2, \cdot\cdot\cdot, l;\ \gamma_i < \gamma_j \ \text{ for } \ i < j\},$$

where γ_i is the rank of non-territorial individual which has the i th rank relative in the non-territorial subpopulation. From these definitions, $N = n + l$. For mathematical convenience, we define the set of all ranks in the considered population by

$$\Xi_N = \Omega_n \cup \Gamma_l = \{1, 2, \ldots, N\}.$$

If an individual could expect to get more resource with keeping its territory, it is more beneficial for the individual to keep its territory. Alternatively if an individual could expect to get more resource without having a territory, it is more beneficial that the individual should not keep territory.

However, the number of territories is assumed to be not beyond n_{max}, so that it is not always possible that all individuals that want to be territorial could have their territories. Any individual that chooses its behaviour to have its territory from the viewpoint of expected amount of resource gain could have its territory as long as the number of territorial sites, n_{max}, could afford it, that is, only if the number of individuals which choose to have their territories is less than n_{max}. We assume that, if the number of the individuals for which it would be more beneficial to keep territory is beyond n_{max}, the individuals of relatively higher ranks among them can have their territories.

Non-territorial individual is assumed to choose its behaviour to be *aggressive* such as to try to invade some territories, or alternatively to be *non-aggressive* without trying to invade any territory. This behavioral choice by the non-territorial depends on the expected amount of resource which it expects to obtain.

We define the set $\Lambda^m_{\Omega_n}$ of ranks of m *aggressive* non-territorial individuals which try to invade one of n territories in Ω_n as follows:

$$\Lambda^m_{\Omega_n} = \{\lambda_i |\ i = 1, 2, \cdots, m;\ \lambda_i < \lambda_j \ \text{ for } \ i < j\},$$

where λ_i is the rank of aggressive non-territorial individual which has the i th rank relative in the aggressive non-territorial subpopulation. The behavioral choice of non-territorial would significantly depend on the existence of territories and on the composition of Ω_n.

1.2 Struggle for Resource in Territory

We assume that the aggressive non-territorial tries to invade one territory per unit time, and that each aggressive non-territorial selects at random the territory which it tries to invade. We ignore any struggle among territorials and among non-territorials. When a territorial succeeds in defending its territory against aggressive non-territorials, any of the aggressive non-territorials could not get any resource of the territory. On the other hand, when a territorial fails to defend its territory against agressive non-territorials, any of them succeeds in its invasion and gets some resource of the territory.

The amount of resource that the aggressive non-territorial of rank λ_j could successfully get per unit time from the territory of the territorial of rank ω_i, f_{ω_i,λ_j}, is assumed to have the following natures:

$$f_{\omega_i,\lambda_k} \geq f_{\omega_i,\lambda_l} \quad \text{for} \ \ \lambda_k < \lambda_l; \tag{1}$$

$$f_{\omega_k,\lambda_j} \leq f_{\omega_l,\lambda_j} \quad \text{for} \ \ \omega_k < \omega_l. \tag{2}$$

The former (1) means that the aggressive non-territorial of lower rank could get smaller amount of resource of the territory than that of higher rank could. The latter (2) means that the aggressive non-territorial could get the larger amount of resource from the territory of lower rank than from that of higher rank.

1.3 Cost for Struggle

Cost for the territorial of rank ω_i in order to defend its territory against a subpopulation of k aggressive non-territorials, L_k ($\subset \Lambda^m_{\Omega_n}$), is now denoted by $C_{\omega_i}(L_k)$ as an ω_i-depending function of L_k, assumed to satisfy the following:

$$C_{\omega_i}(L_k) \leq C_{\omega_j}(L_k) \quad \text{for} \ \ \omega_i < \omega_j. \tag{3}$$

This feature of $C_{\omega_i}(L_k)$ means that the territorial of lower rank should pay the larger cost than that of higher rank should. If there is no aggressive non-territorial for the territory of rank ω_i, that is, when $L_0 = \emptyset$, the territorial does not have to pay the cost for defence, so that $C_{\omega_i}(L_0) = 0$. Further, the following nature of the cost for territorial is assumed for any additional aggressive member l_{k+1}:

$$C_{\omega_i}(L_k) \leq C_{\omega_i}(L_k \cup \{l_{k+1}\}). \tag{4}$$

This reflects the increasing nature of cost in terms of the number of aggressive non-territorials which try to invade the territory.

Moreover, we assume that, if $L_k = \{l_j | j = 1, 2, \cdots, k\}$ is different from $L'_k = \{l'_j | j = 1, 2, \cdots, k\}$ only about a specific member of relative rank q as follows:

$$l_j = l'_j \quad \text{for } \forall j \neq q, \quad \text{and} \quad l_q < l'_q,$$

then,

$$C_i(L_k) \geq C_i(L'_k). \tag{5}$$

The amount of cost depends in general not only on the number of the aggressive non-territorials k but also on the composition of their ranks. Generally speaking, as the member includes the aggressive non-territorial of higher rank, the cost gets larger.

On the other hand, each aggressive non-territorial is assumed to have to pay a cost for trying to invade the territory. We denote by d_{ω_i,λ_j} the cost for the aggressive non-territorial of rank λ_j, which tries to invade the territory of rank ω_i, assuming that

$$d_{\omega_i,\lambda_k} \leq d_{\omega_i,\lambda_l} \quad \text{for} \quad \lambda_k < \lambda_l; \tag{6}$$

$$d_{\omega_k,\lambda_j} \geq d_{\omega_l,\lambda_j} \quad \text{for} \quad \omega_k < \omega_l, \tag{7}$$

where the former (6) means that the aggressive non-territorial of lower rank should pay larger cost than that of higher rank should. The latter (7) means that the aggressive non-territorial should pay larger cost for trying to invade the territory of higher rank than that of lower rank.

1.4 Probability of Invasion Success

Probability that a subpopulation consisting of k aggressive non-territorials, $L_k (\subset \Lambda^m_{\Omega_n})$, succeeds in the invasion into the territory of rank ω_i is now denoted by an ω_i-depending function of L_k, $P_{\omega_i}(L_k)$, assumed to satisfy the following:

$$P_{\omega_i}(L_k) \leq P_{\omega_j}(L_k) \quad \text{for} \quad \omega_i < \omega_j. \tag{8}$$

This feature means that the territory of lower rank is more likely to be successfully invaded by the aggressive non-territorials L_k than that of higher rank is.

Moreover, with the argument similar to that for (5) about two aggressive non-territorial subpopulations L_k and L'_k, we assume the following:

$$P_{\omega_i}(L_k) \geq P_{\omega_i}(L'_k), \tag{9}$$

where L_k and L'_k are defined same as before. The probability of invasion success depends in general on the members of L_k. As the subpopulation L_k includes the individual of higher rank could, the invasion success would be more likely to occur. Further, the following nature is assumed for any additional aggressive member l_{k+1}:

$$P_{\omega_i}(L_k) \leq P_{\omega_i}(L_k \cup \{l_{k+1}\}). \tag{10}$$

This means that, as the number of aggressive non-territorials which try to invade the territory increases, the invasion success would be more likely to occur.

1.5 Expected Resource Gain for Territorial Individual

When the territorial individual of rank ω_i does not need to defend its territory, the expected amount of resource gotten by it is assumed to be $k^{tr}_{\omega_i}$ not beyond r_{ω_i}, where r_{ω_i} is the total amount of resource within the territory kept by the territorial of rank ω_i. It is assumed that the territorial does not necessarily occupy the whole amount of resource in the territory. The resource amount $k^{tr}_{\omega_i}$ is in general a decreasing function of ω_i. That is, the individual of lower rank could get the resource less than that of higher rank, even if it has its territory.

