A Mathematical Model on The Optimal Timing of Offspring Desertion

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Abstract

We consider the offspring desertion as the optimal strategy for the deserter parent, analyzing a mathematical model for its expected reproductive success. It is shown that the optimality of the offspring desertion significantly depends on the offsprings' birth timing in the mating season, and on the other ecological parameters characterizing the innate nature of considered animals. Especially, the desertion is less likely to occur for the offsprings born in the later period of mating season. It is also implied that the offspring desertion after a partially biparental care would be observable only with a specific condition.

Key words: offspring desertion, optimal behavior, optimal timing, reproductive success, mathematical model

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1 INTRODUCTION

Some specific features of the parental care of animals have been attracting many biological researchers (as for an overview, for instance, see Krebs and Davies (1981); Houston *et al.* (2005); Gross (2005)). Theoretical approaches to understand a variety of characteristic natures of the parental care behaviors have grown up, applying some mathematical modellings with, for example, the population genetics (Ihara, 2002), the game theory (Maynard Smith, 1986; McNamara *et al.*, 2002), and the dynamic programming method (Mangel and Clark, 1988; Kelly and Kennedy, 1993).

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In not a few cases of vertebrates, for instance, aardwolf *Proteles cristatus* or striped hyena *Hyaena hyaena*, one of parents (male for these examples) comes not to care the offsprings or to desert them after an early period of offspring care with another parent (Kleiman, 1977; Ridley, 1978; Blumer, 1979; Baylis, 1981). Such offspring desertions ("mate desertion" in Kelly and Kennedy (1993)) have been documented also for birds and fishes (Myers, 1981; Beissinger, 1986, 1990; Blumer, 1986; Ezaki, 1988; Fujioka, 1989; Mendelsohn, 1989; Székely *et al.*, 1996; Jennions and Polakow, 2001; Vélez *et al.*, 2002). Along the theoretical argument of the optimal behavioral strategy, such offspring desertion could be regarded as to increase the fitness of the deserter parent (Houston *et al.*, 2005).

In case of aardwolf *Proteles cristatus*, it has been observed that the male parent deserts the offsprings when the number of offsprings decreases to a critical extent due to some accidents or predations. The deserted offsprings are cared only by the female parent after the desertion. The deserter male parent goes to make another mating with another female.

For the offspring desertion by male in the Panamanian blue acara cichlid *Aequidens coeruleopunctatus*, Vélez *et al.* (2002) found that males with experimentally reduced broods stopped providing parental care earlier than males whose broods were not reduced, and that males with reduced broods stayed longer with their broods as the season progressed. These results indicate that the occurrence of offspring desertion significantly depends not only on the number of offsprings but also on their birth timing in the mating season.

The offspring desertion could be considered to increase the opportunities to get a new mate within the current mating season, so as to increase the expected reproductive success for the deserter male (Houston *et al.*, 2005). With the game theoretic approach, some researchers have considered the offspring desertion in the context of evolutionary stable strategy (ESS) (Grafen and Sibley, 1978; Schuster and Sigmund, 1981; Vehrencamp and Bradbury, 1984; Lazarus, 1990; Yamamura and Tsuji, 1993; Székely *et al.*, 1996). Kelly and Kennedy (1993) considered the offspring desertion of Cooper's Hawks *Accipiter cooperii* in north-central New Mexico, with a sophisticated dynamic programming approach, which they called "dynamic state variable modelling". As in the other mathematical researches with the dynamic programming method, they considered the energy reserves and the intakes of parent and offspring to determine the optimal strategy of parent, depending on the physical conditions of parent and offspring. They showed that the occurrence of offspring desertion significantly depends on the physical conditions of parent and offspring. Their work was specified to consider the offspring desertion of the Cooper's Hawks, so that parameter values were mostly estimated from some observations. Without such data estimated from observations, their model could not have been analyzed enough to give sufficiently valuable ecological insights, since it has

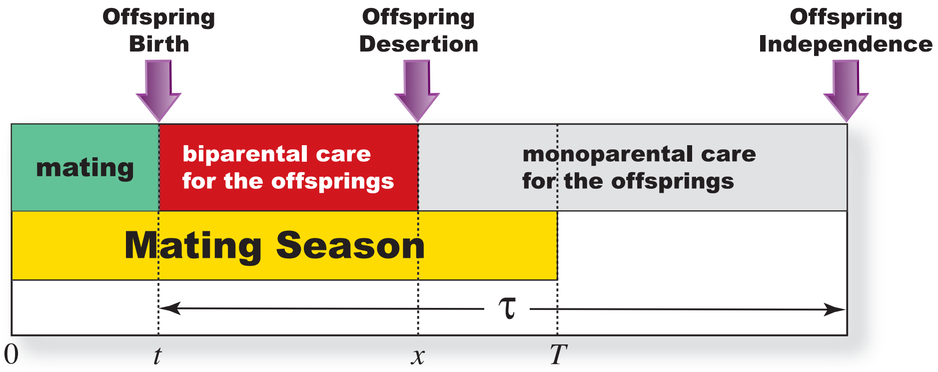

Fig. 1. Schematic illustration of the temporal settings in our model.

much parameters with a degree of freedom. In this sense, although their work has demonstrated the usefulness of dynamic programming method to consider the animal behavior, such models as theirs would have to be considered only with sufficient data from field researches.

