SUGGESTED RUNNING HEAD TYTLE How related is the Size Distribution of Mating Groups

How Related is the Size Distribution of Mating Groups to the Existence and the Frequency of Sneakers?: Some Mathematical Modeling Analyses

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Abstract

1 Introduction

Sexual selection has been viewed as a powerful agent in shaping many traits in behaviour, morphology, and life history (Mayr 1972; Trivers 1972; Warner 1980). It has also been implicated in the maintenance of several reproductive pholymorphisms. Some of those polymorphisms are simple ontogeneric changes by males in species that experience intense sexual selection. In some of these species, younger males with low-cost, nonaggressive mating behaviours coexist with older males who engage in intense competition that has a potentially higher reproductive yield (Gadgil 1972; Howard 1978; Trivers 1972). Other polymorphisms involve the coexistence of two types of males of which one is usually larger and more aggressive than another, and remain distinct throughout their lives (Constantz 1975; Gadgil 1972; Hamilton 1979). Also, apparently stable mixtures of two different sexual types, dioecious and sex-changing hermaphrodite individuals, are common in fishes and pandalid shrimps (Charnov 1979; Reinboth 1970; Ronbertson and Warner 1978; Warner and Ronbertson 1978).

Aspects of the reproductive biology of the labroid fishes which have received considerable attention from evolutionary biologists include the adaptive significance of, and the relationships about: i) the protogynous hermaphroditism and the occurrence and coexistence of various sexual phenotypes, ii) the differently structured social and mating systems, and iii) the existence of distinct, sexspecific color phases. The labroid fishes live on reefs in the tropics and the temperate zone. Many labroid species are hermaphrodites and could change their sex from female to male. In some labroid species, however, there are not only hermaphroditic but also dioecious individuals. The dioecious individuals are born as primary male (not result of sex change). Primary males become sexually mature with the same color to females (initial phase) and make reproductive activity. When primary males become large in size, their color changes to vivid color (terminal phase). On the other hand, females make reproductive activity, and could change sex to male when they become large in size. Those sex-changed males from females change their color to the terminal phase. Two color types of males, which are initial and terminal phases, are observed in dioecious species. Reinboth (Reinboth 1957; Reinboth 1961; Reinboth 962a; Reinboth 962b) reported that mature males with two different color types exist in the labroid fishes, and classified the labroid fishes into two types of species: One has both initial and terminal phase males together (diandric species), and another has only terminal phase males (monandric species).

Terminal and initial phase males have the difference in their mating behaviours. Females of many labroid fishes migrate to specific spawning sites on the outer or the downcurrent edges of reefs (Threshoer 1984). Such spawning sites have been suggested to give the best opportunity for eggs to be carried rapidly off the reef and away from reef-based predators (Johannes 1978; Jones 1981; Moyer and Yogo 1982; Randall and Randall 1963; Robertson 1981; Robertson and Hoffman 1977; Warner and Leigh 1975). Terminal phase males make territories above prominent rocks on the offshore reef slope on which females prefer spawning in mating season. These territories are maintained at the same location during some successive days. Sibuno et al. (Shibuno and Kakuda 1993) studied spawning sites and spawning migration paths of females of the protogynous wrasse, *Halichoeres marginatus*. They observed that small females migrate to the spawning sites near their home range, whereas large females migrate to various spawning sites located within a wide area, including downcurrent sites. Females tend to gather at some specific territorial males selected by the position the territory, the body size and the color. Each territorial male constructs its mating group consisting of females in its territory, and tends to exclude the other males from its territory and to spawn with females in its mating group. Fertilization is made external and with no parental care. Territorial males at the center of the spawning sites can experience significantly higher successful matings than those at the periphery (Moyer and Yogo 1982).

In fishes, the relation between the phylogenesis and the appearance of hermaphroditic fishes is not obvious in general. However, it has been considered that the evolution from dioecious to hermaphrodites has occurred (Smith 1975). Ghiselin (Ghiselin 1969) and Warner (Warner 975a; Warner 1984) constructed and analyzed the size-advantage model, and suggested that if mating system is polygamy and large males can make mating with many females, then hermaphroditic individuals which can make reproductive activity as female in small size are more advantageous than dioecious individuals. Consequently, they theoretically conjectured that the evolution from dioecism to hermaphrodite has occurred. In labroid fishes, indeed, there are many monandric species. How do the initial males make mating? Why are there diandric species in labroid fishes? Initial male of labroid fish makes the two types of mating behaviour. We call one the sneaking, and the other the group spawning. There are two kinds of the sneaking: One is such that the initial phase males invade into the territory of terminal phase male and watch for the mating moment by terminal phase male. At a mating moment, initial phase male rushes into the pair and fertilizes the spawned eggs by shedding gametes into the water. Another is such that the initial phase males follow a female into a territory. When the female tries to court the territory owner, the initial male makes mating with the female by tactile stimulation. In this paper, we call these two types of mating behaviour the sneaking. In contrast, the group spawning is made between group consisting of initial phase males and a female. Those initial phase males pursue the female in the group and subject her to spawn in the group by frequent tactile stimulation.

The reproductive activity of initial phase males could be considered to be also reflected to their proportion in the whole population. In case of *Pseu*- dolabrus japanicus with the small proportion (6%) of initial phase males, only the sneaking is observed, while, in case of *Halichoeres tenuispinis* with the large proportion (50%), the group spawning is mainly observed (Nakazono 1979). Some labroid fish has the proportion of initial phase males and the mating behaviour which be affected by the property of habitat, for instance, as in case of *Thalassoma bifasciatum* (Mayr 1972; Ronbertson and Warner 1978; Warner and Hoffman 980a; Warner and Hoffman 980b; Warner and Ronbertson 1978; Warner and Leigh 1975).

Warner and Hoffman (Warner and Hoffman 980a; Warner and Hoffman 980b) studied how the population of the terminal and the initial phase males of T. bifasciatum changes as the local population gets larger. Local population could be considered in proportion to the area of reef on which it is settled. Warner *et al.* (Warner and Leigh 1975) suggested that the sex-change and the color transition might be socially controlled in each local population. As the local population gets larger, the proportion of terminal phase males tends to decrease (see Fig. 1(a)) and the proportion of initial phase males to increase (see Fig. 1(b)). Only for the local population with the size greater than 200, the group spawning was observed, and it was more likely to be observed as local population gets larger. In the local population with the size less than 200, the sneaking was observed.

In labroid fishes, terminal phase males can efficiently control females of their mating group whose size is small, so the successful matings of initial phase males with the sneaking behaviour from such mating group is expected small. As the mating group size gets larger, terminal phase males could not efficiently control females so that the successful matings of initial phase males with the sneaking behaviour is expected to increase. We can consider that the difference of the size distribution of mating groups could cause to change the expected successful matings of the sneakers.

Hirata and Seno (Hirata and Seno 1996) considered how the spatial size distribution of territories depends on the spatial distribution of resource related to the mating activity, constructing and analyzing the mathematical model. Especially, they considered the territories made by males for purposes of mating and the spatial distribution of females. They considered that the mating group is formed in the territory of each territorial male, and its size significantly depends on the territory size. They introduced the ranking order among territories. When the spatial density distribution of females is given, provided that each territorial male could select their territory size to maximize its mating success, theoretically the expected size distributions of territories and mating groups is determined. They suggested 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. That is, the mating groups have the various size distribution according to the spatial density distribution of resources. In Chapter 2, we consider how the size distribution of mating groups is related to the existence of sneakers. We consider the population in which male has alternative two different mating strategies. One is to make a mating group of females in its territory. Another is to make the sneaking. Male with the sneaking behaviour invades into the territory of another male and watches for the mating moment by its territory owner. He joins a pair at a mating moment and tries to make the mating with the female of it. In this paper, we call these two mating strategies the *mating group strategy* and the it sneaking strategy, and do males with each strategy the *territorial male* and the *sneaker*. In Chapter 2, we construct and analyze a mathematical model for the invasion of sneaking strategy against the mating group strategy, and discuss how the invasion success depends on the size distribution of mating groups.

When the sneaker population is established, how related is the size distribution of mating groups to the frequency of sneakers in the population? In Chapter 3, we construct and analyze a mathematical model for the coexistence of the mating group strategy and the sneaking one, and discuss the dependence of the frequency of sneakers on the size distribution of mating groups. We analyze also the sex ratio derived from the model and imply that it would be also significantly affected by the size distribution of mating groups.

2 Invasion of Sneaking Strategy

In this section, we consider the invasion of the sneaking strategy against the mating group strategy.

2.1 ASSUMPTIONS

Reproductive Behaviour of Territorial Male

Territorial male forms the mating group of females. The frequency distribution f(x) of mating group size x is now assumed to satisfy the following conditions:

$$\frac{df(x)}{dx} \le 0 \tag{1}$$

$$f(x) > 0 \tag{2}$$

$$\int_{min}^{max} f(x)dx = 1,$$
(3)

where min and max denote the minimum and the maximum mating group sizes to be considered. We assume that f(x) continuous function in [min, max]. Each territorial male makes mating with females of own mating group. Female makes mating only one in a mating season. We consider the successful matings as the number of mating in a mating season. As the territorial male keeps the large mating group size, he would spend the greater amount of time and energy to keep its own mating group and to keep females in its territory. In this reason, the available time and energy for matings would decrease. So, now, we assume that territorial male with mating group size x can obtain the mating success A(x) in a mating season, which satisfy the following conditions:

$$\frac{dA(x)}{dx} \ge 0 \tag{4}$$

$$0 \le A(x) < +\infty. \tag{5}$$

Indeed, in labroid fishes, Moyer and Yago (Moyer and Yogo 1982) suggested that territorial males at the center of the spawning site can experience significantly higher successful matings than those at the periphery. Each territorial male make mating with females of own mating group We assume that female make mating only one in a mating season.

We consider the fitness as the expected number of offsprings which survive to the next mating season, and let $W_m(x)$ denote the fitness function of territorial male with mating group size x.