At first, we consider the case when only one territory of rank i exists:

$$\begin{aligned} \Omega_1 &= \{i\}; \\ \Gamma_{N-1} &= \{1, 2, \ldots, i-1, i+1, \ldots, N\}. \end{aligned}$$

In this case, since there is only one territory for the aggressive non-territorials to try to invade, the territorial of rank i needs to defend its territory from all the aggressive non-territorials $\Lambda^m_{\{i\}}$, provided that there would exist a subpopulation $\Lambda^m_{\{i\}}$ of aggressive non-territorials. Hence, the territorial of rank i has to pay the cost $C_i(\Lambda^m_{\{i\}})$. So, the expected amount $K^{tr}_i(\Lambda^m_{\{i\}})$ of resource gotten by the territorial is expressed as follows:

$$K^{tr}_i(\Lambda^m_{\{i\}}) = k^{tr}_i - C_i(\Lambda^m_{\{i\}}). \tag{11}$$

Next, when there are n (> 1) territories, the expected amount of resource gotten by each territorial depends on which aggressive non-territorials come to try to invade its territory. The number of combinations of k individuals out of $\Lambda^m_{\Omega_n}$ is ${}_m\mathrm{C}_k = m!/\{(m-k)!k!\}$, provided that there would exist a subpopulation $\Lambda^m_{\Omega_n}$ of aggressive non-territorials. The probability that each aggressive non-territorial chooses to try to invade the territory of rank ω_i is $1/n$, because the random choice of territory for the aggressive non-territorial is assumed. Therefore, the probability that only k aggressive non-territorials out of $\Lambda^m_{\Omega_n}$ choose to try to invade the territory of rank ω_i is given by

$${}_m\mathrm{C}_k \left(\frac{1}{n}\right)^k \left(1 - \frac{1}{n}\right)^{m-k}. \tag{12}$$

If k aggressive non-territorials choose to try to invade the territory of rank ω_i, the *expected* amount of cost that the territorial should pay is

$$\frac{1}{{}_m\mathrm{C}_k} \sum_{L_k \subset \Lambda^m_{\Omega_n}} C_{\omega_i}(L_k), \tag{13}$$

where the sum is taken over the possible combinations of $L_k \subset \Lambda^m_{\Omega_n}$.

From (12) and (13), the expected amount of cost that the territorial of rank ω_i should pay for the defence of its territory is calculated by the sum in terms of the number k of aggressive non-territorials, and lastly the expected resource gain for the territorial of rank ω_i becomes

$$
\begin{aligned}
K^{tr}_{\omega_i}(\Lambda^m_{\Omega_n}) &= k^{tr}_{\omega_i} - \sum_{k=0}^{m} \left[{}_m\mathrm{C}_k \left(\frac{1}{n}\right)^k \left(1-\frac{1}{n}\right)^{m-k} \left\{ \frac{1}{{}_m\mathrm{C}_k} \sum_{L_k \subset \Lambda^m_{\Omega_n}} C_{\omega_i}(L_k) \right\} \right] \\
&= k^{tr}_{\omega_i} - \sum_{k=0}^{m} \sum_{L_k \subset \Lambda^m_{\Omega_n}} C_{\omega_i}(L_k) \left(\frac{1}{n}\right)^k \left(1-\frac{1}{n}\right)^{m-k}. \qquad (14)
\end{aligned}
$$

1.6 Expected Resource Gain for Non-territorial Individual

Out of territorial region, the expected amount of resource gotten by the non-territorial of rank γ_j, $k^{out}_{\gamma_j}(\Gamma_l)$, is assumed to be a γ_j-depending function of Γ_l, satisfying the following:

$$\sum_{\gamma_j \in \Gamma_l} k^{out}_{\gamma_j}(\Gamma_l) = R - \sum_{\omega_i \in \Omega_n} r_{\omega_i}, \qquad (15)$$

where R is the total amount of resource in the whole habitat region inhabited by the considered population. This means that all the resource out of territorial region is utilized by the non-territorial subpopulation. This does not indicate that the resource utilization of non-territorial would be effective, but does that there exists relatively scarce resource out of the territorial region.

The amount $k^{out}_{\gamma_j}(\Gamma_l)$ is assumed in general to be a decreasing function of γ_j, because the non-territorial individual of lower rank could get the smaller amount of resource out of territorial region than that of higher rank could. In addition, we assume the following nature of $k^{out}_{\gamma_j}(\Gamma_l)$ for any additional rank γ':

$$k^{out}_{\gamma_j}(\Gamma_l) \geq k^{out}_{\gamma_j}(\Gamma_l \cup \{\gamma'\}). \qquad (16)$$

This is because the increase of the number of non-territorials causes the smaller share of resource for each non-territorial out of territorial region.

Especially when there exists no territory in the habitat region, the following must be satisfied:

$$\sum_{j=1}^{N} k^{out}_{j}(\Gamma_l) = R.$$

The expected amount of resource for the non-aggressive non-territorial of rank γ_j, $K^{out-}_{\gamma_j}(\Gamma_l)$, is given by

$$K^{out-}_{\gamma_j}(\Gamma_l) = k^{out}_{\gamma_j}(\Gamma_l). \qquad (17)$$

When there is no territory in the habitat region, the expected amount of resource gotten by the aggressive non-territorial of rank λ_j, $K^{out+}_{\lambda_j}(\Lambda^m_\phi)$, is assumed to be

$$
\begin{aligned}
K^{out+}_{\lambda_j}(\Lambda^m_\phi) &= K^{out-}_{\lambda_j}(\Xi_N) \\
&= K^{out}_{\lambda_j}(\Xi_N) = k^{out}_{\lambda_j}(\Xi_N), \qquad (18)
\end{aligned}
$$

because the aggressive non-territorial has indeed no difference from the non-aggressive one with respect to the behaviour in this case. However, when there exists some territories, the aggressive non-territorial could get some resource also from a territory if it succeeds in the invasion, although it needs to pay a cost in order to try to invade it.

When there is only one territory of rank i, all the aggressive non-territorials try to invade the unique territory. Suppose that there is the subpopulation $\Lambda^m_{\{i\}}$ of m aggressive non-territorials. Then, all the members of $\Lambda^m_{\{i\}}$ try to invade the territory of rank i without any choice. Hence, the expected amount of resource gotten by the aggressive non-territorial of rank λ_j ($\in \Lambda^m_{\{i\}}$) can be obtained as follows:

$$P_i(\Lambda^m_{\{i\}})(f_{i,\lambda_j} - d_{i,\lambda_j}) + (1 - P_i(\Lambda^m_{\{i\}})(0 - d_{i,\lambda_j}) = P_i(\Lambda^m_{\{i\}})f_{i,\lambda_j} - d_{i,\lambda_j}. \quad (19)$$

This is because the aggressive non-territorial could get the amount of resource $f_{i,\lambda_j} - d_{i,\lambda_j}$ from the territory of rank i if the invation is successful with probability $P_i(\Lambda^m_{\{i\}})$, and otherwise it just loses the cost d_{i,λ_j}. Therefore, when there is only one territory of rank i, the expected amount $K^{out+}_{\lambda_j}(\Lambda^m_{\{i\}})$ of resource gotten by the aggressive non-territorial of rank λ_j is

$$K^{out+}_{\lambda_j}(\Lambda^m_{\{i\}}) = k^{out}_{\lambda_j}(\Gamma_{N-1}) + P_i(\Lambda^m_{\{i\}})f_{i,\lambda_j} - d_{i,\lambda_j}. \quad (20)$$

