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Ilkka Hanski: The legacy of a multifaceted ecologist

Conditional reproductive strategies under variable environmental conditions

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Within the framework of adaptive dynamics we consider the evolution by natural selection of reproductive strategies in which individuals may adjust their reproductive behaviour in response to changing environmental conditions. As a specific example we considered a discrete-time model in which possible fluctuations in the environmental conditions are caused by predator–prey interaction. Our main findings include: (1) Coexistence between two fixed strategies (i.e., strategies that do not adjust to changing environmental conditions) is impossible; there exists a best fixed strategy, which invades and ousts all other fixed strategies. (2) A necessary condition for conditional (adjustable) strategies to evolve is that there are fluctuations in the environmental conditions. Predator–prey interactions may cause such fluctuations and under natural assumptions there exists an optimal conditional strategy which is uninvadable and invades and ousts all other strategies.

Introduction

Adaptive dynamics is a framework within which it is possible to explicitly link evolution by natural selection to population dynamics. This is an extremely important aspect of evolutionary theory because population dynamics is shaped by interactions through the environment and the fitness of an individual depends on the environment it experiences. At an ecological equilibrium the environmental conditions remain constant and much of the early work of adaptive dynamics has dealt with questions such as invasion, trait substitution and branching under such steady environmental conditions.

In nature the environmental conditions never remain constant. It is well known that very simple ecological models may lead to cyclic or even chaotic behaviour and even if a particular model would predict convergence to a steady state, the true system would still show fluctuations in the environmental conditions due to "noise", that is, interactions that have been neglected in the model. It is therefore imperative to consider adaptive dynamics in the case of variable environmental conditions (Kisdi & Meszéna 1993, Ripa & Dieckmann 2013).

When the environmental conditions are allowed to fluctuate a new aspect enters the scene of adaptive dynamics: individuals may

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[#] An earlier version of this article was completed while Ilkka Hanski was still alive. The co-authors dedicate the paper to the memory of Ilkka — a friend and collaborator for almost 30 years.

adjust their behaviour in response to the changing conditions. The traits or strategies cannot then any longer be expressed by finite dimensional quantities, but should be functions of the environmental conditions. Adaptive dynamics of function-valued traits have been discussed, among others, by Parvinen *et al*. (2006, 2013), Dieckmann *et al*. (2006) and by Metz *et al*. (2016). In this paper, we give a treatment of adaptive dynamics of such conditional strategies in the context of a class of simple ecological models in discrete time.

The setting

The basic unit of a population is the individual. When modelling the dynamics of populations the first task is to describe the development, survival and reproductive behaviour of individuals. The individual behaviour depends on the *environmental conditions* that usually vary with time. One should not in the first hand think of the environmental conditions an individual perceives as exogenous conditions such as seasonally varying temperature, but rather as quantities summarizing the effect upon the behaviour of the individual of all individuals (both conspecific and others) it is interacting with. In fact, all interactions should be modelled through the environmental conditions, which we therefore also call (*environmental*) *interaction variables* (Diekmann *et al*. 2001, 2003). We collect all the interaction variables into a vector, which we denote by *I*.

In nature there are interactions of many different types. Individuals may cooperate or they may compete for common resources such as food or territory. The interaction variables should then reflect quantities like food density or the availability of territory. In predator–prey interactions the prey density should be an interaction variable for the predators (indeed, that is their food!), whereas predation pressure (which is a function of predator density) should be included among the interaction variables for the prey. In general, the interaction variables are functions of the densities of the interacting populations.

Let us recapitulate the basic modelling setup: The environmental interaction variable I determines individual behaviour, whereas the individuals contribute to the environment (e.g. by consuming food). This leads to a feedback loop.

Mathematically the modelling using interaction variables means that if we cut the feedback loop and assume I to be a given function of time, then the resulting model is *linear* (but time-dependent). The biological interpretation of this thought experiment is that individuals do not interact at all but are independent of each other. Closing the feedback loop one obtains a nonlinear autonomous problem, the solution of which we seek.

In this paper, we shall for expository reasons consider a very simple situation. We consider an unstructured semelparous population in discrete time. The time instants $n = 0, 1, 2, \ldots$ are the instants at which reproduction (and death of the parent) takes place. According to the general modelling principles outlined above, the model takes the following form:

$$x_{n+1} = x_n R_x(I_n). \qquad (1)$$

Here x_n denotes the population density at the the beginning of the nth season (immediately after reproduction). $R_x(I)$ is the *per-capita recruitment*, that is, the expected number of offspring produced by an individual, given the value I of the environmental condition. We shall refer to this population as the *resident* population.

We are interested in the possible success of a *mutant* y using a different strategy, that is, having a different per-capita recruitment $R_y(I)$. We, therefore, couple Eq. 1 with the equation

$$y_{n+1} = y_n R_y(I_n). \qquad (2)$$

The Eqs. 1 and 2 describe competition between the two types x and y. We emphasize once more that all interactions happen through I: the y variable does not appear in the x equation and neither does x appear in the y equation. For most of our arguments the precise form of the feedback function, that is, the function prescribing how I depends on x, y and possibly other interacting populations, is irrelevant.