Reproductive Behaviour of Sneaker

Sneakers are assumed to have the common mating behaviour: Sneakers could make sneaking at each of mating moments by the territorial male. Only one sneaker could make sneaking at each of any mating moments by territorial male. Sneaker is wandering at random around the habitat space and is assumed to encounter a mating moment with probability α .

The probability of sneaking success is assumed to depend on the size of the mating group where the mating occurs. As the mating group size gets larger, the probability of sneaking success would increase. Territorial male keeps on the alert for the sneaker trying to make the mating activity. That is, if the territorial male keeps on the intense alert for the sneaker, the frequency of the successful sneakings would decrease, while that of the successful matings would decrease, too. In labroid fishes, the reproductive activity is made during the specific period of day in the mating season. Therefore, if territorial male tries to mate with the more females, he could keep on the less alert for the sneakers. So, indeed, it is observed that the labroid fishes have such tendency that territorial male makes mating even when the sneaker exists very near the mating site. Sufficient frequency of mating chances could increase the expected fitness gain, even though its loss due to the sneaking would be expected large.

The probability that the sneaker succeeds in sneaking at a mating moment in the mating group with size x is now assumed to be given by p(x) which satisfies the followings:

$$\frac{dp(x)}{dx} \ge 0 \tag{6}$$

$$p(0) = 0 \tag{7}$$

$$p(x) \le 1. \tag{8}$$

When the sneaking is successful, the sneaker can fertilize a portion σ of the average number of eggs per mating.

Let W_s denote the fitness function of sneaker within the considered population.

2.2 MODELING

General Model

At first, we consider the population in which all males take the mating group strategy. We consider the fitness $W_m(x)$ of a male with the mating group size x in the following form:

$$W_m(x) = l_m A(x) E_f \quad \text{for} \quad x \in [min, max], \tag{9}$$

where E_f represents the expected number of spawned eggs per female per mating, and l_m does the survival rate of a eggs fertilized by territorial male till the next mating season. A(x) indicates that the number of mating of territorial male with the mating group size x, we say it the successful matings. We consider that the sufficiently small number of sneakers initially invade in the population in which all males take the mating group strategy. Then we consider the fitness W_s of a sneaker as follows (see Appendix A):

The probability that a territorial male is the male with the mating group in the range of size [x, x + dx] is given by f(x)dx. The total population of territorial male is given now by M_m , so that the total expected number of territorial males with the mating group in the range of size [x, x + dx] is given by

$$M_m f(x) dx.$$

Therefore, the total expected successful matings for the territorial male with the mating group in the range of size [x, x + dx] is given by

$$A(x)M_mf(x)dx.$$

Therefore, the expected successful matings is given by

$$\int_{min}^{max} A(x) M_m f(x) dx.$$
(10)

The probability that a mating is encountered by the sneaker is given by α . Therefore, the probability that a mating in the mating group size x is succeeded in sneaking is given by

 $\alpha p(x).$

If the sneaking is successful, the sneaker can fertilize a portion σ of the average number of eggs E_f per mating. So the expected number of eggs fertilized by a sneaker per mating is given by

 $\alpha p(x)\sigma E_f.$

The expected number of eggs sneaked by a sneaking is

$$\int_{min}^{max} \alpha p(z) \sigma E_f \frac{A(z)M_m f(z)}{\int_{min}^{max} A(y)M_m f(y)dy} dz.$$
(11)

The expected number of eggs deprived by a sneaker in a mating season is given by

$$\int_{min}^{max} \alpha p(z) \sigma E_f A(z) M_m f(z) dx$$

Considering that survival rate l_s of the eggs fertilized by the sneaker till the next mating season, we can obtain w_s as follows:

$$W_s = l_s \int_{min}^{max} \alpha p(x) \sigma E_f A(x) M_m f(x) dx.$$
(12)

where M_m represents the total population of territorial males with the territory, and l_s does the survival rate of a egg fertilized by a sneaker till the next mating season.

Now, the territorial male has the fitness W_m as shown in Fig. 3. If

$$W_s < W_m(x) \quad \text{for} \quad \forall x \in [min, max],$$
(13)

then the sneaking strategy can not invade. If the male individual makes the mating behaviour as sneaker, it is expected for him to obtain the fitness W_s as shown in Fig. 3. The fitness of sneaker is higher than that of the territorial male which has the mating group in the range of size $[min, x^*]$, and less than it in the range of size $[x^*, max]$. Then we consider that the frequency of the sneakers could increase in the population, that is, the sneaking strategy can invade against the mating group strategy. More generally speaking, if

$$\exists x \in [min, max] \quad \text{s.t.} \quad W_s > W_m(x), \tag{14}$$

the sneaking strategy can invade.

Frequency Distribution Function of Mating Group Size

We consider the following frequency distribution function f(x) of mating group size x, which satisfies (1), (2) and (3) (Fig. 4):

$$f(x) = \frac{B}{e^{-Bmin} - e^{-Bmax}}e^{-Bx} \quad \text{for} \quad x \in [min, max], \tag{15}$$

where B is a positive constant related with the extent of the variance of the distribution. As B gets larger, the variance of the distribution gets smaller. As $B \to 0$, f(x) converges to an x-independent constant 1/(max - min), that is, to the uniform distribution. On the other hand, as $B \to +\infty$, f(x) converges to the dirac's delta function $\delta(min - x)$, so that every mating groups have the identical size min.

Probability Function of Sneaking Success

We introduce the following sneaking success probability function p, which satisfies (6), (7) and (8) (Fig. 5):

$$p(x) = 1 - e^{-\beta x} \quad \text{for} \quad x \in [min, max], \tag{16}$$

where β is a positive constant. As x increases, p(x) monotonically approaches 1 from the below. As β gets larger, the easiness of the sneaking success gets larger. As $\beta \to +\infty$, p(x) uniformly converges to the constant probability 1.

Function of Successful Matings

We consider the following function a of the successful matings of territorial male with mating group size x, which satisfies (4) and (5):

$$A(x) = x \quad \text{for} \quad x \in [min, max]. \tag{17}$$

2.3 Analysis

In this section, we analyze the fitness $W_m(x)$ and W_s given by (9) and (12). Now, $W_m(x)$ and W_s are rewritten as follows:

$$W_m(x) = xE_f l_m \quad \text{for} \quad x \in [min, max]$$
 (18)

$$W_{s} = \frac{B\alpha\sigma E_{f}l_{s}M_{m}}{e^{-Bmin} - e^{-Bmax}} \int_{min}^{max} y e^{-By} (1 - e^{-\beta y}) dy.$$
 (19)

When $W_m(x)$ and W_s satisfy (14), the sneaking strategy can invade against the mating group strategy. Now, $W_m(x)$ monotonically increases in terms of x. So if

$$W_s > \min_{x \in [min, max]} W_m(x) = W_m(min), \tag{20}$$

the sneaking strategy can invade.

We consider the dependence of the invasion success of the sneaking strategy on the range of mating group size, that is, on *min* and *max*. We can show that W_s monotonically increases in terms of *max* (see Appendix B). If $W_m(min)$ and $W_s(min, max)$ satisfy

$$W_m(min) \le \lim_{max \to min} W_s(min, max),\tag{21}$$

then $W_m(min) \leq W_s(min, max)$ for any max. (21) is rewritten in the following form:

$$e^{-\beta min} \le 1 - E$$

where

$$E = \frac{l_m}{\alpha \sigma l_s M_m} = \frac{l_m E_f < x >}{\alpha \sigma E_f M_m < x >}$$
$$< x >= \int_{min}^{max} A(y) f(y) dy.$$

 $l_m E_f < x >$ represents the mean fitness of territorial male in terms of the mating group size x. $\alpha \sigma E_f M_m < x >$ represents the fitness of sneaker with the maximum success probability of sneaking, p(x) = 1 for any x. That is, it means the maximum fitness of sneaker. Therefore, we can consider that the parameter E represents the advantage of the sneaking strategy against the mating group strategy. We can consider that, when E < 1, the sneaking strategy has more advantage than the mating group strategy, while, when E > 1, the mating strategy does than the sneaking strategy.

When E < 1 and $\min \ge K = \log(1-E)^{-1/\beta}$, $W_m(\min) \le W_s(\min, \max)$ for any max. When E < 1 and $\min \le K$ or E > 1,

$$W_m(min) > \lim_{max \to min} W_s(min, max).$$

In this case, since $W_s(min, max)$ monotonically increases in terms of max, if min for which $W_m(min)$ and $W_s(min, max)$ satisfy

$$W_m(min) < \lim_{max \to +\infty} W_s(min, max)$$
⁽²²⁾

exists, then the positive root max^* for $W_m(min) = W_s(min, max)$ for such min uniquely exists, and $W_m(min) \leq W_s(min, max)$ for $max \geq max^*$. For min satisfies

$$W_m(min) \ge \lim_{max \to +\infty} W_s(min, max),$$

 $W_m(min) > W_s(min, max)$ for any max.

We classify the invasion success of the sneaking strategy into the case when E < 1 and when E > 1.

At first, we consider the case when E < 1. The dependence of the invasion success on the minimum mating group size *min* and the wide (max - min)of the frequency distribution of females changes according to B and β . The parameter B represents the extent of the variance of the frequency distribution of mating group size, and β does the easiness of sneaking. As B gets larger, the variance decreases. As β gets larger, the easiness increases.

We classify the parameter region of B and β into the two region which are I and II (see Fig. 6(a)). For B and β in the region of I in Fig. 6(a), we show the dependence of the invasion success on min and (max - min) in Fig. 6(a-1), and for II, in Fig. 6(a-2). Fig. 6(a-2) and (a-2) respectively correspond to the larger and the smaller variances.

The common property when E < 1 is that the critical value K, which is given by $\log(1-E)^{-1/\beta}$, exists, and for *min* greater than K, the sneaking strategy can invade for any width (max - min).

Fig. 6(a-1) shows that, for B and β in the region of Iin 6(a), when min < K, the sneaking strategy can not invade for sufficiently small width (max - min). Furthermore, there is the critical value J of the width (max - min), and for (max - min) > J, the sneaking strategy can invade for any min. For the width (max - min) < J, the sneaking strategy can invade for intermediate value of min.

