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"The Timing of Life History Events"

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The Timing of Life History Events

by

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Abstract

We investigate the evolutionarily stable seasonal timing of life history events, such as the start of breeding, when the risk of physical disturbance and advantages of growth or competitive advantage are in conflict. In our model, disturbance is assumed to cause failure of all breeding (or other life history) attempts made before it. For a given probability distribution of the timing of last date of environmental disturbance, individuals starting breeding earlier face a higher risk of being disturbed. On the other hand, the clutch laid earlier has an advantage over those laid later, either having more time to grow or to preempt the nest sites, suitable habitat or foraging sites. The evolutionarily stable population is determined to have a single optimal date on which all individuals start breeding (synchronous breeding), provided the benefit of the earlier start of breeding is given purely by the excess time for growth, not by the competitive advantage, and provided offspring produced from many subpopulations, each having a different date of disturbance, are pooled to form a population over which population regulation occurs. In contrast, an ESS population may include a period of breeding over which some individuals start breeding every day (asynchronous breeding), if [1] early breeding is accompanied by competitive advantage within the local population, or [2] population regulation occurs within the local population before being mixed with offspring produced from other local populations, or [3] disturbance occurs synchronously over the whole population. In short, synchronous breeding should evolve if the spatial scale over which disturbance dates are strongly correlated (denoted by $S_{disturbance}$) is much smaller than the spatial scale of the population in which population regulation occurs (denoted by $S_{regulation}$). Asynchronous breeding is expected to evolve if $S_{disturbance}$ is similar to or larger than $S_{regulation}$.

keywords: life history theory, spatial scales, timing of reproduction, germination, oviposition, bet-hedging,

Introduction

A recurrent problem in life history theory involves the timing of events, for example emergence, germination, breeding or migration to find new sites. In each of these cases, the "early birds" have the greatest potential for high payoffs, and for securing favorable habitat, but may run the greatest risks of uncertain conditions. These tradeoffs exist as well in a number of other situations. For example, even without seasonality, foraging individuals constantly must balance the relative security of a satisfactory patch against the uncertain possibility of finding a higher payoff environment. In foraging as well as larval or seed dispersal, those settling in marginal habitats may experience increased environmental uncertainty but reduced competition. The tradeoffs are familiar ones, but no general approach exists for evaluating the tradeoffs and determining evolutionarily stable strategies. The purpose of this paper is to propose steps in that direction. To the extent that we focus on particular examples, especially timing of reproduction, they should be understood as representing the broader class of problems introduced above.

Suppose that following reproduction or germination there is a risk of disturbance, for example due to frost, storm, herbivory or predation, and that such a disturbance event would kill all offspring already produced. A case in point (Moloney *et al.*, 1992) involves the strategies of various annual plants in serpentine grassland: early germination leads to death if disturbance by gophers occurs early in the season, but gains competitive advantage otherwise. Analogous cases involve the timing of oviposition in insects, or breeding in birds. If the last date of disturbance were known beforehand, the evolutionary tradeoff would be easily resolved: all individuals would germinate or oviposit or breed just after the last disturbance event. However, uncertainty exists regarding dates of disturbance, both locally and regionally. Hence, evolution will select for a compromise, balancing the tradeoffs between the higher risks and higher benefits of early germination.

To be specific, we shall focus henceforth on breeding birds and let x be the last date of disturbance, and $f(x)$ the probability distribution of x. We assume that $f(x)$ has a single peak. We denote the latest possible date of disturbance by t_f. An example of such a distribution is

$$f(x) = C\, x^{a-1}(t_f - x)^{b-1} \qquad , \qquad (1)$$

for $0 < x < t_f$, but zero for other x. This example will be used in illustrations to follow.

Natural selection works every generation to shape a temporal pattern of breeding. Since the success of particular timing involves uncertainty, as determined for example by the probability distribution in Eq (1), a distribution of breeding dates may evolve. In this case, the evolutionarily stable population would include individuals that breed on different dates asynchronously depending on the population structure, spatial scale of disturbance, mode of competition etc.

In this paper we analyze the optimal or evolutionarily stable breeding schedule. Each player chooses the starting date of breeding, denoted by y. In some cases, there is an optimal date y^* on which all individuals are expected to start breeding. In other situations, however, an evolutionarily stable population may include individuals breeding on different dates, and there may be a period over which some individuals start breeding every day.

Case 1: Frequency-independent Fitness

Consider first the simplest case in which there is no frequency dependence, so that breeding success, provided individuals are not killed by the disturbance, decreases with the laying date y. Let $\psi(y \mid x)$ be the breeding success of an individual that begins breeding on day y. For example

$$\psi(y \mid x) = \begin{cases} e^{-by} & , \quad \text{if } y > x \\ 0 & , \quad \text{if } y < x \end{cases} , \tag{2}$$

where b indicates the strength of advantage of starting oviposition earlier. Then the expected reproductive success is simply the success multiplied by the probability of not experiencing disturbance.

$$\begin{aligned} \phi(y) &= \int_0^{t_f} \psi(y \mid x) f(x) dx \\ &= \int_0^{y} f(x) dx \, e^{-by} \end{aligned} . \tag{3}$$

Because $\phi(y)$ is a non-negative continuous function on $[0, t_f]$, it (generally) attains its maximum at a single date y^*. Therefore, there is no possibility for a mixed strategy to evolve.

In the above, we used the arithmetic average with respect to the dates of environmental disturbance in calculating average reproductive success in Eq. (3). Disturbance events have a certain spatial scale, and we may call the area disturbed by a single event "a patch". We assume that the whole population includes a number of patches, each having a different date of disturbance. The fraction of patches having various dates follows $f(x)$ and is constant over generations. The output from reproductive success in these patches will be pooled and redistributed randomly over different patches. This mixing process may be caused by migration. The reproductive success of a particular individual is independent of the behavior of other individuals within the same patch (or subhabitat). This population structure reflects an assumption of hard selection (Christiansen, 1975; van Thienderen, 1991). Because of this assumption, the arithmetic average is the suitable method in calculating the adaptiveness of the breeding date. In addition, the conditional reproductive success of a surviving individual is assumed to be e^{-by}, dependent only on the breeding date y, indicating frequency independence.