When there are n (> 1) territories, we at first consider the probability that a subpopulation which is composed of an aggressive non-territorials of rank λ_j ($\in \Lambda^m_{\Omega_n}$) and the other k aggressive non-territorials, that is, $L_k \cup \{\lambda_j\}$ ($\subset \Lambda^m_{\Omega_n}$), tries to invade the territory of rank ω_i. With the argument similar to that for (12), the probability is obtained as follows:

$${}_{m-1}\mathrm{C}_k \left(\frac{1}{n}\right)^k \left(1 - \frac{1}{n}\right)^{(m-1)-k}. \quad (21)$$

In this case, the probability that the subpopulation $L_k \cup \{\lambda_j\}$ succeeds in invading the territory of rank ω_i is expressed by $P_{\omega_i}(L_k \cup \{\lambda_j\})$. Similarly as for (19), when the subpopulation $L_k \cup \{\lambda_j\}$ tries to invade the territory of rank ω_i, the expected amount of resource gotten by the aggressive non-territorial of rank λ_j is

$$P_{\omega_i}(L_k \cup \{\lambda_j\})f_{\omega_i,\lambda_j} - d_{\omega_i,\lambda_j}. \quad (22)$$

So, from (22), the expected amount of resource gotten by the aggressive non-territorial of rank λ_j when it tries to invade the territory of rank ω_i with the other k aggressive non-territorials can be expressed by

$$\frac{1}{{}_{m-1}\mathrm{C}_k} \sum_{L_k \subset \Lambda^m_{\Omega_n} \setminus \{\lambda_j\}} [P_{\omega_i}(L_k \cup \{\lambda_j\})f_{\omega_i,\lambda_j} - d_{\omega_i,\lambda_j}], \quad (23)$$

where the sum is taken over all the combinations of k aggressive non-territorials except for λ_j. From (21) and (23), with the argument similar to that for (14), when the aggressive non-territorial of rank λ_j tries to invade a territory, the expected amount of resource gotten by the aggressive non-territorial of rank λ_j from the territory can be obtained as follows:

$$
\begin{aligned}
&\frac{1}{n}\sum_{\omega_i\in\Omega_n}\sum_{k=0}^{m-1}{}_{m-1}\mathrm{C}_k\left(\frac{1}{n}\right)^k\left(1-\frac{1}{n}\right)^{(m-1)-k}\\
&\qquad\cdot\left[\frac{1}{{}_{m-1}\mathrm{C}_k}\sum_{L_k\subset\Lambda^m_{\Omega_n}\backslash\{\lambda_j\}}[P_{\omega_i}(L_k\cup\{\lambda_j\})f_{\omega_i,\lambda_j}-d_{\omega_i,\lambda_j}]\right]\\
=\;&\frac{1}{n}\sum_{\omega_i\in\Omega_n}\sum_{k=0}^{m-1}\sum_{L_k\subset\Lambda^m_{\Omega_n}\backslash\{\lambda_j]}\\
&\qquad\{P_{\omega_i}(L_k\cup\{\lambda_j\})f_{\omega_i,\lambda_j}-d_{\omega_i,\lambda_j}\}\left(\frac{1}{n}\right)^k\left(1-\frac{1}{n}\right)^{(m-1)-k}\\
=\;&\frac{1}{n}\sum_{\omega_i\in\Omega_n}\sum_{k=0}^{m-1}\sum_{L_k\subset\Lambda^m_{\Omega_n}\backslash\{\lambda_j\}}P_{\omega_i}(L_k\cup\{\lambda_j\})f_{\omega_i,\lambda_j}\left(\frac{1}{n}\right)^k\left(1-\frac{1}{n}\right)^{(m-1)-k}\\
&\qquad-\frac{1}{n}\sum_{\omega_i\in\Omega_n}d_{\omega_i,\lambda_j}\left\{\sum_{k=0}^{m-1}{}_{m-1}\mathrm{C}_k\left(\frac{1}{n}\right)^k\left(1-\frac{1}{n}\right)^{(m-1)-k}\right\}\\
=\;&\frac{1}{n}\sum_{\omega_i\in\Omega_n}f_{\omega_i,\lambda_j}\sum_{k=0}^{m-1}\sum_{L_k\subset\Lambda^m_{\Omega_n}\backslash\{\lambda_j\}}P_{\omega_i}(L_k\cup\{\lambda_j\})\left(\frac{1}{n}\right)^k\left(1-\frac{1}{n}\right)^{(m-1)-k}\\
&\qquad-\langle d_{\lambda_j}\rangle_{\Omega_n},
\end{aligned}
\tag{24}
$$

where carried out is the sum in terms of the rank ω_i of territorials which the aggressive non-territorial of rank λ_j tries to invade. Since the aggressive non-territorial is assumed to select at random the territory which it tries to invade, the probability that a territory of Ω_n would be selected by an aggressive non-territorial is $1/n$. In the above, we denote by $\langle d_{\lambda_j}\rangle_{\Omega_n}$ the average cost that the aggressive non-territorial of rank λ_j should pay for trying to invade a territory:

$$\langle d_{\lambda_j}\rangle_{\Omega_n}\equiv\frac{1}{n}\sum_{\omega_i\in\Omega_n}d_{\omega_i,\lambda_j}.$$

Lastly, from (24), the expected total amount of resource gotten by the aggressive non-territorial of rank λ_j is obtained as follows:

$$
\begin{aligned}
&K^{out+}_{\lambda_j}(\Lambda^m_{\Omega_n})=\\
&\quad k^{out}_{\lambda_j}(\Gamma_l)+\\
&\quad\frac{1}{n}\sum_{\omega_i\in\Omega_n}f_{\omega_i,\lambda_j}\sum_{k=0}^{m-1}\sum_{L_k\subset\Lambda^m_{\Omega_n}\backslash\{\lambda_j\}}P_{\omega_i}(L_k\cup\{\lambda_j\})\left(\frac{1}{n}\right)^k\left(1-\frac{1}{n}\right)^{(m-1)-k}\\
&\qquad-\langle d_{\lambda_j}\rangle_{\Omega_n}
\end{aligned}
\tag{25}
$$

2 Analysis

2.1 What Condition Makes No Territory Established?

We focus the condition with which no territory would be established from the viewpoint of optimal behaviour. At the beginning, we consider the case when only one territory of rank i exists in the habitat region:

$$\Omega_1 = \{i\};$$

$$\Gamma_{N-1} = \{1, 2, \dots, i-1, i+1, \dots, N\}.$$

We consider at first the combination of members of $\Lambda^{m}_{\{i\}}$ which is a subpopulation of non-territorials that choose to try to invade the territory of rank i from the viewpoint of the expected amount of resource gain.

Suppose that the subpopulation of aggressive non-territorials would be stationarily established, that is, suppose *the stationary state*, which means that any non-aggressive non-territorial does not choose to change to the aggressive one from the viewpoint of the expected amount of resource gain, while any aggressive non-territorial remains as it is. We denote the number of aggressive non-territorials at such stationary state by m_i^* in the case when only the territory of rank i exists.