For II, as shown in Fig. 6(a-2), there are the critical values of min, say min_1 and min_2 ($min_1 < min_2$). For min of the range of size [min_1 , min_2], the sneaking strategy can not invade for any width (max - min).

We show the dependence of the boundary curve for the invasion success on B and β in Fig. 6(b). Fig. 6(b) shows that the region of min and (max-min) for which the sneaking strategy can invade gets small as B gets larger and β does smaller. That is, the invasion of the sneaking strategy becomes more different as the variance of the frequency distribution of mating group sizes and the easiness of sneaking gets smaller.

Additionally, we show the dependence of the invasion success on min and max in Fig. 7(a). For some values of B and β , as shown in Fig. 7(a), there is the values of max, say max_1 and max_2 ($max_1 < max_2$). For max in the region of size [max_1 , K] and [K, max_2], the necessary region of min for the invasion success is divided into discontinuous region (see Fig. 7(a) and (b)).

Next, we consider when E > 1. We show the dependence of invasion success on min and (max - min) in Fig. 8(a). As shown in Fig. 8(a), there is the critical value min^* , and for $min > min^*$, the sneaking strategy can not invade for any width (max - min). For $min < min^*$, a certain width between the minimum and the maximum mating group size is necessary for the invasion of the sneaking strategy, and the necessary width monotonically increases as min gets larger. When E > 1, min^* uniquely exists (see Appendix C). min^* monotonically decreases as B gets larger and β does smaller. As $B \to 0+$, min^{*} becomes $+\infty$, and $\beta \to +\infty$, it does 0 (see Appendix D). As $\beta \to 0+$, min^{*} becomes 0. As $\beta \to +\infty$, min^{*} becomes a constant $1/\{B(1-E)\}$ (see Appendix D). The boundary curve for the invasion success of sneaking strategy depends on B and β . The dependence of its curve on B and β is shown in Fig. 8(b). Fig. 8(b) shows that the boundary for the invasion success of sneaking strategy moves to left as B gets larger, or β does smaller. Fig. 8(b) shows that, similar to the case when E < 1, the invasion of the sneaking strategy becomes more different as the variance of the frequency distribution of mating group sizes and the easiness of sneaking gets smaller.

the frequency of the territorial males with large mating group size decrease. So as B gets larger, succeeding in sneaking is difficult. Therefore, it is considered that the fitness of the sneaker will decrease, and the invasion of the sneaking strategy against the mating group strategy is more difficult.

2.4 DISCUSSION

In this section, we constructed and analyzed the mathematical model for the invasion of the sneaking strategy against the mating group strategy. We analyzed the dependence of the invasion success on the frequency distribution of mating group size, that is, on the parameter B, min, max and (max - min).

When E < 1, as shown in Fig. ??, for sufficiently large *min*, the sneaking strategy can invade, while, when E > 1, as shown in Fig. 8, it can not invade. The opposite results are obtained in these two cases. We assume that the probability of sneaking success gets large as the mating group size gets larger. As *min* gets larger, the frequency of territorial males with large mating group size increases. Therefore, the mean probability of sneaking success increases as *min* gets larger. While, since $W_m(x)$ monotonically increases in terms of $x, W_s(min)$ monotonically increases as *min* gets larger. That is, as *min* gets larger, both territorial with minimum mating group size and sneaker can obtain the more benefit. However, in the case when E < 1, the sneaking strategy is more advantage than the mating group strategy, in the case when E >, it is not. Therefore, these opposite results are obtained.

As the extent of variance of the frequency distribution of mating group size, which is represented by B, gets larger, the frequency of the territorial males with large mating group size decreases, and with small mating group size increases. We assume that the probability of the sneaking success depends on the mating group size, that is, as the mating group size gets larger, the mean probability increases. We showed that B gets larger, the sneaker turned to disadvantage, and the invasion of the sneaking strategy against the mating group strategy becomes difficulty. We can consider that B represents the preference of females against the specific mating site and territorial male. Indeed, in labroid fishes, females prefer the specific spawning sites on the outer or the downcurrent edges of reefs (Threshoer 1984) and tend to gather at a specific territorial male selected by the position of the territory, the body size and the color. In this case, a specific male, which is strong, large and with vivid color, can obtain greater benefit than other males. Under such strong selection against male, the sneaking strategy is likely to appear, however, our result suggests the opposite argument.

3 Frequency of Sneakers at the Equilibrium State

3.1 ASSUMPTIONS AND GENERAL MODEL

In this section, we consider the coexistence of mating group and sneaking strategies. Additionally to the assumptions in the previous modelling for the invasion success of sneaking strategy, we assume the following assumptions:

The population of territorial males M_m and sneakers M_s are at the stationary state. We consider the successful matings as the mating number in a mating season. Female makes mating only one in a mating season. The territorial male with the mating group size x can obtain the successful matings

$$A(x)D(M_s, M_m) \tag{23}$$

where $D(M_s, M_m)$ satisfy the following conditions:

$$\frac{\partial D(M_s, M_m)}{\partial M_s} \le 0 \qquad \frac{\partial D(M_s, M_m)}{\partial M_m} \ge 0 \tag{24}$$

$$0 \le D(M_s, \ M_m) \le 1. \tag{25}$$

Territorial male must defend females from sneakers, however it spend a available time and energy for the mating activity. As the sneaker population gets larger, territorial males must spend much time and energy to defend females from sneakers. While, as the population of territorial males gets larger, the number of sneakers that gather per territorial male must get small, that is, the time and energy which must be spent to defend females from sneakers should decrease. Therefore, we assume that the successful matings of territorial male monotonically decrease in terms of M_s , and monotonically increases in terms of M_m , and (24) and (25) correspond to it.

As the sneaker population gets larger, the probability that a mating moment is encountered by sneakers becomes larger so that the expected number of sneakers per mating moment increases. That is, as the sneaker population gets larger, territorial male comes not to be able to efficiently defend paired female from sneakers, and the probability of sneaking success per mating moment increases. Furthermore, as the mating group size gets larger, the probability of sneaking success increases. In the assumptions in the previous modeling, we assume the probability of sneaking success the probability that sneaker succeeds in sneaking at a mating moment when it is encountered by sneakers, while, in this section, we does it the probability that a mating moment is encounted and succeeded in sneaking by whole sneakers. The probability $p(x, M_s)$ that a mating in the mating group with size x is successfully sneaked conditions:

$$\frac{\partial p(x, M_s)}{\partial x} \ge 0 \qquad \frac{\partial p(x, M_s)}{\partial M_s} \ge 0 \tag{26}$$

$$0 \le p(x, M_s) \le 1. \tag{27}$$

We consider the fitness of territorial male $W_m(x)$ as follows (see Appendix E):

When the sneaking is successful, the sneaker can fertilize a portion σ of the average number of eggs per mating. So the expected number of eggs deprived by sneakers per mating in the mating group with size x is

$$p(x, M_s)\sigma E_f.$$
(28)

Therefore, in a mating season, the expected number of eggs that the whole sneakers deprive a territorial male with mating group size x is given by

$$A(x)D(M_s, M_m)p(x, M_s)\sigma E_f.$$
(29)

So the expected number of eggs that a territorial male with mating group size x can fertilize in a mating season.

$$A(x)D(M_s, M_m)\{1 - p(x, M_s)\sigma\}E_f.$$
 (30)

By considering the survival rate l_m of the eggs fertilized by territorial male till the next mating season, we can define $W_m(x)$ as follows:

$$W_m(x) = l_m A(x) D(M_s, \ M_m) \{ 1 - p(x, M_s) \sigma \} E_f$$
(31)

for
$$x \in [min, max]$$
 (32)

Next, we consider the fitness of sneaker W_s . The probability that a territorial male is in the range of size [x, x + dx] is given by f(x)dx. So the expected number of territorial males in the range of size [x, x + dx] is given by

$$M_m f(x) dx. aga{33}$$

From (29) and (33) the expected number of eggs of which the whole sneakers can deprive the whole territorial males in the range of size [min, max] in a mating season is given by

$$\int_{min}^{max} A(x)D(M_s, \ M_m)p(x, \ M_s)\sigma E_f M_m f(x)dx.$$
(34)

Considering the survival rate l_s of eggs fertilized by sneakers till the next mating season, we can obtain W_s per sneaker as follows:

$$W_s = l_s \frac{1}{M_s} \int_{min}^{max} A(x) D(M_s, \ M_m) p(x, M_s) \sigma E_f M_m f(x) dx$$
(35)

Additionally, we consider the expected fitness W_f of female W_f as the expected number of offsprings which survive to the next mating season:

The probability that a female in the mating group with size x can successfully mate is given by

$$\frac{A(x)D(M_s, M_m)}{x}.$$
(36)

If a female can mate with a territorial male with mating group size x, the expected number of eggs fertilized by the sneaker per mating is given by (28), and that fertilized by a territorial male is given by

$$\{1 - p(x, M_s)\sigma\}E_f.$$
(37)

Considering the survival rates l_m and l_s of eggs fertilized by territorial male and sneaker, when a female can mate in the mating group with size x, the expected number of survival eggs spawned by her is given by

$$l_s p(x, M_s) \sigma E_f + l_m \{1 - p(x, M_s)\sigma\} E_f.$$
 (38)

From (36) and (38), we can define the expected number $W_f(x)$ of survival eggs of a female when she is in the mating group with size x as follows:

$$W_f(x) = \frac{A(x)D(M_s, M_m)}{x} \{ l_s p(x, M_s)\sigma E_f + l_m \{ 1 - p(x, M_s)\sigma \} E_f \}.$$

Therefore, the expected number of survival eggs of a female when she is in the mating group in the range of size [min, max] is given by

$$W_{f} = \int_{min}^{max} W_{f}(x)f(x)dx.$$

$$= \int_{min}^{max} \frac{A(x)D(M_{s}, M_{m})}{x} [l_{s}p(x, M_{s})\sigma E_{f} + l_{m}\{1 - p(x, M_{s})\sigma\}E_{f}\}f(x)dx.$$
(39)

We assume that male can select mating activity as either sneaker or territorial male. While female can select reproductive activity as either female or territorial male. It corresponds to the sex-change observed in labroid fishes that females make mating as territorial male. Females can not make mating activity as sneaker. That is, sneaker is composed of born males, and territorial males can be composed of born males and sex-changed males from females.

