

# A mathematical consideration for the optimal shell change of hermit crab

Yoko Sato<sup>a</sup>, Hiromi Seno<sup>b,\*</sup>

<sup>a</sup>Department of Information and Computer Sciences, Faculty of Science, Nara Women's University, Nara 630-8506, Japan

<sup>b</sup>Department of Mathematical and Life Sciences, Graduate School of Science, Hiroshima University, Higashi-hiroshima 739-8526, Japan

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## Abstract

Shell of the adult hermit crab has some important roles for its fitness. In the same time, the shell size often limits the body growth of its owner. To grow the body size larger, the individual must change the shell to another larger shell. If the individual cannot get another larger one, the individual has to suppress the body size growth as the occupied shell size allows. Growth suppression would result in the lower fitness. With a simple mathematical model, we consider the criterion about whether the individual should try to change the shell or not in order to get the higher fitness. We show that the optimality of a shell change behavior has a relation with the body size and the season length for the shell change. They also affect the optimal timing for the shell change. It is implied that the probability of the success in a shell change and the cost for the shell change behavior do not affect the optimal timing for the shell change at all but significantly do the optimality of the behavioral choice.

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## 1. Introduction

About 800 species of hermit crabs carry empty snail shells as their shelter (Hazlett, 1981; Kuhlmann, 1992; Angel, 2000; Rotjan et al., 2004). In general, the hermit crab grows up to adult after the period of zoea floating in seawater like planktons. Zoea period is 2–5 weeks for the species of the shallow sea. Although the adults are terrestrial, they move to sea for hatching eggs. After several molts in the zoea period, the individual seeks a shell. Only such individual that succeeds in getting its shell can grow up to adult and can increase the body size after several shell changes (Reese, 1962; Hazlett, 1981; Rotjan et al., 2004).

Some species show the reproductive activity throughout year, and the others do only in some specific months. For example, *Calcinus laevimanus* in Hawaii shows a reproductive behavior throughout year except for the period from November to February, while *Clibanarius zebra* inhabiting

in the same region breeds almost just in August (Reese, 1963).

How could the hermit crab get a new shell? We can observe two types of behavior. The first is to obtain a shell just after the snail dies, that is, a vacant shell. In general, such a shell after the snail's death is buried, destroyed and swept away by waves. Even though a hermit crab can encounter such a shell, it may not meet its requirement. The second is to obtain a shell which another crab has, that is a ritualizing behavior. Attacker hermit crab rocks, shakes, and rapps the defender. When the defender gives up its shell, the attacker quickly gets into the defender's shell, and at the same time the ejected defender gets into the attacker's one. In a sense, two crabs exchange the shells from each other (Hazlett, 1981).

A merit to carry the shell is the defense against predators (Hazlett, 1981; Kuhlmann, 1992; Angel, 2000; Rotjan et al., 2004). When a predator comes near, the hermit crab pulls its body into the shell and covers the shell with its claw. Individual with a small shell is much likely subjected to the predation, for instance, by fish (Hazlett, 1981). The shell contributes to the tolerance against some physical

\*Corresponding author. Tel./fax: +81 82 424 7394.

E-mail address: [seno@math.sci.hiroshima-u.ac.jp](mailto:seno@math.sci.hiroshima-u.ac.jp) (H. Seno).

stresses, too (Reese, 1969). In some cases, hermit crabs die for the desiccation or the change of osmotic stress. Species inhabiting in the high intertidal region utilizes the shell to retain sufficient water in it (Bertness, 1981b).

Another merit of the shell is to increase the reproductive success. For female, the shell is to guard its eggs. Some decapod crustacea have difficulty to move with keeping own eggs under the abdomen, whereas the shell is beneficial for the egg protection against predation and physical stresses. As for the reproduction success, the larger shell makes it easier for male to grip the female and guard her from the other males. In the case when male hermit crabs contend for a female, the male with the larger shell could get advantage against the other with the smaller.

On the other hand, the hermit crab has some disadvantages due to keeping the shell. Carrying it requires the cost, although it is beneficial for its survival. Actually, the oxygen consumption by *Coenobita compressus* without shell is estimated to be 67% of that with a shell (Herreid and Full, 1986).

Besides, even when an individual seeks a new shell, it could not always get an appropriate one. Even when the shell becomes damaged or unsuitable for growing the body size, it is in general not easy to find and obtain an appropriate another one. Indeed, the shell selection of hermit crab usually occurs after a lengthy period of investigation (Neil and Elwood, 1986; Brown et al., 1993; Côté et al., 1998; Benvenuto and Gherardi, 2001). It is suggested that some individuals should have to restrict the growth of body size even when there would be enough food to grow up the body size (Markham, 1968; Childress, 1972; Bach et al., 1976; Fotheringham, 1976; Bertness, 1981a; Floeter et al., 2000).

The shell size could limit the reproductive success (Childress, 1972; Bertness, 1981a, b; Hazlett, 1989; Hazlett and Baron, 1989; Elwood et al., 1995; Côté et al., 1998; Floeter et al., 2000). For female, the shell size determines the total amount of eggs that could be kept in the shell. For male, the smaller individual with the smaller shell could get the less opportunity for successful mating than the larger one could (Childress, 1972; Bach et al., 1976; Fotheringham, 1976, 1980; Bertness, 1981a). For several tropical species, it is observed that berried females are with inadequate shell (Bertness, 1981a, b).

The shell is closely related to the survival and the reproductive success of hermit crab. From the viewpoint of the survival or/and the reproductive success, what is the best timing for the shell change? What condition is required for the case that the individual could expect the greater advantage from the suppression of body size growth without changing the shell than from the body size growth with changing the shell? In this paper, we will consider these problems with a mathematical modeling, focusing how the strategy to get the maximal reproductive success depends on the body size and the season length for a shell change. As far as we could have known, our work would be a pioneer one with a mathematical model about these problems.

## 2. Assumptions

### 2.1. Body size

Body size of hermit crab is a function of time. If an individual could use the larger shell, the body size grows up to the larger size as long as the occupied shell could allow.

