Some Mathematical Considerations on the Parent–Offspring Conflict Phenomenon

Hiroki Tokuda and Hiromi Seno†

Department of Mathematics, Faculty of Science, Hiroshima University, Kagamiyama 1-3-1, Higashi-hiroshima, Hiroshima 724, Japan

A stochastic dynamic programming model for parent–offspring conflict is analysed and discussed. We discuss how the conflict is resolved and how the ultimate offspring's independence age is determined between parent and offspring. The results of the mathematical model indicate the possibility that the observed behaviour of parental care may change depending on the parent's age. This is because the compromise conclusion of the parent–offspring conflict depends on the parent's age: that is, essentially, on the parent's expected future reproductive value. Moreover, it is shown that the observed parent–offspring conflict possibly depends also on the parent's age.

1. Introduction

Many researchers in behavioural ecology have been interested in and have discussed the parent–offspring conflict phenomenon: the offspring wants to become independent of the parent and to feed by itself after an age t_o^*, while parent of age a wants to stop feeding after an offspring's age $t_p^*(a)$. The critical day $t_p^*(a)$ from the parent's viewpoint is assumed to depend on the parent's age a. When t_o^* and $t_p^*(a)$ do not coincide with each other, a conflict takes place between parent and offspring. There are possibly two different types of such conflict: $t_o^* < t_p^*(a)$ and $t_o^* > t_p^*(a)$. Under the conflict in the case when $t_o^* < t_p^*(a)$, offspring wants to become independent of parent, while parent wants to feed offspring. On the other hand, in the case when $t_o^* > t_p^*(a)$, offspring wants to be fed, while parent wants to stop feeding. Only when $t_o^* = t_p^*(a)$ does no conflict take place. However, since t_o^* does not depend on the parent's age a, whereas $t_p^*(a)$ does, conflict between parent and offspring is very much observable.

Clark & Ydenberg (1990) treat this phenomenon and consider the optimal t_o^* and $t_p^*(a)$ by using

stochastic dynamic programming models (for example, see Mangel & Clark, 1988). They use the *fitness* concept for constructing the model. In general, fitness for an individual is defined as the probability that the individual can live until its breeding season and can reproduce (for instance, see Maynard Smith, 1986). In Clark & Ydenberg (1990), the parent's fitness is determined by its survival probability in the breeding season, its future reproductive value, and its offspring's fitness, while that for the offspring is determined by its survival probability that it reaches the weight sufficient to reproduce after it becomes independent of the parent. Moreover, the *terminal fitness function* is defined to give the probability that the offspring survives and reaches the reproducible age to reproduce the next generation. In Clark & Ydenberg (1990), it is assumed that the lifespan and reproducible age-span for each individual are infinite, so that the future reproductive value for the parent can be regarded as a constant, independent of the parent's age. Therefore, $t_p^*(a)$ is also independent of the parent's age a, that is, $t_p^*(a) = t_p^*$. In such case, with analytical and numerical calculations, they estimate the optimal t_o^* and t_p^* and discuss the conflict of the type that $t_o^* > t_p^*$.

† Author to whom correspondence should be addressed.

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In this paper we analyse a stochastic dynamic programming model which corresponds to the model constructed by Clark & Ydenberg (1990). In our model, in contrast to their model, the parent is assumed to have a finite reproducible age-span, so that its future reproductive value is explicitly variable depending on the parent's age. A specific growth function and a specific terminal fitness function are introduced. Analysing the model, we discuss the characteristics of the optimal critical ages t_o^* and $t_p^*(a)$, and it is shown that only conflict of the type that $t_o^* > t_p^*(a)$ is possible, independent of the parent's age and the other parameters characterizing the relation between parent and offspring. Further, we discuss how the conflict is resolved and how the ultimate independence age is determined between parent and offspring.

2. Model

2.1. AGES OF PARENT AND OFFSPRING

Let a denote the parent's age, for instance, in years, where $a_f \leqslant a \leqslant a_l$. a_f and a_l are, respectively, the first and the last ages for the parent's reproduction. Hence, the reproducible age-span for every parent is given by $a_l - a_f + 1$. The offspring's age in *days* during a breeding season is denoted by t, where $1 \leqslant t \leqslant T$. T is the length in days of each breeding season (see Fig. 1).

2.2. OFFSPRING'S GROWTH

We use the following specific growth function for offspring:

$$Y(t+1) = \begin{cases} Y(t) + k_1 & \text{for} \quad t = 1, 2, \ldots, t_s - 1 \\ Y(t) + k_2 & \text{for} \quad t = t_s, t_s + 1, \ldots, T - 1 \end{cases}$$

$$(1)$$

$$Y(1) = Y_1, \tag{2}$$

that is,

$$Y(t) = \begin{cases} k_1(t - 1) + Y_1 \\ k_2(t - t_s) + k_1(t_s - 1) + Y_1 \end{cases}$$

$$\begin{aligned} &\text{for} \quad t = 1, 2, \ldots, t_s \\ &\text{for} \quad t = t_s + 1, t_s + 2, \ldots, T, \end{aligned} \tag{3}$$

where $Y(t)$ is the offspring's weight at the beginning of day t, and Y_1 is its weight at birth. t_s is the offspring's age when the parent stops feeding and offspring becomes independent. k_1 is a positive constant which denotes the offspring's daily growth rate with the parent's feeding, while k_2 is a positive constant denoting the independent offspring's daily growth rate (see Fig. 2).

Now, consider the offspring's weight $Y(T; t_s)$ at the beginning of the last day T of the breeding season, under the condition that it becomes independent at day t_s. From (3), $Y(T; t_s)$ is expressed as follows:

$$Y(T; t_s) = k_2(T - t_s) + k_1(t_s - 1) + Y_1. \tag{4}$$

2.3. OFFSPRING'S FITNESS

We define the daily survival probability σ_n for offspring fed by parent, the daily survival probability σ_o for offspring independent of parent, the daily survival probability σ_f for parent feeding offspring, and the daily survival probability σ_p for parent not feeding offspring (see Fig. 1). As Ydenberg (1989) showed in general for alcids, it is naturally assumed that $\sigma_o < \sigma_n$ and $\sigma_f < \sigma_p$. The following events significant to determine the offspring's fitness are assumed on each day: (i) if parent survives and feeds offspring with probability σ_f, the offspring grows according to (3) with survival probability σ_n; (ii) if parent dies with probability $1 - \sigma_f$, the offspring becomes independent to grow according to (3) with survival probability σ_o;
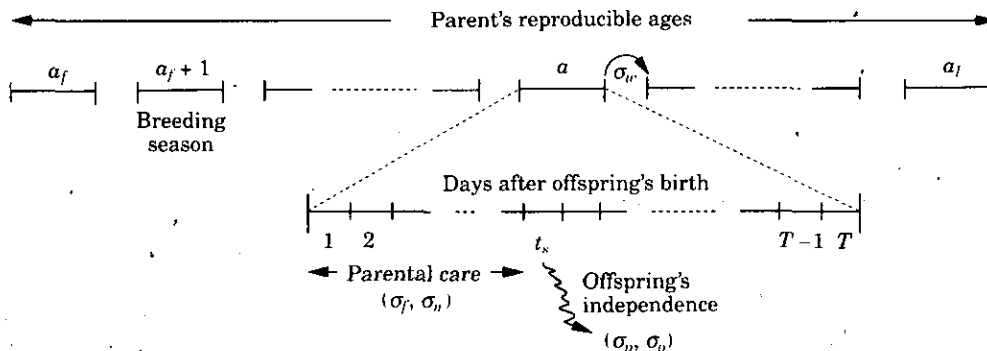

FIG. 1. Modelling the parent–offspring relation. See text for detailed explanation.

(iii) if parent stops feeding the offspring with survival probability σ_p, the offspring becomes independent to grow according to (3) with survival probability σ_o.

Consider the probability $\phi(Y(T; t_s))$ that offspring with weight $Y(T; t_s)$ at the end of the breeding season will survive *after* the breeding season and reach the reproducible age to reproduce the next generation. The probability $\phi(Y(T; t_s))$ is called the *terminal fitness function* for the offspring, and is given as follows:

$$\phi(Y(T; t_s)) = \begin{cases} \gamma(Y(T; t_s) - y_c) & \text{if } Y(T; t_s) > y_c \\ 0 & \text{otherwise,} \end{cases}$$

(5)

where γ is a positive constant translating the advantage of weight gain $Y(T; t_s) - y_c$ to the probability $\phi(Y(T; t_s))$. y_c is the offspring's minimum body weight at the end of the breeding season, sufficient to survive *after* the breeding season and reach its reproducible age to reproduce the next generation (see Fig. 3).