The solution that maximizes Eq. (3) suggests that all the individuals should evolve to start breeding synchronously on the same date. Some of them are killed because the disturbance in their patch comes later than y^*, but reproduction in other patches in which the disturbance ends before y^* will produce the next generation. The population on the whole is quite stable in recruitment because the fraction of disturbed and nondisturbed patches does not change between generations.

As explained later, if some of the conditions described above are violated, for example if the patches are disturbed synchronously or if competition occurs within each local site, then the evolutionary outcome can be very different. We turn to some examples in the sections that follow.

Case 2 Rank-dependent Fitness

Next we examine the case in which the relative advantage of different breeding dates is given not by the absolute date but by the ranking within the local population. To illustrate this, suppose that a limited number (n) of nesting sites are available, and that only those who start breeding in one of these sites are able to breed. Then, to achieve some reproductive success, one must be included among the first n individuals that start breeding after the last disturbance day x.

Alternatively, suppose that offspring from earlier clutches grow faster and, when hatched, enjoy a larger competitive advantage within local populations. Then the reproductive success of an individual starting breeding on y decreases with the number of individuals who start earlier than y, but later than the last disturbance date x. Let $g(y)$ be the distribution of the dates in the population. Suppose that the reproductive success of an individual that starts breeding on day y is

$$\psi(y \mid x) = \begin{cases} \exp\left[-a \int_x^y g(z)dz\right] , & \text{if } y > x \\ 0 , & \text{if } y < x \end{cases} , \qquad (4)$$

where a is a parameter reflecting the intensity of competition. A very large a indicates very strong competition so that only those who start breeding just after the last disturbance can have reasonable reproductive success. In contrast, if a is zero, there is no advantage to start breeding earlier.

The fitness of an individual with parameter y is given by

$$\begin{aligned} \phi(y) &= \int_0^{t_f} \psi(y \mid x) f(x) dx , \\ &= \int_0^y \exp\left[-a \int_x^y g(z)dz\right] f(x) dx . \end{aligned} \qquad (5)$$

The evolutionarily stable population will be comprised of a distribution of individuals, each with a different starting date. To show this, assume otherwise: if the population were composed only of individuals starting on a single "best date" y^*, then a mutant that started breeding just before y^* would have a large advantage, enjoying the best growing success in the population at the cost of a very small increase of risk. Hence, such synchronized breeding is not evolutionarily stable.

Let $g^*(y)$ be an evolutionarily stable distribution of breeding dates. Then all breeding individuals in the ESS will have the same fitness, λ, and the ESS is characterized by the two conditions:

$$\begin{aligned} \phi(y) &= \lambda , && \text{for all } y \text{ such that } g^*(y) > 0 \\ \phi(y) &\leq \lambda , && \text{for a } y \text{ such that } g^*(y) = 0 . \end{aligned} \qquad (6)$$

The first condition reflects the fact that individuals adopting different breeding dates must have the same fitness. The second condition indicates that a mutant breeding outside the

ESS range will have a lower reproductive success. Similar conditions are used in calculating the seasonal pattern of emergence of male butterflies (Iwasa *et al.*, 1983; Parker & Courtney, 1983; Bulmer, 1983); it is a temporal version of the ideal free distribution (Fretwell, 1972).

Indeed, it may be shown (Appendix A) that the evolutionarily stable distribution $g(y)$ is

$$g(y) = \begin{cases} \dfrac{f(y)}{\int_{x_c}^{t_f} f(x)dx} , & \text{for } y > x_c \\ 0 , & \text{for } y < x_c \end{cases} , \qquad (7a)$$

where the critical date x_c is given by:

$$\int_{x_c}^{t_f} f(x)dx = \frac{a}{1+a} . \qquad (7b)$$

Eq. (7b) indicates that the critical date x_c becomes very early (x_c is very close to 0) if competition is very strong (large a); in this case, the evolutionarily stable distribution $g(y)$ becomes close to $f(y)$, the probability distribution of the last disturbance date. In contrast, if the competitive advantage is small (small a), the critical date becomes close to the end of the season (x_c is close to t_f), and breeding should occur only after virtually all possible dates for disturbance have passed.

The distribution $g(y)$ specifies the number of individuals that should start breeding on each day in the ESS population. However, this can be realized in two different ways. The population may be a mixture of individuals having different pure strategies; alternatively all individuals can have a single mixed strategy that causes each individual to follow the probability distribution $g(y)$. The result Eq. (7) derived above does not distinguish among the two cases or from some combination of them.

Case 3: Locally Regulated Population

As stated earlier, use of the arithmetic mean in Case 1 is justified by considering a population composed of many patches that differ in the date of disturbance. In addition, population regulation is assumed to occur after the offspring from different patches are pooled together, which is termed hard selection (Christiansen, 1975; van Tienderen, 1991). In contrast, population size may be regulated within each patch or subhabitat, before being pooled: this is called soft selection. The latter may apply if the difference in the starting date of breeding causes differential growth among individuals, and competition among offspring occurs later in the season within local populations, so that the total reproductive success achieved in the local population is fixed.