### 2.2. Shell change

We assume that the individual could take such a behavior as to change the shell to the larger one except in the breeding season. That is, the individual can choose the behavior of the shell change only in the period between two subsequent breeding seasons, say, the *inter-breeding season*. Furthermore, it is assumed that the individual could change the shell only once in each inter-breeding season. In our modeling, the length of inter-breeding season is given by a constant  $T$ . In reality, the cycle of hermit crab's shell changes is not well known (Gilchrist, 2003). However, in this paper, according to the shell change, we focus on the hermit crab's behavioral choice to maximize the expected reproductive success, that is, on the decision about whether the individual chooses the behavior to seek and change its shell to a new one or not, which is assumed to correlate positively to the reproductive success. In this reason, we assume that the purpose of the behavioral choice about the shell change is to maximize the reproductive success in the subsequent breeding season. So we construct our model with the above-mentioned inter-breeding season, although its given constant length  $T$  is a mathematical simplification in our modeling.

When an individual with body size  $x$  tries to change the shell to another larger one, the probability that the individual succeeds in getting a larger shell is assumed to be given by  $\varphi$ . For mathematical simplification and clarification of our arguments, we assume that the probability  $\varphi$  is constant independently of the body size, although it may generally a function of body size  $x$ . Thus, the probability that the individual fails to get the larger shell is given by  $1 - \varphi$ . We ignore the handling time for the shell change in our modeling. So, a shell change is assumed to occur at a moment in the inter-breeding season if it is successful.

### 2.3. Energy reserve

For our mathematical modeling, we define the *energy reserve* of individual. The energy reserve changes due to the energy input and output by feeding and homeostasis etc., which in general depend on the body size. We assume that the greater energy reserve at the beginning of the breeding season promises the greater reproductive success in the breeding season. Since the behavioral choice in the inter-breeding season can significantly affect the energy reserve, the individual should choose the behavior to make the energy reserve as much as possible at the beginning of the

subsequent breeding season. So we consider the optimality of the behavioral choice with regard to the maximization of the energy reserve at the beginning of the next breeding season, that is, the *terminal energy reserve* at the end of the considered inter-breeding season.

When an individual with body size  $x$  tries to change the shell, the individual is assumed to have to pay an energy cost  $m$  for the behavior to seek an appropriately larger shell, independently of the consequence of the behavior, that is, whether the individual succeeds in getting the larger shell or not. The energy cost  $m$  includes, for instance, an energy consumption to search an appropriate shell. In addition, we may consider an increase of the predation risk during the shell searching behavior, too. In this paper, we assume that the energy cost  $m$  is constant independently of the body size as well as the probability  $\varphi$  is.

### 3. Modeling

Suppose that the body size grows up from  $x$  to  $x + \delta x$  in a time interval  $[t, t + \Delta t]$ . Meantime, the energy reserve of the individual changes by  $E(x + \delta x, t + \Delta t) - E(x, t)$ , where  $E(x, t)$  denotes the energy reserve at time  $t$  and body size  $x$ . On the other hand, we assume that the net *accumulated* energy uptake  $u(x)$  until the body size becomes  $x$  has such a unimodal nature that it monotonically increases for the body size less than a critical value and decreases for the body size more than it. The decrease of net accumulated energy uptake could be regarded as due to the high energy requirement for the homeostasis with the large body size. In our model, we use the following parabolic function for  $u(x)$ :

$$u(x) = -b(x - c)^2 + \text{const.}, \quad (1)$$

where  $b$  and  $c$  are positive constants.

The change of the energy reserve in  $[t, t + \Delta t]$  can be now given by

$$E(x + \delta x, t + \Delta t) - E(x, t) = u(x + \delta x) - u(x). \quad (2)$$

With  $\delta x \rightarrow 0$  and  $\Delta t \rightarrow 0$ , we can obtain the following partial differential equation for the energy reserve  $E(x, t)$  at time  $t$  and body size  $x$ :

$$G(x) \frac{\partial E(x, t)}{\partial x} + \frac{\partial E(x, t)}{\partial t} = \frac{du(x)}{dx} G(x), \quad (3)$$

where  $G(x)$  is the growth function for the body size

$$G(x) = \frac{dx(t)}{dt}. \quad (4)$$

In our model, we assume that the body size grows in a logistic manner:

$$x(t) = x(t; x_0, k) = \frac{k}{1 + (k/x_0 - 1)e^{-rt}}, \quad (5)$$

where  $x_0$  is the initial body size at  $t = 0$ , and  $r$  is the intrinsic rate of body size growth. The carrying capacity  $k$  is now translated to mean the maximal body size allowed by the occupied shell size.

We assume that, if an individual succeeds in its shell change, the individual gets a new shell larger than the previous one, so that the carrying capacity for the body size changes from  $k$  to  $k + \Delta k$  after the shell change. In this model, we assume that the increment  $\Delta k$  of carrying capacity is a constant regardless of the previous or the new shell size. Besides, we assume that the intrinsic growth rate  $r$  is constant independently of the body size  $x$  and the shell change behavior. When the individual fails in changing the shell, the body size growth is limited by the same carrying capacity  $k$ .

From Eqs. (1) and (3), we can get  $E(x, t)$  as the following function  $E(x)$ :

$$E(x, t) = E(x) = E(x_0, 0) + b(x_0 - c)^2 - b(x - c)^2. \quad (6)$$

At first, we consider the case when the individual does not try to change the shell through the inter-breeding season. The terminal energy reserve  $E_{\text{unchange}}$  at  $t = T$  in this case is

$$E_{\text{unchange}}(x_0) = E(X_u), \quad (7)$$

where  $X_u$  is the following terminal body size at  $t = T$  (see Fig. 1):

$$X_u = x(T; x_0, k) = \frac{k}{1 + (k/x_0 - 1)e^{-rT}}. \quad (8)$$

Next, we consider the case when the individual tries to change the shell at time  $t = \tau$  ( $0 \leq \tau \leq T$ ). If the shell change fails, the terminal energy reserve at time  $t = T$  is given by  $E(X_u) - m$ , where the positive constant  $m$  means the energy

