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Ecological Modelling 103 (1997) 193–207

**ECOLOGICAL
MODELLING**

How does the size distribution of male territories depend on the spatial distribution of females?

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Accepted 7 April 1997

Abstract

We consider the relation between the spatial distribution of resource related to the mating activity, for instance, spatially distributed females themselves and the size distribution of territories established by males for purpose of mating. Assuming the ranking related to the position of territory, we construct and analyze a mathematical model to consider how the spatial size distributions of the territories and the mating groups are affected by the spatial distribution of mating resource. Our modelling analyses clearly demonstrate that the size distribution of territories is significantly affected by the spatial distribution of mating resource. Although the general tendency of the spatial size distribution of territories is monotonically increasing as the territorial site becomes far from the most favorable place, a specific spatial distribution of mating resource can realize a monotonically decreasing size distribution of territories. © 1997 Elsevier Science B.V.

Keywords: Territory size; Mating group size; Resource distribution; Mathematical model

1. Introduction

In numerous cases of animals, fishes and insects, territory is established for the various purposes, for example, for foraging and for mating (for instance, see Krebs and Davies, 1981). Keep-

ing territory brings to its owner such benefit that he could advantageously use the resource in his territory, whereas he must spend the time and the energy to maintain and defend his territory. It is considered that the maintenance of the territoriality basically depends on whether the benefit that the territorial individual gains by keeping its territory overcompensates the loss spent for keeping it (Brown, 1964; Davies, 1978; Davies and Houston,

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1984; Myers et al., 1981). The benefit and the loss with keeping the territory depend on the property of habitat where the territory is established, which contains the spatial density distribution of the foods, the mates and the interacting other species including predators.

Horn, 1968 constructed and analyzed the geometrical model for the maintenance of territoriality, and discussed how the maintenance depends on the density distribution of foods. He suggested that, when the food is uniformly distributed in space and is successively recruited, the territoriality could evolve. In contrast, when the spatial density distribution of foods has the small variance, and when the place with the higher density of foods is temporally variable and the prediction about the spatial density distribution is hard, the territoriality could not evolve.

The spatial size distribution of territories depends on the property of habitat. For example, in case of labroid fishes which live on reefs in the tropics and the temperate zone, females migrate to specific spawning sites on the outer or the downcurrent edges of reefs in order to spawn in the mating season. That is, the biased spatial density distribution of females is observed in the mating season. In such case of labroid fishes, the spatial density distribution of females could reflect the spatial distribution of the spawning sites preferred by females. Territorial phase males make territories over prominent rocks on the offshore reef slope where females prefer spawning in the mating season. Those territories are maintained at the same location during some days. Females tend to gather at a specific territorial male selected according to the position of territory, the body size and the color. As a result, each territorial male constructs its mating group consisting of females within its territory, and the territorial male tends to exclude the other males from its territory and to spawn with females of its own mating group. In case of the labroid fish *Halichoeres melanochir*, the size of territory located at the center of the spawning site is smaller than those at the periphery, and the territorial male at the center of spawning site can experience significantly higher successful matings than the other at the periphery (Moyer and Yogo, 1982).

In general, as the territory size gets larger, the amount of time and energy which its owner must spend to keep its territory would increase. Due to such cost of time and energy, the benefit which the territorial individual gains would not necessarily increase as expanding its territory. From the viewpoint of optimality, it could be considered that the territory size is selected so as to maximize the benefit which its owner gains.

Constructing and analyzing a mathematical model, we consider how the spatial size distribution of territories depends on the spatial distribution of resource related to the mating activity. In this paper, we consider the spatial distribution of females and that of territories established by males for purpose of mating such as in case of labroid fishes. The spatial distribution of females reflects the preference of female for the spawning site, the food abundance and the mate keeping territory. The small variance of the spatial distribution of females corresponds to the case when the places or the males preferred by females are distributed in a restricted small region and when the preference of female is intense. We consider the ranked male in terms of the occupation of territory. It is assumed that male with the higher rank can occupy the more favorable place where the female density is higher. The rank reflects the priority to occupy the place with the higher female density. In our modelling, with a given spatial density distribution of females, provided that each territorial male could select their territory size according to the ranking so as to maximize its successful matings, we can theoretically derive the expected size distribution of territories. Furthermore, provided that the mating group is established within the territory of each territorial male, the mating group size is uniquely determined from the female density distribution and the territory size. We discuss the size distribution of mating groups, too.

Our fundamental mathematical modelling will be able to be improved to some more sophisticated mathematical modelling involving some other more concrete factors relevant to the size distribution of territories, and will provide a basic framework to construct and analyze such a more advanced mathematical model.

2. Assumptions and general model

We consider a mathematical model on how the spatial size distribution of territories is determined. We suppose that mating group is established within the territory of each territorial male, and that the group size is uniquely determined from the female density distribution and the territory size.

In case of labroid fishes, terminal phase males make territories in the mating season. Territories are settled at the mating sites. Each territorial male tends to exclude the other males from its own territory and spawn with females of its own mating group. As a result, the best male could occupy the most favorable place, that is, the best territory where the female density is higher than in the other place. So territories could be considered to be settled one after another from the more favorable place to the less. Provided that the territorial male that can occupy the larger territory can keep the more females, the territorial male would spend the greater amount of time and energy to defend its territory and keep females in its territory as it could have the larger territory. Territorial male must defend females from sneakers, too. If mating group size is too large, territorial male could not efficiently guard females from sneakers. Hence, the successful matings of territorial male does not necessarily increase as expanding its territory.

In our mathematical modelling, we consider the 1-dimensional space for the territory. The spatial density distribution of females is now given by $F(x)$, that is, the female density in the region $|x, x + dx|$ by $F(x)dx$. The density function $F(x)$ is assumed to be sufficiently smooth and satisfy the following conditions for $\forall x \geq 0$:

$$\frac{dF(x)}{dx} \leq 0 \tag{1}$$

$$F(x) = F(-x) \tag{2}$$

$$0 \leq F(x) < +\infty \tag{3}$$

These conditions indicate that the most favorable site is at $x=0$, and the female density monotonically decreases as $|x|$ gets higher, that is, as the distance from the most favorable site does

larger. We assume that the better territorial male can occupy the place where the female density is the higher. From (Eq. (2)), since the considered density distribution of females is symmetry in terms of $x=0$, we assume that the spatial distribution of established territories is symmetry, too. So the $2n$ th and the $2n+1$ th males ($n \geq 1$) are considered to have the same size of territory. The best territorial male is assumed to make the territory on $(-x_0/2, x_0/2)$, where x_0 represents the territory size for the best male. From the above-mentioned symmetricity of the spatial distribution of territories, the second and the third males make territories, respectively on $(x_0/2, x_0/2 + x_1)$ and on $(-x_0/2 - x_1, -x_0/2)$. Subsequently, the $2n$ th and the $2n+1$ th males ($n = 1, 2, 3, \dots$), respectively, make the territories on (Z_{n-1}, Z_n) and on $(-Z_n, -Z_{n-1})$, where