The reproductive success of an individual with starting date y is proportional to that given in Eq. (2), but is normalized within each local population. Specifically the reproductive success of an individual with starting date y in a patch with last disturbance date x is:

$$\psi\left(y \mid x\right) = \begin{cases} \dfrac{e^{-by}}{\int_x^{\psi} g(z) e^{-bz} dz} , & \text{if} \quad y > x \\ 0 , & \text{if} \quad y < x \end{cases} \qquad (8)$$

The reproductive success of an individual with breeding date y is the average of ψ over the different local populations included in the whole population:

$$\phi(y) = \int_0^y \frac{e^{-by}}{\int_x^{\psi} g(z) e^{-bz} dz} f(x) dx \qquad (9)$$

The evolutionarily stable distribution is again given by Eq. (6). Namely

$$\int_0^y \frac{e^{-by}}{\int_x^{t_f} e^{-bz} g(z)dz} f(x)dx = \lambda \ , \qquad \text{for } y \ \text{ such that } g(y) > 0 \tag{10a}$$

$$\int_0^y \frac{e^{-by}}{\int_x^{t_f} e^{-bz} g(z)dz} f(x)dx \leq \lambda \ , \qquad \text{for } y \ \text{ such that } g(y) = 0 \tag{10b}$$

where λ is a constant.

According to the calculation in Appendix B, we can determine the ESS distribution *g(y)* satisfying Eq. (10). The solution of these equations is again a truncated distribution, where no oviposition occurs before a critical date x_c but some oviposition occurs every day after x_c. The critical date x_c is the solution of:

$$f(x_c) = b \int_0^{x_c} f(y)dy \ , \tag{11a}$$

and the evolutionarily distribution of oviposition dates is:

$$g(y) = \begin{cases} \dfrac{-1}{b\lambda} e^{by} \dfrac{d}{dy}\{f(y)e^{-by}\} \ , & \text{if} \quad y > x_c \\ 0 \ , & \text{if} \quad y < x_c \end{cases} \ . \tag{11b}$$

where λ is determined by

$$\lambda = \frac{f(x_c)}{b} + \int_{x_c}^{t_f} f(y)dy \ . \tag{11c}$$

Fig. 3 illustrates several examples of Eq. (11). The ESS solution *g(y)* is determined by the environmental disturbance distribution *f(x)* and growth advantage *b*. The critical date, or truncation date x_c decreases with the growth advantage *b*. If the growth advantage *b* is very strong, then the critical date x_c becomes very early, and *g(x)* becomes close to *f(y)* (Fig. 3A), but has a peak later than the peak of *f(y)*. In contrast, if the growth advantage

b is small, the critical date x_c becomes close to t_f and most breeding starts on the date all possible disturbance ends (Fig. 3B). The mean and the variance of the distribution $g(y)$ given by Eq. (11b) and their parameter dependency are derived in Iwasa & Haccou (1994).

Case 4: Synchronized Disturbance

In all three cases discussed above, it is assumed that the arithmetic average of reproductive success is the correct criterion for measuring evolutionary advantage. This is the case if disturbance occurs on a small spatial scale compared with the whole population so that the evironment is fine-grained. However, if instead disturbance is synchronized over the population in which the population regulation occurs, and if the population has no overlapping generations, then fitness is measured as the geometric average of reproductive success, instead of the arithmetic average (Lewontin & Cohen, 1969; Levins, 1962, 1968), because the function maximized is the average of logarithmic reproductive success. Therefore, we write the long-term average of the logarithmic rate of population increase per generation:

$$\phi(y) = \int_0^{t_f} \log[\psi(y \mid x)] f(x) dx \quad , \qquad (12)$$

instead of Eq. (3). We here assume that the fitness $\psi(y \mid x)$ is given by Eq. (2), i.e. we assume neither competition within the local population nor population regulation. Then Eq. (12) is the measure of adaptedness for a pure strategy y, i.e. the individual laying clutch on day y. When disturbances are synchronized, so that the enviornment is coarse-grained, the ESS is a mixed strategy (see Yoshimura & Clark, 1991, 1993; Haccou & Iwasa, 1994; Sasaki & Ellner, 1994), and can be specified by a probability distribution $p(y)$. The logarithmic fitness is given by a functional of $p(y)$:

$$\phi(p(\cdot)) = \int_0^{t_f} \log\left[\int_x^{t_f} e^{-by} p(y)dy\right] f(x)dx \qquad . \qquad (13a)$$

In the population dominated by the evolutionarily stable mixed strategy, no other strategy can have larger logarithmic average fitness as given by Eq. (13); hence the ESS mixed strategy is the one that attains the maximum of the above functional among all distributions satisfying

$$\int_0^{t_f} p(y)dy = 1 \ \text{ and } \ p(y) \geq 0 \qquad . \qquad (13b)$$

This is an optimization problem with constraint, and can be analyzed by Lagrange's method. According to the calculation in Appendix C, the optimal mixture $p^*(y)$ satisfies:

$$\int_0^{y} \frac{e^{-by}}{\int_x^{t_f} e^{-bz} p^*(z)dz} f(x)dx = \lambda \ , \qquad \text{for } y \ \text{ such that } p^*(y) > 0 \ , \qquad (14a)$$

$$\int_0^{y} \frac{e^{-by}}{\int_x^{t_f} e^{-bz} p^*(z)dz} f(x)dx \leq \lambda \ , \qquad \text{for } y \ \text{ such that } p^*(y) = 0 \ , \qquad (14b)$$

where λ is a positive constant. Interestingly, Eqs. (14) are mathematically equivalent to the condition for an evolutionarily stable mixture Eq. (10) if *p*(y)* is replaced by *g(y)*. This implies that the optimal mixed strategy *p*(y)* of case 4 is the same as the solution of the evolutionarily stable mixture *g(y)* obtained for case 3, the mixture solution for locally regulated populations (see Fig. 3). However there is a very important difference between them. In case 3, both a mixed strategy and a mixture of pure strategies achieve an evolutionary equilibrium population. In the present case of bet-hedging, a single mixed strategy, which is to take various behaviors with probability specified by $p^*(y)$, is optimal; but a mixture of pure strategies is not stable.