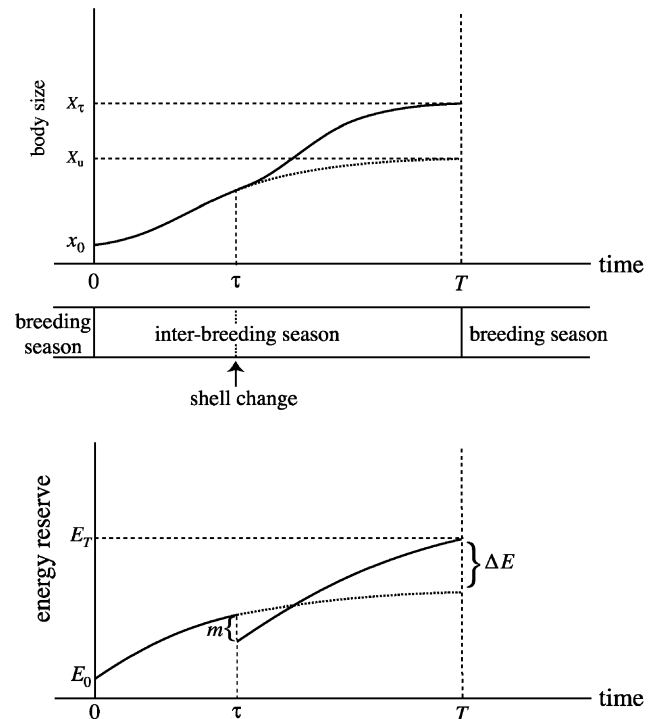


Fig. 1. Temporal variations of the body size and the energy reserve. Illustrative explanation. The solid curve shows the case when the individual tries and succeeds in a shell change at  $t = \tau$ .

cost to seek a new shell. In this case, the terminal body size at  $t = T$  is given by Eq. (8) because the failure of the shell change makes the individual keep the occupied shell and the body size unchange. On the other hand, if the individual succeeds in the shell change at  $t = \tau$ , we can get the energy reserve  $E(X_\tau)$  at  $t = T$ , given by

$$E(X_\tau) = E(X_u) - m + b(X_u - c)^2 - b(X_\tau - c)^2, \quad (9)$$

where the terminal body size  $X_\tau$  at  $t = T$  is given by

$$X_\tau = x(T - \tau; x(\tau; x_0, k), k + \Delta k) \\ = \frac{k + \delta k}{1 + [(k + \delta k)/x(\tau; x_0, k)] - 1} e^{-r(T-\tau)}. \quad (10)$$

This case is assumed to occur with probability  $\phi$ . The size  $X_\tau$  is larger than  $X_u$  given by Eq. (8) because the successful shell change serves the increase of carrying capacity by  $\Delta k$  (see Fig. 1). Besides, we note that  $X_\tau$  is monotonically decreasing in terms of  $\tau$  with  $X_{\tau=0} = x(T; x_0, k + \Delta k) > X_{\tau=T} = X_u$ .

Lastly, we can obtain the *expected* terminal energy reserve  $E_{change}(x_0, \tau)$  at  $t = T$  in the case when the individual with the initial body size  $x_0$  at  $t = 0$  tries to change the shell at  $t = \tau$  ( $0 \leq \tau \leq T$ )

$$E_{change}(x_0, \tau) = (1 - \phi)\{E(X_u) - m\} + \phi\{E(X_u) - m \\ + b(X_u - c)^2 - b(X_\tau - c)^2\}. \quad (11)$$

Now, we consider the *expected* advantage by the shell change behavior. It can be estimated by the energy increment  $\Delta E(x_0, \tau) = E_{change}(x_0, \tau) - E_{unchange}(x_0)$  expected in case of choosing the shell change behavior at time  $\tau$  ( $0 \leq \tau \leq T$ ), compared to the case without choosing it

$$\Delta E(x_0, \tau) = -m + \phi\{b(X_u - c)^2 - b(X_\tau - c)^2\}. \quad (12)$$

If  $\Delta E(x, \tau)$  is positive, the expected energy gain is larger by choosing the shell change behavior than by keeping the occupied shell. In such case, the choice of the shell change behavior in the inter-breeding season is expected to result in the larger energy reserve at the beginning of the subsequent breeding season, that could eventually serve the greater reproductive success in the breeding season.

It should be remarked that, in our modeling, the behavioral choice is assumed to depend not on the *actual* energy gain obtained in case of the successful shell change but on the *expected* energy gain when the individual would choose the behavior to seek the larger shell. Hence, even when  $\Delta E(x_0, \tau) < 0$ , it is likely that the successful shell change could give a sufficiently large energy gain. In such a case, the probability of the successful shell change is so small that the energy gain with the shell change behavior is *expected* to result in much small.

#### 4. Timing for the shell change

Let us consider the timing  $t = \tau^*$  ( $0 \leq \tau^* \leq T$ ) for a shell change, which maximizes  $E_{change}(x_0, \tau)$ . Since  $X_\tau$  is monotonically decreasing in terms of  $\tau$ , we can find from Eqs.

(11) and (12) that  $\tau^* = 0$  if

$$X_{\tau=0} \leq c. \quad (13)$$

With this condition,  $E_{change}(x_0, \tau)$  is monotonically decreasing in terms of  $\tau$  ( $0 \leq \tau \leq T$ ). In contrast, we have  $\tau^* = T$  if

$$X_u \geq c. \quad (14)$$

Then  $E_{change}(x_0, \tau)$  is monotonically increasing in terms of  $\tau$ .