$$Z_0 = \frac{x_0}{2}$$

$$Z_n = Z_{n-1} + x_n = \frac{x_0}{2} + \sum_{k=1}^n x_k \quad (n \geq 1)$$

and x_k is the territory size for the $2k$ th and the $2k+1$ th males. For the symmetricity of the spatial distribution of territories, we hereafter consider just (Z_{n-1}, Z_n) of the territory for the $2n$ th male ($n \geq 1$). The number of females $M_n(x)$ that the $2n$ th male ($n \geq 1$) can keep within the territory size x is given by

$$M_n(x) = \int_{Z_{n-1}}^{Z_{n-1}+x} F(y) dy = \int_0^x F(Z_{n-1} + y) dy \tag{4}$$

$M_n(x)$ is equal to the number of females that the $2n+1$ th male ($n \geq 1$) can keep within the territory size x . The number of females $M_0(x)$ kept by the best male with the territory size x is given by

$$M_0(x) = \int_{-x/2}^{x/2} F(y) dy = 2 \int_0^{x/2} F(y) dy \tag{5}$$

As the territorial male keeps the larger size of territory, he must spend the greater amount of time and energy to defend its own territory and keep females in its territory. In this reason, the available time and energy for matings would de-

crease as the size of territory gets larger. So, now we define the successful matings $W_n(x)$ of the $2n$ th male with the territory size x by

$$W_n(x) = A(x)M_n(x) \tag{6}$$

where $A(x)$ is assumed to satisfy the following conditions for $\forall x \geq 0$:

$$A(x) \geq 0 \tag{7}$$

$$\frac{dA(x)}{dx} \leq 0 \tag{8}$$

$$0 < - \left. \frac{d[\log A(x)]}{dx} \right|_{x=0} < + \infty \tag{9}$$

As the size x of territory gets larger, $M_n(x)$ increases, while $A(x)$ decreases from (Eq. (8)). The above-mentioned negative effect of the territory size on the successful matings is now introduced by the function $A(x)$.

We assume that each territorial male selects the territory size x at which $W_n(x)$ takes the maximum. Eventually, the selected size x_n must satisfy the following conditions:

$$\left. \frac{dW_n(x)}{dx} \right|_{x=x_n} = 0 \tag{10}$$

$$\left. \frac{d^2W_n(x)}{dx^2} \right|_{x=x_n} < 0 \tag{11}$$

We assume that, when the roots for (Eq. (10)) and (Eq. (11)) exist, the territorial male selects the minimum of those roots as its territory size.

3. Analysis

At first, we consider the territory size x_0 for the best male. From (Eq. (10)), we can obtain the following equation:

$$L_0(x) = R(x) \tag{12}$$

where

$$L_0(x) = \frac{F(x/2)}{2 \int_0^{x/2} F(y) dy}$$

$$R(x) = - \frac{d[\log A(x)]}{dx}$$

We can easily show that, when the positive roots for (Eq. (12)) exist, the minimum root satisfies (Eq. (11)), and it is selected as x_0 (see Appendix A).

Next, we consider the territory size x_n for the $2n$ th male ($n \geq 1$). From (Eq. (10)), we can obtain the following equation:

$$L_n(x) = R(x) \tag{13}$$

where

$$L_n(x) = \frac{F(Z_{n-1} + x)}{\int_0^x F(Z_{n-1} + y) dy}$$

and $R(x)$ is the same as before. We can show again that, when the positive roots for (Eq. (13)) exist, the minimum root satisfies (Eq. (11)), and it is selected as x_n ($n \geq 1$) (see Appendix A).

We can prove that, when the appropriate positive root x for (Eq. (12)) exists, and when $L_n(x) > L_{n+1}(x)$ for $\forall n \geq 0$ and $\forall x > 0$, the appropriate root for (Eq. (13)) always exists and the determined territory sizes x_n monotonically decreases in terms of $n \geq 0$ (Appendix B). Otherwise, the territory size is not necessarily decreasing in terms of n . Indeed, the n -dependency of the territory size is considerably affected by the nature of the spatial density distribution of females. In Appendix B, the general condition sufficient for the increasing monotonicity and that for the decreasing monotonicity of the territory size x_n in terms of $n (\geq 1)$ are given.

Now, to demonstrate how the characteristics of the female distribution affects the optimal distribution of male territory sizes, we consider the following distribution functions F of females, which satisfy (Eq. (1), Eq. (2) and Eq. (3)) (see Fig. 1):

Case A: $F(x) \propto e^{-\beta x}$

Case B: $F(x) \propto e^{-\beta x^2}$

Case C: $F(x) \propto H(-x^2 + \beta^2)$
 $\equiv \begin{cases} -x^2 + \beta^2 & \text{for } x < \beta \\ 0 & \text{for } x \geq \beta \end{cases}$