Conventionally, we define the critical day t_c such that $Y(T; t_c) = y_c$, which is given by

$$t_c \equiv \frac{y_c - Y_1 + k_1 - k_2 T}{k_1 - k_2}.$$

(6)

Using the notation t_c, the probability $\phi(Y(T; t_s))$ can be expressed in the following way:

When $k_1 > k_2$,

$$\phi(Y(T; t_s)) = \begin{cases} \gamma(k_1 - k_2)(t_s - t_c) & \text{if } t_s > t_c \\ 0 & \text{otherwise.} \end{cases}$$

(7)

When $k_1 < k_2$,

$$\phi(Y(T; t_s)) = \begin{cases} \gamma(k_2 - k_1)(t_c - t_s) & \text{if } t_s < t_c \\ 0 & \text{otherwise.} \end{cases}$$

(8)

Eventually it is assumed that $1 < t_c < T$. In the case when $k_1 > k_2$, if the offspring's independence day t_s is earlier than the critical day $[t_c] + 1$ given by (6), the offspring's weight $Y(T; t_s)$ at the end of the breeding season is below y_c so that the terminal fitness function $\phi(Y(T; t_s))$ is zero (Fig. 3). In contrast, in the case when $k_1 < k_2$, if the offspring's independence day t_s is later than $[t_c]$, the terminal fitness function $\phi(Y(T; t_s))$ is zero.

Now consider the offspring's fitness $F_o(t_s)$ defined as the probability that it can survive *through* and *after* the breeding season and reach its reproducible age to reproduce the next generation, under the condition that it becomes independent on day t_s of the breeding
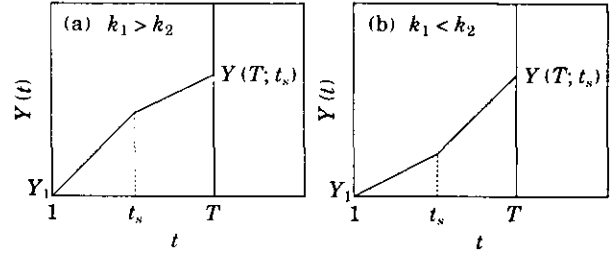

FIG. 2. Offspring's growth function $Y(t)$ for two cases: (a) when $k_1 > k_2$ and the growth rate is larger under the parent's feeding than after the offspring's independence; (b) when $k_1 < k_2$ and the growth rate is the reverse of (a). The offspring has the weight Y_1 at birth. If offspring becomes independent of parent on day t_s, it reaches weight $Y(T; t_s)$ at the end of the breeding season.

season. If the offspring becomes independent on the first day, that is, $t_s = 1$, it survives *through* the breeding season with probability σ_o^T. Growing according to (3), its weight reaches $Y(T; 1)$ at the last day T of the breeding season, which means that *after* the breeding season it has the probability $\phi(Y(T; 1))$ to survive and reach its reproducible age. Hence, its fitness $F_o(1)$ is given by

$$F_o(1) = \sigma_o^T \phi(Y(T; 1)).$$

(9)

In the case when $t_s = 2$, two cases arise. The first is that, if the parent dies on the first day with probability $1 - \sigma_f$, the offspring is not fed by the parent on any day *through* the breeding season. Thus, the offspring is always independent and survives *through* the breeding season with probability σ_o^T. Therefore, the fitness in this case is given by $F_o(1)$ with probability $1 - \sigma_f$. The second case is that, if the parent survives and feeds the offspring on the first day with probability σ_f, the offspring is fed and survives for one day with
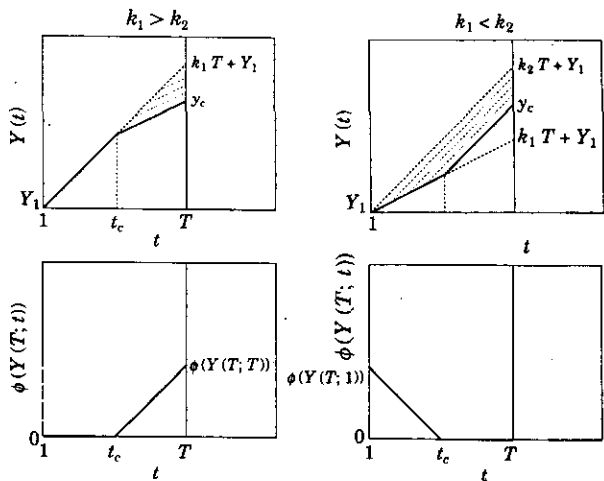

FIG. 3. Terminal fitness function $\phi(Y(T; t))$ given by eqn (5). There exists a critical day for the offspring's independence such that the terminal fitness function $\phi(Y(T; t))$ is zero for any independence day t before or after the critical day.

probability σ_n. For $t_s = 2$, the offspring becomes independent on the second day. Then, the independent offspring survives *through* the rest of the breeding season with probability σ_o^{T-1}. Its weight reaches $Y(T; 2)$ on day T, which means that, *after* the breeding season, it has the probability $\phi(Y(T; 2))$ to survive and reach its reproducible age. Lastly, its fitness $F_o(2)$ is given by

$$F_o(2) = (1 - \sigma_f)\sigma_o^T\phi(Y(T; 1)) + \sigma_f\sigma_n\sigma_o^{T-1}\phi(Y(T; 2)). \tag{10}$$

In the case when $t_s = 3$, three cases arise. The first case is that parent dies on the first day with probability $1 - \sigma_f$. The second case is that the parent survives on the first day with probability σ_f and dies on the second day with probability $1 - \sigma_f$. In this case, from the second day, the offspring becomes independent and survives *through* the rest of the breeding season with probability σ_o^{T-1}. The third case is that the parent survives and feeds the offspring on both of the first and second days with probability σ_f^2. In this case the offspring survives for two days with probability σ_n^2. For $t_s = 3$, it becomes independent on the third day. The independent offspring survives *through* the rest of the breeding season with probability σ_o^{T-2}. Lastly, its fitness $F_o(3)$ is given by

$$
\begin{aligned}
F_o(3) = &(1 - \sigma_f)\sigma_o^T\phi(Y(T; 1)) \\
&+ \sigma_f(1 - \sigma_f)\sigma_n\sigma_o^{T-1}\phi(Y(T; 2)) \\
&+ \sigma_f^2\sigma_n^2\sigma_o^{T-2}\phi(T; 3)). \tag{11}
\end{aligned}
$$

For the case when $t_s = 4, 5, \ldots, T, F_o(t_s)$ is given in the same way.

Consequently, except for the case when $t_s = 1$, $F_o(t_s)$ is expressed in general as follows:

$$
\begin{aligned}
F_o(t_s) = &\sum_{j=1}^{t_s-1} \sigma_f^{j-1}(1 - \sigma_f)\sigma_n^{j-1}\sigma_o^{T-j+1}\phi(Y(T; j)) \\
&+ \sigma_f^{t_s-1}\sigma_n^{t_s-1}\sigma_o^{T-t_s+1}\phi(Y(T; t_s)). \tag{12}
\end{aligned}
$$

2.4. PARENT'S SURVIVAL PROBABILITY

In this section, we consider the parent's survival probability $F_p(t_s)$, which is defined as the probability that the parent survives through the breeding season under the condition that it stops feeding on day t_s in the breeding season. σ_w is defined as the probability that the parent survives through the interval period between two sequent breeding seasons and reaches the next breeding season.