If and only if

$$X_u < c < X_{\tau=0}, \quad (15)$$

we have  $\tau^* = \tau_m$ , such that  $0 < \tau_m < T$ . From Eq. (11), we can explicitly obtain the expression of  $\tau_m$  as follows:

$$\tau_m = \frac{1}{r} \ln \left[ (k + \Delta k) \left\{ \frac{1}{c} - \left( \frac{1}{x_0} - \frac{1}{k} \right) e^{-rT} \right\} - 1 \right] \\ + \frac{1}{r} \ln \frac{k}{\Delta k} + T \\ = \frac{1}{r} \ln \left[ 1 - \frac{k}{\Delta k} (k + \Delta k) \left( \frac{1}{X_u} - \frac{1}{c} \right) \right] + T \\ = \frac{1}{r} \ln \left[ 1 + e^{rT} \frac{k}{\Delta k} (k + \Delta k) \left( \frac{1}{c} - \frac{1}{X_{\tau=0}} \right) \right]. \quad (16)$$

In this case,  $E_{change}(x_0, \tau)$  has the unique maximal extremum at  $\tau = \tau_m$ .

From Eq. (16), we can find that, as  $T$  gets larger,  $(T - \tau_m)/T$  gets smaller (Fig. 2(b)). This means that, as the length of the inter-breeding season gets longer, the optimal timing of a shell change behavior tends to be relatively later within the inter-breeding season.

#### 5. Optimality of the shell change behavior

If and only if  $\Delta E(x_0, \tau) > 0$ , the choice of the shell change behavior at  $t = \tau$  makes sense in order to expect the greater terminal energy reserve at  $t = T$ . In case of  $\Delta E(x_0, \tau) > 0$ , we call the shell change behavior *optimal*. The optimal timing  $\tau = \tau_{opt}$  ( $0 \leq \tau_{opt} \leq T$ ) for a shell change is to maximize  $E_{change}(x_0, \tau)$  with  $\Delta E(x_0, \tau) > 0$ .

When  $\tau = T$  with Eq. (14), we can easily find that  $\Delta E(x_0, T) = -m < 0$ . Thus, if Eq. (14) is satisfied, the shell change behavior is not optimal. Thus, from the viewpoint of the optimal shell change, it never occurs at the end of inter-breeding season.

For  $\tau = \tau_m$  given by Eq. (16), the necessary and sufficient condition for  $\Delta E(x_0, \tau_m) > 0$  is given by

$$\frac{X_u}{1 - \sqrt{\beta}} < c \quad (17)$$

with  $\beta = (1/bc^2)(m/\phi) < 1$ . Therefore, with the condition (15) for  $\tau^* = \tau_m$ , the necessary and sufficient condition for  $\tau_{opt} = \tau_m$  is given by

$$\frac{X_u}{1 - \sqrt{\beta}} < c < X_{\tau=0} \quad (18)$$



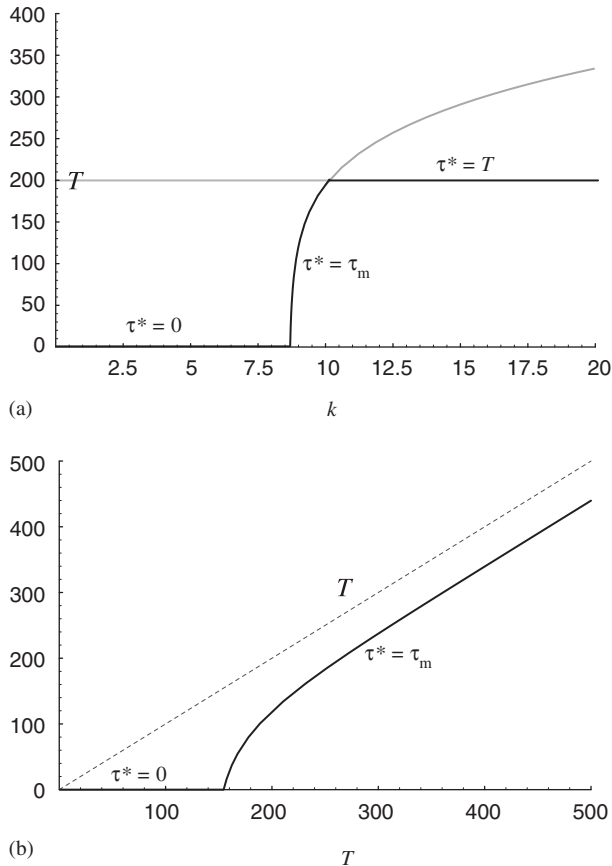


Fig. 2. Dependence of  $\tau^*$  on (a) the carrying capacity  $k$  and (b) the length of the inter-breeding season  $T$ . Numerical calculation with  $T = 200.0$  for (a),  $k = 9.0$  for (b). Commonly  $r = 0.02$ ;  $c = 10.0$ ;  $x_0 = 5.0$ ;  $\Delta k = 1.5$ .

with  $\beta < 1$ . When  $\tau_{opt} = \tau_m$ , if the shell change is successful, from Eqs. (10) and (16), the terminal body size  $X_\tau$  at the end of inter-breeding season is given by  $X_{\tau=\tau_m} = c$ .

For  $\tau = 0$ , from Eq. (12), the condition for  $\Delta E(x_0, 0) > 0$  is given by

$$\left(1 - \frac{X_u}{c}\right)^2 - \left(1 - \frac{X_{\tau=0}}{c}\right)^2 \geq \beta. \quad (19)$$

With the condition (13) for  $\tau^* = 0$ , we can get the following condition for  $\tau_{opt} = 0$ , that is the case when a shell change at the beginning of inter-breeding season is optimal:

$$c \left[ 1 - \sqrt{\left(1 - \frac{X_u}{c}\right)^2 - \beta} \right] \leq X_{\tau=0} \leq c,$$

$$X_u \leq c(1 - \sqrt{\beta}). \quad (20)$$

When  $\tau_{opt} = 0$ , if the shell change is successful, the terminal body size  $X_\tau$  is given by Eq. (10) with  $\tau = 0$ , that is,  $X_{\tau=0} = x(T; x_0, k + \Delta k)$ .

These results indicate that, if the shell change behavior is optimal, the condition that  $\beta < 1$  is necessary. In case of  $\beta \geq 1$ , the shell change behavior is never optimal.