Case D: $F(x) \propto \frac{1}{e^{\lambda x - \beta} + 1}$

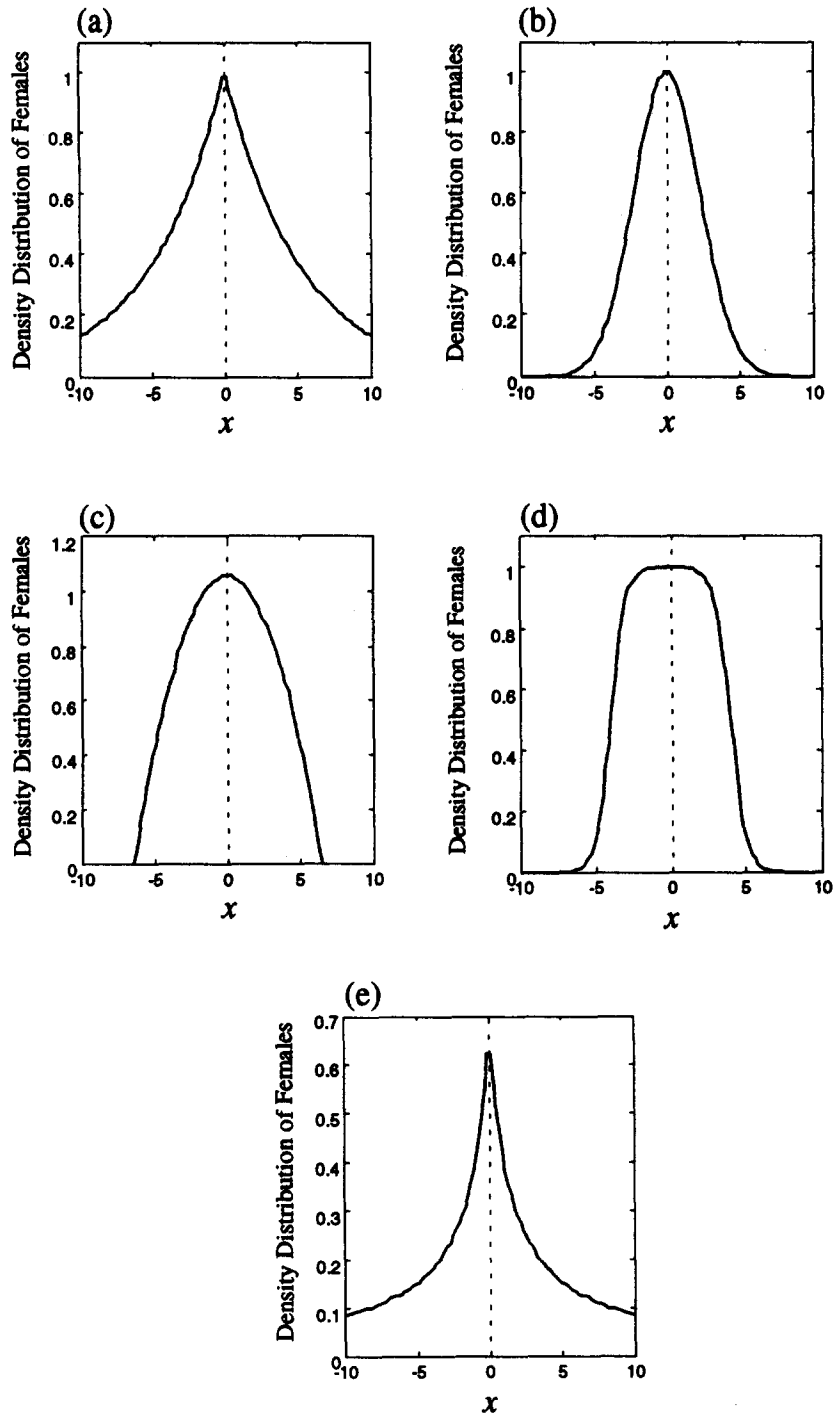


Fig. 1. The female density distribution functions F : (a) $F(x) = \exp(-\beta x)$, $\beta = 0.1$; (b) $F(x) = \exp(-\beta x^2)$, $\beta = 0.2$; (c) $F(x) = c(-x^2 + \beta^2)$, $c = 0.025$, $\beta = 6.5$; (d) $F(x) = 1/\{\exp(\lambda x - \beta) + 1\}$, $\lambda = 2.0$, $\beta = 8.0$; (e) $F(x) = 1/(\beta x + 1)$, $\beta = 1.5$.

$$\text{Case E: } F(x) \propto \frac{1}{\beta x + 1}$$

where β and λ are positive constants.

At first, we consider the following function A which represents the effect of the territory size on the successful matings, satisfying Eq. (7), Eq. (8) and Eq. (9):

$$A(x) \propto e^{-\alpha x} \quad (14)$$

where α is a positive constant that represents the extent of energy share for keeping the territory with size x . As α gets larger, the available time and energy for matings decrease, whereas, as α does smaller, they increase. For $A(x)$ given by (Eq. (14)), $R(x)$ becomes constant α . Then, we can show that the mating group size $M_n(x_n)$ kept by the $2n$ th male satisfies the below relation for any spatial female density distribution function F satisfying Eq. (1), Eq. (2) and Eq. (3), so that it monotonically decreases in terms of n (Appendix C):

$$M_n(x_n) > M_{n+1}(x_{n+1}) \text{ for } n \geq 0 \quad (15)$$

For each function F in the above-described cases, we show in Fig. 2 the territory size (grey) and the mating group size (black) of each male, calculated numerically with (Eq. (14)).

Numerical demonstration Fig. 2a corresponds to Case A with (Eq. (14)). For Case A, whenever the positive root 2 for (Eq. (12)) exists, the appropriate one for (Eq. (13)) exists, and then the determined territory sizes have the following relations for any function A satisfying Eq. (7), Eq. (8) and Eq. (9) (Appendix D):

$$x_0 > x_1 \quad (16)$$

$$x_n = x_{n+1} \text{ for } n \geq 1 \quad (17)$$

This result indicates that the territory size of the best male is larger than any other males, and all the other males have the same territory size.

From Eq. (16) and Eq. (17), we can show that the mating group sizes for Case A have the relation (Eq. (15)) for any function A satisfying Eq. (7), Eq. (8) and Eq. (9) (Appendix D). This indicates that the mating group size monotonically decreases as the rank of territorial male becomes lower. Consequently, the mating group size is

smaller in the less favorable region than in the more favorable region with the higher female density.

Also for Cases B, C and D, as shown in Fig. 2(b–d), the territory size x_n monotonically decreases in terms of n . That is, the size of territory located at the more favorable site with the higher female density is larger than that at the less favorable.

For Case C, the spatial density distribution of females is restricted in $[-\beta, \beta]$. As shown in Fig. 2c, the territories located relatively near the more favorable site could have almost the same size. However, the territory size becomes smaller rapidly as the distance from the most favorable site gets much larger. Only males ranked less than the 18th have the territories. Fig. 2c could be regarded as the case when the size of territories settled in the periphery of the spatial distribution of females is much smaller than the others within the range of female distribution.

For Case D, as shown in Fig. 2d, the territories located in the sufficiently favorable region have almost the same size. Because of the nature of the female density distribution shown by Fig. 1d, the size of territories located in the region with a intermediate range of female density rapidly decreases as the distance from the most favorable site gets larger. The territories located in the less favorable region with the lower female density have almost the same size distinctly smaller than the size for those in the sufficiently favorable region. Hence, in this case, the territories could be roughly classified into two characteristic sizes.