We shall now simplify matters further and assume that the interaction variable I is a scalar. This means that we assume that everything that is population dynamically relevant about the environment can be summarized in a single real number. We choose I non-negative such that $I = 0$ corresponds to a population-free, or *virgin*, environment and such that an increase in any of the interacting populations leads to an increase in I.

To model the unavoidable detrimental effects of crowding upon birth and the decreased survival due to crowding and/or the activity of other interacting populations (e.g. predators), we assume that greater I entails lower recruitment. In the monomorphic case one can then always (after a suitable rescaling of I) write the per-capita recruitment as

$$R(I) = \beta \exp(-kI). \tag{3}$$

If one in the monomorphic case takes $I = x$, Eqs. 1 and 3 reduce to the well-known model first introduced by Ricker (1954). It should be stressed that Eq. 3 is not merely the result of a mathematical transformation: mechanistic derivations of Eq. 3 in the single-species case can be found for instance in the book by Thieme (2003).

In the polymorphic case a transformation of the per-capita recruitment to the form in Eq. 3 that would hold for the different types simultaneously is of course not possible in general. We now make the *assumption* that the per-capita recruitment is of the form in Eq. 3, with type specific parameters k and β, when there are more that one type present. In the Appendix we derive a concrete predator–prey model, in which the parameters k and β are given clearcut biological interpretations. Here we are content with the following qualitative description: The parameter k in Eq. 3 measures the strength of the density-dependence or the competitive ability and β can be interpreted as the average clutch size at low density, when there is no negative effect of density on reproduction. (We use the term 'clutch' as a shorthand for a 'batch of offspring born at the same time', with no intention of restricting the results to species for which 'clutch' is generally used in the biological literature.)

We assume that the parameters k and β are subject to selection and evolvable.

Finally we assume a trade-off between reproductive effort and competitive ability by making k a function of β. We assume that individuals producing small clutches do better in competition than individuals producing large clutches. This assumption has substantial empirical support for many organisms (Stearns 1992), and requires k to be an increasing function of β. If the population densities are low the trade-off is usually less pronounced than if the densities are high. One should therefore allow k to depend explicitly on the environment I. A convenient assumption that covers quite a number of potential forms of the trade-off, at least qualitatively, is that k is a product of a function depending only on I and a function depending only on β:

$$k = k(I,\beta) = k_1(I)k_2(\beta). \tag{4}$$

From what has been said above it follows that k_1 should be nondecreasing and k_2 increasing. Inserting Eq. 4 into Eq. 3 of the per-capita recruitment one obtains

$$R(I) = \beta \exp(-k_2(\beta)k_1(I)I). \tag{5}$$

If we now redefine the environment as $k_1(I)I$, we see that we can assume that the function $k = k_2$ depends on β only. We shall follow this convention throughout the paper.

Individual reproductive choices may be affected by the current environment. Breeding females of many animals are capable of responding to changing environmental conditions by for instance reducing clutch size, resorbing embryos and possibly by selectively lactating only some of their offspring. We shall distinguish between fixed and conditional reproductive strategies. A *fixed* reproductive strategy is modelled by assuming that an individual at each reproductive event produces on average a fixed number β of young. In a *conditional* strategy the clutch size β depends on the environmental interaction variable I. In the latter case the per-capita recruitment has the form

$$R(I) = \beta(I)\exp\big(-k(\beta(I))I\big). \tag{6}$$

If the population dynamics is such that the system settles down to a steady state, then the interaction variable will be constant. It is self-evident that under such steady environmental conditions there cannot be any advantage of conditional strategies, simply because under steady conditions they cannot be distinguished from fixed ones. We shall therefore assume an underlying ecological model, which leads to fluctuating populations and hence changing varying environmental conditions. The most obvious ecological interaction leading to fluctuations is predator–prey interaction. The numerical examples given in this paper are based on a predator–prey model originally derived by Gyllenberg *et al*. (1996) and for completeness reproduced in the Appendix. The details of the model are irrelevant for the results presented in this paper. As all biologically relevant models, this model predicts that population sizes remain bounded — a fact that will be used frequently in the mathematical elaborations.

Invasion

We consider competition between different reproductive strategies. Two fundamental questions are of course those of invadability and outcompetition of a resident type by a mutant following a different strategy.