## 6. Discussion

### 6.1. Length of the inter-breeding season

For our model, in Fig. 3, we numerically show the parameter region for the optimal shell change behavior. In the case when the shell change behavior is optimal for a given initial body size, the optimal timing for the shell change behavior significantly depends on the length of the inter-breeding season (see also Fig. 2(b)). When  $\beta$  is sufficiently small, that is, when the shell change is sufficiently easy with small  $m$  and large  $\varphi$ , the shell change behavior is optimal for any inter-breeding season longer than a critical value (Fig. 3(a)). In contrast, for sufficiently large  $\beta$ , the shell change behavior cannot be optimal.

If the occupied shell and the body size are sufficiently small, as in case of Fig. 3(d), the shell change behavior is optimal except for when the inter-breeding season is sufficiently short.

In case of Fig. 3(b) or (c), the shell change behavior could be optimal only for an intermediate length of the inter-breeding season. For sufficiently short or sufficiently long inter-breeding season, it cannot be optimal. As a consequence, for sufficiently short inter-breeding season, the shell change behavior cannot be optimal. Further, from Figs. 2(b) and 3(a, b), we find that, as the inter-breeding season gets longer, the optimal timing for the shell change behavior tends to be relatively later.

In conclusion, the length of the breeding season could affect the optimality of a shell change behavior. Only with an intermediate length of the breeding season, the shell change behavior would be optimal. As the breeding season is longer, the individual would show the shell change behavior relatively earlier in the inter-breeding season. In other words, in an environment with long breeding season, the individual would show the shell change behavior relatively early in the inter-breeding season. In a harder environment with short breeding season, the individual would not show the shell change behavior and suppress the body size growth.

### 6.2. Initial body size

In our model, the initial body size means the body size at the beginning of inter-breeding season. So it becomes greater year by year. As indicated in Fig. 3, we could find some cases with an upper limit of the initial body size for which the shell change behavior could be optimal. If the initial body size is larger than the upper limit, the increment of the net energy uptake following the body size growth is so low while the energy consumption is so large that the individual could not compensate the cost for the shell change behavior until the end of inter-breeding season, or that the *expected* terminal energy reserve becomes too small to compensate the cost due to sufficiently small probability  $\varphi$ , or that the individual cannot get a sufficient large increase of the terminal energy

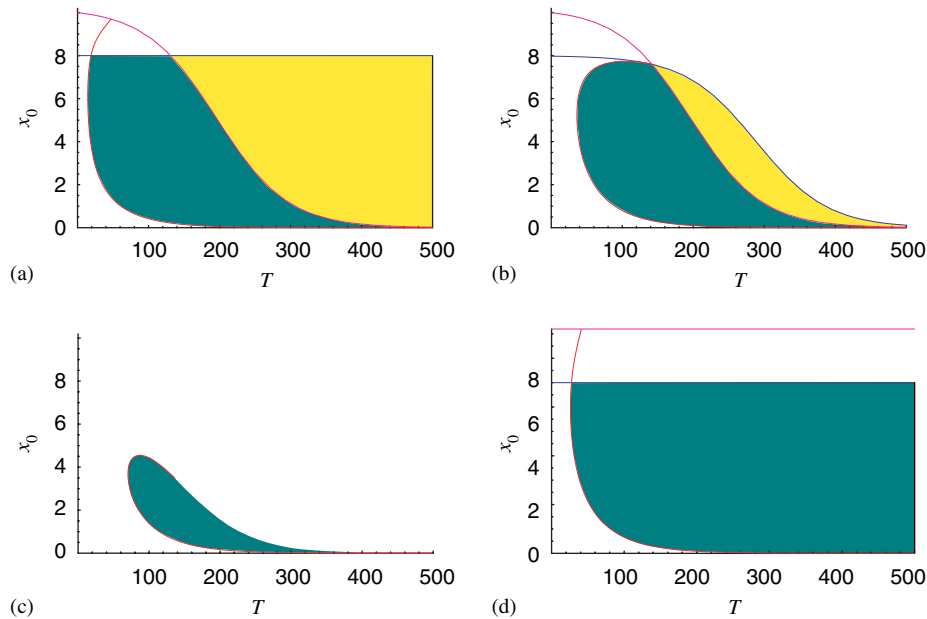


Fig. 3.  $(x_0, T)$ -dependence of the optimal behavioral choice. Numerical calculations for Eqs. (18) and (20). (a)  $\beta = 0.02$  with  $k = 8.0$ ; (b)  $\beta = 0.041$  with  $k = 8.0$ ; (c)  $\beta = 0.06$  with  $k = 8.0$ ; (d)  $\beta = 0.041$  with  $k = 7.0$ . Commonly,  $r = 0.02$ ;  $c = 10.0$ ;  $\Delta k = 2.2$ . The dark region is for  $\tau_{opt} = 0$ , and the light dark one for  $\tau_{opt} = \tau_m$ . The case of (a) is when  $k/(1 - \sqrt{\beta}) < c < k + \Delta k$ , while those of (b) and (c) are when  $k/(1 - \sqrt{\beta}) < c < k + \Delta k$ . The case of (d) is when  $k + \Delta k < c$ .

reserve with the shell change due to too short inter-breeding season.

In contrast, as shown in Fig. 3, the shell change behavior is not optimal for the individual with sufficiently small initial body size, either. This implies that the shell change behavior is not optimal for the individual in the earlier stage of the body size growth. The individual would begin the shell change behavior after its body size grows sufficiently large.

Further, we can show that, when a shell change behavior is optimal for a length of the inter-breeding season, the optimal timing for the shell change behavior becomes relatively later in the inter-breeding season as the body size gets larger (see Fig. 2(a)).

### 6.3. Body size growth

We illustrate some examples of the history of the body size growth in our model, making use of numerical calculations (Fig. 4). Since the body size grows fundamentally in a logistic manner, it asymptotically approaches its saturated value, the carrying capacity determined by the occupied shell size, as shown in Fig. 4(a). If the shell is successfully changed to an appropriately larger one, the growth rate is changed with the shell change, so that the growth curve of the body size shows a cuspidal point at the moment of the shell change, indicated by upward arrows in Fig. 4. The shell change occurs in the period with an intermediate body size, while it does not with sufficiently small or large body size.