Firstly, we can obtain the following lemma with respect to the existence of m_i^* (Appendix A):

Lemma 1. If and only if the following condition is satisfied, there exists a $\Lambda^{m_i^*}_{\{i\}}$ which is a subpopulation of non-territorials that try to invade the existing unique territory of rank i:

$$P_i(\{\lambda_1\}))f_{i,\lambda_1} - d_{i,\lambda_1} > 0. \tag{26}$$

With the arguments given in Appendix B, we can determine the elements of $\Lambda^{m_i^*}_{\{i\}}$ at the stationary state with the following two lemmas:

Lemma 2. Suppose that there exists only one territory of rank i. If the condition (26) is satisfied, and $\Lambda^{m_i^*}_{\{i\}}$ is not vacant, then

$$\Lambda^{m_i^*}_{\{i\}} = \{\lambda_1, \lambda_2, \dots, \lambda_{m_i^*}\}.$$

This means that, if $\Lambda^{m_i^*}_{\{i\}}$ is not vacant, it is composed of individuals from the highest rank to the m_i^* th in the non-territorial subpopulation.

Lemma 3. Suppose that there exists only one territory of rank i, and the condition (26) is satisfied. Then, if and only if

$$P_i(\Gamma_{N-1})f_{i,\gamma_{N-1}} - d_{i,\gamma_{N-1}} > 0,$$

all the non-territorials would be aggressive, that is, $m_i^* = N-1$. In contrast, if

$$P_i(\Gamma_{N-1})f_{i,\gamma_{N-1}} - d_{i,\gamma_{N-1}} < 0,$$

the subpopulation $\Lambda_{\{i\}}^{m_i^*}$ of aggressive non-territorials which try to invade the territory of rank i at the stationary state satisfies the following conditions:

$$\begin{aligned} P_i(\Lambda_{\{i\}}^{m_i^*})f_{i,\gamma_{m_i^*}} - d_{i,\gamma_{m_i^*}} &> 0; \\ P_i(\Lambda_{\{i\}}^{m_i^*} \cup \{\gamma_{m_i^*+1}\})f_{i,\gamma_{m_i^*+1}} - d_{i,\gamma_{m_i^*+1}} &< 0, \end{aligned}$$

then there exists a m_i^* such that $1 < m_i^* < N-1$.

Further, with the arguments given in Appendix C, we can prove the following:

Lemma 4. Suppose that there exists only one territory. If there exists a subpopulation of aggressive non-territorials at the stationary state, then as for the number of aggressive non-territorials, m_i^* for the territory of rank i, and m_j^* for that of rank j, the following holds:

$$m_i^* \leq m_j^* \quad \text{for} \quad i < j.$$

This lemma means that, when there exists only one territory in the habitat region, the number of aggressive non-territorials at the stationary state increases as the rank of the unique territorial individual becomes lower.

On the other hand, from (11), when only the territory of rank i exists, the expected amount $K_i^{tr}(\Lambda_{\{i\}}^{m_i^*})$ of resource gotten by the territorial at the stationary state is

$$K_i^{tr}(\Lambda_{\{i\}}^{m_i^*}) = k_i^{tr} - C_i(\Lambda_{\{i\}}^{m_i^*}). \tag{27}$$

From (18), when there is no territory in the considered habitat region, the expected amount K_i^{out} of resource gotten by the individual of rank i is

$$K_i^{out}(\Xi_N) = k_i^{out}(\Xi_N). \tag{28}$$

If $K_i^{tr}(\Lambda_{\{i\}}^{m_i^*}) < K_i^{out}(\Xi_N)$, the territorial individual of rank i should stop keeping the territory and change to a non-territorial from the viewpoint of the expected amount of resource gain.

With the above lemmas, (27) and (28), we can obtain the following proposition about the necessary condition that no territory is established at the stationary state within the considered population:

Proposition 1. When there exists no territory in the habitat region, if (26) and the following condition are satisfied for $\forall i \in \Xi_N$, the state with no territory is stationary:

$$k_i^{tr} - k_i^{out}(\Xi_N) > C_i(\Lambda_{\{i\}}^{m_i^*}).$$

In addition, with the arguments in Appendix D, we can derive the following corollary about the nature of cost $C_i(\Lambda_{\{i\}}^{m_i^*})$ for the unique territorial of rank i at the stationary state:

Corollary. $C_i(\Lambda_{\{i\}}^{m_i^*})$ is an increasing function of rank i of the unique territorial.

From Proposition 1, we can make some more detail arguments with some additional assumptions. First, we consider the case when $k_i^{tr} - k_i^{out}(\Xi_N)$ is a decreasing function of rank i. This means that, as the rank i becomes lower, k_i^{tr} decreases more steeply than $k_i^{out}(\Gamma_N)$ does. In this case, from Corollary, if

$$k_1^{tr} - k_1^{out}(\Xi_N) > C_1(\Lambda_{\{1\}}^{m_1^*}), \tag{29}$$

the condition of Proposition 1 is satisfied, so that there exists no territory at the stationary state.

Second, we consider the case when $k_i^{tr} - k_i^{out}(\Xi_N)$ is a constant independent of rank i. In this case, if condition (29) is satisfied, the condition of Proposition 1 is also satisfied, and there exists no territory at the stationary state.

Third, we consider the case when $k_i^{tr} - k_i^{out}(\Xi_N)$ is an increasing function of rank i. This means that, as the rank i becomes lower, $k_i^{out}(\Xi_N)$ decreases more steeply than k_i^{tr} does. In this case, if the condition (29) is satisfied and $k_i^{tr} - k_i^{out}(\Xi_N) = C_i(\Lambda_{\{i\}}^{m_i^*})$ would not be realized for any i $(= 2, 3, \ldots, N)$, the condition of Proposition 1 is satisfied, so that there exists no territory at the stationary state. Since the functions $k_i^{tr} - k_i^{out}(\Xi_N)$ and $C_i(\Lambda_{\{i\}}^{m_i^*})$ increasing in i take their maximal values at $i = N$, if

$$k_1^{tr} - k_1^{out}(\Xi_N) > C_N(\Lambda_{\{N\}}^{m_N^*}),$$

Proposition 1 holds and no territory is established at the stationary state.

Moreover, we consider the case when $k_i^{tr} - k_i^{out}(\Xi_N)$ is an unimodel function. Then, if its maximum is less than $C_1(\Lambda_{\{1\}}^{m_1^*})$, the condition of Proposition 1 is satisfied, so that there exists no territory at the stationary state.

2.2 When Could The Stationary State with Some Territories Not Be Realized?

We consider the condition with which a state with some territories would not be stationary from the viewpoint of optimal behaviour. At first, we suppose the following state:

$$\begin{aligned}\Omega_n &= \{\omega_1, \omega_2, \dots, \omega_n\};\\ \Gamma_l &= \{\gamma_1, \gamma_2, \dots, \gamma_l\};\\ \Lambda_{\Omega_n}^{m^*} &= \{\lambda_1, \lambda_2, \dots, \lambda_{m^*}\}.\end{aligned}$$

For a given Ω_n, we here suppose that $\Lambda_{\Omega_n}^{m^*}$ is uniquely determined as a stationary state for the non-territorial subpopulation in the sense mentioned in the previous section.

For our mathematical model, if the following is satisfied for $\exists\omega_i \in \Omega_n$, the considered state is not stationarily maintained:

$$K_{\omega_i}^{tr}(\Lambda_{\Omega_n}^{m^*}) < K_{\omega_i}^{out+}(\Lambda_{\Omega_n}^{m^*} \cup \{\omega_i\}) \quad \text{for} \quad \exists\omega_i \in \Omega_n. \tag{30}$$

Then, from Appendix E, we can obtain the following proposition about the necessary condition that satisfies (30), when the state with any territories could not be stationarily realized:

Proposition 2. If the following condition is satisfied, the stationary state with any territories could not be stationarily realized:

$$k_1^{tr} < k_N^{out}(\Xi_N) + P_1(\{N\})f_{1,N} - d_{1,N}.$$

This proposition means that, if the expected resource gain for the territorial of rank 1 without defending its territory is less than the expected resource gain gotten by the aggressive non-territorial of rank N trying alone to invade the territory of rank 1, the stationary state could not be stationarily realized.