Combinations of different mechanisms

We can also study combinations of the three mechanisms that promote the evolution of asynchronous life history events. For example, we may consider the case in which fitness is locally regulated and, in addition, the last date of disturbance is synchronized over all the patches in the population. This problem is a combination of cases 3 and 4. Let the evolutionarily stable mixture be $p^*(x)$, and the probability distribution used by the mutant strategy be $p^*(x)$. Then the fitness of the mutant in the population dominated by the ESS type is

$$\phi(p(\cdot)) = \int \log\left[\int_x^{t_f} p(y)\frac{e^{-by}}{\int_x^{t_f} p^*(z)e^{-bz}dz}dy\right] f(x)dx \quad , \qquad (15)$$

where the fitness is normalized within each patch. This equation can be rewritten as

$$\phi(p(\cdot)) = \int \log\left[\int_x^{t_f} p(y)e^{-by}dy\right] f(x)dx - \int \log\left[\int_x^{t_f} p^*(z)e^{-bz}dz\right] f(x)dx \quad , \qquad (16)$$

where the second term is independent of the mutant strategy. The fitness must be largest when $p(x) = p^*(x)$. Hence the ESS type is simply the one that maximizes the first term of Eq. (16) and hence is the same as the one calculated in case 3 and in case 4. We conclude that the ESS mixed distribution when both local population regulation and synchronized disturbance operate together is the same as that when only one of the two mechanisms operates.

In Appendix D, we analyze (1) the case in which the population is regulated within local populations and the fitness is rank dependent, which is a combination of cases 2 and 3. The ESS is either a mixture of pure strategies or a mixed strategy. We also analyze (2) the case in which the fitness is rank dependent and disturbance occurs synchronously over the population, which is a combination of cases 2 and 4, and finally (3) the case corresponding to synchronized disturbance, local regulation, and rank-dependent fitness. The mixed strategy that evolves for both of these is exactly the same as a mixture of distributions from cases 2 and 3.

Discussion

In matters involving the timing of life history events, the evolutionarily stable population may exhibit general synchrony or a distribution of individual times that equalize fitness through frequency dependence. In this paper, we provide a framework for investigating this question, focusing on the seasonal timing of the start of breeding. We first consider the case (hard selection) in which fitness is frequency independent and the environment is fine-grained, so that natural selection operates on the average fitness over different local patches differing in disturbance date. In this case, the ESS involves a synchronous start of breeding.

In other situations (e.g. Case 2) asynchronous breeding may evolve. If, as is generally the case, the success of a strategy depends to some extent on whether others have acted first, fitnesses are frequency dependent, and determined by order or rank; in such a situation, asynchronous starts of breeding may evolve, either as a mixture of individuals having pure strategies, or as a population composed of genotypes each showing a mixed strategy, i.e. to choose the breeding date according to a probability distribution. Combinations of these can also occur. In a parallel situation, asynchronous pupation was demonstrated to be the evolutionarily stable solution for insect life cycles when competition among feeding larvae slows down the growth rate (Iwasa, 1991).

Asynchronous breeding can also result under soft selection, if the population size is regulated within local populations before being mixed together with many others, and if those individuals within local populations experience disturbance on the same date (Case 3) In this case the growth benefit may be frequency independent, with growth performance being a function of breeding date only; however because of population regulation within local populations, the fitness of a particular individual depends on the success of other individuals within the local population, which creates frequency dependence if viewed from the perspective of the whole population.

Asynchronous breeding can also result, however, in the absence (Case 4) of frequency dependence, provided disturbance is synchronized over all patches. In this case, a bet-hedging strategy will emerge, leading to an optimal mixed strategy formally equivalent to the equation for a mixed strategy for Case 3. However, there is an important difference: the ESS in this case is a strategy; one cannot have a mixure of many pure strategies, as was the case for Case 2 and Case 3. We also investigate combinations of these different mechanisms, examing the roles of frequency dependence and disturbance scale. Disturbance scale is well known to have important effects (Levin, 1992), introducing correlations that are of both ecological and evolutionary importance.

Let $S_{regulation}$ be the spatial scale of the population over which population regulation occurs, and $S_{disturbance}$ be that of a single disturbance event. In Case 1 above, $S_{regulation}$ is assumed to be much larger than $S_{disturbance}$ so that the population over which regulation occurs includes many local patch each created by a single disturbance event; genotypic fitness is calculated by averaging reproductive success over local patches. In this case, a pure strategy is expected to evolve though kin selection (not investigated here) may modify this. In Case 3, though the population includes many local subpopulations that differ in the timing of disturbance, population regulation occurs within each subpopulation, before averaging occurs. Hence $S_{disturbance}$ is the same as or even larger than $S_{regulation}$. In this case, a mixed strategy or a mixture of pure strategies is expected to evolve. The same is true for Case 2, rank-dependent fitness, where a mixture of pure strategies evolves. In Case 4, in which spatial structure is unimportant ($S_{regulation} = S_{disturbance}$), a mixed strategy results.

In short, we may conclude that a pure strategy should evolve if the spatial scale of each disturbance event is smaller than the spatial scale of the population in which regulation occurs. Otherwise, either a mixture of pure strategies or a r[illegible]d strategy, or some combination of them can evolve.

This paper is just a first step in the investigation of complex life history events, in which risks and benefits associated with timing of events must be balanced. The focus here has been on breeding, but the considerations are the same for a wide variety of other situations. Frequency dependence and spatial scale are both shown to be considerations of general importance.