In this paper, we qualitatively consider the offspring desertion as the optimal strategy for the deserter parent, analyzing a mathematical model for the deserter's expected reproductive success. Especially, we focus the offspring desertion timing that makes the expected reproductive success maximum. The desertion timing was not discussed well even in the nice work by Kelly and Kennedy (1993). We show that the optimality of the offspring desertion significantly depends on the offsprings' birth timing in the mating season, and on the other ecological parameters characterizing the innate nature of considered animals: the duration of mating season, the survival rates of offsprings with a single parent and with both, and the feasibility of additional matings for the deserter parent. Especially, it is shown that the length of the rest period of mating season after the offspring desertion is essential for the occurrence of offspring desertion.

2 MODEL

2.1 Assumptions and modelling

The period $[0, T]$ denotes each mating season. The offsprings are assumed to be born at time t ($0 \leq t \leq T$) between a pair of male and female parents. Suppose that one of parents deserts the offsprings at time x ($t \leq x \leq T$) and does not care them any more. The offspring desertion is assumed to occur only in the mating season, and not to occur after the season. For the offsprings, $[t, x]$ gives the period of biparental care. The deserter parent who becomes free from the care for the offsprings of the first mating goes looking for the other new partner to mate with and breed again (see Fig. 1).

For the offsprings born at time t, we consider the offspring's survival rate $\sigma_2(x-t)$ during $x-t$ under the biparental care, and the survival rate $\sigma_1(t+\tau-x)$ during $t+\tau-x$ under the care by a single parent, where we assume that the offspring needs period $\tau \geq T$ after the birth to grow up and become independent. The survival rate for the offspring to become reproductive after its independence is now assumed constant. Hence, the survival probability for the deserted offspring from the birth to the reproductive age is assumed to be proportional to $\sigma_2(x-t)\sigma_1(t+\tau-x)$. Thus, for the deserter parent, we consider the expected reproductive success by the first mating, given by

$$\langle n_1 \rangle_{x-t} = \overline{n}\sigma_2(x-t)\sigma_1(t+\tau-x), \tag{1}$$

where $\overline{n}$ is the number of offsprings by the first mating. We can regard $\langle n_1 \rangle_{x-t}$ as a function of $x-t$.

The deserter parent may take various kinds of behaviors for the additional matings. In this paper, the expected reproductive success for the deserter parent by the additional matings as a whole could be determined separately from that by the first mating, and could be given by an average value, except for the contribution of the probability of the additional *mating* success in the rest period of mating season after the offspring desertion for the first mating.

Now, $P(T-x)$ denotes the probability for the deserter to succeed in some subsequent matings during period $T-x$ after the (first) offspring desertion. We assume the expected number $\overline{\nu}$ of survival offsprings by the additional mating success. The expected number $\overline{\nu}$ involves the survival probability up to the offsprings' independence, that is, it means the expected number of offsprings that successfully become independence. If the offspring desertion does not occur for the additional mating, $\overline{\nu}$ could be described in the form of $\overline{\nu} = \overline{n}'\sigma_2(\tau)$, where $\overline{n}'$ is the number of offsprings in the (second) additional mating. More generally, the expected reproductive success by the additional matings for the deserter during the rest period $T-x$ of the mating season is now assumed to be given by

$$\langle n_{\mathrm{add}} \rangle_{T-x} = \overline{\nu}P(T-x), \tag{2}$$

where $\overline{\nu}$ gives the maximal expected reproductive success possible by the additional successful matings. Similarily with (1), we can regard $\langle n_{\mathrm{add}} \rangle_{T-x}$ as a function of $T-x$.

Lastly, the expected total reproductive success $N(t;x)$ for the deserter about the mating season is given as a whole by the sum of (1) and (2): $N(t;x) = \langle n_1 \rangle_{x-t} + \langle n_{\mathrm{add}} \rangle_{T-x}$.

Let us note that the offspring desertion could be optimal only when $N(t;x)$ is greater for some x than the expected reproductive success $\overline{N}_*$ in case of no offspring desertion when both parents care the offsprings up to their independence. If no x in $[0,T)$ satisfies $N(t;x) > \overline{N}_*$, then the behavior of the offspring desertion can not be optimal. In such a case, both parents care their offsprings born in the first mating as the optimal behavior to get the expected maximal reproductive success.

In the case that the offspring desertion could realize the reproductive success greater than the biparental care without the desertion could, the optimal behavior for the deserter parent is to maximize $N(t;x)$ with the choice of the optimal desertion timing $x = x^*$ $(t \le x^* \le T)$. In our analysis, $x^* = t$ means that the offspring desertion occurs at the moment of the offsprings' birth, so that the deserter has taken no care of those offsprings at the first mating. In contrast, $x^* = T$ means that the offspring desertion does not occur, and the first offsprings are always cared by both parents without the occurrence of desertion. In the case when $t < x^* < T$, the deserter parent contributes just in part to the care of those offsprings born in the first mating.