Now, we consider the case when the difference in quality among individuals is small. This case would be realized when the size of cosidered population is sufficiently large, because the struggle for the survival and the growth would be so hard that the individual of highest rank could not have had any large advantage related to the difference of quality. In such a case, when the population size is sufficiently large, compared to when the population size is relatively small, k_1^{tr} and $k_N^{out}(\Xi_N)$ might be relatively small, because the large population size makes the resource share out of the territorial region small. In contrast, $P_1(\{N\})f_{1,N} - d_{1,N}$ could be relatively large, because the small difference among individuals in quality could cause the relatively large probability of successful invasion of non-territorials into the territory with the relatively small cost for the invasion. Therefore, we conjecture that Proposition 2 might be more likely to hold for the sufficiently large population, and the territory might be hard to be stationarily established.

On the other hand, in case of sufficiently small size of population, the difference among individuals in quality would be small, too, because the struggle for the survival and the growth could be rather weak, and each individual could grow with relatively high quality. Since the population size is sufficiently small, the difference between k_1^{tr} and $k_N^{out}(\Xi_N)$ would be rather small because the non-territorial could get a relatively large resource share out of the territorial region. On the other hand, $P_1(\{N\})f_{1,N} - d_{1,N}$ could be relatively large because of the relatively small difference in quality. So, the same as for the previous case, also for the case of sufficiently small size of population, we conjecture that Proposition 2 might be more likely to hold, and the territory might be hard to be established.

Along the above arguments, in case of some intermediate size of population, the difference among individuals in quality could be relatively large, so that $P_1(\{N\})f_{1,N} - d_{1,N}$ would be relatively large. Therefore, for the case of some intermediate size of population, we conjecture that Proposition 2 might be hard to hold, and the territory might be more likely to be established.

2.3 Case With No Quality Difference Among Individuals

In this section, with some detail mathematical assumptions and concrete formulas for the probability of successful invasion and the cost for territory defense, we numerically analyze our mathematical model of the case when the individuals have no difference among them, that is, when the ranks could not exist among them.

When the number of territorials is n, and that of non-territorials l, we assume a frequency q of aggressive non-territorials in the non-territorial subpopulation. Then, the number of aggressive non-territorials is given by ql. Probability that non-territorials succeed in invading a territory is now assumed to be given by

$$P(k) = \begin{cases} \dfrac{p_0}{a_c} k & \text{if } k \le a_c \\ p_0 & \text{if } k > a_c, \end{cases}$$

where the probability depends on the number of territorials, n, and that of aggressive non-territorials, k, which try to invade the territory, because there is no difference among individuals in their quality (Fig. 1). p_0 is the maximum probability that non-territorials succeed in invading the territory, which is realized when aggressive non-territorials more than a_c try to invade a territory. Since we assume that each aggressive non-territorial chooses at random a territory to invade per unit time, the mean number of aggressive non-territorials per territory is ql/n.

Cost that the territorial should pay for the defence of its territory is now assumed to be given by

$$C(k) = ck, \tag{31}$$

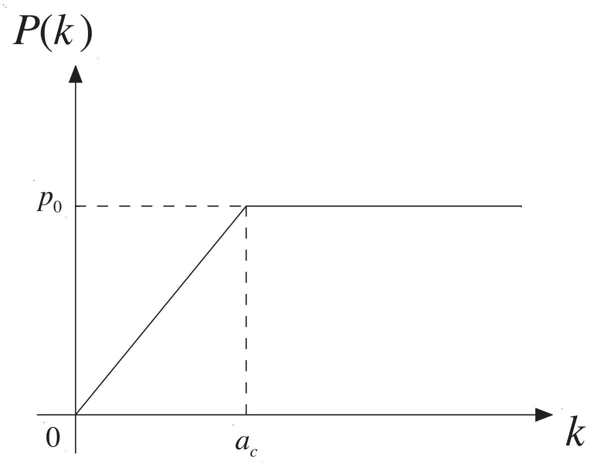

Figure 1: Probability that non-territorials succeed in invading a territory. It depends on the number of territorials, n, and that of non-territorials, k, which try to invade the territory. p_0 is the maximum probability that non-territorials succeed in invading the territory, which is realized when aggressive non-territorials more than a_c/q try to invade a territory.

where c is a positive constant that means the cost for territory defence against one aggressive non-territorial. Cost for territory defence is assumed to depend only on the number of aggressive non-territorials which try to invade the territory.

Now, since there is no difference among individuals, non-territorials evenly share the resource out of territorial region with each other, so that the expected amount of resource gotten by a non-territorial out of territorial region is given from (15) by

$$k^{out}(l) = \frac{R - rn}{l}, \tag{32}$$

where, as defined before, R is the total amount of resource in the whole habitat region, and r is the total amount of resource within the territory.

Both the expected amount f of resource that each aggressive non-territorial could get from a territory and the expected cost d that each non-territorial must pay for trying to invade a territory are assumed to be common among non-territorials, because there is no difference among individuals.

From (25) and (32), and the above-mentioned assumptions, the expected resource gain for the aggressive non-territorial, $K^{out+}(l)$, is given by

$$K^{out+}(ql) = \frac{R - rn}{l} + P\left(\frac{ql}{n}\right) f - d. \tag{33}$$

From (17) and (32), the expected resource gain for non-aggressive non-territorial,

$K^{out-}(l)$, is the following:

$$K^{out-}(l) = \frac{R - rn}{l}. \tag{34}$$

From (33) and (34), the expected resource gain averaged over the non-territorial subpopulation, $K^{out}(l)$, is obtained as follows:

$$\begin{aligned} K^{out}(l) &= qK^{out+}(l) + (1-q)K^{out-}(l) \\ &= \frac{R - rn}{l} + qP\left(\frac{ql}{n}\right) f - qd. \end{aligned} \tag{35}$$

From (14), if the expected total amount of resource which a territorial would lose from its territory due to the successful invasion of non-territorials, $P(ql/n)fql/n$, is smaller than $r - k^{tr}$, the expected amount of resource gain for the territorial would be

$$K^{tr}(ql) = k^{tr} - C\left(\frac{ql}{n}\right), \tag{36}$$

where k^{tr} is the expected resource gain for the territorial with no cost for the defence of territory. On the other hand, if $P(pl/n)fql/n > r - k^{tr}$, the expected resource gain for territorial would be

$$K^{tr}(ql) = r - P\left(\frac{ql}{n}\right) f\frac{ql}{n} - C\left(\frac{ql}{n}\right). \tag{37}$$

In case of (36), the successful invasion of the non-territorials is not expected to reduce the expected amount of resource gain for the territorial, although, in case of (37), it is expected to do.

With some mathematical and numerical analyses for $K^{out}(l) - K^{tr}(ql)$, we can see that there could be three possible cases with respect to the stationary establishment of territory within the considered population.

First case is that the stationary state with some territories could be stationarily realized. In this case, as shown in Fig. 2, the stationary state with some territories less than n_{max} would be stationarily realize. In this case, for our analysis, there could be two kinds of stationary states depending on the non-territorial frequency, as in the first case (see Fig. 2). One is that there would exist some territories less than n_{max}. At this stationary state, all the individuals in the considered population could choose the optimal behaviour with some established territories less than n_{max}. Another stationary state is that there could exist no territory. If the non-territorial frequency is smaller than a critical value corresponding to a in Fig. 2, there could exist stationarily some territories in the habitat region at the stationary state. On the contrary, if the non-territorial frequency is beyond the critical value, there could exist no territory at the stationary state.