If the parent never feeds the offspring on any day throughout the breeding season, that is, if $t_s = 1$, the

parent survives through the breeding season with probability σ_p^T. Then it can reach the next breeding season with probability σ_w. Hence, its survival probability $F_p(1)$ is given by

$$F_p(1) = \sigma_p^T\sigma_w. \tag{13}$$

If the parent feeds the offspring on the first day and stops feeding on the second day, that is, if $t_s = 2$, the parent survives on the first day with probability σ_f and through the rest of the breeding season with probability σ_p^{T-1}. Hence, its survival probability $F_p(2)$ is given by

$$F_p(2) = \sigma_f\sigma_p^{T-1}\sigma_w. \tag{14}$$

In the case when $t_s = 3$, two cases arise. The first is that the parent feeds the offspring on the first day with survival probability σ_f, while the offspring dies on the first day with probability $1 - \sigma_n$. Then, the parent survives through the rest of the breeding season with probability σ_p^{T-1}. The second case is that the parent feeds the offspring on the first day with survival probability σ_f, while the offspring survives on the second day with survival probability σ_n. Parent feeds offspring also on the second day with survival probability σ_f. For $t_s = 3$, the parent stops feeding on the third day. Then, it survives through the rest of the breeding season with probability σ_p^{T-2}. Lastly, its survival probability $F_p(3)$ is given by

$$F_p(3) = \{(1 - \sigma_n)\sigma_f\sigma_p^{T-1} + \sigma_n\sigma_f^2\sigma_p^{T-2}\}\sigma_w. \tag{15}$$

The cases when $t_s = 4, 5, \ldots, T, F_p(t_s)$ is given in the same way.

Consequently, except for the case when $t_s = 1$ or $t_s = 2, F_p(t_s)$ is expressed in general as follows:

$$
\begin{aligned}
F_p(t_s) = &\left\{\sum_{j=1}^{t_s-2} \sigma_n^{j-1}(1 - \sigma_n)\sigma_f^j\sigma_p^{T-j} \right. \\
&\left. + \sigma_n^{t_s-2}\sigma_f^{t_s-1}\sigma_p^{T-t_s+1}\right\}\sigma_w. \tag{16}
\end{aligned}
$$

2.5. PARENT'S FITNESS

Consider the parent's fitness at age a, under the condition that it stops feeding on day t_s of the breeding season. The parent's fitness $J(t_s; R(a))$ is defined by its survival probability $F_p(t_s)$, its offspring's fitness $F_o(t_s)$, and the parent's expected future reproductive value $R(a)$ at the last day of the breeding season at age a, which satisfies the following:

$$R(a) = \sigma_w J(t_s; R(a + 1)) \quad (a = a_f, a_f + 1, \ldots, a_l - 1). \tag{17}$$

$J(t_s; R(a + 1))$ denotes the parent's fitness at its age $a + 1$. Since σ_w denotes the probability that the parent

survives between the end of the breeding season at age a and the beginning of the next breeding season at age $a + 1$, the right-hand side of (17) denotes the expected future reproductive value. Note that $R(a)$ should be monotonically decreasing in terms of the age a, and $R(a_l) = 0$ because a_l is the last age for the parent's reproduction.

As in Clark & Ydenberg (1990), $J(t_s; R(a))$ is given in this paper as follows: .

$$J(t_s; R(a)) = F_o(t_s) + R(a)F_p(t_s).$$ (18)

From (17) and (18), we can obtain the backward recurrence equation to determine the expected future reproductive value $R(a)$ for every age a. It is assumed that, since the expected future reproductive value $R(a)$ is considered only for parent to determine its behaviour $t_p^*(a)$ from its viewpoint, it has no relation with t_o^* from the offspring's viewpoint. Thus, since $R(a_l) = 0$, the expected future reproductive value $R(a_l - 1)$ for the age $a_l - 1$ is determined by

$$R(a_l - 1) = \sigma_w J(t_p^*(a_l); R(a_l)) = \sigma_w F_o(t_p^*(a_l)),$$ (19)

and, further, in general, the value $R(a_l - i)$ $(i = 1, 2, \ldots, a_l - a_f)$ for the age $a_l - i$ is given by the following backward recurrence equation:

$$R(a_l - i) = \sigma_w J(t_p^*(a_l - i + 1); R(a_l - i + 1)).$$ (20)

3. Analysis

3.1. THE OPTIMAL OFFSPRING'S INDEPENDENCE AGE FROM THE OFFSPRING'S VIEWPOINT

The optimal offspring's independence age t_o^* from the offspring's viewpoint is defined as the day in which the offspring's fitness $F_o(t_s)$ in the breeding season is maximized. Therefore, by analysing $F_o(t_s)$ given by (9) and (12) (for the method of analysis, see Appendix A), t_o^* can be obtained as follows (Fig. 4):

When $k_1 > k_2$,

$$t_o^* = T.$$ (21)

When $k_1 < k_2$,

$$t_o^* = \begin{cases} 1 & \text{if } t_c < v + 2; \\ n & \text{if } v + n < t_c \leqslant v + n + 1 \end{cases}$$

$$(n = 2, 3, \ldots, T-1),$$ (22)

where

$$v \equiv \frac{1}{\sigma_n/\sigma_o - 1}.$$ (23)

Since $\sigma_n > \sigma_o$ from the assumption, $0 < v < \infty$. For convenience, we will hereafter use the notation v.

As shown in Fig. 4, those conditions for t_o^* in the case when $k_1 < k_2$, given by (22), are complementary
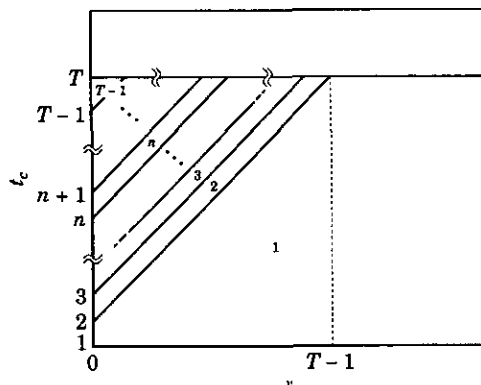

FIG. 4. In the case when $k_1 < k_2$, the optimal offspring's independence age t_o^* from the offspring's viewpoint on the parameter space (v, t_c) is shown. For $1 < t_c < T$, $t_o^* < T$.

to each other, and the possibly maximal $F_o(t_s)$ is $T - 1$ in this case.

3.2. THE OPTIMAL OFFSPRING'S INDEPENDENCE AGE FROM THE PARENT'S VIEWPOINT

The optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint is defined as the offspring's age t_s at which the parent's fitness $J(t_s; R(a))$ is maximized. By analysing $J(t_s; R(a))$ given by (18), $t_p^*(a)$ can be obtained for the parent's age a, when $R(a) > 0$, that is, when $a_f \leqslant a \leqslant a_l - 1$, as follows: When $k_1 > k_2$,

$$t_p^*(a) = \begin{cases} 1 & \text{if } t_c > g_2(v; a); \\ n & \text{if } n - 1 \leqslant t_c < n \quad \text{and} \quad h_{n+1}(v; a) \\ & \leqslant t_c < g_n(v; a), \\ & \text{or if } t_c < n - 1 \quad \text{and} \quad h_{n+1}(v; a) \leqslant t_c \\ & < h_n(v; a) \quad (n = 2, 3, \ldots, T-1); \\ T & \text{if } T - 1 \leqslant t_c < T \quad \text{and} \quad t_c < g_T(v; a), \\ & \text{or if } t_c < T - 1 \quad \text{and} \quad t_c < h_T(v; a). \end{cases}$$ (24)

When $k_1 < k_2$,

$$t_p^*(a) = \begin{cases} 1 & \text{if } t_c < h_1(v; a); \\ n & \text{if } h_n(v; a) < t_c \leqslant h_{n+1}(v; a) \end{cases}$$

$$(n = 2, 3, \ldots, T-1),$$ (25)

where

$$g_n(v; a) \equiv n + \frac{\rho^{T-n+2}}{K(a)} \frac{v}{v + 1}$$ (26)

$$h_n(v; a) \equiv n + \left(1 - \frac{\rho^{T-n+2}}{K(a)}\right)v$$ (27)
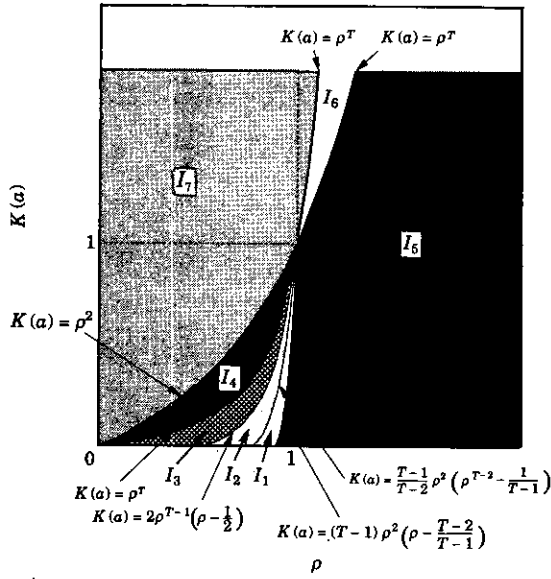
$$\rho \equiv \frac{\sigma_p}{\sigma_o}$$ (28)