2.2 Expected reproductive success by the first mating

In our model, the survival rate σ_2 for the offspring under the biparental care during $[t,x]$ is given by

$$\sigma_2(x-t) = e^{-\delta_2(x-t)}, \tag{3}$$

where δ_2 denotes the expected death rate in a unit time, while the survival rate σ_1 under the care by a single parent during $[x, t+\tau]$ is given by

$$\sigma_1(t+\tau-x) = e^{-\delta_1(t+\tau-x)}, \tag{4}$$

where δ_1 is the expected death rate in a unit time. We assume that $\delta_2 < \delta_1$.

With the above survival rate functions, we consider the following expected reproductive success by the first mating:

$$\langle n_1 \rangle_{x-t} = \overline{n} e^{-\delta_1\tau + (\delta_1-\delta_2)(x-t)}. \tag{5}$$

2.3 Expected reproductive success by additional matings

We assume that the probability of the success of additional matings depends only on the length $T - x$ of the rest mating season and is given by

$$P(T - x) = 1 - e^{-a(T-x)}, \tag{6}$$

where a is a positive constant which means the easiness of successful additional matings. The larger a means the easier additional matings. The occurrence of additional matings is assumed to be random, so that the non-occurrence probability decreases exponentially as the length of the rest mating season gets longer. Now, in our model, we consider the following expected additional reproductive success:

$$\langle n_{\mathrm{add}} \rangle_{T-x} = \overline{\nu} \left\{ 1 - e^{-a(T-x)} \right\}. \tag{7}$$

2.4 Expected reproductive success without offspring desertion

From (5), in our model, the expected reproductive success $\overline{N}_*$ in case of no offspring desertion when both parents care the offsprings by the first mating until their independence is given by

$$\overline{N}_* = \overline{n} e^{-\delta_2 \tau}. \tag{8}$$

2.5 Expected total reproductive success for the deserter parent

From (5), (7) and (8), we can get the following expression of the expected total reproductive success $N(t;x) = \langle n_1 \rangle_{x-t} + \langle n_{\mathrm{add}} \rangle_{T-x}$ for the deserter parent:

$$N(t;x) = \overline{N}_* \left[e^{-a\mu\{\tau-(x-t)\}} + \rho \left\{ 1 - e^{-a(T-x)} \right\} \right], \tag{9}$$

where $\rho = \overline{\nu}/\overline{N}_*$ and $\mu = (\delta_1 - \delta_2)/a > 0$.

3 ANALYSIS

3.1 Optimality of offspring desertion

We investigate the expected total reproductive success $N(t;x)$ as a function of the desertion timing x ($t \leq x \leq T$) with fixed offsprings' birth timing t ($0 \leq t \leq T$), and determine at which x it takes its maximum in $[t,T]$.

The expected total reproductive success $N(t;x)$ is monotonic or has a unique miminal/maximal extremum at $x = x^{\dagger}$ in (t,T) (Appendix A):

$$x^{\dagger} = t + \frac{1}{1-\mu}\left\{T - t + \frac{1}{a}\log\left(\frac{\mu}{\rho}e^{-a\mu\tau}\right)\right\}. \tag{10}$$

At first, when $N(t;x)$ is monotonically increasing in terms of x, $N(t;x)$ takes its maximum at $x = T$ in $[t,T]$. Therefore, the offspring desertion is not optimal because the deserter could not get any mate after the time T out of the mating season. Indeed, in this case, from (9), since

$$N(t;T) = \overline{N}_{*}e^{-a\mu\{\tau-(T-t)\}}, \tag{11}$$

the condition that $N(t;T) > \overline{N}_{*}$ is never satisfied.

In contrast, when $N(t;x)$ is monotonically decreasing for any x in (t,T), if $N(t;t) > \overline{N}_{*}$, the offspring desertion at $x = t$ is optimal to maximize the expected reproductive success for the deserter parent. In such case, the deserter parent does not care the offsprings at all in the first mating.

When $N(t;x)$ has its maximal extremum at $x = x^{\dagger}$ in (t,T), if $N(t;x^{\dagger}) > \overline{N}_{*}$, the offspring desertion at $x = x^{\dagger}$ is optimal for the deserter parent. In contrast, when $N(t;x)$ has its minimal extremum for an x in $[t,T]$, it has its maximum at $x = t$ or $x = T$. Therefore, in such case, if $N(t;t) > \overline{N}_{*}$, the offspring desertion at $x = t$ is optimal for the deserter parent. If $N(t;t) < \overline{N}_{*}$, the offspring desertion is not optimal.

Lastly, the offspring desertion is optimal if and only if $N(t;t) > \overline{N}_{*}$ or $N(t;x^{\dagger}) > \overline{N}_{*}$ at $x = x^{\dagger}$ in (t,T). In other words, if and only if $N(t;t) \leq \overline{N}_{*}$ and $N(t;x^{\dagger}) \leq \overline{N}_{*}$ at $x = x^{\dagger}$ in (t,T), the offspring desertion is not optimal while the biparental care for the offsprings of the first mating provides the greater reproductive success.