We assume the following assumption:

Assumption

Female and sneaker change into territorial male at the minimum mating group size for which each fitness equals to the fitness of territorial.

Probability Function of Sneaking Success

In this paper, we consider the following sneaking success probability function p, which satisfies (26) and (27):

$$p(x, M_s) = \alpha (1 - e^{-\beta x})(1 - e^{-\delta M_s}) \quad \text{for} \quad x \in [min, max],$$

$$(40)$$

where $\alpha (\leq 1)$, β and δ are positive constants, and as those parameters gets larger, the easiness of the sneaking success gets larger.

Function of Successful Matings

We consider the following function A(x) for the successful matings for a territorial male with mating group size x (Fig. 9):

$$A(x) = c(1 - e^{-ax}) \quad \text{for} \quad x \ge 0,$$
 (41)

where c and a are positive constants to satisfy $ca \leq 1$. c indicates that the maximum number of mating made in a mating season. As a gets larger, the easiness of mating with females gets larger.

3.2 Analysis

In this section, we analyze the model (3.1), (35) and (39). (3.1), (35) and (39) are rewritten as follows:

$$W_m(x) = c(1 - e^{-ax})D(M_s, M_m)\{1 - \alpha\sigma(1 - e^{-\delta M_s})(1 - e^{-\beta x})\}E_f l_m (42)$$

for $x \in [min, max]$

$$W_{s} = M_{m} \frac{D(M_{s}, M_{m})(1 - e^{\delta M_{s}})}{M_{s}} \frac{Bc\alpha\sigma}{e^{-Bmin} - e^{-Bmax}} W_{s,1} E_{f} l_{s}$$
(43)

$$W_f = \frac{B}{e^{-Bmin} - e^{-Bmax}} \int_{min}^{max} e^{-Bx} \frac{W_F(x)}{x} dx$$
(44)

where

$$W_{s,1} = \int_{min}^{max} e^{-Bx} (1 - e^{-ax})(1 - e^{-\beta}) dx$$
$$W_F(x) = a(1 - e^{-ax}) D(M_s, M_m)$$
$$\{1 - \alpha \sigma (1 - e^{-\delta M_s})(1 - e^{-\beta x})(1 - \frac{l_s}{l_m})\} E_f.$$

Existence of Equilibrium State

In this section, we consider how relation $W_m(x)$, W_s and W_f have when the frequency of sneakers can be at the equilibrium state. Since we assume that female and sneaker change into territorial male at the minimum mating group size for which each fitness equals to the fitness of territorial male. Therefore, $W_m(x)$, W_s and W_f satisfy that $W_m(min) = W_s$ or $W_m(min) = W_f$. $W_m(x)$ is not necessary monotonically increase in terms of x There is the case that $W_m(x)$ has the maximum and the minimum in terms of x (see Appendix F). When x = 0, $W_m(x) = 0$ and $dW_m(x)/dx > 0$, so for the mating group size at which female and sneaker change into the territorial male the derivation of $W_m(x)$ is positive. At first, we consider the case when $W_m(x)$ monotonically increases in terms of x in [min, max].

At first, we consider when $W_f \geq W_s$. When $W_s = W_m(min)$ (see Fig. 10(a)), even if males that make mating as territorial male with smaller mating group size than min appear, they can not obtain higher fitness than males making mating as sneaker. So the frequency of such males in the population can not increase. On the contrary, even if males that make mating as sneaker at the larger mating group size than min appear, their fitness was less than territorial males with such mating group size. So the frequency of such males in the population can not increase. Therefore, when $W_s = W_m(min)$, we consider the mating strategy of male that he makes mating as sneaker in smaller mating group size than min and in the range of mating group size [min, max] as territorial male can be the equilibrium state. That is, in this case, we consider that the frequency of sneakers can be at the equilibrium state.

When $W_s = W_m(min)$, concerning to the fitness of female, there are two cases, one is when $W_m(min) < W_f \leq W_m(max)$, the other is when $W_f > W_m(max)$. When $W_m(min) < W_f \leq W_m(max)$ (see Fig. 10(a)), even if females that make mating as territorial male with smaller mating group size than x_1 appear, they could not obtain higher fitness than females. On the contrary, even if females that make mating as female at the larger mating group size than x_1 appear, they could not obtain higher fitness than females making mating as territorial male with such mating group size. So when $W_m(min) < W_f \leq W_m(max)$, we can consider that the reproductive strategy of female that she makes mating as female in smaller mating group size than x_1 and does mating as territorial male in larger mating group size than x_1 and the equilibrium state. Therefore, in this case, we can consider that territorial males with mating group in the range of size $[min, x_1]$ are composed of born males and in the range of size $[x_1, max]$ are of both born males and sex-changed males.

Next, we consider when $W_f \leq W_s$. In this case, similarly to the case when $W_f > W_s$, we can show that the frequency of sneakers can be at the equilibrium state only when $W_f = W_m(min)$.

When $W_f = W_m(min)$, concerning to the fitness of sneaker, there are two cases, one is when $W_m(min) < W_s \leq W_m(max)$, the other is when $W_s > W_m(max)$.

When $W_m(min) < W_s \leq W_m(max)$ (see Fig. 10(b)), we consider that territorial males with mating group in the range of size $[min, x_2]$ are composed of sex-changed males and in the range of size $[x_2, max]$ are of both born and sex-changed males.

When $W_s > W_m(max)$, sneaker can obtain higher fitness than territorial males with any mating group size. So we consider that territorial male are composed of only sex-changed males.

Next, we consider the case when $W_m(x)$ does not monotonically in terms of x in [min, max]. When $W_f \geq W_s$, there is the case as shown in Fig. 10. In this case, male change from sneaker to territorial male at min. In the range of size $[min, x_3]$ and $[x_4, max]$, the territorial male can obtain higher fitness than the sneaker. However, in the range of size $[x_3, x_4]$, the sneaker can obtain the higher fitness than the territorial male. In labroid fishes, the sneaker can change into the territorial male, and its color also changes. It has not been observed that the terminal phase male changes into the initial phase male, and it is not likely to be in aspect of physiology. Therefore, we consider that territorial males also keep territory in the range of size $[x_3, x_4]$. In this case, we consider that the mating strategy of male that he makes mating as sneaker in smaller mating group size than min and in the range of size [min, max] as territorial male can be the equilibrium state.

Similarly, when $W_f < W_s$, we consider that the reproductive strategy of female that she makes mating as female in smaller mating group size than min and in the range of size [min, max] as territorial male can be the equilibrium state.

From the argument in this section, when female and sneaker change into territorial male at the minimum mating group size for which each fitness equals to the fitness of territorial male, the frequency of sneakers can be at the equilibrium state.

For a given the frequency distribution of mating group size, we can classify the case that the frequency of sneakers can be at the equilibrium state into following two cases:

Case A:
$$\begin{cases} W_f \ge W_s \\ W_s = W_m(min) \end{cases}$$
(45)

Case B:
$$\begin{cases} W_f \le W_s \\ W_f = W_m(min). \end{cases}$$
(46)

Parameter Region for the Equilibrium State

Along the argument in previous sections, the frequency of sneakers can be at the equilibrium state in Case A and Case B.

At first, we consider the Case A.

Considering the condition that dW/dx(min) > 0 and Case A exists, we show the parameter region of *min* and *max* for which the frequency of sneakers can be at the equilibrium state in Case A in Fig. 11 and 12. When $\alpha\sigma \leq$ $1/(1+e^{-2})$, $W_m(x)$ monotonically increases in terms of x. So any min satisfies dW/dx(min) > 0. The parameter region of min and max for Case A is shown in Fig. 11. There is a boundary value of min, say min_1 . The frequency of sneakers can be at the equilibrium state in Case A for any max for $min \leq min_1$, and it could not be for any max for $min > min_1$. For min and max of the region of $Theta_I$ in Fig. 11, M_s can exist in $M_s > 0$ (see Table. 13). For min and max of Θ_{II} in Fig. 11 , a positive value $M_{s,1}^*$ exists and M_s could exist in $M_s > M_{s,1}^*$. When $\alpha \sigma > 1/(1+e^{-2})$, we show the parameter region of min and max for Case A in Fig. 12. In this case, $W_m(x)$ monotonically increases in terms of x for a and β of the region Phi_A in Fig. 12(a). For a and β of Φ_A , when β is small, the parameter region of min and max for Case A has the form as shown in Fig. 11. For $min \in [min_1, min_2]$, when max is sufficiently large, Case A can not exist. While, when β is large, it is shown in Fig. 12(b). Case A can exist for any min and max, while, for $min \ge min_4$, it can not exist for any max. For a and β of Φ_B in Fig. 12(a), $W_m(x)$ has the maximum and minimum in terms of x. For a and β of Φ_B , the parameter region of min and max for Case A is shown in Fig. 12(c). For min and max of Θ_{III} , the positive values $M_{s,1}^*$ and $M_{s,2}^*$ $(M_{s,1}^* < M_{s,2}^*)$ exist, and M_s can exist in $M_{s,1}^* < M_s < M_{s,2}^*$.

From $W_s = W_m(min)$ and $W_f > W_m(min)$, in Case A, M_m and M_s have the following relation (see Appendix G):

$$M_m = R(M_s). \tag{47}$$

47 indicates that M_s is any value in each range shown in Fig. 13, and M_m is uniquely determined by $R(M_s)$. When $\alpha\sigma(1-e^{-\beta min}) \leq 1/2$, $R(M_s)$ monotonically increases in terms of M_s (see Fig. 14(a)), while, when $\alpha\sigma(1-e^{-\beta min}) > 1/2$, as shown in Fig. 14(b), it has the minimum in terms of M_s .