Assume that the dynamics of a resident type x with per-capita recruitment $R_x(I)$ has settled down to an attractor. We shall refer to the corresponding sequence of environments as (I_1^{res}, I_2^{res}, ...). Consistency then requires that

$$\lim_{n\to\infty}\frac{1}{n}\sum_{i=1}^{n}\log R_x\left(I_i^{\text{res}}\right)=0. \qquad (7)$$

Assume now that a mutant type y with per-capita recruitment $R_y(I)$ enters the population. To begin with it will appear in very small numbers and it will therefore not perturb the resident population density from the attractor very much. The environment experienced by the mutant will therefore be given by the sequence (I_1^{res}, I_2^{res}, ...). Invasion will be successful if and only if the logarithm of the per-capita recruitment of the mutant is positive on average, that is, if and only if

$$\lim_{n\to\infty}\frac{1}{n}\sum_{i=1}^{n}\log R_y\left(I_i^{\text{res}}\right)>0. \qquad (8)$$

With the choice (Eq. 6) of the per-capita recruitment the criterion (Eq. 8) takes on the form

$$\lim_{n\to\infty}\frac{1}{n}\sum_{i=1}^{n}\left(\log\beta_y\left(I_i^{\text{res}}\right)-k\left(\beta_y\left(I_i^{\text{res}}\right)I_i^{\text{res}}\right)\right)>0. \qquad (9)$$

If the resident attractor is very complicated it is of course in general hard to determine whether the condition in Eq. 9 is valid or not. But if the mutant y adopts a fixed strategy the parameter β_y is a constant and the invasion criterion reduces to

$$\frac{\log\beta_y}{k\left(\beta_y\right)}>I_{\text{ave}}^{\text{res}}, \qquad (10)$$

where $I_{\text{ave}}^{\text{res}}$ denotes the average of the environmental interaction variable calculated over the resident attractor. This result gains in interest when we realize that the left hand side of Eq. 10 is the value $I_{\text{fix}}^{\text{mut}}$ of the environmental interaction variable when the mutant is at a fixed point. We can thus rewrite Eq. 10 as

$$I_{\text{fix}}^{\text{mut}}>I_{\text{ave}}^{\text{res}}, \qquad (11)$$

and state the result as follows: *A mutant adopting a fixed strategy can invade if and only if the the value of the environmental interaction variable corresponding to a fixed point of the mutant is greater than the average value of the environment calculated over the resident attractor. This result holds regardless of whether the resident adopts a fixed or a conditional strategy*.

Fixed reproductive strategies

If both the resident and the mutant adopt fixed strategies the analysis can be considerably refined. Dividing Eq. 2 by Eq. 1 one obtains

$$\frac{y_{n+1}}{x_{n+1}}=\frac{y_n\beta_y\exp\left(-k\left(\beta_y\right)I_n\right)}{x_n\beta_x\exp\left(-k\left(\beta_x\right)I_n\right)} \qquad (12)$$

from which it follows that

$$\frac{y_{n+1}^{1/k\left(\beta_y\right)}}{x_{n+1}^{1/k\left(\beta_x\right)}}=\frac{\beta_y^{1/k\left(\beta_y\right)}}{\beta_x^{1/k\left(\beta_x\right)}}\frac{y_n^{1/k\left(\beta_y\right)}}{x_n^{1/k\left(\beta_x\right)}}. \qquad (13)$$

If

$$I_{\text{fix}}^{\text{mut}}=\frac{\log\beta_y}{k\left(\beta_y\right)}>\frac{\log\beta_x}{k\left(\beta_x\right)}=I_{\text{fix}}^{\text{res}} \qquad (14)$$

then $\beta_y^{1/k(\beta_y)}\big/\beta_x^{1/k(\beta_x)}>1$ and hence $y_n^{1/k(\beta_y)}\big/x_n^{1/k(\beta_x)}$

tends to infinity as n tends to infinity independently of the initial state. Since all orbits are bounded, this is possible only if x_n tends to zero. We thus conclude that *in the case of fixed reproductive strategies the mutant invades and outcompetes the resident if and only if the mutant in the absence of the resident gives rise to a higher value of the environmental interaction variable at the fixed point than the resident*.

We emphasize that this result is independent of the actual dynamics. Even in the case of chaotic dynamics it is the fixed point value of I that determines whether invasion and outcompetition takes place.

The result has an interesting corollary. Assume that Eq. 14 does not hold. Then because of the interchangeability of the mutant and the resident (both adopt fixed strategies!), the resident will outcompete the mutant, which means that the mutant could never have invaded. Thus invasion is actually equivalent with the seemingly stronger condition of invasion and outcompetition. It follows that

$$I_{\text{fix}}^{\text{res}} = I_{\text{ave}}^{\text{res}}, \tag{15}$$

in other words: *The average value of the environmental interaction variable corresponding to a type adopting a fixed reproductive strategy equals the value of the environmental interaction variable at the fixed point*.

It is funny to see how easily this result was achieved when density dependence and interaction is modelled using the environment variable I. We have not been able to prove it directly from the difference equation.

Even if the resident attractor contains infinitely many points the sign of the dominant Lyapunov exponent

$$\log\beta_y - k(\beta_y)I_{\text{ave}}^{\text{res}} \tag{16}$$

is determined by the scalar property $I_{\text{ave}}^{\text{res}}$ of the attractor. Adopting the terminology of Meszéna and Metz (1999), the *effective dimension of the environmental feedback* therefore equals one. According to the general principle of competitive exclusion put forward by Géza Meszéna and collaborators (Meszéna & Metz 1999, Diekmann *et al*. 2003, Gyllenberg and Meszéna 2005, Meszéna *et al*. 2006, Barabas *et al*. 2012) the number of types that can robustly coexist is lower than or equal to the effective dimension of the environmental feedback. In the one dimensional case coexistence is therefore not possible. This is in concordance with our result above.