Second case is that there could be two kinds of stationary states, depending on the frequency of non-territorial individuals in the whole population. One is that there would exist n_{max} territorials and the other non-territorials even though

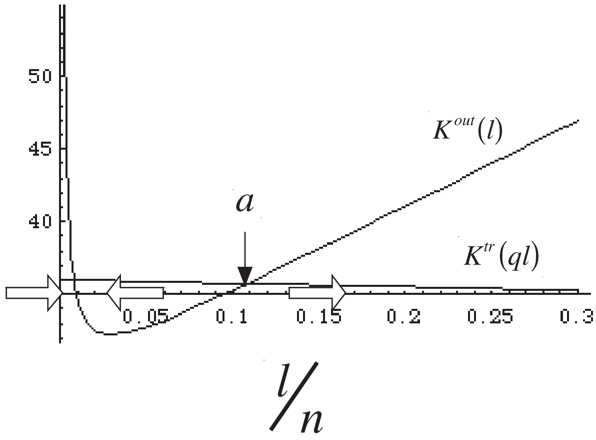

Figure 2: Dependence of $K^{out}(l)$ and $K^{tr}(ql)$ on the non-territorial subpopulation size l. In this case, if the non-territorial frequency is smaller than a critical value corresponding to a, the stationary state would be such that n_{max} territories are established and there exists some non-territorials for which it is more beneficial to keep their territories. Otherwise, there could exist no territory at the stationary state. $N = 10.4; n_{max} = 9.5; r = 20; k_t = 15; f = 10; a_c = 0.4; d = 8$.

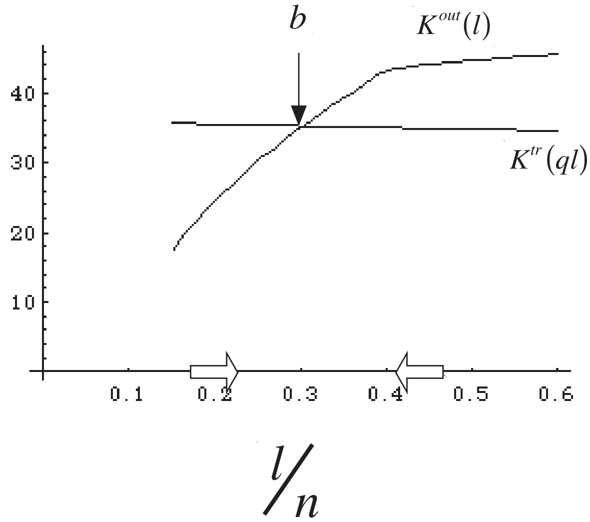

Figure 3: Dependence of $K^{out}(l)$ and $K^{tr}(ql)$ on the non-territorial subpopulation size l. In this case, if the non-territorial frequency is smaller than a critical value corresponding to b, the stationary state would be such that some territories are established and all the individuals could choose the optimal behaiviour. Otherwise, there could exist no territory at the stationary state. $N = 11.04; n_{max} = 6.25; r = 20; k_t = 15; f = 10; a_c = 0.4; d = 8$.

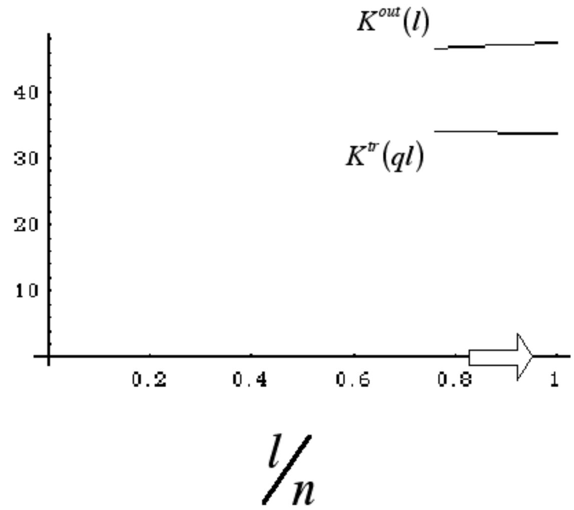

Figure 4: Dependence of $K^{out}(l)$ and $K^{tr}(ql)$ on the non-territorial subpopulation size l. $N = 11.04; n_{max} = 9.5; r = 20; k_t = 15; f = 10; a_c = 0.4; d = 8$.

it would be more beneficial for some non-territorials to keep their territories. Another stationary state is that there could exist only non-territorials with no territory in the habitat region. If the non-territorial frequency is smaller than a critical value corresponding to b in Fig. 3, the stationary state would be such that n_{max} territories are established in the habitat region. Otherwise, there could exist no territory at the stationary state.

Third case is that the stationary state with any territories less than n_{max} would not be stationarily realize. In this case, the non-territorial could be always expected to get the larger amount of resource than the territorial could (Fig. 4).

Further, from the results given in Fig. 5 that shows the (N, n_{max})-dependence of occurence of the above-mentioned three cases about the stationary state, we can conjecture that, for the sufficiently large or sufficiently small population, the second case mentioned in the above would be more likely to occur than the others.

We can regard the value n_{max} as an index to reflect the quality of habitat. As the habitat has the better quality, the value n_{max} gets larger. From the result given in Fig. 5, we see that, for sufficiently small n_{max}, that is, for sufficiedntly low quality of habitat, the above-mentioned second case would be likely to occur. Consequently, the result given by Fig. 5 implies that the territory would be hard to be established in the sufficiently low quality of habitat, and the population would contain only non-territorial individuals.

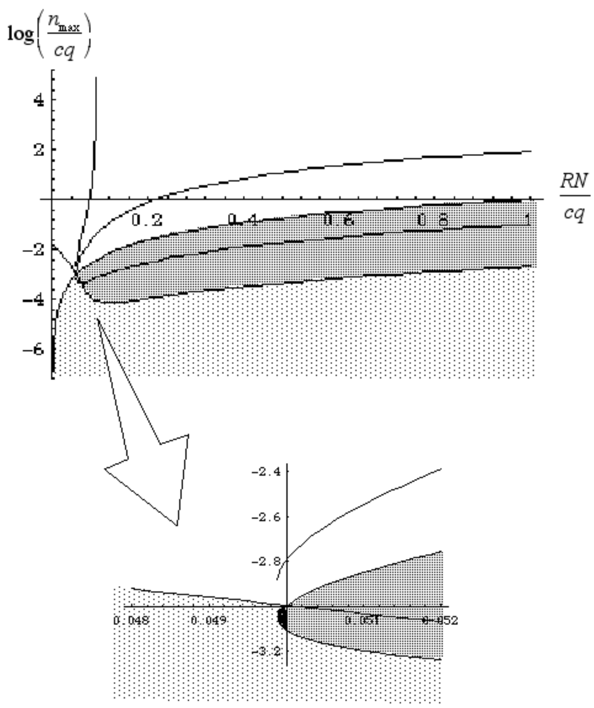

Figure 5: (N, n_{max})-dependence of the occurence of three cases about the stationary state. Black painted region corresponds to the case of Fig. 1, Dark meshed region to that of Fig. 2, Light meshed to that of Fig. 3. Blanked region corresponds to the case when $N < n_{max}$, which we did not take into account for our modelling consideration. For detail, see the text. $r = 20; k_t = 15; f = 10; a_c = 0.4; d = 8$.