Next, we consider Case B. The parameter region of min and max for Case B is Θ_{II} and Θ_{III} in Fig. 11 and 11. For min smaller than 1, Case B could not exist for any max. From $W_f = W_m(min)$ and $W_s \ge W_m(min)$, in Case B, a value of M_s , say $M_{s,1}^*$, uniquely exist for min and max in Θ_{II} or Θ_{III} and M_m and M_s have the following relation:

$$M_s = M_{s,1}^*$$
 (48)

$$M_m \ge R(M_s^*).$$

That is, the population of sneakers is uniquely determined by $M_{s,1}^*$, and the territorial population can be any value larger than $R(M_{s,1}^*)$.

For min and max of the region Θ_{II} and Θ_{III} , Case Å and Case B coexist. For min and max of Θ_{II} , we show the relation of between Case A and Case B in Fig. 15. There are two type of the equilibrium state which depend on the relation between the fitness of sneaker and female. We consider the ratio of sneakers and territorial males and the sex ratio in the following sections.

Ratio of Sneakers and Territorial Males

In this section, we consider the ratio of sneakers and territorial males, which is given as following form:

$$M_{ra} = \frac{M_s}{M_m + M_s}.$$
(49)

 M_{ra} means that the proportion of territorial males in total population of males. For Case A, M_s can be any value of the region which is classified into some cases in Table 13, and M_m is given by $R(M_s)$. Therefore, for Case A, (49) is given by following form:

$$M_{ra} = \frac{M_s}{R(M_s) + M_s}.$$
(50)

(50) monotonically increases in terms of M_s , and as $M_s \to +\infty$, it converges to a positive value (see Appendix G).

For Case B, a positive value M_s^* uniquely exists, and M_m can be any value greater or equal to $R(M_s^*)$. So (49) is given by

$$M_{ra} = \frac{M_s^*}{M_m + M_s^*}.$$
(51)

In each case, we consider the dependence of M_{ra} on the frequency distribution of mating group size, that is, on B, max and min. The parameter B represents the extent of the variance of the frequency distribution of mating group size. As B gets larger, the variance decreases. The parameter max and min respectively represent the minimum and the maximum mating group size. In the following analyses, we use the parameters min and max in Θ_{II} when $\alpha \sigma > 1/(1 + e^{-2})$.

At first, we consider how M_{ra} depends on the parameters B, max and min when the population of territorial males M_m is given. We show the dependence of M_{ra} for Case A and Case B on B, max and min in Fig. 16 by numerical calculation. Fig. 16(a) show the dependence of M_{ra} on B. As B gets larger, the extent of variance of the frequency distribution of the mating group size gets small. In the range of large variance, as the variance gets smaller, M_{ra} decreases, that is, the population of sneaker decreases. In the range of small variance, for Case A in which the fitness of female is higher than the sneaker, as the variance gets smaller, M_{ra} increases, while, for Case B in which the fitness of female is less than the sneaker, it decreases.

Fig. 16(b) show the dependence of M_{ra} on max. In both Case A and Case B, as max gets larger, in the range of small max, M_{ra} increases rapidly, while, in the range of sufficiently large max, it takes a constant value. On the other word, however large max is, M_{ra} can not beyond a constant value.

Fig. 16(c) show the dependence of M_{ra} on min. In the range of sufficiently small min, only Case A exists, as min gets larger, M_{ra} decreases. In the range of sufficiently large min, as min gets larger, M_{ra} for both Case A and B increases.

As *min* gets larger, the frequency of territorial male with larger mating group increases, and the average probability of sneaking success also does. Therefore, the sneakers turn to advantages.

It is considered that, in the range of large *min*, sneakers decrease the competition for a mating in them by decreasing the population of themselves, and increase their fitness. While, in the range of small *min*, sneakers intercept the matings of territorial male by increasing their population and decrease the fitness of territorial males, and increase their fitness relatively.

Next, we consider how M_{ra} depends on the population of territorial males when the frequency distribution of mating group size is given, that is, on M_m when B, max and min are given. We show the dependence of M_{ra} on M_m in Fig. 17. In Case A, we show that M_{ra} monotonically increases in terms of M_m . In Case B, M_s^* is determined independent on M_m , so M_{ra} obviously monotonically decreases in terms of M_m .

Next, we consider how M_{ra} depends on B, max and min when the population of sneakers M_s is given. In Case A, we can obtain the similar result to one as shown in Fig. 16 which show the dependence of M_{ra} on B, max and min when the population of territorial males M_m is given. As B and min gets larger, at first, M_{ra} monotonically decreases, and when B becomes large, it monotonically increases. On the contrary, as max get larger when max is small, M_{ra} monotonically increases, while, when max is large, it monotonically decreases.

In Case B, M_s is uniquely determined by M_s^* , and M_m is any value in $M_m \ge R(M_s^*)$. Therefore, in Case B, considering the dependence of M_{ra} on B, max and min when M_s is given corresponds to considering the dependence of it on these parameters when M_m is given, and it is shown Fig. 16.

Sex Ratio

In this section, we consider how the sex ratio depends on the frequency distribution of mating group size. We consider the population of females M_f as the total population of composing the mating groups. Then M_f is given by

$$M_f = M_m M_{f0} \tag{52}$$

where

$$M_{f0} = \int_{min}^{max} x f(x) dx.$$

We consider the sex ratio as following form:

$$Sra = \frac{M_f}{M_m + M_s} = \frac{M_m M_{f0}}{M_m + M_s}.$$
(53)

In Case A, the sex ratio is as follows:

$$Sra = \frac{R(M_s) + M_s}{R(M_s)M_{f0}}.$$
(54)

 S_{ra} monotonically decreases in terms of M_s . As $M_s \to 0+., S_{ra}$ becomes M_{f0} , while, as $M_s \to +\infty$, it converges to a positive value S_{ra}^* .

In Case B, the sex ratio is as follows:

$$Sra = \frac{M_m M_{f0}}{M_m + M_s^*}.$$
(55)

 M_m can be any value greater than or equal to $R(M_s^*)$. For Case B, S_{ra} monotonically increases in terms of M_m . As $M_m \to +\infty$, S_{ra} converges to M_{f0} .

In each case, we consider the dependence of S_{ra} on the frequency distribution of mating group size, that is, on the parameters B, max and min.

At first, we consider how S_{ra} depends on B, max and min when the population of territorial males M_m is given. We show the dependence of S_{ra} on B in Fig. 18(a-1) by numerical calculation. In the range of sufficiently small variance of the frequency distribution of mating group size, for Case A in which the fitness of female is higher than the sneaker, as the variance gets smaller, the sex ration decreases, while, for Case B in which the fitness of female is less than the sneaker, it increases.

Fig. 18(b) shows the dependence of S_{ra} on max. In both Case A and Case B, the sex ratio monotonically increases as max gets larger. In both Case A and Case B, as max gets larger, in the range of small max, M_{ra} increases rapidly, while, in the range of sufficiently large max, it takes a constant value. On the other word, however large max is, M_{ra} can not beyond a constant value. As max gets larger, the frequency of territorial males with large mating group size gets large. So when M_m is given by a constant, the population of females gets larger as max gets larger. As max gets larger, simultaneously, the population of sneakers also changes. The population of sneakers has the same property to the dependence of M_{ra} on max shown in Fig. 17(b). From Fig. Mra-dep-Mm(b), the population of sneakers has the maximum in terms of max. Therefore, it is not trivial that the sex ratio monotonically increases as max gets larger.

We show the dependence of the sex ratio on min in Fig. 18(c). In Case A, S_{ra} monotonically increases as min gets larger, while, in Case B, it decreases.

As min gets larger, the frequency of territorial males with large mating group size gets large, and the population of females will get large. The dependence of the population of sneakers in Case B has the same property to the dependence of M_{ra} on min shown in Fig. 17(c). From Fig. 17(c), the population of sneakers in Case B monotonically increases in terms of min. In Case B, the increase of the population of sneakers will be more rapid than females, so it is considered that the sex ratio does not monotonically increase. Next, we consider how the sex ratio depends on the population of territorial males M_m when the frequency distribution of mating group size is given, that is, when the parameter B, max and min are given. We show the dependence of the sex ratio on M_m in Fig. 19. In Case A, the sex ratio monotonically decreases as M_m gets larger, while, in Case B, it monotonically increases. As the population of territorial males gets larger, the number of territories gets larger. So the population of females gets large. Simultaneously, the population of sneakers also gets changes according to the population of territorial males. Fig. 19 indicates that there are two type of the dependence of the sex ratio on the population of the territorial males in the same frequency distribution of mating group size.

Next, we consider how the sex ratio depends on B, max and min when the population of sneakers M_s is given. In Case A, we can obtain the similar result to one as shown Fig. 18 which shows the dependence of the sex ratio on B, max and min when the population of the territorial males M_m is given.

In Case A, considering the relation between M_{f0} and 1, and between S_{ra} and 1, we can classify the sex ratio into the following three cases:

Case (a):
$$S_{ra} < 1$$
 for $\forall M_s > 0$ (56)

Case (b):
$$\exists M_{s,1}$$
 s.t. $0 < S_{ra} < 1$ $0 < M_s < M_s^*$
 $S_{ra} \ge 1$ $M_s \ge M_s^*$
Case (c): $S_{ra} > 1$ for $\forall M_s > 0$ (57)

Case (a) indicates that the sex ratio is less than 1 for any value of $M_s > 0$, and Case (b) does that a positive value $M_{s,1}$ exists and it is less than 1 for $0 < M_s < M_{s,1}$, and greater than or equal to 1 for $M_s \ge M_{s,1}$. Case (c) indicates that the sex ratio is greater than 1 for any value of $M_s > 0$.