Fig. 5. In the case when $k_1 > k_2$, the parameter space $(\rho, K(a))$ is categorized into I_1-I_7, depending on the type of the division of the parameter space (v, t_c) in terms of the value of $t_p^*(a)$.

$$K(a) \equiv \frac{\gamma(k_1 - k_2)}{R(a)} \frac{\sigma_p/\sigma_w}{\sigma_p/\sigma_f - 1}. \qquad (29)$$

Note that the above conditions for $t_p^*(a)$ are not complementary to each other. For example, in

the case when $k_1 > k_2$, there exist parameters such that $g_2(v; a) < t_c < h_T(v; a) < T - 1$. This means that, with such parameters, $t_p^*(a)$ should be 1 *or* T. In this case, $t_p^*(a)$ can be ultimately determined by comparing $J(1; R(a))$ with $J(T; R(a))$. In this paper, to avoid messy calculations, we no longer discuss the ultimately determined $t_p^*(a)$ in such a case, because our presented analyses give sufficiently significant qualitative results valuable for the discussion on the parent–offspring conflict phenomenon.

As indicated by those conditions for $t_p^*(a)$, given by (24) and (25), the ultimately determined $t_p^*(a)$ strongly depends on parameters (Figs 6, 7 and 9). The parameter space (v, t_c) can be divided into subregions depending on which value is possible for $t_p^*(a)$. The way of the division depends on the other parameters ρ and $K(a)$ (Figs 5 and 8).

In the case when $k_1 > k_2$, depending on the type of the division of the parameter space (v, t_c), we categorize the parameter region of $(\rho, K(a))$ into regions I_1-I_7 as shown in Fig. 5 (for the method of analysis, see Appendix B). According to those parameter subregions of $(\rho, K(a))$, the ultimately determined $t_p^*(a)$ is shown in the parameter space (v, t_c), as in Figs 6 and 7. In the cases of I_1, I_2, and I_4, the possible value of $t_p^*(a)$ is T or less than an N, while, in the case of I_3,
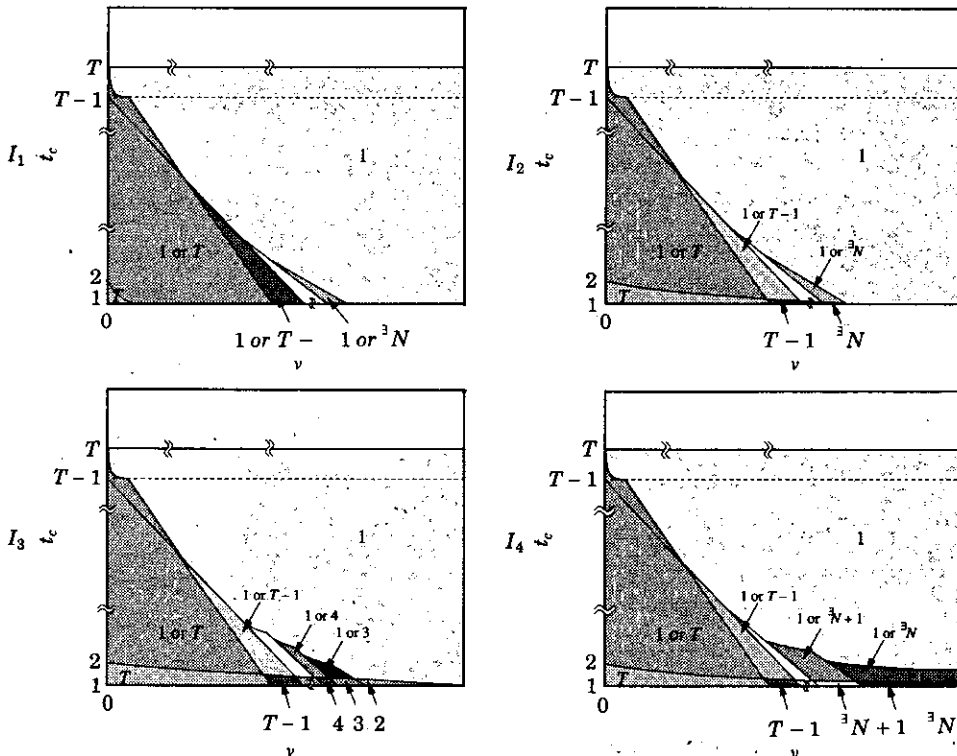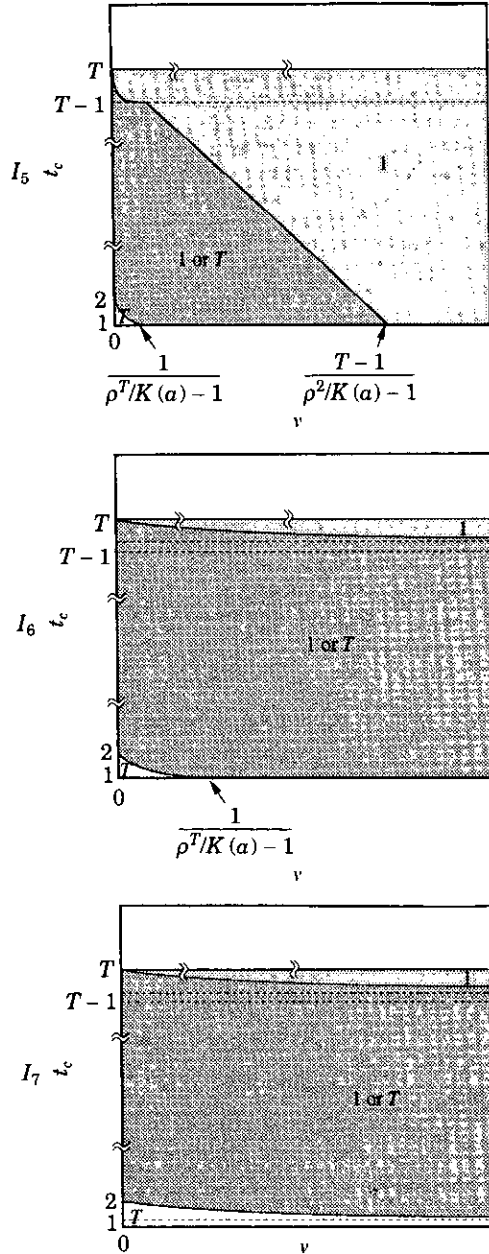

Fig. 6. In the case when $k_1 > k_2$, the optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint on the parameter space (v, t_c) for the parameter sets I_1-I_4 of the parameter space $(\rho, K(a))$ is shown.

considered, any value from 1 to $T - 1$ is possible for $t_p^*(a)$.

When $a = a_l$, since $R(a_l) = 0$ from the defintion, it follows that $J(t_s; R(a_l)) = J(t_s; 0) = F_o(t_s)$. Therefore, $t_p^*(a_l) = t_o^*$ given by (21) and (22), and no conflict occurs between parent and offspring.

The offspring's independence age $\tilde{t}_p$ to maximize the parent's survival probability $F_p(t_s)$ is always 1 independently of the values of parameters, because $F_o(t_s)$ is monotonically decreasing. Indeed, since $\sigma_p > \sigma_f$, for any t_s,

$$F_p(t_s+1)-F_p(t_s) = \sigma_n^{t_s-1}\sigma_f^{p-1}\sigma_p^{T-t_s}(\sigma_f - \sigma_p)\sigma_w < 0.$$

$$(30)$$

From the definition (18), when parent is sufficiently young and $R(a)$ is so large, it is expected that $t_p^*(a)$ is near $\tilde{t}_p$, because $J(t_s; R(a)) \approx R(a)F_p(t_s)$. Indeed, as seen in Figs 6, 7 and 9, the parameter region for $t_p^*(a) = \tilde{t}_p = 1$ is relatively larger for smaller $|K(a)|$ than for the larger.