As indicated in Fig. 4(b), the energy reserve is monotonically increasing in time except for the moment of the

shell change if no cost is charged in the breeding season. In contrast, as shown in Fig. 4(c), if a cost is charged in the breeding season, for instance, due to some breeding activity, the energy reserve goes decreasing as the body size is near the saturated value. As the growth rate of the body size gets sufficiently small, the increase of the energy reserve with the body size growth cannot cover its decrease due to the cost in the breeding season. This might be translated as an appearance of the aging.

Generally, the younger individual corresponds to one with smaller body size and the elder does to one with larger body size. So we can translate the relation between the optimal timing for a shell change and the body size as follows: the younger individual would show the shell change behavior relatively earlier after the breeding season, and the elder would not show the shell change behavior and suppress the body size.

### 6.4. Cost for the shell change behavior

In our model, the ratio  $m/\phi$  in the parameter  $\beta$  is one of important factors which determine the optimality of a shell change behavior, whereas the ratio  $m/\phi$  does not affect the optimal timing for a shell change at all. If  $m/\phi$  gets larger, the optimality conditions (17) and (20) are harder to be satisfied.

The smaller  $m/\phi$ , that is, the smaller cost for the shell change behavior and/or the larger probability of the successful shell change increases the optimality of the shell change behavior.

Our results indicate that the cost for a shell change behavior and the probability of its success have no relation

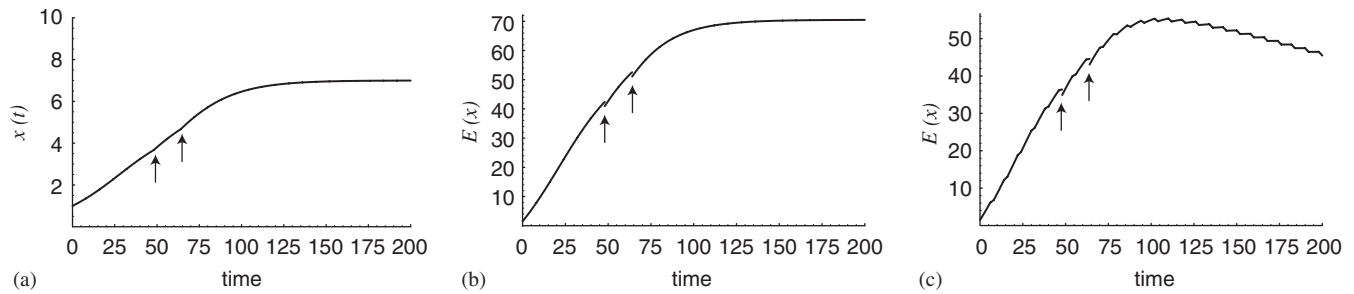


Fig. 4. A temporal variation of the body size  $x$  and the energy reserve  $E$ . Upward arrows indicate the moment of a shell change. Numerical calculation with  $r = 0.05$ ;  $x(0) = 1.0$ ;  $k_{i=0} = 5.0$ ;  $\Delta k = 1.0$ ;  $b = 1.0$ ;  $c = 10.0$ ;  $T = 6.0$ ;  $E(x(0)) = 4.0$ ;  $m = 1.5$ ;  $\varphi = 1$ . The length of breeding season = 2.0: (a) body size; (b) energy reserve with no cost for the breeding activity; (c) energy reserve with a time-proportionally increasing cost for breeding activity (cost per time = 0.1). Except for the cost of the shell change or the breeding activity, no cost is charged in these calculations. In these calculations, as the result, every shell change appears at the beginning of an inter-breeding season.

to the optimal *timing* for the shell change, while, with the small cost for a shell change, the optimality itself is high. Environment in which the hermit crab could easily find a new shell corresponds to the case of a large probability of the successful shell change. Sufficiently large probability could make the shell change behavior optimal. In such an environment, we could observe the shell change behavior frequently.

#### 6.5. Net accumulated energy uptake $u$

In our modeling, the net accumulated energy uptake  $u$  is assumed to be a unimodal function of the body size  $x$ . For not only a parabolic function but also another unimodal function, our results would be expected to hold. Furthermore, this assumption of the unimodality may not be necessary for the existence of the optimal timing for a shell change behavior. Indeed, for the existence of the optimal timing for a shell change, the function  $u$  should have an appropriate nonlinearity, because its existence requires some nonlinearity of the function  $E_{\text{change}}$ . Therefore, we expect that our results would hold for a wide range of modeling about the same/similar problem.

#### 6.6. A simpler modeling

As described in Appendix A.1, we can consider a simpler model that can derive some essential results corresponding to those for our model analysed in our main text: Under those same assumptions described in the previous section, we assume for the mathematical modeling that the body size growth is sufficiently fast once the individual succeeds in getting a new shell. At the moment when the shell change is succeeded in, the body size grows up to the maximal size as the occupied shell allows. Only when the individual succeeds in changing the shell to the larger one, the individual can increase the body size by  $\Delta x$ , where the increment  $\Delta x$  is a positive constant independent of the previous body size  $x$ . So, once the shell change is

successful in at time  $\tau$ , the body size is assumed to increase simultaneously by  $\Delta x$ . In this modeling, differently from that shown in our main text, we ignore the time required for the body size growth from  $x$  to  $x + \Delta x$ . This assumption mathematically means that the body size grows up from  $x$  to  $x + \Delta x$  in a discontinuous manner like a step function of time.

Even though this modeling may seem oversimplified, as briefly shown in Appendix A.1, we can obtain the results quantitatively same as those from the model of our main text. Some simple model could grasp the essential factors relevant for the problem and provide some satisfactory results to discuss theoretically the phenomenon.

### 7. Conclusion

Analysing a mathematical model, we showed that the hermit crab would have a range of the initial body size and the length of breeding season to make the shell change behavior optimal. Our results imply that the individual with sufficiently large body size would not show the shell change behavior and suppress the body size growth. With regard to the optimal timing for a shell change, the individual with the larger body size would show the shell change behavior relatively later in the inter-breeding season. The individual with the smaller body size would show the behavior relatively earlier.