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Appendix A

Analysis of the ESS for Case 2 (rank-dependent fitness):

To investigate the dependence of fitness on breeding date y, differentiate (5) to yield

$$\frac{d\phi}{dy} = f(y) - a\, g(y)\phi(y) \quad . \qquad \text{(A1)}$$

For an interval in which $g(y) = 0$ holds, $\phi(y)$ increases since

$$\frac{d\phi}{dy} = f(y) > 0 \quad .$$

This means that, for an ESS, $g(y)$ can be 0 on an interval, but not for any y greater than the first for which $g(y) > 0$. Hence the ESS must be of the form:

$$\begin{array}{lll} g(y) = 0 \quad , & \text{for} & 0 < y < x_c \\ g(y) > 0 \quad , & \text{for} & x_c < y < t_f \end{array}$$

For $0 < y < x_c$, ϕ increases with y and reaches its maximum at $y = x_c$:

$$\phi(x_c) = \int_0^{x_c} f(x)dx \quad , \qquad \text{(A2)}$$

From Eq. (6), $\phi(y) = \phi(x_c)$ for $x_c < y < t_f$. Hence, Eq. (A1) yields

$$g(y) = \frac{f(y)}{a\,\phi(x_c)} \quad . \qquad \text{(A3)}$$

By integrating (A3) from x_c to t_f, we have

$$1 = \frac{1}{a\,\phi(x_c)}\int_{x_c}^{t_f} f(y)dy$$

which together with Eq. (A2) results in (7b) in the text.

Appendix B

To investigate soft selection, we begin by considering the case in which the evolutionary equilibrium includes two intervals separated by a critical date x_c, and that $g(y) = 0$ holds before x_c but $g(y) > 0$ after x_c. Then the critical date x_c and the shape of $g(y)$ are determined as follows:

First we note that, for $y > x_c$, Eq. (9) may be rewritten as

$$\phi(y) = \int_0^{x_c} f(x)\frac{e^{-by}}{\int_{x_c}^{t_f} g(z)e^{-bz}dz}dx + \int_{x_c}^{y} f(x)\frac{e^{-by}}{\int_{x}^{t_f} g(z)e^{-bz}dz}dx \qquad \text{(B1)}$$

where integrals with respect x are separated into pieces before and after the critical date. Differentiating Eq. (B1), and noting that $\phi(y) = \lambda$ holds for $y \geq x_c$, we have:

$$0 = -b\lambda + \frac{f(y)e^{-by}}{\int_{y}^{t_f} g(z)e^{-bz}dz} \qquad . \qquad \text{(B2)}$$

By rearranging factors and differentiating, we have

$$g(y) = \frac{-1}{b\lambda}e^{by}\frac{d}{dy}\left[f(y)e^{-by}\right] \qquad , \qquad \text{(B3)}$$

for $y > x_c$. Since the integral of g from x_c to t_f must be equal to one, we have

$$1 = \frac{-1}{b\lambda}\int_{x_c}^{t_f} e^{by}\frac{d}{dy}\left[f(y)e^{-by}\right]dy \qquad \text{(B4)}$$

By integration by parts, Eq. (B4) can be rewritten as

$$\lambda = \frac{f(x_c)}{b} + \int_{x_c}^{t_f} f(y)dy \tag{B5}$$

On the other hand, since $g(y) = 0$ before the critical date x_c, Eq. (9) at the critical date x_c yields:

$$\lambda = \frac{e^{-bx_c}}{\int_{x_c}^{t_f} g(z)e^{-bz}dz} \int_0^{x_c} f(x)dx \tag{B6}$$

By combining (B6) and (B2) with $y = x_c$, we have Eq. (11a), by which we can detemine the critical date.

In general, the time axis may be composed of more than two intervals so that $g(y) > 0$ and $g(y) = 0$ hold alternatively. With some additional argument, we can prove that the evolutionarily stable solution must have the form explained above. Here we take an easy step. The problem we are analyzing here is mathematically equivalent to the model studied elsewhere in a very different context -- the seasonal pattern of male butterfly emergence (Iwasa *et al.*, 1983). By reversing the time axis by making the substitutions $t_f - x \rightarrow x$, $t_f - y \rightarrow y$, and $t_f - z \rightarrow z$, we can rewrite Eq. (9) as

$$\phi(y) = \int_y^{t_f} \frac{f(x)e^{-b(x-y)}}{\int_0^y g(z)e^{-b(x-z)}dz} dx \tag{B7}$$

This is the same as the fitness discussed by Iwasa *et al.* (1983), in which $f(x)$ and $g(x)$ are the number of males and females emerging on day x , b is the daily mortality of adult males and $\phi(y)$ is the expected number of matings for a male emerging on day y. Then Eq. (6) is the condition for the evolutionarily stable male emergence curve for a given female emergence curve. In the Appendix of Iwasa *et al.* (1983) it is proved that there exists a single solution $g(y)$ and, if the function $f(x)e^{-bx}$ has a single peak, the evolutionarily stable emergence curve is a truncated distribution, such that some males should emerge before it, and no males after it. By reversing the time axis, we have the same solution as for Case 2 and Case 3 of the present paper.

Appendix C

The problem of optimization of Eq. (13a) under the equality constraint (13b) (the value of the integral is always 1), can be transformed to an optimization problem without equality constraint:

$$\tilde{\phi}(p(\cdot)) = \int_0^{t_f} \log\left[\int_x^{t_f} e^{-by} p(y)dy\right] f(x)dx - \lambda \int_0^{t_f} p(y)dy \qquad \text{(C1)}$$

under the remaining inequality condition ($p(y) \geq 0$, for all y), where λ is a positive constant, called Lagrange's multiplier.