In contrast to these cases, Case E is an example to satisfy the sufficient condition for the increasing monotonicity of the territory size x_n in terms of n (≥ 1), given in Appendix B. In labroid fishes, it has been reported that the territory size monotonically increases as the distance from the most favorable spawning site with the higher female density gets larger (Moyer and Yogo, 1982). When the parameter β is small, the territory size x_0 for the best male is larger than that for the second, while the territory size x_n monotonically increases in terms of $n \geq 1$ (see Fig. 2e-1). When β is sufficiently large, as shown in Fig. 2e-2, x_n monotonically increases in terms of $n \geq 0$. In this

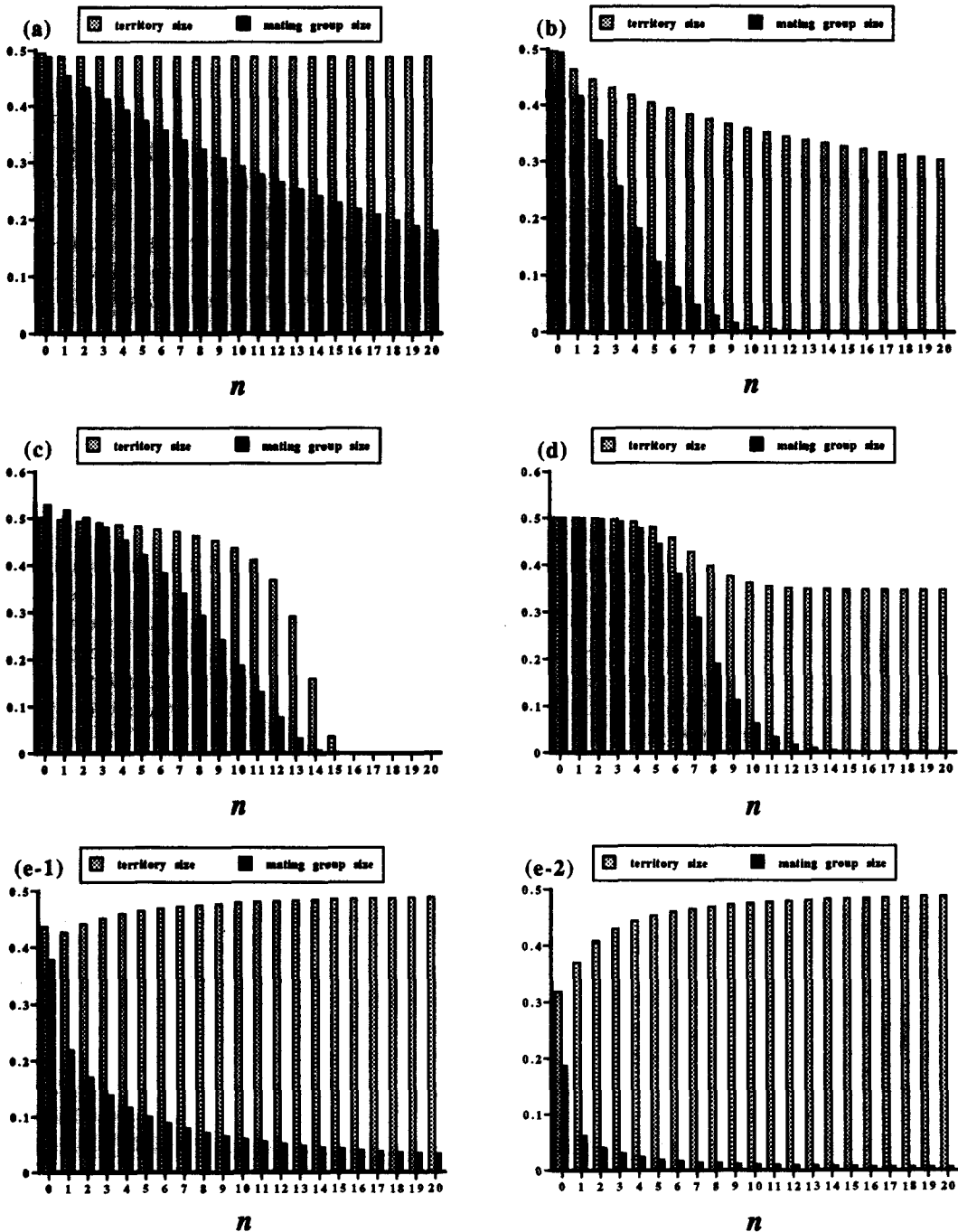


Fig. 2. The territory size x_n (grey) and the mating group size M_n (black) for the $2n + 1$ th male ($n = 0, 1, 2, \dots$). $n = 0$ Corresponds to the territory of the best male in the text. $A(x) = \exp(-\alpha x)$, $\alpha = 2.0$. (a) $F(x) = \exp(-\beta x)$, $\beta = 0.1$; (b) $F(x) = \exp(-\beta x^2)$, $\beta = 0.2$; (c) $F(x) = c/(-x^2 + \beta^2)$, $c = 0.025$, $\beta = 6$; (d) $F(x) = 1/(\exp(\lambda x - \beta) + 1)$, $\lambda = 2.0$, $\beta = 8.0$; (e-1) $F(x) = 1/(\beta x + 1)$, $\beta = 1.5$; (e-2) $F(x) = 1/(\beta x + 1)$, $\beta = 10.5$.

case, the parameter β represents the extent of the variance of spatial density distribution of females. As β gets larger, the variance becomes smaller. When the variance gets smaller, the size of territory located in the more favorable region with the higher female density tends to become smaller than that in the less favorable region.

For each case, we show in Fig. 3 the mating group size per territory size of each male, $M_n(x_n)/x_n$, that is corresponding to the mean female density within the territory (grey), and the successful matings $W_n(x_n)$ defined by (Eq. (6)) (black). Fig. 3(a–e), respectively correspond to Cases A, B, C, D and E. For every considered cases, both the mean female density and the successful matings are larger for the territory located at the more favorable site with the higher female density than for that at the less favorable. In Fig. 3d for Case D, the males with their territories in the sufficiently favorable region have almost the same larger successful matings. In Fig. 3e-1 and Fig. 3e-2 for Case E, the mean female density is small and roughly similar for the territories located in the less favorable region with the lower female density. Fig. 3e-1 and Fig. 3e-2, respectively correspond to the cases when β is small and when it is sufficiently large. As the variance of the density distribution of females gets larger, the successful matings of any male becomes smaller.

From Fig. 2 and Fig. 3, we can see that the nature of the successful matings is regarded as significantly related to the nature of the mating group size and of the mean female density within the territory.

Fig. 4 gives the spatial distributions of the successful matings per territory size (grey) and per mating group size (black). The former can be regarded as the mean efficiency of the utilization of territory area for the mating success, or as the value of the unit territory area according to the mating success. The latter corresponds to the mating success averaged over the females within the territory, so that it can be regarded as the value of one female according to the mating success. The successful matings per territory size shows the nature similar to that of the mating group size (Fig. 3) or the mating group size per territory size (Fig. 4). It monotonically decreases as the distance from

the most favorable site gets larger. This result indicates that the merit of the wider territory according to the mating success becomes the less as the territory is located at the less favorable site. Especially, as seen from Fig. 4d, Case D shows that the value of the unit territory area rapidly decreases as the distance of territory from the most favorable site gets over a critical.