When $\alpha\sigma < 1/(1 + e^{-2})$, we show the parameter region of min and max for these three cases in Fig. 20(a). The parameter region of Ψ_a , Ψ_b and Ψ_c respectively corresponds to Case (a), Case (b) and Case (c). When B > 1, a positive value of min, say $min_1 = 1 - 1/B$, exists, and for min less than min_1 , the sex ratio is less than 1 for any max. Fig. 20 indicates that the sex ratio is greater than 1 when both min and max are large, while, when both are small, it is less than 1. As min and max gets larger, the frequency of territorial males with large mating group size gets large. So as min and max gets larger, the population of females get large. We show that the sex ratio monotonically increases as min and max get larger in Fig. 18. The result shown in Fig. 20 corresponds to this argument.

For a and β of Φ_A when $\alpha \sigma \leq 1/(1+e^{-2})$, we show the parameter region of min and max for the three cases in Fig. 20(b). For Φ_B , it is same property.

Next, for Case B, considering the relation between M_{f0} and 1, and between $R(M_s^*)M_{f0}/\{R(M_s^*)+M_s^*\}$ and 1, we can classify the sex ratio into the following three cases:

Case (a):
$$S_{ra} < 1$$
 for $\forall M_m \ge R(M_s^*)$ (58)

Case (b):
$$\exists M_{m,1} > R(M_s^*)$$
 s.t. $0 < S_{ra} < 1$ $M_m^* > M_m > R(M_s^*)$
 $S_{ra} \ge 1$ $M_m \ge M_m^*$
Case (c): $S_{ra} > 1$ for $\forall M_m > R(M_s^*)$ (59)

Case (a) indicates that the sex ratio is less than 1 for any value of $M_m > R(M_s^*)$, and Case (b) does that a positive value $M_{m,1} > R(M_s^*)$ exists and it is less than 1 for $R(M_s^*) < M_m < M_{m,1}$, and greater than or equal to 1 for $M_m \ge M_{m,1}$. Case (c) indicates that the sex ratio is greater than 1 for any value of $M_m > R(M_s^*)$.

When $\alpha\sigma < 1/(1 + e^{-2})$, we show the parameter region of *min* and *max* for these three cases in Fig. 21(a). The parameter region of Ψ_a , Ψ_b and Ψ_c respectively corresponds to Case (a), Case (b) and Case (c). In this case, the sex ratio is always greater than 1.

For a and β of Φ_A when $\alpha \sigma \leq 1/(1 + e^{-2})$, we show the parameter region of min and max for the three cases in Fig. 21(b). When min is sufficiently small or large, the sex ratio is greater than 1. While, for the intermediate value of min, the sex ratio is less than 1. For Φ_B , it is the same property.

3.3 Discussion

We analyzed a mathematical model for the coexistence of sneaking strategy and the mating group strategy. We showed that there are two types of the equilibrium states. For these two cases, we considered how the frequency distribution of mating group size depends on the ratio of sneakers and territorial males and the sex ratio.

For example, we could obtain the result as shown in Fig. 16(a) and Fig. 18(a) for the dependence of the ratio of sneakers and the sex ratio on the variance of the size distribution of mating groups.

As the variance gets smaller, the frequency of territorial male with large mating group size decreases, and the sneakers turn to disadvantage. Our results shown in Fig. 16 and Fig. 18, show that the frequency of sneakers gets large even if it is disadvantage for them. It is considered that, in the range of large

variance, sneakers decrease the competition for a mating in them by decreasing the population of themselves, and increase their fitness. While, in the range of small variance, sneakers intercept the matings of territorial male by increasing their population and decrease the fitness of territorial males, and increase their fitness relatively. Indeed, in labroid fish, as the frequency of the sneakers gets larger, the successful matings of territorial male becomes small because they must the invasion of sneakers. That is, the sneaker make the advantage for theirselves by interfering the territorial male. In our model, it is reflected in that the probability of sneaking success gets large as the frequency of sneakers gets larger. However, in the point that the sneaker make the disadvantage for territorial males, we can say that our results corresponds to the phenomenon observed in labroid fishes.

4 Conclusion

In this paper, at first, we considered how the size distribution of mating groups is related to the existence of sneakers. We constructed and analyzed a mathematical model for the invasion of sneaking strategy against the mating group strategy, and discuss how the invasion success depends on the size distribution of mating groups. We obtained the result that as the variance of the distribution gets smaller, the existence of sneaker becomes difficult.

When the population of the sneaker is established, how related is the size distribution of mating groups to the frequency of sneakers in the population? In Chapter 3, we constructed and analyzed a mathematical model for the coexistence of the mating group strategy and the sneaking one, and discuss the dependence of the frequency of sneakers on the size distribution of mating groups.

Even if it is disadvantage for the sneaker, the ratio of sneakers can get large. For example, we analyzed how the variance of the distribution depends on the ratio of sneakers and the sex ratio. In the range of large variance of the distribution, sneakers decrease the competition for a mating in them by decreasing the population of themselves, and increase their fitness. While, in the range of small variance, sneakers intercept the matings of territorial male by increasing their population and decrease the fitness of territorial males, and increase their fitness relatively. That is, the sneaker make the advantage for theirselves by interfering the territorial male.

Thus we analyzed the ratio of sneakers and the sex ratio derived from our model and showed that it would be also significantly affected by the size distribution of mating groups.

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A Modelling for the Invasion of Sneaking Strategy

In this appendix, we show the way to derive W_s given by (9) when a sufficiently small number of sneakers appear in the population in which all males take the mating group strategy. The probability that a territorial male is the male with the mating group in the range of size [x, x + dx] is given by f(x)dx. The total population of territorial male is given now by M_m , so that the total expected number of territorial males with the mating group in the range of size [x, x+dx]is given by

$$M_m f(x) dx.$$

Therefore, the total expected successful matings for the territorial male with the mating group in the range of size [x, x + dx] is given by

$$A(x)M_mf(x)dx.$$

Therefore, the expected successful matings over all the territorial males is given by

$$\int_{min}^{max} A(x) M_m f(x) dx.$$
(60)

The probability that a mating is encountered by sneakers is given by a constant α . Therefore, the probability that a sneaker is successful in the sneaking against a mating in the mating group size x is given by

 $\alpha p(x).$

If the sneaking is successful, the sneaker can fertilize a portion σ of the average number E_f of eggs per mating. So the expected number of eggs fertilized by a sneaker per mating is given by

$$\alpha p(x)\sigma E_f.$$

The probability that the successful mating in the mating group in the range of size [x, x + dx] is encountered by a sneaker is given by

$$\alpha \frac{A(x)M_m f(x)dx}{\int_{min}^{max} A(x)M_m f(y)dy}.$$
(61)

Hence, the expected number of eggs that a sneaker can deprive of the encountered mating in the mating group in the range of size [x, x + dx] is given by

$$\alpha p(x)\sigma E_f \frac{A(x)M_m f(x)dx}{\int_{min}^{max} A(x)M_m f(y)dy}$$

So the expected number of eggs sneaked by a sneaking is

$$\int_{min}^{max} \alpha p(z) \sigma E_f \frac{A(z)M_m f(z)}{\int_{min}^{max} A(y)M_m f(y)dy} dz.$$
(62)

Since the expected total number of successful matings in a mating season is given by (60). The expected number of eggs deprived by a sneaker in a mating season is given by

$$\{\int_{min}^{max} A(x)M_m f(x)dx\}\{\int_{min}^{max} \alpha p(z)\sigma E_f \frac{A(z)M_m f(z)}{\int_{min}^{max} A(x)M_m f(x)dx}dz\}$$
$$=\int_{min}^{max} \alpha p(z)\sigma E_f A(z)M_m f(z)dx.$$

Considering that survival rate l_s of the eggs fertilized by the sneaker till the next mating season, we can obtain the expected fitness W_s for the sneaker as follows:

$$W_s = l_s \int_{min}^{max} \alpha p(x) \sigma E_f A(x) M_m f(x) dx.$$

B The monotonicity of fitness of sneaker

We show that $W_s(min, max)$ monotonically increases in terms of max ($max \ge min$). The derivative of $W_s(min, max)$ in terms of max is as follows:

$$\frac{\partial W_s(\min, \max)}{\partial \max} = F_1(\min, \max)F_2(\min, \max)$$
(63)

where

$$F_1(min, max) = g(max) - W_s(min, max)$$

$$F_2(min, max) = \frac{Be^{-Bmax}}{e^{-Bmin} - e^{-Bmax}}$$

$$g(max) = \alpha E_f l_s \sigma max(1 - e^{-\beta max}) > 0.$$
(64)

As $max \to min$, (63) becomes

$$\frac{\alpha E_f l_s \sigma (1 - e^{\beta min} + \beta e^{-\beta min})}{2} > 0.$$
(65)

For max > min, $F_2(min, max)$ is a positive function, so the sign of $F_2(min, max)$ determines the sign of (63). g(max) monotonically increases in terms of max. As $max \to min$, dg(max)/dmax becomes

$$\alpha E_f l_s \sigma (1 - e^{-\beta min} + \beta e^{-\beta min})$$

$$=2\lim_{\max\to\min}\frac{\partial W_s(\min,\max)}{\partial max}>0,$$

and we can show that simultaneously,

$$\lim_{\max \to \min} W_s(\min, \max) = \lim_{\max \to \min} g(\max) > 0.$$

Therefore, in neighborhood of min, W_s is smaller than g(max). If W_s decreases in terms of max, W_s must beyond g(max). However, on the function g(max), the derivative of W_s in terms of max equals to 0, so W_s can not beyond g(max). Therefore, $W_s < g(max)$, that is, W_s monotonically increases in terms of max.

C Boundary of Mating Group Size for Invasion Success of Sneaking Strategy

We show the condition for the existence of min and max which satisfy $W_m(min) \leq W_s(min, max)$. $W_s(min, max)$ monotonically increases in terms of max. So if $W_m(min)$ and $W_s(min, max)$ satisfy

$$W_m(min) \le \lim_{max \to min} W_s(min, max) \quad \text{for a fixed} min,$$
 (66)

then $W_m(min) \leq W_s(min, max)$ for any max. (66) is rewritten in the following form:

$$e^{-\beta min} \le 1 - E,$$

where

$$E = \frac{l_m}{\alpha \sigma l_s M_m}$$

Thus, when E < 1 and $\min \ge \log(1 - E)^{-1/\beta}$, $W_m(\min) \le W_s(\min, \max)$ for any max.