From these arguments, we can derive the following condition with which the

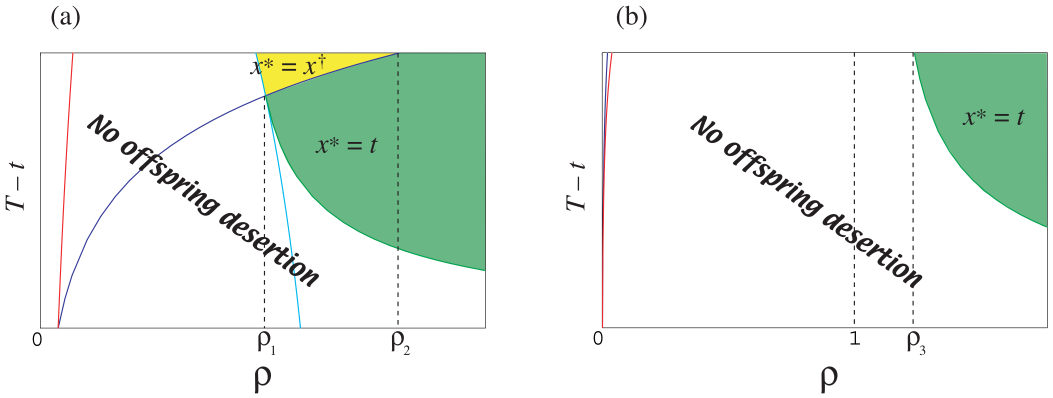

Fig. 2. $(\rho, T-t)$-dependence of the occurrence of offspring desertion. (a) $\mu < 1$; (b) $\mu \geq 1$. $T-t$ means the rest length of the mating season after the offspring birth by the first mating. $\rho_1 = 1-(1-\mu)e^{-a\mu\tau}$; $\rho_2 = \mu e^{-a(\mu\tau - T)}$; $\rho_3 = (1-e^{-a\mu\tau})/(1-e^{-aT}) > 1$. Also see Fig. 3. Numerically drawn for (a) $\mu = 0.2$; (b) $\mu = 1.2$ with $\tau = 2.0$, $T = 1.0$, and $a = 3.0$. Difference in parameter values makes no qualitative difference on these figures.

offspring desertion is optimal (Appendices B and C):

$x^* = t$:

$$-\frac{1}{a}\log\left\{1-\frac{1}{\rho}\left(1-e^{-a\mu\tau}\right)\right\} < T-t \leq -\frac{1}{a}\log\left(\frac{\mu}{\rho}e^{-a\mu\tau}\right) \qquad \text{with } \rho > \mu e^{-a\mu\tau}+1-e^{-a\mu\tau}. \tag{12}$$

$x^* = x^\dagger$ in (t, T):

$$\begin{cases} \mu < 1; \\ -\dfrac{1}{a}\log\left(\dfrac{\mu}{\rho}e^{-a\mu\tau}\right) \leq T-t \leq -\dfrac{1}{a\mu}\log\left(\dfrac{\mu}{\rho}e^{-a\mu\tau}\right) \text{ with } \rho > \mu e^{-a\mu\tau}; \\ \rho \geq 1 \text{ or } \begin{cases} \rho < 1; \\ T-t > -\dfrac{1}{a}\log\left(\dfrac{\mu}{\rho}e^{-a\mu\tau}\right) - \dfrac{1-\mu}{a\mu}\log\left(\dfrac{1-\mu}{1-\rho}e^{-a\mu\tau}\right). \end{cases} \end{cases} \tag{13}$$

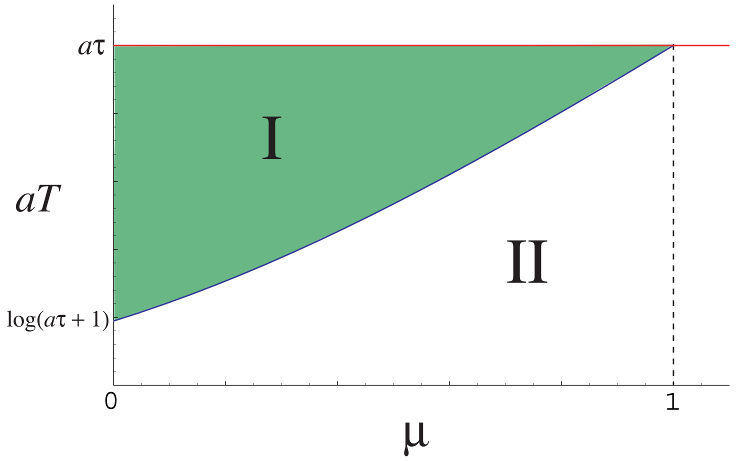

Fig. 3. (μ, aT)-dependence of the occurrence of offspring desertion. For the region II, only the offspring desertion with no biparental care could occur. For the region I, the offspring desertion with a partially biparental care could occur. Also see Fig. 2.

3.2 Occurrence of offspring desertion

From conditions (12) and (13), we can find two cases of the occurrence of offspring desertion from the viewpoint of its optimality as shown in Figs. 2 and 3. Although those figures are numerically drawn, their qualitative natures are the same independently of chosen values for the numerical calculation. If $\mu \geq 1$, only the offspring desertion with no biparental care could occur. That is, in this case, the optimal behavior of offspring desertion is to desert the offsprings just after or before their birth. Only if $\mu < 1$, the offspring desertion with a partially biparental care could be optimal. The parameter $\mu = (\delta_1 - \delta_2)/a > 0$ is the ratio of the difference of death rates with the monoparental or biparental care to the easiness of additional matings. Thus, only in a situation that an additional mating would be sufficiently easy, the offspring desertion with a partially biparental care could be optimal. If the additional mating is relatively hard, only the offspring desertion with no biparental care would be observable in the case when it could be optimal.