Our models have the special feature that the environment I is a one-dimensional variable. Moreover, in the case of fixed strategies the basic reproduction numbers of the types are decreasing functions of I. Diekmann and Mylius (1995) (*see* also Metz *et al*. 2008, Gyllenberg *et al*. 2011) showed that it follows from this that if population dynamics leads to a steady state with constant I, then a type x is evolutionarily stable if and only if the function which assigns to a type the environmental value at which the population will be steady has a maximum at x. The results above show that for our model of fixed strategies the same is true even if stabilization of population dynamics does not occur.

Fisher (1930) and Charlesworth (1980) noted that selection maximizes mean population size under certain conditions in single-species models. This principle is violated for many multi-species systems including predator–prey systems (Levins 1975, Roughgarden 1976, León and Charlesworth 1978). In our model of fixed reproductive strategies selection maximizes the mean value $I_{\text{ave}}^{\text{res}}$ of the environmental interaction variable I. For the particular predator–prey model of the Appendix, $I_{\text{ave}}^{\text{res}} = \log\beta_x/k(\beta_x)$ is the mean prey population size *in the absence of predation* (and in the absence of the mutant). But maximizing this quantity is not the same as maximizing mean population size. This is illustrated in Fig. 1 in which panel **a** depicts $I_{\text{ave}}^{\text{res}} = \log\beta_x/k(\beta_x)$ as a function of β for a particular choice of the trade-off $k(\beta)$, and panel **b** shows the mean prey population size obtained from the predator–prey model. The curve in **b** attains its maximum for a smaller value of β than the curve in **a** and therefore the maximum mean prey population size is not selected for.

Conditional reproductive strategies

As shown in the previous section, coexistence

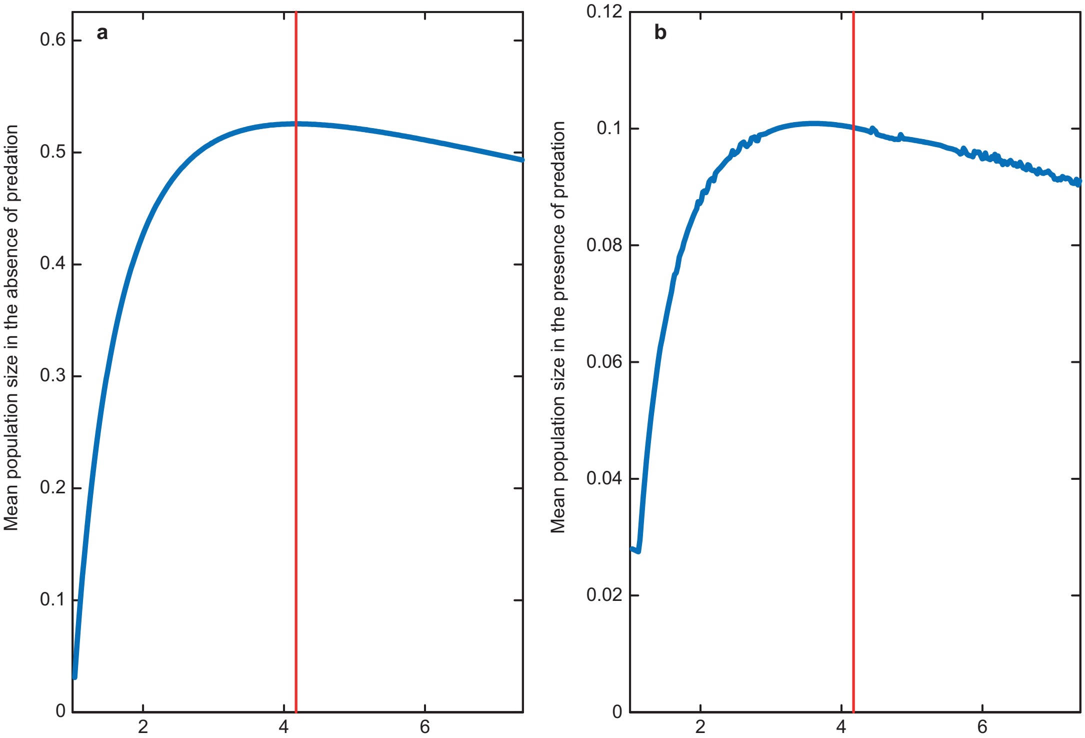

Fig. 1. Mean population size for the prey in (**a**) the absence of predation for the parameter values $am\mathcal{F} = 21.0$, $\mathcal{F} = 0.4$, $k(\beta) = \beta^p$ and $p = 0.7$; and (**b**) the presence of predation for the same parameter values. The selected fixed strategy marked with a vertical line has clutch size $\beta = 4.1727$ in both cases.

between two fixed strategies is not possible since the type with larger I_{ave} will always outcompete the other type. On the other hand, two conditional strategies may very well coexist. As a matter of fact, even a fixed and a conditional strategy may invade each other and thus coexist. This is demonstrated by the following example.