On the other hand, when E > 1,

$$W_m(min) > \lim_{max \to min} W_s(min, max).$$

In this case, since $W_s(min, max)$ monotonically increases in terms of max, if min for which $W_m(min)$ and $W_s(min, max)$ satisfy

$$W_m(min) < \lim_{max \to +\infty} W_s(min, max) \tag{67}$$

exists, then the positive root max^* with $W_m(min) = W_s(min, max)$ for such min uniquely exists, and $W_m(min) \leq W_s(min, max)$ for $\forall max \geq max^*$. Otherwise, for such min as to satisfy the following:

$$W_m(min) \ge \lim_{max \to +\infty} W_s(min, max).$$

 $W_m(min) > W_s(min, max)$ for any max. As $max \to +\infty$, $W_s(min, max)$ converges to

$$B\alpha\sigma E_f l_s \{\frac{1}{B}(min+\frac{1}{B}) - \frac{1}{B+\beta}e^{-\beta min}(min+\frac{1}{B+\beta})\}.$$

So, (67) can be rewritten in the following form:

 $H(\min, B, \beta) > 0,$

where

$$H(\min, B, \beta) = (1 - E)\min - \frac{B}{B + \beta}\min e^{-\beta\min} - \frac{B}{(B + \beta)^2}e^{-\beta\min} + \frac{1}{B}.$$

When E > 1, the derivative of $H(min, B, \beta)$ in terms of min is

$$\frac{\partial H(\min, B, \beta)}{\partial \min} = 1 - E - \frac{B}{B + \beta} e^{-\beta \min} (1 + \beta \min + \frac{\beta}{B + \beta}),$$

that is a negative function. Therefore, $H(min, B, \beta)$ monotonically decreases in terms of min. When min = 0, $H(min, B, \beta)$ is

$$\frac{(2B+\beta)\beta}{B(B+\beta)^2} > 0.$$

As $min \to +\infty$, $H(min, B, \beta)$ becomes $-\infty$. Therefore, the positive root min^* for $H(min, B, \beta) = 0$ uniquely exists, and $H(min, B, \beta) > 0$ for $min \in [0, min^*)$.

D Dependence of Boundary Value for Invasion Success of Sneaking Strategy on Parameters

In this appendix, we show the dependence of min^* on B and β when E > 1, where min^* is the positive root for the following equation(see Appendix C):

$$(1-E)min - \frac{B}{B+\beta}mine^{-\beta min} - \frac{B}{(B+\beta)^2}e^{-\beta min} + \frac{1}{B} = 0.$$
 (68)

At first, we show the dependence of min^* on B. (68) is rewritten in the following form:

$$G(min, B, \beta) = e^{-\beta min},$$

where

$$G(min, B, \beta) = \frac{(B+\beta)\{min(1-E) + 1/B\}}{B\{min + 1/(B+\beta)\}}.$$

The derivative of $G(min, B, \beta)$ in terms of min can be obtained as follows:

$$\frac{\partial G(\min,B,\beta)}{\partial \min} = -(\frac{B+\beta}{B^2} + \frac{E-1}{B})\frac{1}{\{\min+1/(B+\beta)\}^2} < 0.$$

Therefore, $G(min, B, \beta)$ monotonically decreases in terms of min (see Fig. 24(a)). The derivative of $G(min, B, \beta)$ in terms of B becomes:

$$\frac{\partial G(\min, B, \beta)}{\partial B}$$
$$= \frac{B(B+\beta)}{B^2 \{B(B+\beta)\min + B\}^2} [-\beta \{B\min(1-E)+1\} \{(B+\beta)\min + 1\}\}$$

 $-B^2min(E-1)-(B+\beta)^2min-\beta].$ From Fig. 24(a), since min^* uniquely exists in $[0, 1/\{B(E-1)\}]$. $\partial G/\partial B < 0$. That is, $G(min, B, \beta)$ monotonically decreases in terms of B. From Fig. 24(b), min^* monotonically decreases in terms of B. As seen from Fig. 24(a), $B \to +\infty$, min^* converges to 0. We show that min^* diverges to $+\infty$ as $B \to 0+$. min^* which is the positive root of min for the below equation is $min^{\#}$ less than min^* , because $G(min, B, \beta)$ monotonically decreases in terms of min and B (see Fig. 24(b)):

$$G(min, B, \beta) = 1 \ (\geq e^{-\beta min}).$$

We can obtain $min^{\#}$ as follows:

$$min^{\#} = \frac{\beta(2B+\beta)}{B(B+\beta)\{(B+\beta)(E-1)+B\}}$$

As $B \to 0+$, $min^{\#}$ diverges to $+\infty$. Since $min^{\#} \leq min^*$, as $B \to 0+$, min^* diverges to $+\infty$, too

Next, we show the dependence of min^* on β . The derivative of $G(min, B, \beta)$ in terms of β is as follows:

$$\frac{\partial G(\min,B,\beta)}{\partial\beta} = \frac{(B+\beta)[\{B\min(1-E)+1\}\{(B+\beta)+1\}+B\min+1]}{\{B(B+\beta)\min+B\}^2}.$$

Since the region of *min* that we consider is $[0, 1/\{B(E-1)\}], \partial G/\partial \beta > 0$. That is, $G(min, B, \beta)$ monotonically increases in terms of β , while $e^{-\beta min}$ monotonically decreases in terms of β . Therefore, as shown in Fig. 24(c), *min** monotonically decreases in terms of β . As $\beta \to 0+$, *min** converges to 0, and as $\beta \to +\infty$, it does to $1/\{B(E-1)\}$.

E Modelling for Coexist of Sneaking and Mating Group Strategies

In this appendix, we show the way to derive $W_m(x)$, W_s and W_f when the sneaker population is established. At first, we derive $W_m(x)$. The maximum expected successful matings for a territorial male with mating group size x is given by A(x). When the total population of territorial males and sneakers are M_m and M_s , we consider the successful matings of a territorial male with mating group size x:

$$A(x)D(M_s, M_m). (69)$$

The probability that a mating in the mating group with size x is successfully sneaked is given by $p(x, M_s)$. When the sneaking is successful, the sneaker can fertilize a portion σ of the average number of eggs per mating. So the expected number of eggs deprived by the whole sneakers per mating in the mating group with size x is

$$p(x, M_s)\sigma E_f. \tag{70}$$

Therefore, a mating season, the expected number of eggs that the whole sneakers deprive a territorial male with mating group size x is given by

$$A(x)D(M_s, M_m)p(x, M_s)\sigma E_f.$$
(71)

So the expected number of eggs that a territorial male with mating group size x can fertilize in a mating season is

$$A(x)D(M_s, M_m)\{1 - p(x, M_s)\sigma\}E_f.$$
(72)

By considering the survival rate of the eggs fertilized by territorial male till the next mating season, we can define $W_m(x)$ as follows:

$$l_m A(x) D(M_s, M_m) \{ 1 - p(x, M_s) \sigma \} E_f.$$
 (73)

Next, we consider W_s . The expected number of eggs of which the whole sneakers can deprive a territorial male with mating group size x in a mating season is given by (71). The probability that a territorial male is in the range of size [x, x + dx] is given by f(x)dx. So the expected number of territorial males in the range of size [x, x + dx] is given by

$$M_m f(x) dx. \tag{74}$$

From (71) and (74) the expected number of eggs of which the whole sneakers can deprive the whole territorial males in the range of size [x, x+dx] in a mating season is given by

$$A(x)D(M_s, M_m)p(x, M_s)\sigma E_f M_m f(x)dx.$$
(75)

Therefore, in the range of size [min, max], it becomes

$$\int_{min}^{max} A(x)D(M_s, \ M_m)p(x, \ M_s)\sigma E_f M_m f(x)dx.$$
(76)

By considering the survival rate l_s of eggs fertilized by sneakers till the next mating season and converting it into per sneaker, we can obtain W_s as follows:

$$W_s = l_s \frac{1}{M_s} \int_{min}^{max} A(x) D(M_s, \ M_m) p(x, M_s) \sigma E_f M_m f(x) dx.$$

Next, we consider W_f . The expected successful matings of a territorial male with mating group size x is given by (69), that is, it represents the number of females that can make mating in the mating group with x females. a females was in the mating group with size x. The probability that a female in the mating group with size x can successfully mate is given by

$$\frac{A(x)D(M_s, M_m)}{x}.$$
(77)

If a female can mate with a territorial male with mating group size x, the expected number of eggs fertilized by the sneakers per mating is given by (70), and that fertilized by a territorial male is given by

$$\{1 - p(x, M_s)\sigma\}E_f.$$
 (78)

Considering the survival rates l_m and l_s of eggs fertilized by territorial male and sneaker, when a female can mate in the mating group with size x, the expected number of survival eggs spawned by her is given by

$$l_s p(x, M_s) \sigma E_f + l_m \{ 1 - p(x, M_s) \sigma \} E_f.$$
 (79)

From (77) and (79), we can define the expected number $W_f(x)$ of survival eggs of a female when she is in the mating group with size x as follows:

$$W_f(x) = \frac{A(x)D(M_s, M_m)}{x} \{ l_s p(x, M_s)\sigma E_f + l_m \{ 1 - p(x, M_s)\sigma \} E_f \}.$$
(80)

The probability that a female is in the mating group in the range of size [x, x + dx] is given by f(x)dx. Therefore, the expected number of survival eggs of a female when she is in the mating group in the range of size [x, x + dx] is given by

$$W_f(x)f(x)dx.$$
(81)

So, in the range of size [min, max], it becomes

$$W_f = \int_{min}^{max} W_f(x) f(x) dx.$$
(82)

F Monotonicity of Fitness of Territorial Male

The derivation of $W_m(x)$ in terms of x is as follows:

$$\frac{dW_m(x)}{dx} = cD(M_s, M_m)E_f l_m [a - \alpha\sigma(1 - e^{-\delta})\{a(1 - e^{-\beta}) + (1 - e^{-ax})\beta e^{-\beta x}\}].$$
(83)

When the root x for $dW_m(x)/dx = 0$ exists, it satisfies the following equation:

$$S_e(x) = T_e(x) \tag{84}$$

where

$$S_e(M_s) = \frac{a}{\alpha\sigma(1 - e^{-\delta M_s})}$$
(85)

$$T_e(x) = a(1 - e^{-\beta x}) + (1 - e^{-ax})\beta e^{-\beta x}$$
(86)

The right side of (84) monotonically decreases in terms of M_s , and as $M_s \to +\infty$, it converges to $a/(\alpha\sigma)$. Since α and σ are less than 1, $a/(\alpha\sigma) < a$. That is, the minimum of the right hand is a. The derivation of $T_e(x)$ in terms of x is as follows:

$$\frac{dT_e(x)}{dx} = \beta e^{-\beta x} \{ a - \beta + (a + \beta)e^{-ax} \}.$$
(87)

When $a \geq \beta$, $dT_e(x)/dx > 0$ for $\forall x > 0$. When x = 0, $T_e(x) = 0$, and as $x \to +\infty$, $T_e(x)$ converges to a. Therefore, when $a \geq \beta$, $S_e(M_s) > T_e(x)$. In this case, $dW_m(x)/dx > 0$ for x > 0.