The occurrence of offspring desertion significantly depends on the value of ρ. For sufficiently small ρ, it cannot be optimal (Fig. 2). Since $\rho = \overline{\nu}/\overline{N}_*$ means the ratio of the expected number of survival offsprings by the additional matings to that by the first mating without the offspring desertion, this result means that, if the additional matings are expected to be so poorly successful, the offspring desertion could not be optimal. Moreover, if the number of offsprings by the first mating is sufficiently large, it could not be optimal. Only if the number of offsprings by the first mating is sufficiently small, it could be optimal.

Further, the offspring desertion could be optimal only for the first mating in the relatively early period of the mating season. This is because the probability of the occurrence of successful additional matings depends on the length of the rest length of the mating season after the offspring birth by the first mating, as the definition (6) indicates. Sufficiently large reproductive success by the additional matings is hardly expected if the rest of the mating season is so short that the successful additional mating is expected difficult. Therefore, from this result, the offspring desertion could be observed only in the relatively early period of the mating season.

The offspring desertion with a partially biparental care could be optimal only for a finite range of ρ, and could not be optimal for sufficiently large ρ. As shown in Fig. 2(a), we obtain the result that the optimal offspring desertion with a partially biparental care could occur in rather early period of the mating season and the desertion just after the offspings' birth could occur in the later (not too later) period of the mating season.

As indicated in Fig. 2, a necessary condition for the occurrence of the optimal offspring desertion with a partially biparental care is given by $\rho_1 < \rho_2$ in the figure, that is,

$$aT > \log\left(1 + \frac{1 - e^{-a\tau\mu}}{\mu e^{-a\tau\mu}}\right). \tag{14}$$

This condition is illustratively shown in Fig. 3. The offspring desertion with a partially biparental care could be more observable if the mating season is sufficiently long.

3.3 Dependence on offsprings' birth timing

As mentioned in the previous section, the optimality of the offspring desertion significantly depends on the birth timing of offsprings by the first mating. Fig. 4 shows the dependence of the expected maximized total reproductive success $N(t;x^*)$, the optimal timing of offspring desertion x^*, and the optimal duration of biparental care for the offsprings by the first mating $x^* - t$ on the birth timing of offspings by the first mating. As the offsprings' birth gets later in the mating season, the optimality of the offspring desertion gradually diminishes and loses after a critical time within the mating season. Independently of whether a period of the biparental care exists or not, the offspring desertion for the offsprings born in the earlier period of the mating season is expected to realize the larger reproductive success.

It is interesting that there exists a critical birth timing of the offsprings, after which the offspring desertion cannot be optimal, while the offspring deser-