3.3. EXISTENCE OF PARENT–OFFSPRING CONFLICT

Comparison of Fig. 4 with Figs 6, 7 and 9, the parent–offspring conflict presents a wide range of parameters.

In the case when $k_1 > k_2$, as shown in Figs 6 and 7, especially for relatively large value of t_c, the parent–offspring conflict can exist, because $t_o^* = T$. The type of conflict is eventually for $t_o^* > t_p^*(a)$, that is, during conflict, parent tends to stop feeding its offspring, while offspring wants to be fed. Only for sufficiently small values of t_c and v, $t_o^* = t_p^*(a) = T$, and, throughout the breeding season, the parent continues feeding its offspring, which wants to be fed.

Also, in the case when $k_1 < k_2$, as shown in Fig. 9, only one type of conflict, $t_o^* > t_p^*(a)$, is possible. This result can be easily proved: any slope of boundary lines parameter regions in (v, t_c), given by (27), is greater than 1.

3.4. PARENT'S AGE DEPENDENCE OF CONFLICT

The optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint for a breeding season is determined depending on the value of $K(a)$, that is, of $R(a)$ as shown by the above analysis. Following the definition, $|K(a)|$ is monotonically increasing to infinite as the parent's age a increases, since $R(a)$ monotonically decreases as a increases, and reaches zero at the age a_l. Therefore, as the parent's age increases, the parameter point moves up in the parameter space $(\rho, |K(a)|)$.

In the case when $k_1 > k_2$ and $0 < K(a)$, if $\rho \geqslant 1$, as the parent's age increases, the parameter point

FIG. 7. In the case when $k_1 > k_2$, the optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint on the parameter space (v, t_c) for the parameter sets I_5–I_7 of the parameter space $(\rho, K(a))$ is shown.

it is any value from 1 to N. In the cases of I_5–I_7, only 1 or T is possible for $t_p^*(a)$.

In contrast, in the case when $k_1 < k_2$, we categorize the parameter region of $(\rho, |K(a)|)$ into regions C_0, C_n ($n = 2, 3, \ldots, T - 2$), and C_{all} as shown in Fig. 8 (Appendix B). For those regions, the ultimately determined $t_p^*(a)$ is shown in the parameter space (v, t_c) as in Fig. 9. Independently of which case is
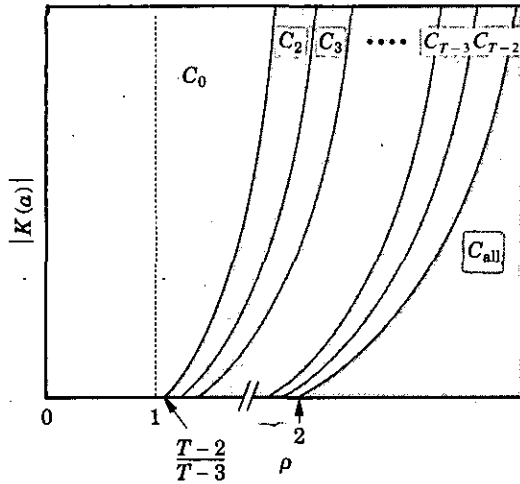
FIG. 8. In the case when $k_1 < k_2$, the parameter space $(\rho, |K(a)|)$ is categorized into C_0, C_{all}, and C_2-C_{T-2}, depending on the type of the division of the parameter space (v, t_c) in terms of the value of $t_p^*(a)$.

$(\rho, K(a))$ moves as $I_5 \to I_6 \to I_7$ in Fig. 5. Therefore, since $t_0^* = T$ in this case, whenever the conflict occurs, $t_p^*(a) = 1$, and parent tends to stop feeding its offspring on every day of the breeding season, while offspring wants to be fed throughout the breeding season. Otherwise, when conflict does not occur, the parent keeps feeding its offspring through the breeding season. Moreover, for some parameters of (v, t_c), as seen in Fig. 7, conflict does not occur for a parent older than a critical age determined by the parameter (v, t_c), while conflict does occur for a younger parent.

If $\rho < 1$ when $k_1 > k_2$, as the parent's age increases, the parameter point $(\rho, K(a))$ moves up in Fig. 5 through the following order of parameter regions in it: $I_5 \to I_1 \to I_2 \to I_3 \to I_4 \to I_7$. The parameter point $(\rho, K(a))$ does not pass any region with any order inverse to this order. The argument similar to that for $\rho \geq 1$ is applicable for this case. As the parent's age increases, $t_p^*(a)$ tends to be the same or to increase, therefore, it is likely that after a critical parent's age, conflict does not occur and the parent keeps feeding through the breeding season.

As previously mentioned, at the parent's last age a_l in the reproducible age-span, in the case when $k_1 > k_2$, conflict does not occur and $t_p^*(a) = t_o^* = T$, so that the parent feeds through the breeding season.

It is concluded that, for the case when $k_1 > k_2$, the optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint stays the same or tends to become larger toward T as the parent's age a increases, and conflict of the type for $t_o^* > t_p^*(a)$ comes not to occur after a parent's age; thus the parent keeps feeding through the breeding season.
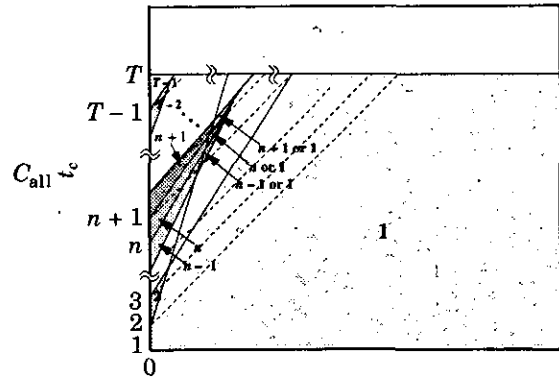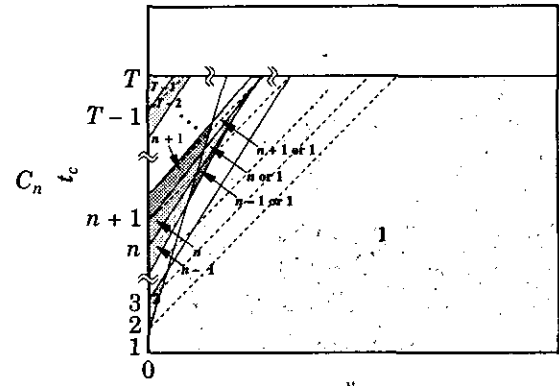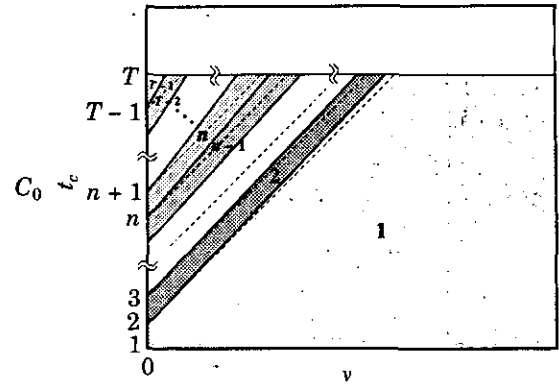
FIG. 9. In the case when $k_1 < k_2$, the optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint on the parameter space (v, t_c) for the parameter sets, C_0, C_{all}, and C_n $(n = 2, 3, \ldots, T - 2)$ of the parameter space $(\rho, |K(a)|)$ is shown.

Moreover, in the case when $k_1 < k_2$ and $K(a) < 0$, as the parent's age a increases, the parameter point $(\rho, |K(a)|)$ moves up, as shown in Fig. 8, through the following order of parameter regions in it: $C_{all} \to C_{T-2} \to C_{T-3} \to \cdots \to C_3 \to C_2 \to C_0$. The parameter point $(\rho, |K(a)|)$ does not pass any region with any order inverse to this order. Therefore, as seen in Fig. 9, since the conflict is only of the type such that $t_o^* > t_p^*(a)$, the conflict can come not to occur after a critical age of parent for some parameters of (v, t_c).

For the other parameters of (v, t_c), the conflict of the type such that $t_o^* > t_p^*(a)$ occurs through the parent's reproducible age-span except for the last age a_l. In both cases, the optimal offspring's independence age $t_p^*(a)$ from the parent's viewpoint stays the same or tends to become the larger as the parent's age a increases, as well as in the case when $k_1 > k_2$.