To know the maximum of a smooth function in general, we calculate the derivative of the function. The same is true for the optimization of the functional (C1), but we need a functional derivative which is a partial derivative of a functional with an infinite number of variables. We calculate the sensitivity of $\tilde{\phi}$ to the perturbation made to $p(z)$ around the day y.

$$\begin{aligned} \frac{\delta\tilde{\phi}}{\delta p(y)} &= \lim_{\varepsilon \to 0} \frac{\tilde{\phi}(p(z)+\varepsilon\delta(z-y)) - \tilde{\phi}(p(z))}{\varepsilon} \\ &= \int_0^{y} \frac{e^{-by}}{\int_x^{t_f} e^{-bz} p(z)dz} f(x)dx - \lambda \end{aligned} \qquad \text{(C2)}$$

The condition for optimality under the inequality condition $p(y) \geq 0$, for all y, is that the derivative (C2) is zero if $p(y) > 0$, but (C2) is negative or zero if $p(y) = 0$. This is Eq. (14a and b) in the text

Appendix D

Locally regulated population with rank-dependent fitness:

We may consider the case of a locally regulated population with rank dependent fitness, which is a combination of Case 2 and Case 3. The fitness of an individual is

$$\phi(y)=\int_0^y \frac{\exp\left[-a\int_x^y g(z)dz\right]}{\int_x^{t_f} g(u)\exp\left[-a\int_x^u g(z)dz\right]du} f(x)dx=\lambda \quad , \qquad \text{for} \quad g(y)>0, \tag{D1a}$$

$$\phi(y)=\int_0^y \frac{\exp\left[-a\int_x^y g(z)dz\right]}{\int_x^{t_f} g(u)\exp\left[-a\int_x^u g(z)dz\right]du} f(x)dx\leq\lambda \quad , \qquad \text{for} \quad g(y)=0. \tag{D1b}$$

Multiply both sides of (D1a) by $g(y)$ and integrate over y, to obtain

$$\int_0^{t_f}\phi(y)g(y)dy=\int_0^{t_f}\int_0^{t_f}\frac{\chi(y>x)\,g(y)\exp\left[-a\int_x^y g(z)dz\right]}{\int_x^{t_f} g(u)\exp\left[-a\int_x^u g(z)dz\right]du} f(x)dxdy$$

$$=\int_0^{t_f} f(x)dx=1$$

where $\chi(y>x)=1$ if $y>x$; $\chi(y>x)=0$ otherwise. Hence $\lambda=1$. Eq. (D1a) can then be rewritten as

$$\exp\left[-a\int_0^y g(z)dz\right]\int_0^y \frac{f(x)}{\int_0^{t_f} g(u)\exp\left[-a\int_0^u g(z)dz\right]du}dx = 1 \qquad \text{(D2)}$$

which holds for $g(y) > 0$.

The ESS distribution $g(y)$ satisfying Eq. (6) has a critical date x_c: $g(y) = 0$ for $y < x_c$, and $g(y) > 0$ for $y > x_c$. After some algebra, we rewrite the equality (D2) as:

$$\int_y^{t_f} f(z)dz = \int_y^{t_f} g(z)dz + \frac{1}{a}\left(\exp\left[-a\int_y^{t_f} g(z)dz\right] - 1\right) \qquad \text{(D3)}$$

From which we can compute the ESS distribution $g(y)$. Since the integral of $g(y)$ is one, the critical date x_c is determined by:

$$\int_{x_c}^{t_f} f(z)dz = \frac{1}{a}\left(e^{-a} - 1 + a\right) \qquad \text{(D4)}$$

Using an expression for $g(y) = 0$ similar to (D2), we can confirm that $\phi(y)$ increases with y for $y < x_c$.

Synchronized disturbance and rank-dependent fitness:

Now we consider the case in which disturbance date is synchronized over the population and the fitness is rank dependent. This is a combination of cases 2 and 4. Let $p^*(x)$ be the ESS mixed strategy and $p(x)$ be the probability distribution of traits x for the mutant that is very low in frequency. The logarithmic average fitness of the mutant is:

$$\phi(p(\cdot)) = \int \log\left[\int_x^{t_f} p(y)\exp\left[-\int_x^{t_f} p^*(z)dz\right]dy\right] f(x)dx$$

which is to be maximized when $p(x) = p^*(x)$. The optimality conditions under the constraints ($\int_0^{t_f} p(y)dy = 1$ and $p(y) \geq 0$) are:

$$\frac{\delta\Phi}{\delta p(w)} = \int \frac{\chi(y > x)\exp\left[-\int_y^{t_f} p^*(z)dz\right]}{\int_x^{t_f} p(y)\exp\left[-\int_x^{t_f} p^*(z)dz\right]} f(x)dx - \lambda$$

is zero for $p^*(w) > 0$, and is negative for $p^*(w) = 0$, where λ is a Langrange's multiplier. An analysis similar to that for case 4 leads to Eq (D1a) and (D1b) if $p^*(x)$ is replaced by $g(x)$. Hence the optimal mixture distribution $p^*(x)$ for rank-dependent fitness with synchronized disturbance (combination of Case 2 and Case 4) is the same as the ESS mixture $g(x)$ for a locally regulated population with rank-dependent fitness (combination of Case 2 and Case 3).

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Figure legends

Fig. 1. Illustration of population structure assumed in the models.

(A) Globally regulated population. The population regulation occurs in the pool after offspring from different subpopulations are mixed together. The different subpopulations receive disturbance at different dates. This corresponds to Case 1 in the text. A single pure strategy should evolve.

(B) Locally regulated population. The population regulation occurs within each subpopulation. This corresponds to Case 3 in text. Either a mixture of pure strategies or a single mixed strategy should evolve.

(C) Synchronized disturbance. The dates of disturbance for different subpopulations are synchronized. This corresponds to Case 4 in text. A single mixed strategy should evolve.

Fig. 2 The evolutionary stable distribution of starting date for Case 2 (rank dependent fitness). $f(t) = 2.968\times10^{-5}x^3(10 - x)^{2.5}$. In (A) competitive advange of starting breeding early is large (a= 1.5) and truncation occurs relatively early (x_c = 4.886). In (B), the competitive advantage is small(a = 0.3) and the truncation date is late (x_c = 6.705).