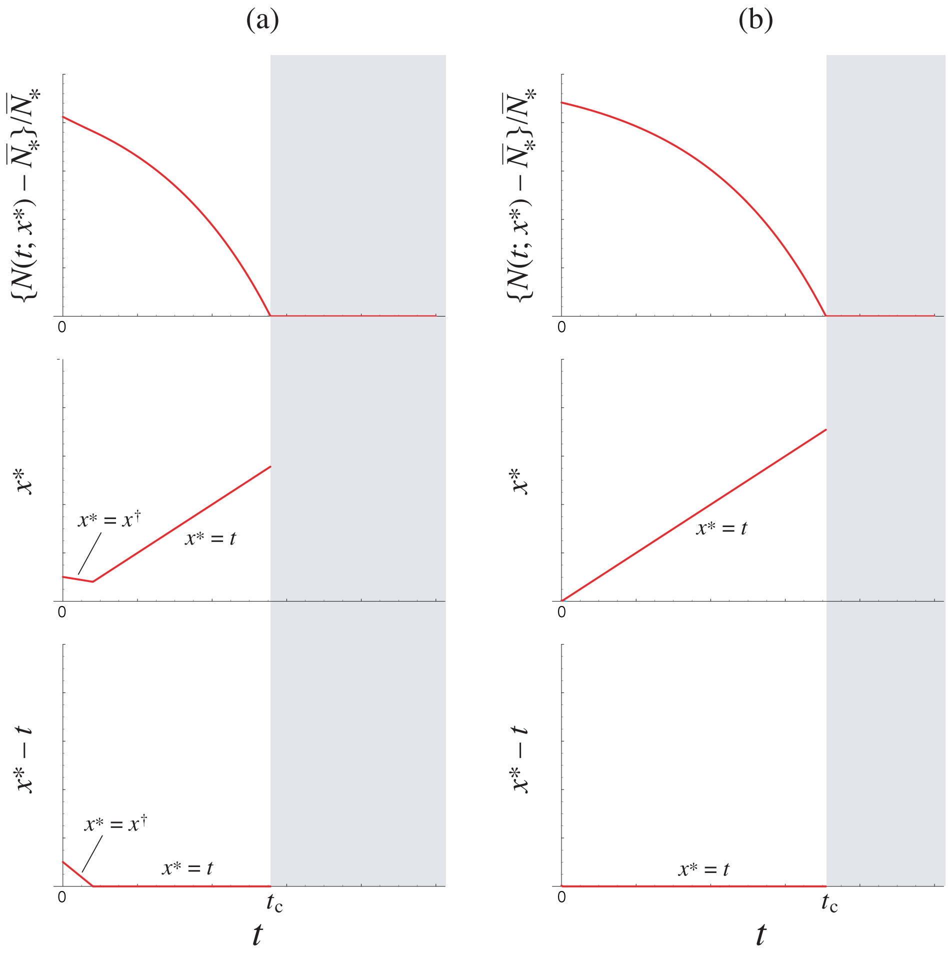

Fig. 4. Dependence of the offspring desertion on the birth timing of offsprings by the first mating. (a) In the case when the optimal offspring desertion with a partially biparental care appears; (b) In the case when only the optimal offspring desertion with no biparental care appears. For $t \geq t_c$, the offspring desertion is not optimal. Numerically drawn for (a) $\rho = 0.9$; (b) $\rho = 1.2$ with $\overline{N}_* = 1.0$, $\tau = 2.0$, $T = 1.0$, $a = 3.0$, and $\mu = 0.2$. Difference in parameter values makes no qualitative difference on these figures.

tion with no biparental care is optimal for the offsprings born just before the critical.

3.4 Dependence on the duration till the offspring independence

As indicated by Fig. 5, the offspring desertion is less likely to be optimal about the offsprings which require the longer duration of parental care for their independence. Only for the offsprings which require a sufficiently short duration of parental care for their independence, the offspring desertion with a partially biparental care is likely to be optimal.

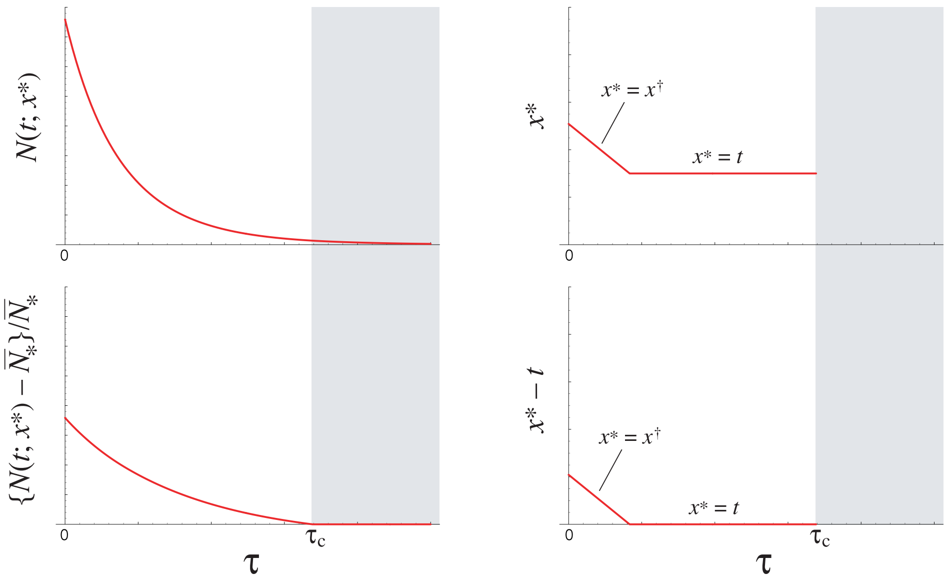

Fig. 5. Dependence of the offspring desertion on the duration of parental care necessary for the offspring's independence. For $\tau \geq \tau_c$, the offspring desertion is not optimal. Numerically drawn with $\overline{N}_* = e^{-\tau}$, $\tau = 2.0$, $T = 1.0$, $t = 0.3$, $a = 3.0$, $\rho = 0.99$, and $\mu = 0.2$. Difference in parameter values makes no qualitative difference on these figures.

It is interesting again that there exists a critical duration of the parental care, beyond which the offspring desertion cannot be optimal, while the offspring desertion with no biparental care is optimal for the duration of parental care just below the critical.

4 CONCLUDING REMARKS

In our modelling, the expected total additional reproductive success for the deserter parent is assumed to depend only on the length of the rest period of mating season after the offspring desertion. This assumption might seem one of oversimplifications in our modelling. However, especially in the case when the additional mating success would be hardly expectable, or be much easily available, we could expect that our modelling analysis provides some perspectives to understand the behavior of offspring desertion.

In our result given by Figs. 2 and 4, the offsprings' birth timing significantly contributes to the determination of parent's optimal behavior about the offspring care and desertion. It is indicated that the offspring desertion is more likely to occur for the offsprings born in the earlier period than for those in the later of the mating season. It is shown that there exists the critical birth timing, after which the offspring desertion cannot be optimal (see Fig. 4). For example, Marques (2003, 2004) reported that, in case of the Spanish Sparrow, *P. hispaniolensis*, the desertion usually occurs early in the breeding cycle, during incubation. Vélez *et al.* (2002) found that males with reduced broods in the Panamanian blue acara cichlid *Aequidens coeruleopunctatus* stayed longer with their broods as the season progressed.