3.5. RESOLUTION OF PARENT–OFFSPRING CONFLICT

By the above analysis, it is shown that the parent–offspring conflict possibly occurs depending on those parameters including the parent's age. The conflict is resolved once the parent or the offspring yields to the other. In this section we discuss how the conflict is resolved and how the compromised day $t^*(a)$ when the offspring becomes independent is determined.

For the resolution of the parent–offspring conflict, the cost of the conflict is taken into account. The cost is assumed to be introduced as the decrease of fitness (M. Higashi and N. Yamamura, personal communication). That is, during the conflict, it is assumed that the offspring must pay a cost c to counter the parent, while the parent must pay a cost αc to counter the offspring, where c is monotonically increasing as the duration of the behaviour to counter the other side per conflict, and α is a positive constant. At the beginning of any day during the conflict situation, $c = 0$ because the behaviour to counter the other side has not yet started. These costs are subtracted from the fitnesses of parent and offspring.

In the following, we consider the resolution of the parent–offspring conflict, making use of the cost mentioned above, for two distinct cases: $t_o^* > t_p^*(a)$ and $t_o^* < t_p^*(a)$.

Case A: $t_o^* > t_p^*(a)$

The compromised day $t^*(a)$ naturally satisfies $t_p^*(a) \leqslant t^*(a) \leqslant t_o^*$. The fitness gain $D_p(t; a)$ for the parent on day t during the conflict (expected for the case in which parent wins the conflict and succeeds in making the offspring independent), relative to the fitness that the parent yielded to the offspring initially and let the offspring depend on its feeding, is now given by

$$D_p(t; a) = J(t; R(a)) - J(t + 1; R(a)) - \alpha c. \quad (31)$$

On the other hand, the fitness gain $D_o(t; a)$ for offspring on day t during the conflict (expected for the case in which it wins the conflict and succeeds in making the parent feed it), relative to the fitness and the offspring initially yielded to the parent and became independent, is now given by

$$D_o(t; a) = F_o(t + 1; a) - F_o(t; a) - c. \quad (32)$$

When $t_p^*(a) \leqslant t < t^*(a)$, the fitness gains $D_p(t; a)$ and $D_o(t; a)$ must eventually decline from positive toward zero on day t, because the cost c is temporally increasing as the behaviour of the conflict continues. Therefore, when $D_p(t; a)$ becomes zero while $D_o(t; a)$ is still positive, the parent yields to the offspring and feeds it. Thus, when $t_p^*(a) \leqslant t < t^*(a)$, there exists a value of c such that $D_p(t; a) = 0$ and $D_o(t; a) > 0$. On the other hand, on the day when $t = t^*(a)$, the parent does not yield to the offspring before the offspring yields to the parent from the definition of $t^*(a)$. This means that there exists a value of c such that $D_o(t; a) = 0$ and $D_p(t; a) \geqslant 0$. It is clear that $t^*(a) \leqslant t_o^*$, because $D_o(t_o^*; a) \leqslant -c$ from the definition of t_o^* so that the compromised independence day does not be beyond day t_o^*. This argument can be simplified with the following function $\theta(t; \alpha, a)$:

$$\begin{aligned}
\theta(t; \alpha, a) &\equiv \alpha\{F_o(t + 1; a) - F_o(t; a)\} \\
&\quad + \{J(t + 1; R(a)) - J(t; R(a))\} \\
&= (\alpha + 1)\{F_o(t + 1; a) - F_o(t; a)\} \\
&\quad + R(a)\{F_p(t + 1; a) - F_p(t; a)\} \\
&= (\alpha + 1)\left\{J\left(t + 1; \frac{R(a)}{\alpha + 1}\right) - J\left(t; \frac{R(a)}{\alpha + 1}\right)\right\}.
\end{aligned}$$
$$(33)$$

Note that $\theta(t; \alpha, a) > 0$ when $t_p^*(a) \leqslant t < t^*(a)$, while $\theta(t; \alpha, a) \leqslant 0$ when $t = t^*(a)$. Therefore, the compromised day $t^*(a)$ is given by

$$t^*(a) = \min_t \{t | \theta(t; \alpha, a) \leqslant 0, t_p^*(a) \leqslant t \leqslant t_o^*\}. \quad (34)$$

Case B: $t_o^* < t_p^*(a)$

As before, the compromised day $t^*(a)$ naturally satisfies that $t_o^* \leqslant t^*(a) \leqslant t_p^*(a)$. Contrarily to Case A, the fitness gain $D_p(t; a)$ for parent on day t during the conflict (expected for the case in which the parent wins the conflict and succeeds in keeping offspring under the parent's feeding), relative to the fitness that the parent initially yielded to the offspring and let it become independent, is now given by

$$D_p(t; a) = J(t + 1; R(a)) - J(t; R(a)) - \alpha c. \quad (35)$$

The fitness gain $D_o(t; a)$ for the offspring on day t during the conflict (expected for the case in which it wins the conflict and succeeds in becoming independent), relative to the fitness that is initially yielded to the parent and accepted the parent's feeding, is now given by

$$D_o(t; a) = F_o(t; a) - F_o(t + 1; a) - c. \quad (36)$$

By the same argument as in Case A, when $t_o^* < t < t^*(a)$, there exists a value of c such that $D_p(t; a) > 0$ and $D_o(t; a) = 0$. On the day when $t = t^*(a)$, there exists a value of c such that $D_o(t; a) \geqslant 0$ and $D_p(t; a) = 0$. Also in this case, it is assumed that $t^*(a) \leqslant t_p^*(a)$, because $D_p(t_p^*(a); a) \leqslant -\alpha c$ from the definition of $t_p^*(a)$. This argument can be simplified with the same function (33), $\theta(t; \alpha, a)$. Moreover, the compromised day $t^*(a)$ is given by the following equation which is similar to (34):

$$t^*(a) = \min_t \{t | \theta(t; \alpha, a) \leqslant 0, t_o^* \leqslant t \leqslant t_p^*(a)\}. \quad (37)$$

We note that, since the considered signature of $\theta(t; \alpha, a)$ is determined by the difference of $J(t; R(a)/(\alpha + 1))$, $t^*(a)$ is regarded as the smallest value that gives the maximal of $J(t; R(a)/(\alpha + 1))$ when $\min\{t_o^*, t_p^*(a)\} \leqslant t \leqslant \max\{t_o^*, t_p^*(a)\}$. Existence of such $t^*(a)$ is assured by the above argument.

From the results of our model, it can be seen that the conflict is only of the type $t_o^* > t_p^*(a)$, that is, Case A, and as the parent's age a increases and the expected future reproductive value $R(a)$ decreases, $t_p^*(a)$ stays the same or becomes the larger and approaches t_o^* from below. Therefore, the above result indicates that the compromise between parent with expected future reproductive value $R(a)$ and its offspring shifts the offspring's independence day to that corresponding to the favourable (not necessarily optimal!) independence age from the viewpoint of parent with the expected future reproductive value $R(a)/(\alpha + 1)$. Eventually, the compromised independence day $t^*(a)$ is nearer to t_o^* the larger the value of α.

In the case when $k_1 > k_2$ and $\rho \geqslant 1$, $t_o^* = T$ and $t_p^*(a)$ is 1 or T, as shown the previous section (Fig. 7). Thus, the compromise can cause only two alternative conclusion of the parent–offspring conflict: the offspring becomes independent on the first day of breeding season, or the parent keeps feeding the offspring throughout the breeding season. Since $t_p^*(a)$ is 1 or T by our analysis, if the parent yields to the offspring on the first day of the breeding season, the offspring's independence does not occur until the last day of the breeding season.

On the other hand, in the case when $k_1 > k_2$ and $\rho < 1$, the compromise can cause the offspring's independence on the day $t^*(a)$ such that $1 < t^*(a) < T$ (see Fig. 6). Depending on the parameters, the compromise conclusion is the same as in the case when $k_1 > k_2$, and $\rho \geqslant 1$ still possibly occurs.

In the case when $k_1 < k_2$, both t_o^* and $t_p^*(a)$ can take any value less than T, depending on the par-

ameters, whereas $t_o^* > t_p^*(a)$ is always satisfied in the previous section (Fig. 9). Therefore, the compromise can cause the offspring's independence on the day $t^*(a)$ as defined by $t_p^*(a) \leqslant t^*(a) \leqslant t_o^*$.