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Appendix A

We assume that there exists only one territory of rank i in the habitat region. From (17) and (20), we can easily prove that, if the condition (26) is satisfied, the following is satisfied, too:

$$K_{\gamma_1}^{out-}(\Xi_N) < K_{\gamma_1}^{out+}(\{\gamma_1\}). \tag{38}$$

This means that, even if no individual of rank lower than the highest would try to invade the territory, the non-territorial of the highest rank should choose to try, so that $\Lambda_{\{i\}}^{m^*}$ must be exist if the condition (26) is satisfied.

In contrast, if

$$P_i(\{\gamma_1\})f_{i,\gamma_1} - d_{i,\gamma_1} < 0, \tag{39}$$

then

$$K_{\gamma_1}^{out-}(\Xi_N) > K_{\gamma_1}^{out+}(\{\gamma_1\}),$$

which means that the non-territorial of the highest rank would not choose to be aggressive without any other aggressive non-territorials.

From (1), (6) and (9), we can derive the following inequality:

$$P_i(\{\gamma_k\})f_{i,\gamma_k} - d_{i,\gamma_k} < P_i(\{\gamma_1\})f_{i,\gamma_1} - d_{i,\gamma_1} \quad \text{for} \quad \gamma_2 \leq \forall\gamma_k \leq \gamma_{N-1}. \tag{40}$$

Then, if the condition (39) is satisfied, we have

$$P_i(\{\gamma_k\})f_{i,\gamma_k} - d_{i,\gamma_k} < 0 \quad \text{for} \quad \gamma_2 \leq \forall\gamma_k \leq \gamma_{N-1}.$$

This means that no non-territorial would choose to be aggressive without any other aggressive non-territorials.

Therefore, as long as the condition (39) is satisfied, no non-territorial chooses to try to invade a territory, and $\Lambda_{\{i\}}^{m^*}$ can not exist.

Appendix B

Suppose that there exists only one territory of rank i:

$$\Omega_1 = \{i\};$$

$$\Gamma_{N-1} = \{1, 2, \cdot\cdot, i-1, i+1, \cdot\cdot, N\}.$$

We assume that there exists a $\Lambda_{\{i\}}^{m}$ at the stationary state. Any of non-territorials included in $\Lambda_{\{i\}}^{m}$ gains more resource when it is an aggressive non-territorial than when it is a non-aggressive non-territorial. Alternatively, any of non-territorials which is not included in $\Lambda_{\{i\}}^{m}$ gains more resource as a non-aggressive non-territorial than as an aggressive non-territorial. We denote by λ_j the lowest rank in $\Lambda_{\{i\}}^{m}$. Because λ_j is included in $\Lambda_{\{i\}}^{m}$, the following must be satisfied:

$$K_{\lambda_j}^{out+}(\Lambda_{\{i\}}^{m}) > K_{\lambda_j}^{out-}(\Gamma_{N-1}),$$

that is,

$$P_i(\Lambda^m_{\{i\}})f_{i,\lambda_j} - d_{i,\lambda_j} > 0. \tag{41}$$

We now suppose that there would exist a non-aggressive non-territorial of rank γ_k higher than λ_j. From (1), (6) and (10), the following must be satisfied:

$$P_i(\Lambda^m_{\{i\}} \cup \{\gamma_k\})f_{i,\gamma_k} - d_{i,\gamma_k} \geq P_i(\Lambda^m_{\{i\}})f_{i,\lambda_j} - d_{i,\lambda_j}. \tag{42}$$

From (41) and (42), we have

$$P_i(\Lambda^m_{\{i\}} \cup \{\gamma_k\})f_{i,\gamma_k} - d_{i,\gamma_k} > 0, \tag{43}$$

which means that the non-territorial of rank γ_k must be aggressive instead of non-aggressive from the viewpoint of the expected amount of resource gain. This is contradictionary to the assumption that the non-territorial of rank γ_k is non-aggressive *at the stationary state*. Consequently, there could not exist such any rank γ_l at the stationary state that

$$\gamma_l < \lambda_j \quad \text{and} \quad \gamma_l \notin \Lambda^m_{\{i\}}.$$

In other words, at the stationary state, $\Lambda^m_{\{i\}}$ is composed of non-territorial individuals from the highest rank to the relatively m th, that is,

$$\Lambda^m_{\{i\}} = \{\gamma_1, \gamma_2, \ldots, \gamma_m\}.$$

Next, we focus the non-aggressive non-territorials at the stationary state. Now, let us consider the highest rank γ_j of non-territorial which is not included in $\Lambda^m_{\{i\}}$. As γ_j is not included in $\Lambda^m_{\{i\}}$, the non-territorial of rank γ_j is expected to get more resource when it is non-aggressive than when aggressive, so that the following must be satisfied:

$$P_i(\Lambda^m_{\{i\}} \cup \{\gamma_j\})f_{i,\gamma_j} - d_{i,\gamma_j} < 0. \tag{44}$$

Suppose that there would exist an aggressive non-territorial of rank λ_k ($\in \Lambda^m_{\{i\}}$) lower than γ_j. From (1), (6) and (10), we have the following inequality:

$$P_i(\Lambda^m_{\{i\}} \cup \{\gamma_j\})f_{i,\lambda_k} - d_{i,\lambda_k} \leq P_i(\Lambda^m_{\{i\}} \cup \{\gamma_j\})f_{i,\gamma_j} - d_{i,\gamma_j}. \tag{45}$$

From (10), (44) and (45),

$$P_i(\Lambda^m_{\{i\}})f_{i,\lambda_k} - d_{i,\lambda_k} < 0. \tag{46}$$

This inequality means that the non-territorial of rank λ_k ($\in \Lambda^m_{\{i\}}$) must be non-aggressive instead of aggressive from the viewpoint of optimal behaviour. Therefore, the assumption that there would exist an aggressive non-territorial of rank λ_k lower than γ_j is contradictory. Thus, at the stationary state, all of non-territorials of ranks lower than the highest of non-aggressive non-territorial must be non-aggressive. Lastly, these arguments have proved Lemma 2.

With these arguments, we can conclude that, at the stationary state with $\Lambda^m_{\{i\}}$, the followings must be satisfied:

$$\Lambda^m_{\{i\}} = \{\gamma_1, \gamma_2, \ldots, \gamma_m\};$$

$$P_i(\Lambda^m_{\{i\}}) f_{i,k} - d_{i,k} > 0 \quad \text{for } \forall k \leq m; \tag{47}$$

$$P_i(\Lambda^m_{\{i\}} \cup \{\gamma_l\}) f_{i,\gamma_l} - d_{i,\gamma_l} < 0 \quad \text{for } \forall l \geq m; \tag{48}$$

These conditions (47) and (48) determine the number m^* of aggressive non-territorials at the stationary state for given i, P_i, f_{i,γ_k}, and d_{i,γ_k}. So Lemma 3 has been proved.

Appendix C

We compare a stationary subpopulation $\Lambda^{m_i^*}_{\{i\}}$ of non-territorials to try to invade the existing unique territory of rank i with $\Lambda^{m_j^*}_{\{j\}}$ which is to try to invade the territory of rank j. Suppose that $j > i$. From (2), (7) and (8),

$$P_j(\Lambda^{m_i^*}_{\{i\}}) f_{j,\gamma_{m_i^*}} - d_{j,\gamma_{m_i^*}} > P_i(\Lambda^{m_i^*}_{\{i\}}) f_{i,\gamma_{m_i^*}} - d_{i,\gamma_{m_i^*}}. \tag{49}$$

Since $\gamma_{m_i^*} \in \Lambda^{m_i^*}_{\{i\}}$ so that the righthand side of (49) is positive, and therefore

$$P_j(\Lambda^{m_i^*}_{\{i\}}) f_{j,\gamma_{m_i^*}} - d_{j,\gamma_{m_i^*}} > 0. \tag{50}$$

From Lemma 3 and the arguments in Appendix B, this inequality (50) indicates that the non-territorial of rank $\gamma_{m_i^*}$ should join in the subpopulation $\Lambda^{m_i^*}_{\{i\}}$ aggressive for the unique territory of rank j. This means that $\gamma_{m_i^*} \in \Lambda^{m_j^*}_{\{j\}}$. Since

$$\Lambda^{m_j^*}_{\{j\}} = \{\gamma_1, \gamma_2, \ldots, \gamma_{m_j^*}\}$$

from Lemma 2, we conclude that $\gamma_{m_i^*} \leq \gamma_{m_j^*}$, so that $m_i^* \leq m_j^*$.