Naturally, the possibility of the occurrence of the offspring desertion depends on the nature of the expected additional reproductive success after the desertion, which is determined by the expected total number of offsprings by the additional matings, the probability of additional mating success, etc. As Fig. 2(b) clearly shows, in our model, if $\mu = (\delta_1 - \delta_2)/a \geq 1$ and $\rho = \overline{\nu}/\overline{N}_* \leq 1$, the offspring desertion is not optimal. With the sufficiently large number of offsprings by the first mating, the offspring desertion hardly occurs. Inversely, as the number of offsprings by the first mating gets smaller, it is more likely to occur. For the offspring desertion by male in the Panamanian blue acara cichlid *Aequidens coeruleopunctatus*, Vélez *et al.* (2002) found that males with experimentally reduced broods stopped providing parental care earlier than males whose broods were not reduced. In case of waterfowl, Armstrong and Robertson (1988), Ackerman *et al.* (2003) and Ackerman and Eadie (2003) suggest that the nest desertion in waterfowl is determined largely by attributes of the remaining clutch size (e.g., proportion of the clutch remaining). Their cases would correspond to our case. Moreover, as the expected number of offsprings by the additional matings gets larger, and eventually as the expected reproductive success by the additional matings gets larger, the offspring desertion is more likely to occur. The case of aardwolf *Proteles cristatus* would correspond to this result. It is remarked that, in the framework of our model, the occurrence of the offspring desertion appears to depend on the ratio ρ of the offspring numbers instead of the absolute amounts themselves.

When the additional matings are rather easily available, that is, the parameter a is so large that μ is rather small, Figs. 2(a) and 3 indicate that the partial biparental care is rather observable before the offspring desertion. In the case when the additional mating is hardly available, that is, the parameter a is so small that μ is rather large, Figs. 2(b) and 3 show that the offspring desertion is hard to occur.

The death rate of offsprings significantly contributes to the optimality of the offspring desertion, too. With a sufficiently high death rate of offsprings cared by a single parent, compared to that of offsprings cared by both, the offspring desertion is very likely to occur just after the offsprings' birth. This result might seem strange, because the high death rate of deserted offsprings is intuitively considered to lead to increase the disadvantage of the offspring desertion and to reduce the expected reproductive success by the first mating. This would be because the expected reproductive success by the additional matings is assumed to have no explicit dependence on those death rates of offsprings. The dependence on the death rates should be considered to be implicitly included in the parameter $\overline{\nu}$, which would become smaller as the death rate gets larger. Thus, for biological discussion, we must pay attention to such an implicit relationship between parameters δ_1, δ_2 and $\overline{\nu}$ of our model. From this point, in the framework of our modelling, the μ-dependence of the occurrence of the offspring desertion, given by Fig. 3, might have to be considered just as a referential result.

It is interesting that, in our results, the offspring desertion with a partially biparental care could occur only for the offsprings born in the sufficiently early period of mating season. Further, although the offspring desertion would be hard to be observable in the period before the end of mating season, the offspring desertion observed in the later period would be only that with no biparental care, that is, such that the deserter parent goes away without caring the offsprings of the first mating. As a consequence, the offspring desertion with a partially biparental care is not of an intermediate type between the desertion with no biparental care and the non-desertion, but of a specific case.

Kelly and Kennedy (1993) concluded from their analysis on their mathematical model with the dynamic programming method that the female parent that makes the offspring desertion is in a poor physical condition, though all female parents do not make the desertion behavior even in such a condition. In their model, the temporal variation of the physical condition is introduced, which depends on the chosen behavior. In our model, the physical condition of deserter parent is not explicitly considered, and only the first mating success is discriminated from those additional mating successes. The physical condition may be regarded to be involved in the easiness of successful additional matings (parameter a). In the case when the mating season is relatively short, results for our model would be at least intuitively useful to consider the behavior of offspring desertion, because the change of the physical condition of the parent would be negligible in the short mating season.

Models present a simplified view of the world while trying to capture some of its essential features. We expect that our analysis would be so and could give some intuitive or perspective views to consider biologically or theoretically the offspring desertion behaviors by a variety of animals.

APPENDIX

A $N(t;x)$ as a function of x

We can explicitly get the following x-derivative of $N(t;x)$:

$$\frac{\partial N(t;x)}{\partial x} = a\rho \cdot \overline{N}_* e^{-a\mu\{\tau-(x-t)\}} \left[\frac{\mu}{\rho} - e^{a\{\mu\tau-(T-t)\}} e^{a(1-\mu)(x-t)} \right]. \tag{A.1}$$

Then we can easily find that $N(t;x)$ has a unique maximal extremum at $x = x^\dagger$, given by (10), as a function of x.

From (A.1), we can easily see that $N(t;x)$ is monotonically decreasing for any x in (t,T) if $\mu < 1$ and $x^\dagger \leq t$ or if $\mu > 1$ and $x^\dagger \geq T$, while it is monotonically increasing for any x in (t,T) if $\mu > 1$ and $x^\dagger \geq T$ or if $\mu < 1$ and $x^\dagger \leq t$. If and only if $\mu < 1$ and $t < x^\dagger < T$, $N(t;x)$ has its maximal extremum for an x in $[t,T]$. In contrast, if $\mu > 1$ and $t < x^\dagger < T$, $N(t;x)$ has its minimal extremum for an x in $[t,T]$, and has its maximum at $x = t$ or $x = T$.