In contrast, the successful matings per mating group size does not necessarily have such nature as common for every cases. Commonly for Cases A, B, C and D, as seen from Fig. 4(a–d), the successful matings per mating group size is monotonically increasing in the male rank n , that is, in the distance from the most favorable site. For Case E, as seen from Fig. 4e-1 and Fig. 4e-2, roughly saying, it is monotonically decreasing, although it is larger for the second rank male than for the best in case of Fig. 4e-1.

For Case A, the value of one female according to the mating success does not have much difference among territories as seen from Fig. 4a. So, from the viewpoint of female, the mating success is affected little by which territory it belongs to. Differently from Case A, the value of one female in Case C could show a drastic change for the territories sufficiently far from the most favorable site.

In Fig. 4c, the value of one female for the territories at the periphery of the most favorable site is rather high, whereas has little difference among the territories located within a range of distance from the most favorable site. In other words, the female in the territory located as the peripheral site has a rather high value for the territorial male according to the mating success. From the viewpoint of such female, it could expect the higher mating success, compared with the female belonging to the territory located at the better site. As for the female belonging to the territory within a range of distance from the most favorable site, as seen from Fig. 4c, it could expect little difference depending on which territory it belongs to, as long as belonging to the territory located with the range.

Also for Case D, as seen from Fig. 4d, the value of one female has the characteristics similar to that for Case C. However, compared with the case of

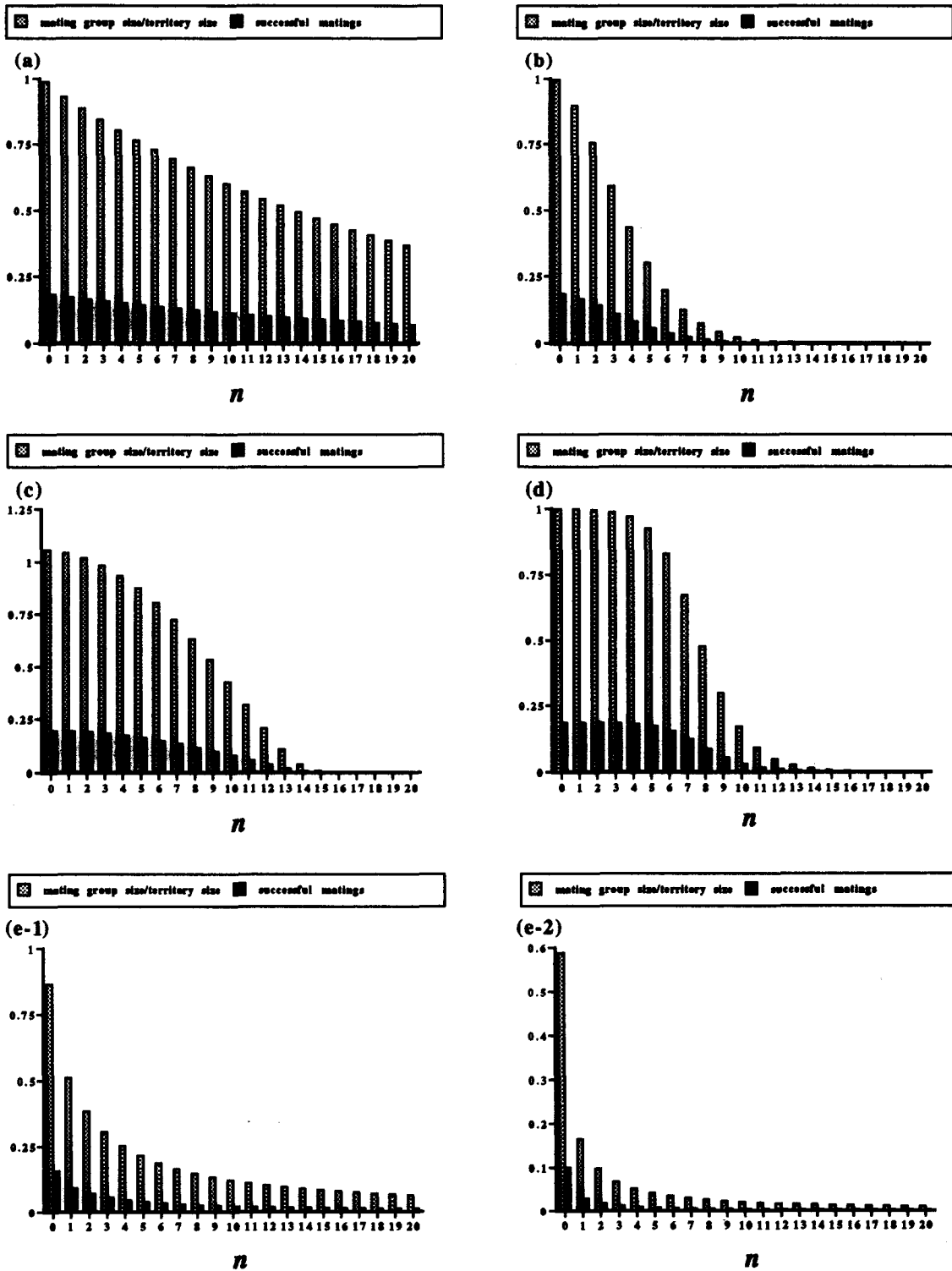


Fig. 3. The mating group size per territory size $M_n(x_n)/x_n$ (grey), and the successful matings $W_n(x_n)$ (black) for the $2n + 1$ th male ($n = 0, 1, 2, \dots$). $A(x) = \exp(-\alpha x)$, $\alpha = 2.0$. (a) $F(x) = \exp(-\beta x)$, $\beta = 0.1$; (b) $F(x) = \exp(-\beta x^2)$, $\beta = 0.2$; (c) $F(x) = c(-x^2 + \beta^2)$, $c = 0.025$, $\beta = 6.5$; (d) $F(x) = 1/(\exp(\lambda x - \beta) + 1)$, $\lambda = 2.0$, $\beta = 8.0$; (e-1) $F(x) = 1/(\beta x + 1)$, $\beta = 1.5$; (e-2) $F(x) = 1/(\beta x + 1)$, $\beta = 10.5$.