Appendix D

$C_i(\Lambda^{m_i^*}_{\{i\}})$ is the cost for the territorial of rank i in order to defend its territory against the subpopulation $\Lambda^{m_i^*}_{\{i\}}$ at the satisionary state. As defined, m_i^* is the number of aggressive non-territorials at stationary state. From Lemma 2,

$$\Lambda^{m_i^*}_{\{i\}} = \{\gamma_1, \gamma_2, \ldots, \gamma_{m_i^*}\}; \tag{51}$$

$$\Lambda^{m_j^*}_{\{j\}} = \{\gamma_1, \gamma_2, \ldots, \gamma_{m_j^*}\}. \tag{52}$$

From Lemma 4, if $i < j$, then $\gamma_{m_i^*} < \gamma_{m_j^*}$ and $m_i^* < m_j^*$. We consider hereafter the case when $i < j$.

At first, we suppose that the individual of rank j is a member of subpopulation $\Lambda_{\{i\}}^{m_i^*}$. In this case, since $i < j < \gamma_{m_i^*} < \gamma_{m_j^*}$, $\Lambda_{\{j\}}^{m_j^*}$ satisfies the following:

$$\Lambda_{\{j\}}^{m_j^*} = \Lambda_{\{i\}}^{m_i^*} \setminus \{j\} \cup \{i\} \cup \{\gamma_{m_i^*+1}, \ldots, \gamma_{m_j^*}\}.$$

Hence, from (3) and (5),

$$C_i(\Lambda_{\{i\}}^{m_i^*}) < C_j(\Lambda_{\{j\}}^{m_j^*}). \tag{53}$$

Next, we suppose that the individual of rank j is not included in the subpopulation $\Lambda_{\{i\}}^{m_i^*}$. In this case, since $\gamma_{m_i^*} < j$ and $\gamma_{m_i^*} < \gamma_{m_j^*}$, $\Lambda_{\{j\}}^{m_j^*}$ satisfies the following:

$$\Lambda_{\{j\}}^{m_j^*} = \Lambda_{\{i\}}^{m_i^*} \cup \{\gamma_{m_i^*+1}, \ldots, \gamma_{m_j^*}\}. \tag{54}$$

From (3) and (4), also in this case, the inequality (53) holds. Therefore, Corollary has been proved.

Appendix E

We focus the condition which satisfies

$$K_{\omega_i}^{tr}(\Lambda_{\Omega_n}^{m^*}) < K_{\omega_i}^{out+}(\Lambda_{\Omega_n}^{m^*} \cup \{\omega_i\}).$$

From (14) and (25),

$$\begin{aligned}
&k_{\omega_i}^{tr} - k_{\omega_i}^{out}(\Gamma_l \cup \{\omega_i\}) \\
&- \quad \frac{1}{n-1} \sum_{k=0}^{m} \sum_{L_k \subset \Lambda_{\Omega_n}^{m^*}} \left(\frac{1}{n-1}\right)^k \left(1 - \frac{1}{n-1}\right)^{m-k} \sum_{h \in \Omega_n \setminus \{\omega_i\}} P_h(L_k \cup \{\omega_i\}) f_{h,\omega_i} \\
&\qquad + \frac{1}{n-1} \sum_{i \in \Omega_n \setminus \{\omega_i\}} d_{h,\omega_i} \\
&\qquad < \sum_{k=0}^{m} \sum_{L_k \subset \Lambda_{\Omega_n}^{m^*}} \left(\frac{1}{n}\right)^k \left(1 - \frac{1}{n}\right)^{m-k} C_{\omega_i}(L_k).
\end{aligned} \tag{55}$$

We have the following inequality:

$$\sum_{k=0}^{m} \sum_{L_k \subset \Lambda_{\Omega_n}^{m^*}} \left(\frac{1}{n-1}\right)^k \left(1 - \frac{1}{n-1}\right)^{m-k} P_h(L_k \cup \{\omega_i\}) > P_h(\{\omega_i\}). \tag{56}$$

Thus, from (56),

$$
\begin{aligned}
&k^{tr}_{\omega_i} - k^{out}_{\omega_i}(\Gamma_l \cup \{\omega_i\}) \\
&- \quad \frac{1}{n-1}\sum_{k=0}^{m}\sum_{L_k \subset \Lambda^{m^*}_{\Omega_n}} \left(\frac{1}{n-1}\right)^k \left(1-\frac{1}{n-1}\right)^{m-k} \sum_{h\in\Omega_n\setminus\{\omega_i\}} P_h(L_k \cup \{\omega_i\}) f_{h,\omega_i} \\
&\qquad\qquad + \frac{1}{n-1}\sum_{i\in\Omega_n\setminus\{\omega_i\}} d_{h,\omega_i} \\
&\qquad\qquad < k^{tr}_{\omega_i} - k^{out}_{\omega_i}(\Gamma_l \cup \{\omega_i\}) - \frac{1}{n-1}\sum_{h\in\Omega_n\setminus\{\omega_i\}} P_h(\{\omega_i\}) f_{h,\omega_i} + d_{h,\omega_i}.
\end{aligned} \tag{57}
$$

Therefore, if

$$
k^{tr}_{\omega_i} < k^{out}_{\omega_i}(\Gamma_l \cup \{\omega_i\}) + \frac{1}{n-1}\sum_{h\in\Omega_n\setminus\{\omega_i\}} P_h(\{\omega_i\}) f_{h,\omega_i} - d_{h,\omega_i} \quad \text{for } \exists \omega_i \in \Omega_n, \tag{58}
$$

the inequality (55) can be satisfied, so that $K^{out+}_{\omega_i}(\Lambda^{m^*}_{\Omega_n} \cup \{\omega_i\})$ is greater than $K^{tr}_{\omega_i}(\Lambda^{m^*}_{\Omega_n})$.

Moreover,

$$
\begin{aligned}
k^{tr}_{\omega_i} &< k^{tr}_1; && (59)\\
k^{out}_{\omega_i}(\Gamma_l \cup \{\omega_i\}) &> k^{out}_N(\Xi_N); && (60)\\
\frac{1}{n-1}\sum_{h\in\Omega_n\setminus\{\omega_i\}} P_h(\{\omega_i\}) f_{h,\omega_i} - d_{h,\omega_i} &> P_1(\{N\}) f_{1,N} - d_{1,N}. && (61)
\end{aligned}
$$

Lastly, from (58), (59), (60), and (61), if

$$
k^{tr}_1 < k^{out}_N(\Xi_N) + P_1(\{N\}) f_{1,N} - d_{1,N},
$$

the inequality (58) can be satisfied for $\forall \omega_i \in \Omega_n$. This indicates the satisfaction of inequality (55), so that $K^{out+}_{\omega_i}(\Lambda^{m^*}_{\Omega_n} \cup \{\omega_i\})$ is greater than $K^{tr}_{\omega_i}(\Lambda^{m^*}_{\Omega_n})$.