3.6. ATLANTIC PUFFINS

Clark & Ydenberg (1990) made numerical calculations for their model with parameters estimated from the data for Atlantic puffins (Ydenberg, 1989). Following their parameters, those for our model can be given as follows: $\sigma_p = 0.9955$; $\sigma_n = 0.9998$; $\sigma_o = 0.9962$; $Y_1 = 58.75$ g; $T = 40$; $y_c = 300$ g; $\gamma = 0.3$. Since the growth function for an offspring fed by its parent in Clark and Ydenberg (1990) was given by a two-stage function with a different growth rate, we should take another estimation for the parameter k_1 of our model in which the corresponding growth function is a single stage. Since, following their parameters, offspring fed through the whole breeding season could grow to about 350 g by the last day, we take $k_1 = 7.3$, with which an offspring fed throughout the breeding season reaches 350.75 g in our model. Clark & Ydenberg (1990) numerically analysed how the offspring's independence days from the respective viewpoints of parent and offspring depend on the offspring's growth rate k_2 after its independence, the daily survival probability σ_f for parent feeding offspring, and the probability σ_w for the parent to survive through the period between two sequential breeding seasons. In their analysis, in contrast to ours, it is assumed that the lifespan and reproducible age-span for each individual are infinite, so that the future reproductive value for parent can be regarded as a constant, independent of its age, and thus $t_p^*(a)$ is also independent of the parent's age: that is, $t_p^*(a) = t_p^*$.

When $\sigma_w = 0.96$, we obtain $\nu = 231.5$, $\rho = 0.9993$, and

$$t_c = 40 - \frac{43.45}{7.3 - k_2}$$

$$K(a) = \frac{7.3 - k_2}{R(a)} \frac{0.3125}{1/\sigma_f - 1.0045}.$$

Calculated for some values of k_2 and σ_f, these parameter values are given in Table 1. Note that, since it is required that $1 < t_c < T$, we assume that $k_2 \leqslant 6.1858 < k_1$. On the other hand, from this assumption, $\sigma_f < \sigma_p = 0.9955$. Note that ν is rather large and ρ is very close to and less than 1. Therefore, if σ_f is sufficiently large or $R(a)$ is sufficiently small, then $K(a)$ is rather large and is bounded by the parameter region I_1 of Fig. 5. However, if σ_f is sufficiently small or $R(a)$ is sufficiently large, then $K(a)$ is bounded by

TABLE 1

Parameter values of t_c *and* $K(a)R(a)$

k_2	σ_f	t_c	$K(a)R(a)$
4	0·990	26·83	184·1
	0·995		1963·9
5	0·990	21·11	128·3
	0·995		1368·8
6	0·990	6·58	72·5
	0·995		773·7

Parameter values of t_c and $K(a)R(a)$ for $k_1 = 7\cdot3$; $k_2 = 4$, 5, 6; $\sigma_f = 0\cdot990$, $0\cdot995$; $\sigma_p = 0\cdot9955$; $\sigma_n = 0\cdot9998$; $\sigma_o = 0\cdot9962$; $\sigma_w = 0\cdot96$; $Y_1 = 58\cdot75$; $T = 40$; $y_c = 300$; $\gamma = 0\cdot3$. From the definition, $v = 231\cdot5$ and $\rho = 0\cdot9993$ in this case.

the parameter region I_1–I_5 of Fig. 5. As k_2 increases to k_1, since $K(a)$ monotonically decreases, $t_p^*(a)$ decreases (refer to our result about the parent's age dependence of conflict). This result corresponds to that of Clark & Ydenberg (1990). However, t_o^* is also monotonically decreasing in their analysis, while t_o^* in our model is constant, that is, $t_o^* = T = 40$ when $k_1 > k_2$. Further, as σ_f gets larger, since $K(a)$ monotonically increases, $t_p^*(a)$ increases. This result also corresponds to that of Clark and Ydenberg.

When $k_2 = 5$ and $\sigma_f = 0\cdot995$, the value of $K(a)R(a)$ lies in the range 1314–1878 for $\sigma_w = 0\cdot7$–$1\cdot0$. This value of $K(a)R(a)$ is rather large. Therefore, it is very likely that $K(a)$ is large enough to lie in the parameter region I_7. Since $t_c = 21\cdot11$ and $v = 231\cdot5$ in this case, it is likely that $t_p^*(a) = 1$. This result is different from the numerical result of Clark & Ydenberg (1990). Only when the parent is so young that $R(a)$ is large enough to make the value of $K(a)$ sufficiently small, then $K(a)$ is in the parameter region I_1–I_5, and it is likely that $t_p^*(a) > 1$. This is similar to the result of Clark & Ydenberg (1990), since t_p^* takes the value less than but near to t_o^* in their result. This result can be explained by the fact that the parent in their model is assumed to be eternally young.

For $\rho = 0\cdot9993$ independently of the parent's age, the parameter regions I_1–I_4 occupy relatively so small an interval of $K(a)$ that the behaviour corresponding to such parameter regions seem rarely observable. Hence, relatively, the behaviour for the region I_5 or I_7 seems expected to be so observable. Thus, it is very likely that $t_p^* = 1$ or $t_p^* = T = 40$, and it is expected that, as in the parent–offspring relation of Atlantic puffins, the parent feeds the offspring through the breeding season, or the parent–offspring conflict starts to occur in an early period of the breeding season that offspring becomes independent early in the breeding season.

4. Conclusion

The results of our mathematical model indicates the possibility that the observed behaviour of parental care may change depending on the parent's age. This is because the compromise conclusion of the parent–offspring conflict depends on the parent's age, i.e. essentially on the parent's expected future reproductive value. Moreover, the observed parent–offspring conflict possibly depends also on the parent's age.

In the framework of our mathematical model the observed parent–offspring conflict is of the type such that $t_o^* > t_p^*(a)$, that is, the parent intends to stop feeding its offspring, while the offspring wants to be fed. However, if another type of conflict is observed, such that $t_o^* < t_p^*(a)$, that is, the parent intends to feed, while the offspring wants to become independent, some improved mathematical model will be required for the mathematical theoretical explanation of it.

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APPENDIX A

In this appendix, we show how to determine t_o^* and $t_p^*(a)$ analytically. The optimal offspring's independence age t_o^* from its own viewpoint is defined as the day on which the offspring's fitness $F_o(t_s)$ in the breeding season is maximized. Thus, t_o^* should be one of maximals of $F_o(t_s)$ for $t_s = 1, 2, \ldots, T$. The necessary condition for $t_o^* = 1$ is

$$F_o(2) - F_o(1) < 0.$$

In the same way, the necessary condition for $t_o^* = T$ is

$$F_o(T) - F_o(T - 1) > 0,$$

where it is assumed that, if $F_o(T) = F_o(T-1)$, then, $t_o^* \leqslant T - 1$. In contrast, the necessary condition for $t_o^* = n$ $(n = 2, 3, \ldots, T - 1)$ is as follows:

$$\begin{cases} F_o(n) - F_o(n-1) > 0 \\ F_o(n+1) - F_o(n) \leqslant 0. \end{cases}$$

Some cumbersome analyses of these necessary conditions can lead to possible values of t_o^* given as eqns (21) and (22) in the text.

Also as for $t_p^*(a)$, the same argument is adaptable for $J(t_s; R(a))$ given by eqn (18) in the text. In this case, as long as parent–offspring relation within a breeding season is considered, the expected future reproductive value can be regarded as a non-negative constant independent of t_s. Therefore, the same method of analysis can be carried out for $J(t_s; R(a))$ and those possible values of $t_p^*(a)$ are given as (24) and (25) in the text.

APPENDIX B

In this appendix, some outlines of the way of analysing the parameter dependence of the optimal offspring's independence age from parent's viewpoint (given by Figs 5 and 8 in the text) are given.