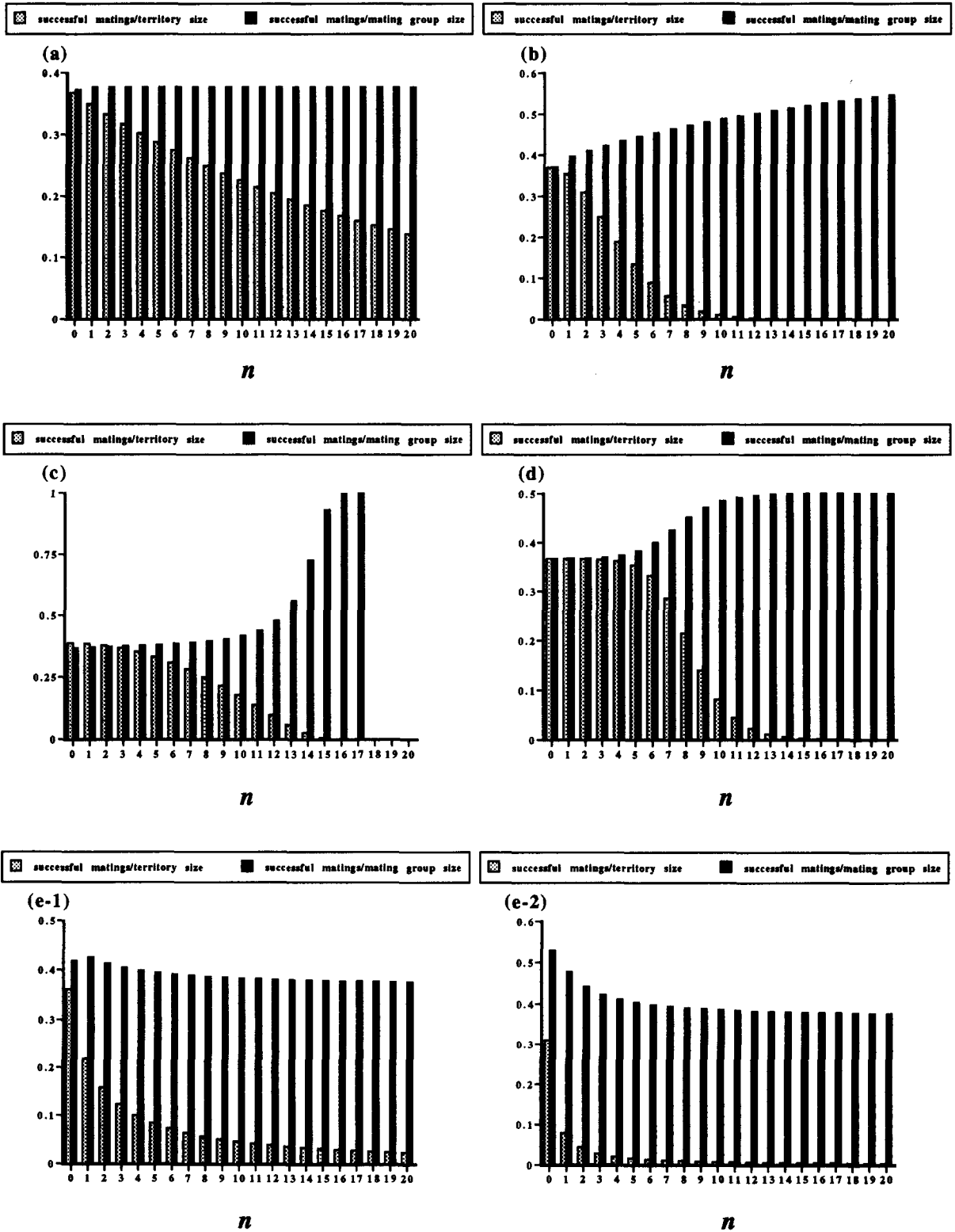


Fig. 4.

Case C, Case D shows a classification of the value into two characteristic groups, as resulted for the territory size distribution indicated by Fig. 2d. For a group of territories (for instance, from the 0th to the 4th in Fig. 4d) within a range of distance from the most favorable site, the value of one female has little difference among them. In the same time, for another group of territories (from the 11th to the 20th in Fig. 4d) sufficiently far from the most favorable site, too, the value has little difference among them. The value for the latter group is significantly larger than that for the former. Roughly saying, the value of one female becomes significantly larger as the location of territory gets out of a critical site (around the 7th or the 8th in Fig. 4d).

For Case E, the result shows the characteristics difference from those in the other cases. The value of one female is relatively higher around the most favorable site than in the peripheral sites far from the most favorable. In case of Fig. 4e-1 and Fig. 4e-2, the value for the territories located in the peripheral region far from the most favorable site has little difference among them.

Through those results shown in Fig. 4, the distribution of the value of one female has tendency reflecting the characteristics of the distribution of territory size rather than the mating group size. That is, the female tends to have the higher value in the smaller territory. So, this result indicates the significant relationships between the territory size and the value of one female, independently of the female distribution in space.

4. Discussion

In our model, we considered the 1-dimensional space for territory, and analyzed a mathematical model to consider how the spatial size distributions of the territories and the mating groups are determined, depending on the spatial distribution of

resource related to the mating activity, for instance, that of females themselves. We analyzed the model for some different spatial density distribution functions of the resource. In some cases of labroid fish, as observed by Moyer and Yogo, 1982, the territory size is smaller at the more favorable mating site with the higher female density than at the less favorable site. Our mathematical model can realize such nature of the size distribution of territories (see Fig. 2e). However, as shown in Fig. 2, the results opposite to such observed nature could be realized by our mathematical model, too, depending on the spatial distribution of females. Therefore, our results could apparently demonstrate that the spatial size distribution of territories considerably depends on how the resource related to the mating activity, including the female density, is distributed in space.

In some cases of labroid fish, the territorial male must defend the mating group against the sneakers. Such situation might make the amount of time and energy for the territorial to defend its territory increase. The density of sneakers might have tendency to be higher at the more favorable mating site. As a result, such situation would considerably work to reduce the territory size at the favorable mating site. In our mathematical modelling, such effect of sneaking could be introduced into the model by the nature of both functions F and A . This is because the spatial distribution of sneakers must be significantly relevant to the female distribution F , and the mating loss due to the sneaking could be to A .

In reality, the spatial distribution of territories is to be considered in the 2-dimensional space. However, when the territories are formed in the region centered at the unique favorable mating site, we could expect that there would be the similar property of the distribution as resulted for our 1-dimensional model. Provided that both the territory size and the mating group size at the less favorable site would be smaller than those at the more favorable site, we could consider that the size distribution of mating groups monotonically decreases. How-

Fig. 4. The successful matings per territory size $W_n(x_n)/x_n$ (grey), and the successful matings per mating group size $W_n(x_n)/M_n(x_n)$ (black) for the $2n+1$ th male ($n=0, 1, 2, \dots$). $A(x) = \exp(-\alpha x)$, $\alpha = 2.0$. (a) $F(x) = \exp(-\beta x)$, $\beta = 0.1$; (b) $F(x) = \exp(-\beta x^2)$, $\beta = 0.2$; (c) $F(x) = c(-x^2 + \beta^2)$, $c = 0.025$, $\beta = 6.5$; (d) $F(x) = 1/\{\exp(\lambda x - \beta) + 1\}$, $\lambda = 2.0$, $\beta = 8.0$; (e-1) $F(x) = 1/(\beta x + 1)$, $\beta = 1.5$; (e-2) $F(x) = 1/(\beta x + 1)$, $\beta = 10.5$.

ever, as demonstrated in our analysis for the model of Case E, there is such case that the territory size is larger at the less favorable site than at the more favorable site. So it is likely that both the territory size and the mating group size at the less favorable site might be larger than at the more favorable site.