Fig. 3 The evolutionary stable distribution of starting date for Case 3 (locally regulated population). $f(t)$ is the same as in Fig. 2. In (A) growth advange is large (b = 1.5) and the truncation occurs relatively early (x_c = 2.298). In (B) , the growth advantage is small(b = 0.3) and the truncation date is late (x_c = 6.167). If we regard $g(y)$ as a probability distribution for a mixed strategy, the same graph gives the optimal mixed strategy for Case 4.

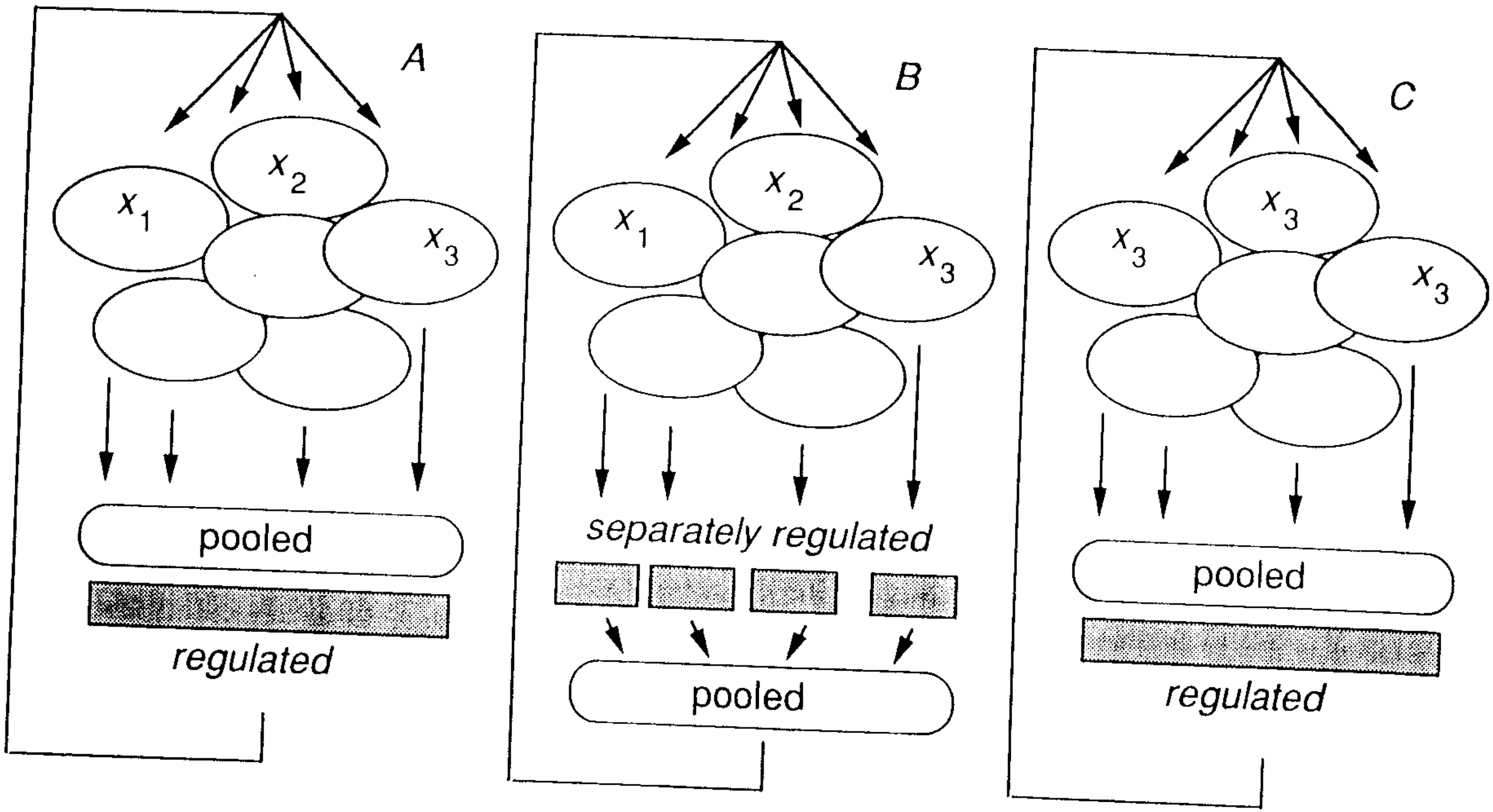
A
x_1
x_2
x_3
pooled
regulated
B
x_1
x_2
x_3
separately regulated
pooled
C
x_3
x_3
x_3
pooled
regulated