Length of the breeding season could affect the optimality of a shell change behavior. Only with an intermediate length of the breeding season, the shell change behavior would be optimal. As the breeding season is longer, the individual would show the shell change behavior relatively earlier in the inter-breeding season.

Our results indicate that the cost for a shell change behavior and the probability of its success have no relation to the optimal *timing* for the shell change, while, with the small cost for a shell change, the optimality itself is high. Sufficiently large probability of the successful shell change could make the shell change behavior optimal.

## Appendix A

### A.1. A simpler model with a step-wise growth of the body size

In this appendix, we consider a simpler model that can derive some essential results corresponding to those for our model in the main text. Now, we assume that the body size growth is sufficiently fast once the individual succeeds in getting a new shell: at the moment when the shell change is succeeded in, the body size is assumed to grow up to the maximal size as the occupied shell allows. Only when the individual succeeds in changing the shell to the larger one, the individual can increase the body size by  $\Delta x$ , where the increment  $\Delta x$  is a positive constant independent of the previous body size  $x$ . So, once the shell change is successful in at time  $\tau$ , the body size is assumed to increase simultaneously by  $\Delta x$  (Fig. A.1). In this modeling, differently from that in the main text, we ignore the time required for the body size growth from  $x$  to  $x + \Delta x$ . This assumption mathematically means that the body size grows up from  $x$  to  $x + \Delta x$  in a discontinuous manner like a step function of time (see Fig. A.1). When the individual fails in changing the shell, the body size growth is assumed to be suppressed and unchanged.

The energy reserve of individual with body size  $x$  at time  $t$  is assumed to be determined by the net energy uptake  $\varepsilon(x)$  per unit time at body size  $x$  and the initial energy reserve  $E(x, 0)$  at the beginning of the inter-breeding season with the initial body size  $x$ . Eventually, the energy reserve of individual with body size  $x$  is given by  $E(x, 0) + \varepsilon(x)t$  at time  $t$  in the inter-breeding season.

In the case when the individual with the initial body size  $x$  successfully changes the shell at time  $\tau$  ( $0 \leq \tau \leq T$ ) in an inter-breeding season, the terminal energy reserve at  $t = T$  is given by

$$E(x, 0) + \varepsilon(x)\tau - m + \varepsilon(x + \Delta x)(T - \tau) \quad (\text{A.1})$$

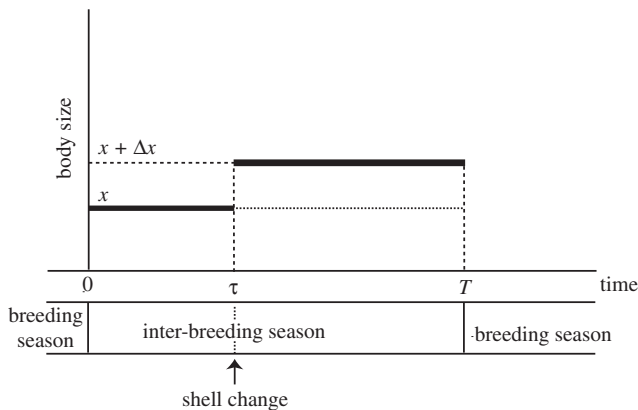


Fig. A.1. Step-wise growth of body size. The solid line shows the case when the individual tries the shell change and succeeds in it at  $t = \tau$ . At the moment of the successful shell change, the body size immediately changes from  $x$  to  $x + \Delta x$ .

with the terminal body size  $x + \Delta x$ . On the other hand, in the case when the individual with body size  $x$  tries and fails to get the larger shell at time  $\tau$  ( $0 \leq \tau \leq T$ ), the body size is unchanged, and the terminal energy reserve is given by  $E(x, 0) + \varepsilon(x)T - m$  with the terminal body size  $x$ .

Therefore, when the individual with the initial body size  $x$  would seek the larger shell, the *expected* terminal energy reserve  $E_{\text{change}}(x, \tau)$  is given by the following with probability  $\phi$  to succeed in the shell change:

$$E_{\text{change}}(x, \tau) = E(x, 0) + \varepsilon(x)T - m + (T - \tau)\phi\{\varepsilon(x + \Delta x) - \varepsilon(x)\}. \quad (\text{A.2})$$

In contrast, in the case when the individual with the initial body size  $x$  would *not* seek the larger shell but keep the occupied shell through the inter-breeding season, the terminal energy reserve  $E_{\text{unchange}}(x)$  at time  $T$  is given by

$$E_{\text{unchange}}(x) = E(x, 0) + \varepsilon(x)T. \quad (\text{A.3})$$

Hence, the expected difference  $\Delta E(x, \tau) = E_{\text{change}}(x, \tau) - E_{\text{unchange}}(x)$  is given by

$$\Delta E(x, \tau) = -m + (T - \tau)\phi\{\varepsilon(x + \Delta x) - \varepsilon(x)\}. \quad (\text{A.4})$$

#### A.1.1. Timing for the shell change

We consider here the optimal timing  $\tau = \tau_{\text{opt}}$  to change the shell in terms of the maximization of  $E_{\text{change}}(x, \tau)$  given by (A.2).

If  $\varepsilon(x + \Delta x) - \varepsilon(x) > 0$ , the  $\tau$ -dependent part of  $E_{\text{change}}(x, \tau)$  is decreasing in  $\tau$ . Thus, since  $E_{\text{change}}(x, \tau) \leq E_{\text{change}}(x, 0)$  for any  $\tau$  ( $0 \leq \tau \leq T$ ), the optimal timing for shell change is  $\tau_{\text{opt}} = 0$  just after the previous breeding season, that is, at the beginning of the considered inter-breeding season. In contrast, if  $\varepsilon(x + \Delta x) - \varepsilon(x) < 0$ , the  $\tau$ -dependent part of  $E_{\text{change}}(x, \tau)$  is increasing in  $\tau$ , and  $E_{\text{change}}(x, \tau) \leq E_{\text{change}}(x, T)$  for any  $\tau$  ( $0 \leq \tau \leq T$ ), the optimal timing is  $\tau_{\text{opt}} = T$  at the beginning of the next breeding season, that is, at the end of the considered inter-breeding season. Since the body size increment  $\Delta x$  is a constant independent of  $\tau$  for a given inter-breeding season, the sign of  $\varepsilon(x + \Delta x) - \varepsilon(x)$  is uniquely determined for the inter-breeding season. So these arguments indicate that the optimal timing for shell change could be alternatively  $\tau_{\text{opt}} = 0$  or  $\tau_{\text{opt}} = T$ . There could not exist such an optimal timing  $\tau_{\text{opt}}$  as  $0 < \tau_{\text{opt}} < T$  in this model.