When $a < \beta$, there is the root x^* for $dT_e(x)/dx = 0$,

$$x_* = -\frac{1}{a}\log(\frac{\beta-a}{\beta+a}).$$
(88)

$$\frac{dT_e(x)}{dx} \ge 0 \quad \text{for} \quad 0 < x \le x^* \tag{89}$$

$$\frac{dT_e(x)}{dx} < 0 \quad \text{for} \quad x > x^*.$$
(90)

That is, $T_e(x)$ has the maximum for x^* , and it is given by

$$T_e(x^*) = a - \left(\frac{\beta - a}{\beta + a}\right)^{\frac{\beta}{a}} \{a - \beta\left(1 - \frac{\beta - a}{\beta + a}\right)\}.$$
(91)

 $T_e(x^*)$ is greater than a. Considering the relation between T_e^* and $a/(\alpha\sigma)$, when $T_e^* \leq a/(\alpha\sigma)$, $S_e(M_s) > T_e(x)$. Therefore, $dW_m(x)/dx > 0$. When $T_e^* > a/(\alpha\sigma)$, there is a positive value M_s^* , which is given by

$$M_s^* = -\frac{1}{\delta} \log(1 - \frac{a}{\alpha \sigma T_e^*}).$$
(92)

When $0 < M_s \leq M_s^*$, $dW_m(x)/dx > 0$. When $M_s > M_s^*$, the positive roots, which are x_1^* and x_2^* ($x_1^* \leq x_2^*$), exist, and

$$dW_m(x)/dx > 0$$
 for $0 < x < x_1^*$ (93)

$$dW_m(x)/dx \le 0$$
 for $x_1^* < x < x_2^*$ (94)

$$dW_m(x)/dx > 0 \quad \text{for} \quad x > x_2^* \tag{95}$$

G Equilibrium State

From $W_m(min) = W_s$, we can obtain $R(M_s)$ as follows:

$$R(M_s) = R_1(\min, \max)R_2(\min, M_s).$$

$$R_1(min, max) = \frac{(1 - e^{-amin})E_f l_m}{W_{s,1}W_{s,2}}$$

where

$$W_{s,1} = \frac{B\alpha\sigma E_f l_s}{e^{-Bmin} - e^{-Bmax}}$$
$$W_{s,2} = \int_{min}^{max} e^{-Bx} (1 - e^{-ax})(1 - e^{-\beta x}) dx.$$
$$R_2(min, M_s) = \frac{M_s \{1 - \alpha\sigma (1 - e^{-\delta M_s})(1 - e^{-\beta min})\}}{1 - e^{-\delta M_s}}.$$

 M_{ra} is given as follows:

$$M_{ra} = \frac{M_s}{R_1(\min,\max)R_2(\min,\max) + M_s}.$$

At first, we show that M_{ra} monotonically in terms of M_s . The derivation of M_{ra} is as follows:

$$\frac{\partial M_{ra}}{\partial M_s} = \frac{R_1 \delta e^{-delta M_s} M_s}{(R_1 R_2 + M_s)^2 (1 - e^{-\delta M_s})}.$$

Since $R_1 > 0$, it is positive. So M_{ra} monotonically increases in terms of M_s . As $M_s \to +\infty$, M_{ra} converges to

$$\frac{R_1\{1 - \alpha\sigma(1 - e^{-\beta min})\}}{R_1\{1 - \alpha\sigma(1 - e^{-\beta min})\} + 1}.$$
(96)

Figure Caption

Fig. 1. Proportion of terminal phase populations; (b) Size of terminal phase population of *T. bifasciatum*.

Fig. 2. Proportion of initial phase male population of *T. bifasciatum*.

Fig. 3. When $W_m(x)$ and W_s have the relation shown in this figure, the invasion success of sneaking strategy against the mating group strategy.

Fig. 4. Frequency distribution f(x) for mating group size x. For larger B, the extent of variance of f(x) becomes smaller.

Fig. 5. The probability function p(x) of sneaking success for mating group size x. For larger β , the extent of easiness of p(x) becomes larger.

Fig. 6. The invasion success of the sneaking strategy against the mating group strategy when E < 1. The dependence of the invasion success is classified into the two cases I and II in the parameter region of B and β : (a) E = 0.6. The invasion success depends on parameter (min, wh = max - min): E = 0.6. (a-1) B = 2.5, $\beta = 0.5$; (a-2) B = 3.5, $\beta = 0.5$. (b) shows the dependence of the boundary curve of the invasion success on B and β .

Fig. 7. The dependence of the invasion success of the sneaking strategy on min and max. (a) E = 0.6, B = 3.0, $\beta = 0.5$.

Fig. 8. The invasion success of the sneaking strategy against the mating group strategy when E > 1. The invasion success depends on parameter (*min*, *wh*): (a) E = 2.4., B = 1.0, $\beta = 0.5$. (b) shows the dependence of the boundary curve for the invasion success on B and β .

Fig. 9. The successful matings A(x) of the territorial male with the mating group size. For larger a, the successful matings becomes larger.

Fig. 10. The case that the frequency of sneakers can be at the evolutionally stably state.

Fig. 11. Parameter region of *min* and *max* for the existence of equilibrium state Case A when $\alpha \sigma \leq 1/(1 + e^{-2})$. $\alpha = 1.0, \sigma = 0.5, \beta = 0.5, a = 0.05, c = 10.0, \delta = 0.1, E_f = 10.0, l_m = 0.6, l_s = 0.5.$

Fig. 12. Parameter region of *min* and *max* for the existence of equilibrium state Case A when $\alpha\sigma < 1/(1 + e^{-2})$. $\alpha = 1.0, \sigma = 0.9, a = 0.05, B = 1.5$,

 $c = 10.0, \ \delta = 0.1, \ E_f = 10.0, \ l_m = 0.6, \ l_s = 0.5.$ (a) $\beta = 0.517$, (b) $\beta = 0.53$.

Fig. 14. (a): $\alpha \sigma < 1/(1 + e^{-2})$. $R(M_s)$ monotonically increases in terms of M_s . (b): $\alpha \sigma \ge 1/(1 + e^{-2})$. $R(M_s)$ has the minimum in terms of M_s .

Fig. 15. The relation M_m and M_s in Case A and Case B.

Fig. 16. The dependence of M_{ra} on the parameters when M_m is given. $\alpha = 1.0, \sigma = 0.5, \beta = 0.5, a = 0.05, c = 10.0, \delta = 0.1, E_f = 10.0, l_m = 0.6,$ $l_s = 0.5, M_m = 100.0$. (a) min = 1.2, max = 15.0; (b) B = 1.5, min = 1.2; (c) B = 1.5, max = 15.0.

Fig. 17. The dependence of M_{ra} on M_m when parameters are given. $B = 1.5, \alpha = 1.0, \sigma = 0.5, \beta = 0.5, a = 0.05, c = 10.0, \delta = 0.1, E_f = 10.0,$ $l_m = 0.6, l_s = 0.5, min = 1.2, max = 15.0.$

Fig. 18. The dependence of the sex ratio on B, min and max when M_m is given. $\alpha = 1.0, \sigma = 0.5, \beta = 0.5, a = 0.05, c = 10.0, \delta = 0.1, E_f = 10.0, l_m = 0.6, l_s = 0.5, M_m = 100.0$. (a) min = 1.2, max = 15.0; (b) B = 1.5, min = 1.2; (c) B = 1.5, max = 15.0.

Fig. 19. The dependence of *thesexratio* on M_m when parameters B, *min* and *max* are given. B = 1.5, $\alpha = 1.0$, $\sigma = 0.5$, $\beta = 0.5$, a = 0.05, c = 10.0, $\delta = 0.1$, $E_f = 10.0$, $l_m = 0.6$, $l_s = 0.5$, *min* = 1.2, *max* = 15.0.

Fig. 20. The region of *min* and *max* for the each case of sex ratio in Case A. B = 1.5, $\alpha = 1.0$, $\sigma = 0.5$, a = 0.05, c = 10.0, $\delta = 0.1$, $E_f = 10.0$, $l_m = 0.6$, $l_s = 0.5$. (a) $\beta = 0.5$; (b) $\beta = 0.53$.

Fig. 21. The region of *min* and *max* for the sex ratio in Case B. B = 1.5, $\alpha = 1.0, \sigma = 0.5, a = 0.05, c = 10.0, \delta = 0.1, E_f = 10.0, l_m = 0.6, l_s = 0.5$. (a) $\beta = 0.5$; (b) $\beta = 0.53$.

Fig. 22. The dependence of the function $G(min, B, \beta)$ on B and β .

Table. 13. Region which M_s can be at the equilibrium state.























Mating Group Size









(min, max)	The Region of <i>M_S</i>
Θ_{I}	
Θπ	
Θ_{III}	



 $M_{\rm s}$