In this paper, we considered that the spatial density distribution of females could reflect the spatial distribution of the spawning site preferred by females. We can consider the other factors which could reflect the preferability for mating, for example, the food or the predation risk. For the case of food distribution, $W(x)$ could be regarded as corresponding to the number of offsprings or the energy that the territorial keeping the territory size x could expect to obtain.

Acknowledgements

The authors greatly thank Yasuhiro Nakajima and Junji Maruyama for their valuable comments.

Appendix A. Adaptability of the minimum root

The derivative of $L_0(x)$ in terms of x is obtained as follows:

$$\frac{dL_0(x)}{dx} = \frac{1}{4\{M_0(x)\}^2} \left[\frac{dF}{dx} \left(\frac{x}{2} \right) M_0(x) - \left\{ F \left(\frac{x}{2} \right) \right\}^2 \right]$$

$M_0(x)$ is given by (Eq. (5)). Therefore, from (Eq. (1)) and (Eq. (3)), $dL_0(x)/dx < 0$, that is, $L_0(x)$ monotonically decreases in terms of x . From (Eq. (1)) and (Eq. (3)), $M_0(x)$ satisfies the following inequality:

$$xF \left(\frac{x}{2} \right) < M_0(x) < xF(0)$$

Thus, $L_0(x)$ satisfies the following inequality:

$$\frac{F(x/2)}{xF(0)} < L_0(x) < \frac{1}{x} \tag{A1}$$

From (Eq. (1)) and (Eq. (3)), as $x \rightarrow +0$, $F(x/2)/\{xF(0)\}$ and $1/x$ diverge to $+\infty$. As $x \rightarrow +\infty$, they converge to 0. Therefore, from (Eq. (A1)), $L_0(x)$ diverges to $+\infty$ as $x \rightarrow +0$, and converges to 0 as $x \rightarrow +\infty$. Now, $dW_0(x)/dx > 0$ when $L_0(x) > R(x)$, and $dW_0(x)/dx < 0$ when $L_0(x) < R(x)$. Since $A(x)$ satisfies (Eq. (9)), $0 < R(0) < \lim_{x \rightarrow +0} L_0(x) = +\infty$. Therefore, when the positive roots for (Eq. (12)) exist, $L_0(x)$ and $R(x)$ have the relation shown in Fig. A1. As a result, when the positive roots for (Eq. (12)) exist, $W_0(x)$ takes the maximum at the minimum root of them, so that the minimum positive root satisfies (Eq. (11)). In the similar way, we can show that $L_n(x)$ monotonically decreases in terms of x , and it diverges to $+\infty$ as $x \rightarrow +0$, and converges to 0 as $x \rightarrow +\infty$. Therefore, when the positive roots for (Eq. (13)) exist, $W_n(x)$ takes the maximum at the minimum root of them.

Appendix B. Monotonicity of territory sizes

At first, we consider the decreasing monotonicity of the territory size x_n in terms of n . When the appropriate positive root for (Eq. (12)) exists, $L_0(x)$ and $R(x)$ have the relation as shown in Fig. B1. Then, when $L_n(x) > L_{n+1}(x)$ for $\forall n \geq 0$ and $\forall x > 0$, as shown in Fig. B1, the positive root for (Eq. (13)) always exists and the determined territory sizes satisfy $x_n > x_{n+1}$. So, in this case, we can obtain the following condition sufficient for the decreasing monotonicity of the territory size x_n in terms of n :

$$\frac{\partial L(x, z)}{\partial z} < 0 \text{ for } \forall z, x > 0,$$

where

$$L(x, z) = \frac{F(x+z)}{\int_0^x F(y+z) dy}$$

$L_n(x)$ in the main text corresponds to $L(x, z_{n-1})$ ($n \geq 1$). When $L(x, z)$ monotonically decreases in

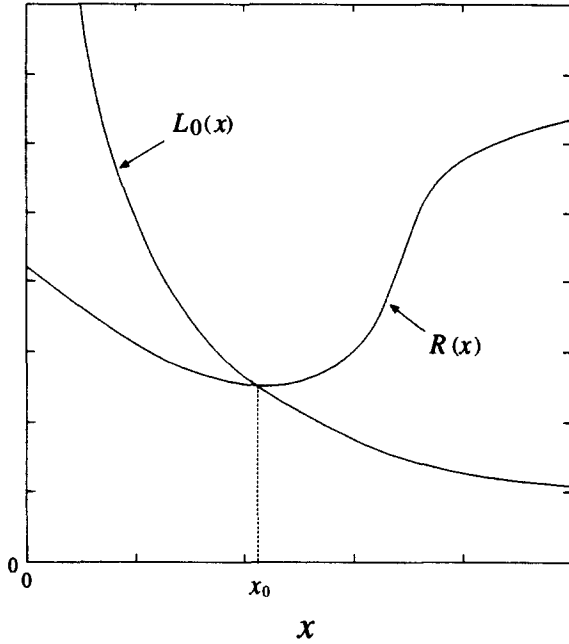


Fig. A1. Relation between $L_0(x)$ and $R(x)$ when the positive root for $L_0(x) = R(x)$ exists.

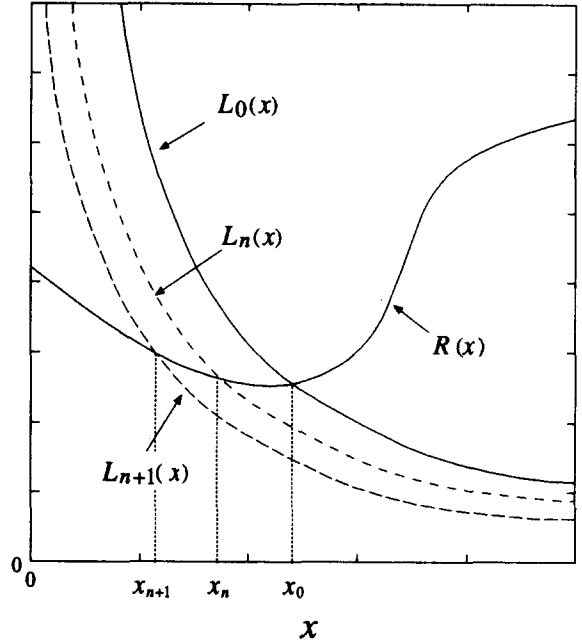


Fig. B1. Relation between $L_n(x)$ and $R(x)$ ($n \geq 0$) when the positive root for $L_0(x) = R(x)$ exists, and when $L_n(x) > L_{n+1}(x)$.

terms of z , $L_n(x) > L_{n+1}(x)$ so that the territory size x_n ($n \geq 1$) monotonically decreases in terms of n .