Example

Let $k(\beta) = \beta$. Since $\log\beta/\beta$ assumes its maximum at $\beta = e$, the best fixed strategy is to produce on average $\beta = e$ offspring. The average value of the environment corresponding to the best fixed strategy is $1/e$. Assume that a conditional strategy is given by

$$\beta(I) = \frac{M}{I+d}, \tag{17}$$

In the following, we choose $M = 3.8$ and $d = 2.25$. Again we take the predator–prey model of the Appendix as the underlying ecological model. For the parameters describing predator behaviour we choose $a = 120$, $\mathcal{F} = 0.15$ and $m = 1$.

We first consider the case in which the resident adopts the best fixed strategy. Simulations show that the attractor lies on an invariant curve in the (x,I)-plane and that the dynamics on this curve are complicated (quasiperiodic or chaotic). Mathematically inclined readers will realize that the nontrivial fixed point has lost its stability through a Hopf bifurcation. Furthermore

$$\lim_{n\to\infty} \frac{1}{n} \sum_{i=1}^{n} \log R_y\left(I_i\right) \approx 0.06 > 0 \tag{18}$$

showing that the conditional strategy can invade the best fixed strategy provided predators exist in the population. Assume now that the resident follows the conditional strategy. The attractor looks very similar to the one corresponding to the best fixed strategy, but the amplitude is considerably smaller. This is due to the general stabilizing effect of conditional strategies (Gyllenberg *et al*. 1996). Can a mutant adopting the best fixed strategy invade? The average value of the resident environment was found to be $I^{\text{res}}_{\text{ave}} \approx 0.35$ which is less than $I^{\text{mut}}_{\text{fix}} = 1/e$ and so the best fixed strategy can indeed invade. Figure 2 shows the resident attractor for the cases in which the resident adopts either the fixed or the conditional strategy and the projection of the attractor onto the (x,y)-coordinate plane in the case of coexistence, between the best fixed strategy x and the conditional strategy. The three-dimensional situation is depicted in Fig. 3.

In order to compare the amplitudes of the different oscillations we plotted the resident attractor of the fixed strategy, the resident attractor of the conditional strategy, and the slanted projection of the coexistence attractor in the same log-scaled plane (Fig. 4). It is now clearly visible that the amplitude of the coexistence attractor is strictly located between the amplitudes of the fixed and the conditional attractor, respectively.

An optimization principle

It is intuitively clear that a type, which under all environmental conditions has a greater per-capita recruitment than its competitors, has an advantage. We already saw an example of this in the section 'Fixed reproductive strategies' in the case of competition between two fixed strategies.

The best an individual can achieve is to maximize its contribution to the next generation. With a per-capita recruitment given by Eq. 3 and trade-off given by k this amounts to having a per-capita recruitment equal to

$$R(I) = \sup_{0<\beta\le M(I)} \beta\exp\left(-k(\beta)\right), \qquad (19)$$

where $M(I)$ is the maximum clutch size when the environment is I. For physiological reasons individuals cannot produce an arbitrarily large number of offspring and therefore $M(I) < \infty$ for all I.

Next we show that under natural assumptions such an optimal reproductive strategy exists indeed. We assume that

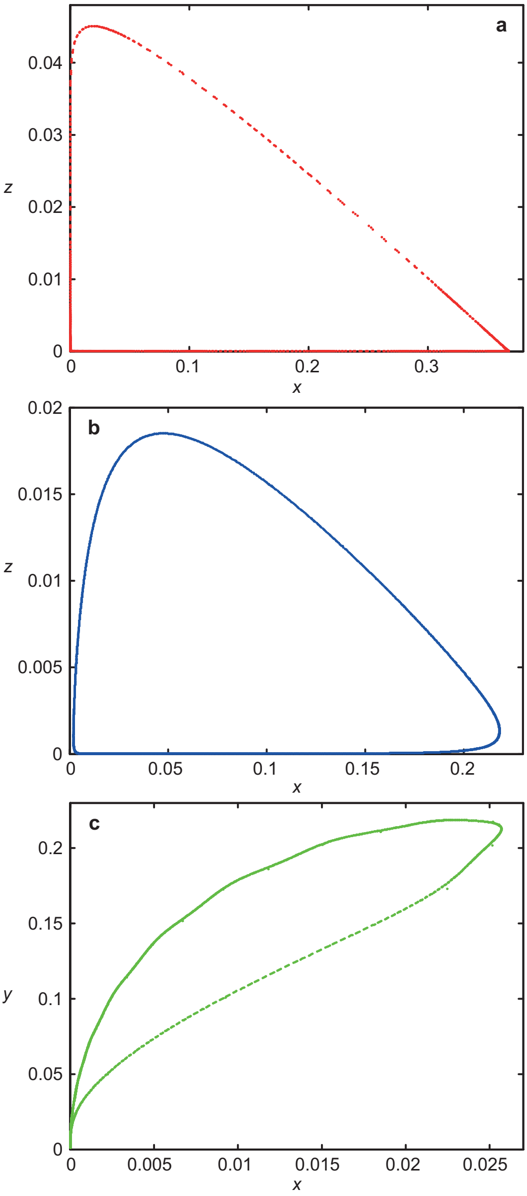

Fig. 2. The resident attractor when (**a**) the prey adopts the best fixed strategy, and (**b**) the prey adopts the conditional strategy given by Eq. 17. (**c**) The projection onto the *xy*-coordinate plane of (the attractor describing coexistence between the best fixed strategy and the conditional strategy. Parameter values: $M = 3.8$, $d = 2.25$, $a = 120$, $\mathcal{F} = 0.15$ and $m = 1$.