Fig. 2a

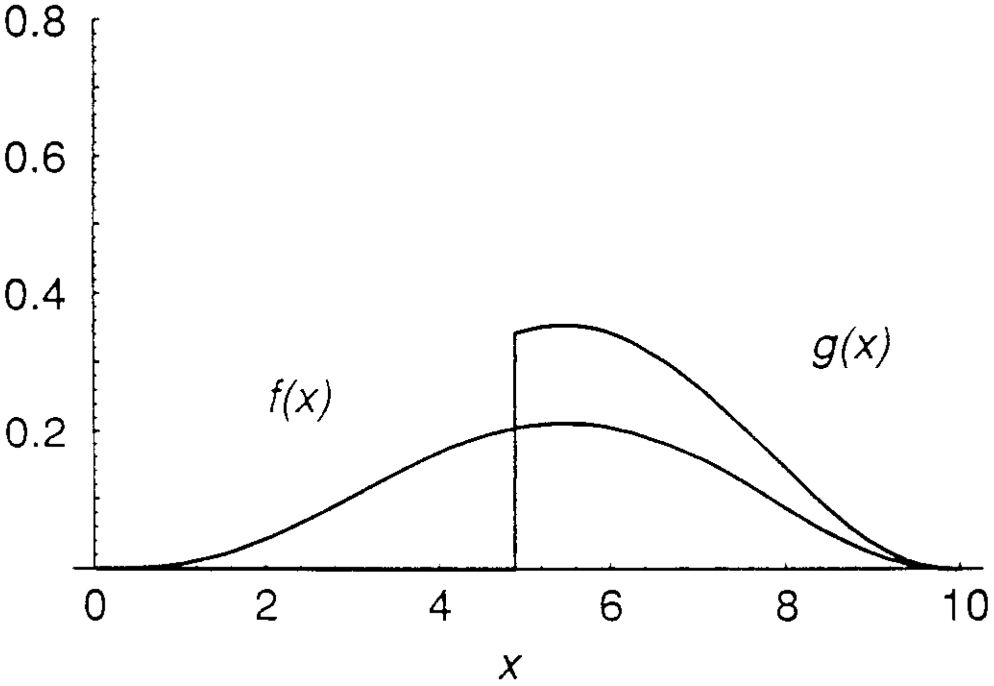

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Fig. 2b

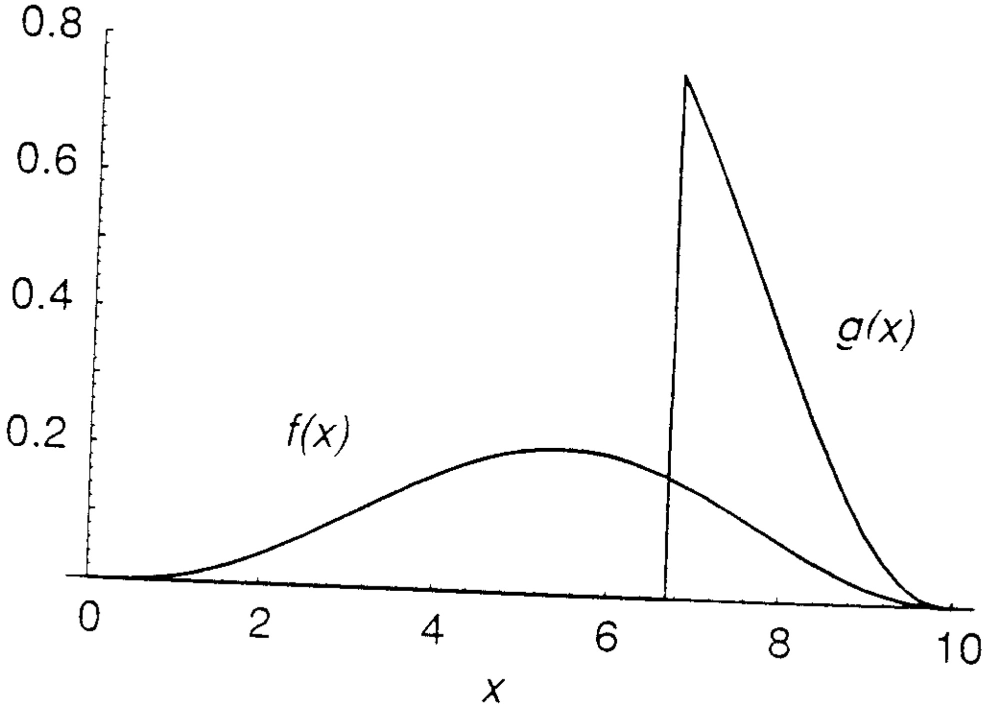

Fig. 3a

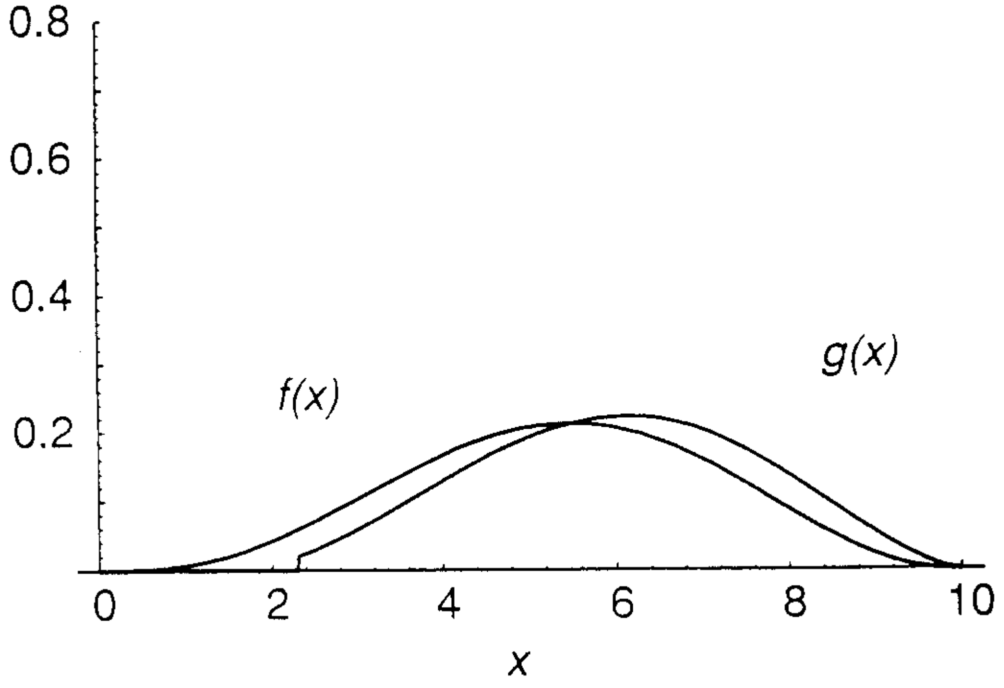

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Fig. 3b