From these arguments, $N(t;x)$ is monotonic or has a unique extremum in (t,T) in terms of x. Therefore, only from the x-derivatives of $N(t;x)$ at $x = t$ and $x = T$, we can identical the monotonicity and the existence of minimal/maximal extremum in (t,T). From (A.1), we have

$$\begin{aligned} \left.\frac{\partial N(t;x)}{\partial x}\right|_{x=t} &= a\rho \cdot \overline{N}_* e^{-a\mu\tau} \left\{ \frac{\mu}{\rho} - e^{a\{\mu\tau-(T-t)\}} \right\}; \\ \left.\frac{\partial N(t;x)}{\partial x}\right|_{x=T} &= a\rho \cdot \overline{N}_* e^{-a\mu\{\tau-(T-t)\}} \left\{ \frac{\mu}{\rho} - e^{a\mu\{\tau-(T-t)\}} \right\}. \end{aligned} \tag{A.2}$$

From (A.2), $N(t;x)$ is monotonically decreasing for any x in (t,T) if and only if the following condition is satisfied:

$$\begin{cases} T - t \leq \mu\tau - \dfrac{1}{a} \log \dfrac{\mu}{\rho}; \\[2ex] T - t \leq \tau - \dfrac{1}{a\mu} \log \dfrac{\mu}{\rho}, \end{cases} \tag{A.3}$$

where the condition that $\rho > \mu e^{-a\mu\tau}$ is necessary. In contrast, $N(t;x)$ is monotonically increasing for any x in (t,T) if and only if the following condition is satisfied:

$$\begin{cases} T - t \geq \mu\tau - \dfrac{1}{a} \log \dfrac{\mu}{\rho}; \\[2ex] T - t \geq \tau - \dfrac{1}{a\mu} \log \dfrac{\mu}{\rho}. \end{cases} \tag{A.4}$$

On the other hand, $N(t;x)$ has a minimal extremum at $x = x^\dagger$ in (t,T) if and only if the following condition is satisfied:

$$\begin{cases} T - t \leq \mu\tau - \dfrac{1}{a}\log\dfrac{\mu}{\rho}; \\ T - t \geq \tau - \dfrac{1}{a\mu}\log\dfrac{\mu}{\rho}, \end{cases} \tag{A.5}$$

where the condition that $\rho > \mu e^{-a\mu\tau}$ is necessary. Next, $N(t;x)$ has a maximal extremum at $x = x^\dagger$ in (t,T) if and only if the following condition is satisfied:

$$\begin{cases} T - t \geq \mu\tau - \dfrac{1}{a}\log\dfrac{\mu}{\rho}; \\ T - t \leq \tau - \dfrac{1}{a\mu}\log\dfrac{\mu}{\rho}. \end{cases} \tag{A.6}$$

This condition (A.6) implies the condition that $\mu < 1$ and $\rho > \mu e^{-a\mu\tau}$.

B Condition for $x^* = t$

If $x^* = t$, it is necessary that $N(t;x)$ is monotonically decreasing or has a minimal extremum in (t,T) in terms of x. From the conditions (A.3) and (A.5) in Appendix A, the necessary condition is given by

$$T - t \leq \mu\tau - \frac{1}{a}\log\frac{\mu}{\rho} \quad \text{with} \quad \rho > \mu e^{-a\mu\tau}. \tag{B.1}$$

Furthermore, from (9), since

$$N(t;t) = \overline{N}_* \left[e^{-a\mu\tau} + \rho\left\{1 - e^{-a(T-t)}\right\}\right], \tag{B.2}$$

the condition that $N(t;t) > \overline{N}_*$ is given by

$$T - t > -\frac{1}{a}\log\left\{1 - \frac{1}{\rho}\left(1 - e^{-a\mu\tau}\right)\right\} \quad \text{with} \quad \rho > 1 - e^{-a\mu\tau}. \tag{B.3}$$

Lastly, from (B.1) and (B.3), we can get the condition (12) for $x^* = t$.

C Condition for $x^* = x^\dagger$

If $x^* = x^\dagger$ in (t, T), it is necessary that $N(t; x)$ has a maximal extremum in (t, T) in terms of x, which condition is given by (A.6) in Appendix A. Furthermore, from (9), the condition that $N(t; x^\dagger) > \overline{N}_*$ is equivalent to the following:

$$e^{-a\mu\{\tau-(x^\dagger-t)\}} + \rho\left\{1 - e^{-a(T-x^\dagger)}\right\} > 1. \tag{C.1}$$

Making use of (10), the condition (C.1) can be rewritten as follows:

$$e^{-a(T-x^\dagger)}\frac{1-\mu}{\mu} > \frac{1-\rho}{\rho}. \tag{C.2}$$

Therefore, from (10) and the implied condition that $\mu < 1$, the condition (C.2) results in the following ones:

$$\rho \geq 1 \text{ or } \begin{cases} \rho < 1; \\ T - t > \tau - \dfrac{1}{a}\log\dfrac{\mu}{\rho} - \dfrac{1-\mu}{a\mu}\log\dfrac{1-\mu}{1-\rho}. \end{cases} \tag{C.3}$$

Lastly, the conditions (A.6) and (C.3) gives the condition (13) for $x^* = x^\dagger$.

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