H1 Function $M : [0, \infty) \to (0, \infty)$ is continuous.

H2 Function $k : [0, \infty) \to [0, \infty)$ is increasing and positive for $\beta > 0$,

H3 Function k is twice continuously differentiable and $\beta k''(\beta) + k'(\beta) > 0$ for all $\beta \in (0,\infty)$.

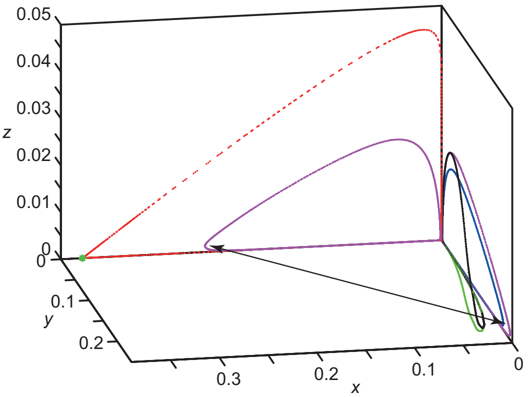

Fig. 3. Three-dimensional situation. The resident attractor when the prey adopts the best fixed strategy is marked with red dots. The resident attractor when the prey adopts the conditional strategy given by Eq. 17 is marked with blue dots. The coexistence attractor and its projection onto the *xy*-plane is denoted by black dots and green dots, respectively (cf. Fig. 2). Slanted projections of the coexistence attractor onto the *xz*- and *yz*-planes are marked with magenta dots and pointed by the arrow. The coexistence attractor seems to have strictly smaller amplitude than the resident attractor for the fixed strategy in red whereas it has strictly larger amplitude than the resident attractor for the conditional strategy in blue. Parameter values: $M = 3.8$, $d = 2.25$, $a = 120$, $\mathcal{F} = 0.15$ and $m = 1$. The fixed strategy equilibrium without predators ($1/e$,0,0) that cannot be invaded by the conditional strategy is denoted by a green star.

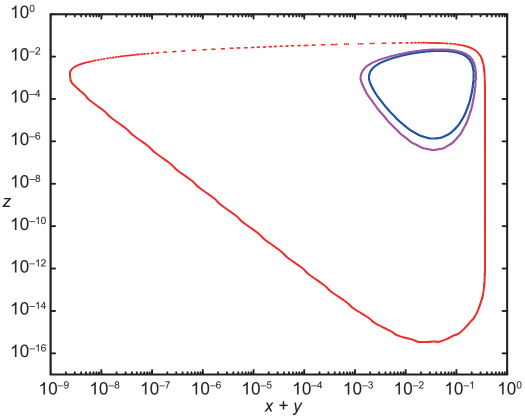

Fig. 4. On a logarithmic scale it is evident that the amplitude of cycles of the conditional strategy (blue dots) is strictly smaller than the amplitude of (the cycles of the fixed strategy (red dots). The amplitude of the slated projections of the coexistence attractor is strictly between those two strategies (magenta dots). Parameter values: $M = 3.8$, $d = 2.25$, $a = 120$, $\mathcal{F} = 0.15$ and $m = 1$.

As already pointed out, assumption H2 reflects that individuals producing smaller clutches do better in competition than individuals producing larger clutches. Assumption H3 is more technical in nature, but it ensures the existence of a *unique* optimal reproductive strategy. For instance the power function $k(\beta) = \beta^p$ satisfies H2 and H3 for all $p > 0$.

Theorem: Assume H1–H3.

i. The supremum in Eq. 19 is a maximum, and for every $I \in [0,\infty)$ it is attained at precisely one $\beta \in (0,M(I)]$.
ii. The unique $\beta =: \tilde{\beta}(I)$ found in (i) defines a continuous function $\tilde{\beta} : [0,\infty) \to [0,\infty)$.
iii. There exists an $\varepsilon > 0$ such that $\tilde{\beta}(I) = M(I)$, $I \in [0,\varepsilon)$.

Proof: For every $I \in [0,\infty)$ the continuous function

$$\psi_I(\beta) := \beta\exp(-k(\beta)I)$$

attains its maximum in the compact interval $[0,M(I)]$. As ψ_I is positive and $\psi_I(0) = 0$ the maximum is in fact attained in $(0,M(I)]$. If it is attained at $\beta \in (0,M(I))$, then

$$\psi_I'(\beta) = \left(1 - \beta k'(\beta)I\right)\exp\left(-k(\beta)I\right) = 0. \qquad (20)$$

Equation 20 holds if and only if

$$\chi(\beta) := \frac{1}{\beta k'(\beta)} = 0. \qquad (21)$$

It follows from H3 that χ is strictly decreasing and continuous on $(0,\infty)$ and hence equation (21) can have at most one solution in $(0,M(I))$. This proves *i*.