#### A.1.2. Optimality of the shell change behavior

Only if  $\Delta E(x, \tau_{\text{opt}}) > 0$ , the shell change behavior at time  $\tau_{\text{opt}}$  could be optimal. From the arguments in the above, since alternatively  $\tau_{\text{opt}} = 0$  or  $\tau_{\text{opt}} = T$ , we now consider just  $\Delta E(x, 0)$  and  $\Delta E(x, T)$ . From (A.4), in the case when  $\tau_{\text{opt}} = T$ ,  $\Delta E(x, T)$  is equal to  $-m$  and negative for any  $x$ , so that consequently the shell change behavior in such a case is not optimal than such behavior as to keep the occupied shell. On the other hand, in the case when  $\tau_{\text{opt}} = 0$ , the condition that  $\Delta E(x, 0) > 0$



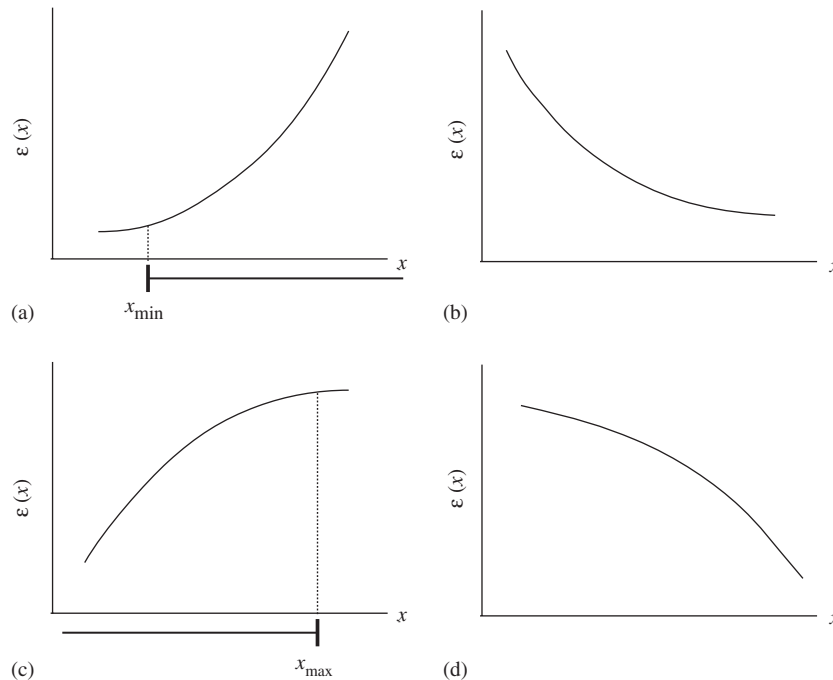


Fig. A.2. Four types of the body size dependence of the net energy uptake  $\varepsilon(x)$  per unit time at body size  $x$ . The interval indicated by the thick segment schematically shows such a range that the condition (A.5) is satisfied. For detail, see the text.

corresponds to the following:

$$\varepsilon(x + \Delta x) - \varepsilon(x) > \frac{m}{\varphi T}. \quad (\text{A.5})$$

This condition (A.5) is necessary for the optimality of shell change behavior in this model.

If the length of inter-breeding season  $T$  is sufficiently long, the right-hand side of (A.5) becomes sufficiently small so that the condition for  $\Delta E(x, 0) > 0$  is satisfied. Therefore, as a consequence, the longer inter-breeding season makes the shell change behavior more observable as the optimal strategy, as well as shown for the model in our main text.

As well as the model in our main text, the condition (A.5) clearly indicates that the smaller  $m/\varphi$ , that is, the smaller cost for the shell change behavior and/or the larger probability of the success in a shell change, increases the optimality of shell change behavior.

#### A.1.3. Limitation of body size

Now, we consider the relation between the choice of shell change behavior and the body size  $x$ . If the condition (A.5) is satisfied for any  $x$  larger than a critical size  $x_{\min}$  (see Fig. A.2(a)), that is, when  $\Delta E(x, 0) > 0$  for any  $x > x_{\min}$ , any individual with size  $x > x_{\min}$  is expected to advantage with the shell change behavior in terms of the expected reproductive success. Unless the condition (A.5) is satisfied for any  $x$  (see Figs. A.2(b) and (d)), that is, when  $\Delta E(x, 0) \leq 0$  for any  $x$ , the individual with any body size is not expected to advantage with the shell change behavior in terms of the expected reproductive success. So no individual would be expected to show the shell change

behavior. Therefore, in such a case with a net energy uptake function  $\varepsilon(x)$  decreasing in terms of  $x$ , the body size is limited only by the size of shell occupied first in the life.

If the condition (A.5) is satisfied for  $x < x_{\max}$  (see Fig. A.2(c)), only individual with body size  $x < x_{\max}$  is expected to advantage with the shell change behavior. Thus, only the hermit crab with body size smaller than  $x_{\max}$  is expected to show the shell change behavior. The individual with body size more than  $x_{\max}$  is expected not to try to change the shell but to suppress the body size growth up to the maximal body size afforded by the occupied shell size. The net energy uptake rate per unit time would be increasing in body size, while the larger body requires the larger energy for its homeostasis or metabolism. Hence it would be most likely to have the shape of Fig. A.2(c).

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