Next, we consider the increasing monotonicity of the territory size. For $\forall n \geq 0$ and $\forall x > 0$, when $L_n(x) < L_{n+1}(x)$, and when the appropriate positive roots x for $L_n(x) = R(x)$ and $L_{n+1}(x) = R(x)$ exist, with the argument similar to that for the decreasing monotonicity of the territory size, we can show that the determined territory sizes x_n and x_{n+1} satisfy $x_n < x_{n+1}$. In this case, for $n \geq 1$, we can obtain the following sufficient condition for the increasing monotonicity of x_n in terms of n :

$$\frac{\partial L(x, z)}{\partial z} > 0 \text{ for } \forall z, x > 0.$$

When $L(x, z)$ monotonically increases in terms of z , $L_n(x) < L_{n+1}(x)$. Then, when $L_n(x) < L_{n+1}(x)$, and when the appropriate positive roots x for $L_n(x) = R(x)$ and $L_{n+1}(x) = R(x)$ exist, we can show that the determined territory sizes x_n and x_{n+1} satisfy $x_n < x_{n+1}$.

Appendix C. Decreasing monotonicity of mating group sizes

For the function $A(x)$ given by (Eq. (14)), $R(x)$ is constant α . Since $M_0(x_0)$ is given by (Eq. (5)) and $x = x_0$ satisfies (Eq. (12)), the following relation can be obtained:

$$M_0(x_0) = \frac{1}{\alpha} F\left(\frac{x_0}{2}\right) = \frac{1}{\alpha} F(z_0)$$

Since $M_1(x_1)$ is given by (Eq. (5)) and x_1 satisfies (Eq. (13)), the following can be also obtained:

$$M_1(x_1) = \frac{1}{\alpha} F\left(\frac{x_0}{2} + x_1\right) = \frac{1}{\alpha} F(z_0 + x_1)$$

From (Eq. (1)) and (Eq. (3)), $F(z_0) > F(z_0 + x_1)$. Hence, the above relations show that $M_0(x_0)$ and $M_1(x_1)$ satisfy the following relation:

$$M_0(x_0) > M_1(x_1)$$

Similarly, for $n \geq 1$, $M_n(x_n)$ and $M_{n+1}(x_{n+1})$ become

$$M_n(x_n) = \frac{1}{\alpha} F(z_{n-1} + x_n)$$

$$\begin{aligned} M_{n+1}(x_{n+1}) &= \frac{1}{\alpha} F(z_n + x_{n+1}) \\ &= \frac{1}{\alpha} F(z_{n-1} + x_n + x_{n+1}) \end{aligned}$$

Since $F(z_{n-1} + x_n) > F(z_n + x_{n+1})$ for $n \geq 1$, the argument same as above concludes that $M_n(x_n)$ and $M_{n+1}(x_{n+1})$ satisfy the following relation:

$$M_n(x_n) > M_{n+1}(x_{n+1})$$

Appendix D. Territory and mating group sizes for Case A

At first, we show that x_n has the relation (Eq. (16)) and (Eq. (17)) for Case A. L_0 in this case is given by

$$L_0(x) = \frac{\beta}{2} \frac{1}{e^{\beta x/2} - 1}$$

and

$$L_n(x) (\forall n \geq 1)$$

by

$$L_n(x) = \frac{\beta}{e^{\beta x} - 1}$$

When the positive roots for (Eq. (12)) exist, $L_0(x)$ and $R(x)$ have the relation as shown in Fig. 6. We can easily show that $L_0(x) > L_n(x) (\forall n \geq 1)$. Therefore, as shown in Fig. 6, when the positive roots for (Eq. (12)) exist, (Eq. (13)) also has the positive roots. The minimum root is smaller for (Eq. (13)) than for (Eq. (12)). This proves (Eq. (16)). Since each $x_n (n \geq 1)$ is the root determined commonly for (Eq. (13)) which is now independent of n , they are all identical. This proves (Eq. (17)).

Next, we show that $M_n(x_n) (n \geq 0)$ in Case A monotonically decreases in terms of n . $M_0(x_0)$ and $M_1(x_1)$ are respectively obtained as follows:

$$\begin{aligned} M_0(x_0) &= \frac{2}{\beta} (1 - e^{-\beta x_0/2}) \\ M_1(x_1) &= \frac{e^{-\beta x_0/2}}{\beta} (1 - e^{-\beta x_1}) \end{aligned}$$

Since $x_0 > x_1$, $M_0(x_0)$ and $M_1(x_1)$ have the following relation:

$$\begin{aligned} M_0(x_0) - M_1(x_1) &= \frac{1}{\beta} \{2(1 - e^{-\beta x_0/2}) - e^{-\beta x_0/2}(1 - e^{-\beta x_1})\} \\ &> \frac{1}{\beta} \{2(1 - e^{-\beta x_0}) - (1 - e^{-\beta x_1})\} \\ &= \frac{1}{\beta} \{(1 - e^{-\beta x_0}) + (e^{-\beta x_1} - e^{-\beta x_0})\} > 0 \end{aligned}$$

$M_n(x_n)$ and $M_{n+1}(x_{n+1}) (n \geq 1)$ are respectively obtained as follows:

$$\begin{aligned} M_n(x_n) &= \frac{e^{-\beta z_{n-1}}}{\beta} (1 - e^{-\beta x_n}) \\ M_{n+1}(x_{n+1}) &= \frac{e^{-\beta z_n}}{\beta} (1 - e^{-\beta x_{n+1}}) \end{aligned}$$

Since $x_n = x_{n+1}$ for $\forall n \geq 1$, $M_n(x_n)$ and $M_{n+1}(x_{n+1})$ have the following relation:

$$\begin{aligned} M_n(x_n) - M_{n+1}(x_{n+1}) &= \frac{1 - 2e^{-\beta x_n} + e^{-\beta(x_n + x_{n+1})}}{\beta e^{\beta z_{n-1}}} \\ &= \frac{(1 - e^{-\beta x_n})^2}{\beta e^{\beta z_{n-1}}} > 0 \text{ for } \forall n \geq 1 \end{aligned}$$

Therefore, $M_n(x_n)$ monotonically decreases in terms of n .

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