The above construction immediately shows that

$$\tilde{\beta}(I) = \min\left\{\chi^{-1}(I), M(I)\right\}.$$

Hence $\tilde{\beta}$ is continuous.

Finally, since $\chi(M(0)) > 0$ it follows by continuity that $I < \chi(M(I))$ for all sufficiently small values of I. This proves *iii*.

Remark: Since increasing I amounts to increasing intraspecific competition (and/or increasing predator density in the case of the model in the Appendix) one expects the maximum clutch size M to be a deceasing function of I. As the proof of the theorem shows the optimal clutch size $\tilde{\beta}$ is then a decreasing function of I. By conclusion *iii* the optimal strategy is to produce the maximal possible number of offspring when I is small, that is, when density dependent effects are not pronounced. But as I increases it pays to *suppress* reproduction, that is, to produce less offspring than is physiologically possible.

Next we consider invadability and outcompetition when one of the competing types adopts the optimal reproductive strategy.

First of all, it is rather obvious that the optimal strategy is uninvadable. To see this, let the resident x adopt the optimal strategy. Then (using Eq. 7)

$$\lim_{n\to\infty}\frac{1}{n}\sum_{i=1}^{n}\log R_y\left(I_i^{\mathrm{res}}\right)=\lim_{n\to\infty}\frac{1}{n}\log\frac{R_y\left(I_i^{\mathrm{res}}\right)}{R_x\left(I_i^{\mathrm{res}}\right)}\le 0, \quad (22)$$

since by optimality $R_y(I_i^{\mathrm{res}})/R_x(I_i^{\mathrm{res}}) \le 1$ for all i.

Let us now assume that the mutant adopts the optimal strategy. Arguing precisely as in Eq. 22, we see that

$$\lim_{n\to\infty}\frac{1}{n}\sum_{i=1}^{n}\log R_y\left(I_i^{\mathrm{res}}\right)\ge 0. \quad (23)$$

But will the optimal strategy actually invade? As a matter of fact it need not. To see why, assume that the resident is in a fixed point. The environment set by the resident is then a constant I^{res}. Assume further that $\beta_x(I^{\mathrm{res}}) = \tilde{\beta}(I^{\mathrm{res}})$. This does not mean that the resident also adopts the optimal strategy, only that for this particular value of the environment its clutch size coincides with that of the optimal strategy. It follows that in this case

$$\lim_{n\to\infty}\frac{1}{n}\sum_{i=1}^{n}\log R_y\left(I_i^{\mathrm{res}}\right)=0, \quad (24)$$

and invasion does not take place. The result is easy to understand in intuitive terms: If the environment does not fluctuate, nothing can be gained from a potential ability to adjust as a response to environmental changes.

Assume now that the mutant y adopting the optimal strategy has invaded. Will it oust the resident? To answer this question we have to consider the actual population dynamics. Optimality implies that

$$\frac{R_y\left(I_i\right)}{R_x\left(I_i\right)}\ge 1 \text{ for all } i = 1, 2, \ldots. \quad (25)$$

The condition in Eq. 25 means that at each generation the mutant y gains ground at the expense of the resident x. It implies that

$$\frac{y_{n+1}}{x_{n+1}}\ge\frac{y_n}{x_n}\; n = 1, 2, \ldots, \quad (26)$$

and hence that the fraction y_n/x_n either tends to infinity or to a positive constant C. Since all orbits remain bounded the resident will go extinct in the former case. In the latter case there will be coexistence.

Let us have a closer look at the case

$$\lim_{n\to\infty}\frac{y_n}{x_n}=C>0.$$

The ω-limit set (the set on which the asymptotic dynamics occur) then lies on the straight line

$$y = Cx, \quad (27)$$

and when the system is in the ω-limit set the equation

$$R_x(I) = R_y(I) \quad (28)$$

holds. Adding Eqs. 1 and 2 and taking Eq. 28 into account one finds that

$$(x + y)_{n+1} = (x + y)_n R_x(I_n). \quad (29)$$

This shows that in the ω-limit set the total population $x + y$ has precisely the same dynamics as the resident in the absence of the mutant. Let A be the (projection onto the x-axis of the) resident attractor. It follows from Eqs. 27 and 29 that in the case of coexistence between mutant and resident, the ω-limit set must be a subset of

$$\left\{(x,y):x+y\in A\right\}\bigcap\left\{(x,y):y=Cx\right\}$$

for some $C > 0$.