In the case when $k_1 > k_2$, t_p^* is given by (24) in the text. Function $g_n(v; a)$ has the following asymptote:

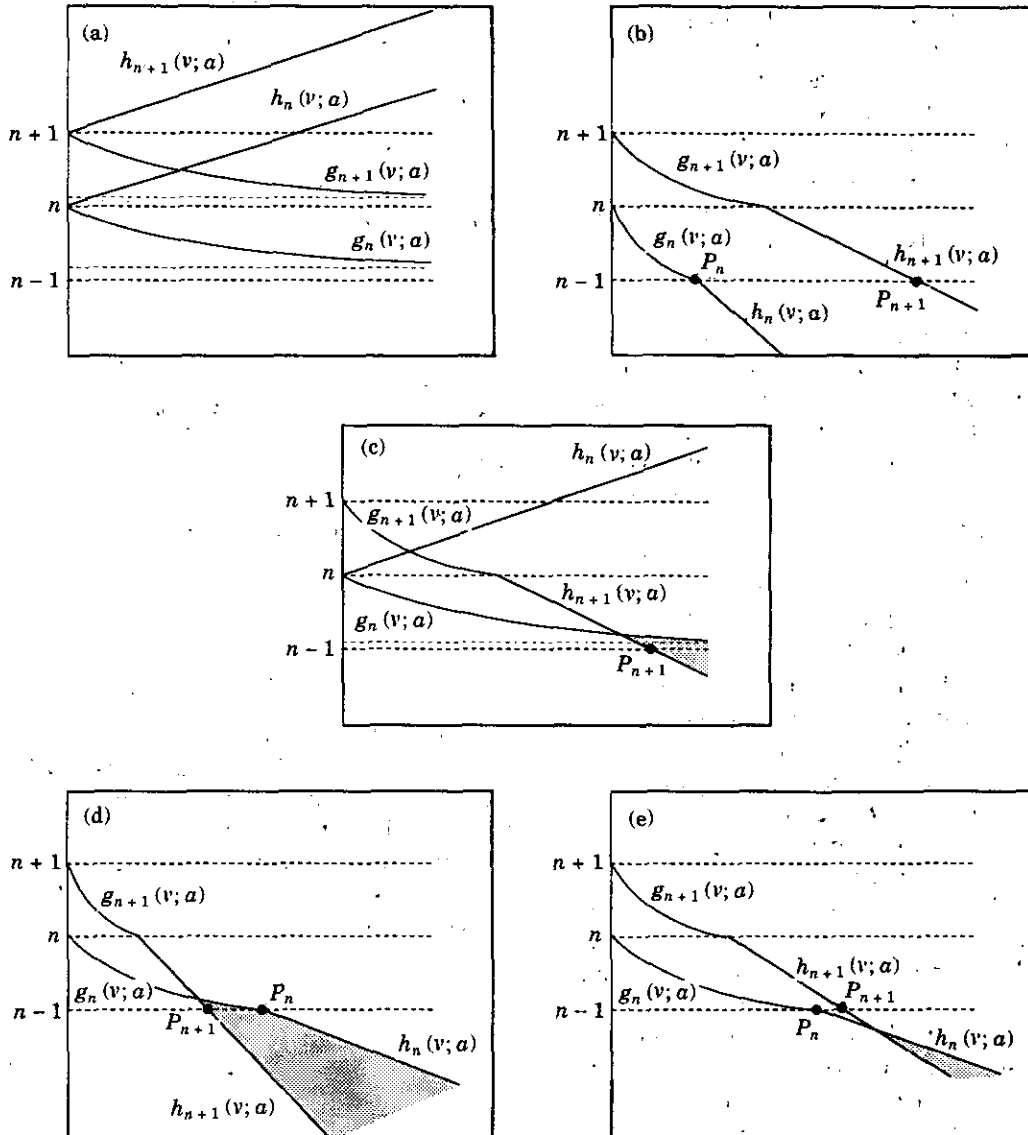$$t_c = n - \frac{\rho^{T-n+2}}{K(a)}.$$

Fig. A1. Schematic description of the configuration pattern for $g_n(v; a)$ and $h_n(v; a)$. See text for detailed explanation.
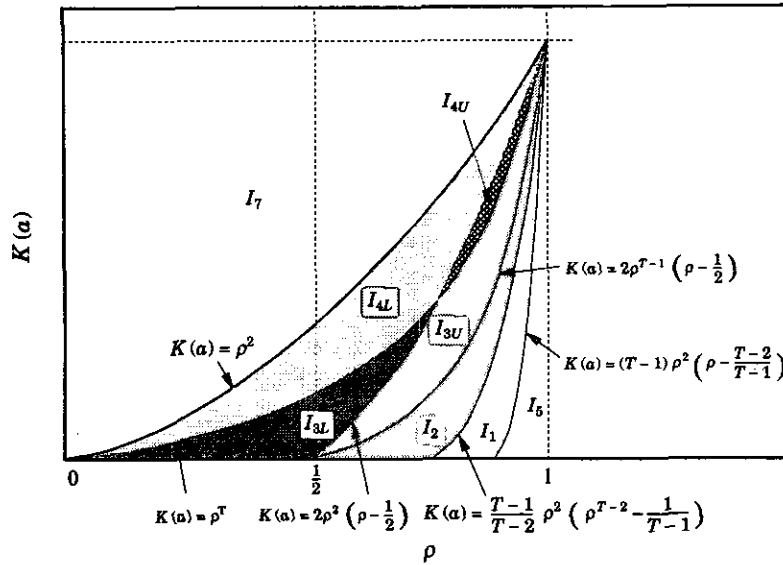
FIG. A2. In the case when $k_1 > k_2$ and $\rho \leqslant 1$, the parameter space $(\rho, K(a))$ consists of a detailed structure depending on the type of the division of the parameter space (v, t_c) in terms of the value of $t_p^*(a)$. Compare with Fig. 5 in the main text.

Therefore, depending on the position of the above asymptote, the valid condition of eqn (24) switches, because the positional relation among the functions $g_n(v; a)$ and $h_n(v; a)$ changes (see Fig. A1). Further, the positional relation depends also on n. Thus, as seen in the cases of I_1, I_2 and I_4 of Fig. 6 in the text, there is a case such that t_p^* cannot be less than $^3N > 1$. For $n < {}^3N$ in such a case, the positional relation corresponds to (a) or (b) in Fig. A1. As indicated in this figure, the positional relation can be analytically categorized by analysing the positional relation among these points P_n and P_{n+1}, given by

$$P_n : \left(n - 1, \frac{1}{\rho^{T-n+2}/K(a) - 1} \right)$$

$$P_{n+1} : \left(n - 1, \frac{2}{\rho^{T-n+1}/K(a) - 1} \right).$$

If P_{n+1} is located to the left of P_n, there exists some region for $t_p^* = n$, seen in case (d) of Fig. A1. Even if P_{n+1} is located to the right of P_n, when $\rho < 1$, there can exist a region for $t_p^* = n$, seen as case (e) of Fig. A1, under the following condition:

$$\frac{n}{\rho^{T-n+1}/K(a) - 1} < \frac{n - 1}{\rho^{T-n+2}/K(a) - 1}.$$

This condition means that the cross section of $h_{n+1}(v; a)$ on the v axis is located to the left of that of $h_n(v; a)$. In Fig. 5 in the text, no distinction is indicated between the two cases (d) and (e) of Fig. A1. In these cases, the parameter region of $(\rho, K(a))$ further shows a detailed structure, when $k_1 > k_2$, as shown in Fig. A2: these regions I_3 and I_4 are respectively divided into two distinct regions. For parameters of I_{3U}, with increasing n for $t_p^* = n$, both cases (d) and (e) from Fig. A1 occur, while, for those of I_{3L}, only case (d) occurs. Similarly, for parameters of I_{4U}, with increasing n, if $n < {}^3N$, case (a) occurs, and when $n = {}^3N$, (c) occurs. Then, for $n > {}^3N$, both cases (d) and (e) occur. However, for those of I_{4L}, case (e) does not occur; it is replaced by (d). As another case, if the following condition is satisfied for ^3N when $\rho < 1$,

$$\frac{\rho^{T-N+2}}{K(a)} \leqslant 1 < \frac{\rho^{T-N+1}}{K(a)},$$

there exist some region for $t_p^* = N$, given by (c) in Fig. A1. This case is included in the region I_4 of Fig. 5, as seen in Fig. 6 in the text.

In the case when $k_1 < k_2$, the analogous analysis can be carried out for $h_n(v; a)$ and $h_{n+1}(v; a)$. For parameters of C_n, the region of (v, t_c)-space for $t_p^* = j$ less than $n + 1$ and more than 1 appears as a triangle because $h_n(v; a)$ and $h_{n+1}(v; a)$ intersect, as shown in Fig. 9 in the text.