So far our discussion has been independent of the strategy of the resident and of the underlying population dynamical model. If the per-capita recruitment $R_x(I)$ corresponding to the resident strategy is convex and satisfies some other natural assumptions, Eq. 28 has precisely one solution I^*. This is the case for instance if the resident adopts a fixed strategy (Gyllenberg *et al.* 1996). The equation (29) then holds in the ω-limit set with $I_n = I^*$ for all n. But since Eq. 29 is equivalent to the equation describing the residence attractor we conclude that $Rx(I^*) = Ry(I^*) = 1$, which means that the ω-limit set consists of a fixed point.

Predator–prey interaction results typically in either fixed point dynamics or quasi-periodic dynamics after a Hopf bifurcation has occurred. We refer to (Gyllenberg *et al.* 1996) for a detailed description of the bifurcations in the case of fixed strategies. When predator-prey oscillations prevail, the fixed point has lost its stability and hence cannot be in the ω-limit set. As a consequence the mutant adopting the optimal strategy will oust the resident.

We summarize our findings as follows: *The optimal strategy is uninvadable. If the resident attractor describes predator–prey oscillations, then the optimal strategy will invade and oust a nonoptimal resident.*

Discussion

We have considered the evolution of reproductive strategies under varying environmental conditions. The fluctuations in the environment are due to the population dynamics. A typical example of ecological interactions leading to such fluctuations is predator–prey interaction. A predator–prey model in discrete time has served as a concrete example to illustrate the theoretical results.

These density dependent effects were incorporated in the model by introducing an environmental interaction variable which increases both with increasing prey density and increasing predator density. The fact that the environmental variable is one dimensional was crucial for many of our results. On the other hand, the precise functional forms of the environmental variable and the type of ecological interaction were in most cases irrelevant.

If the environment is given as a function of time, then the equation for the dynamics of the prey is linear (but time dependent). Modelling the nonlinear interaction (both inter- and intraspecies interaction) through feedback to the environment is extremely helpful. Many results that we have not been able to prove directly from the difference equations were now obtained relatively easily.

In the context of our model coexistence between two fixed reproductive strategies is impossible. There exists a best fixed strategy, which invades and ousts all other fixed strategies. The criterion of being best is independent of the actual population dynamics.

On the other hand, in the case of conditional reproductive strategies, invadability and outcompetition depends heavily on the dynamics. If the system is in a steady state there is obviously nothing to be gained by the ability to adjust the behaviour in response to changes in the environment since such changes will not occur. A necessary condition for such conditional strategies to evolve is therefore that there are fluctuations in the environmental interaction variable. Predator-prey interactions may cause such fluctuations and indeed we showed that with natural assumptions there exists an optimal conditional strategy which is uninvadable and invades and ousts all other strategies.

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References

Barabas, G., Pigolotti, S., Gyllenberg, M., Dieckmann, U. & Meszena, G. 2012: Continuous coexistence or discrete species? A new review of an old question. — *Evolutionary Ecology Research* 14: 523–554.

Charlesworth, B. 1980: *Evolution in age-structured populations*. — Cambridge University Press, Cambridge.

Dieckmann, U., Heino, M. & Parvinen, K. 2006: The adaptive dynamics of function-valued traits. — *Journal of Theoretical Biology* 241: 370–389.

Diekmann, O., Gyllenberg, M., Huang, H., Kirkilionis, M., Metz, J. & Thieme, H. 2001: On the formulation and analysis of general deterministic structured population models. II. Nonlinear theory. — *Journal of Mathematical Biology* 43: 157–189.

Diekmann, O., Gyllenberg, M. & Metz, J. 2003: Steady state

analysis of structured population models. — *Theoretical Population Biology* 63: 309–338.
Diekmann, O. & Mylius, S. 1995: About ESS, maximisation and the need to be specific about density dependence. — *Oikos* 74: 218–224.
Fisher, R. A. 1930: *The genetical theory of natural selection*. — Clarendon Press, Oxford.
Gyllenberg, M., Hanski, I. & Lindström, T. 1996: A predator–prey model with optimal suppression of reproduction in the prey. — *Mathematical Biosciences* 134: 119–152.
Gyllenberg, M., Hanski, I. & Lindström, T. 1997: Continuous versus discrete single species population models with adjustable reproductive strategies. — *Bulletin of Mathematical Biology* 59: 679–705.
Gyllenberg, M. & Meszéna, G. 2005: On the impossibility of coexistence of infinitely many strategies. — *Journal of Mathematical Biology* 50: 133–160.
Gyllenberg, M., Metz, J. A. & Service, R. 2011: When do optimisation arguments make evolutionary sense? — In: Chalub, F. A. C. C & Rodrigues, J. R. (eds.), *The mathematics of Darwins legacy*: 233–268. Birkhäuser, Basel.
Kisdi, É. & Meszéna, G. 1993: Density dependent life history evolution in fluctuating environments. — *Lecture Notes in Biomathematics* 98: 26–62
Lack, D. 1986: *The natural regulation of animal numbers*. — Clarendon Press, Oxford.
León, J. A. & Charlesworth, B. 1978: Ecological effects of natural selection. — *Ecology* 59: 457–464.
Levins, R. 1975: Evolution in communities near equilibrium. — In: Cody, M. L. & Diamond, J. M. (eds.), *Ecology and evolution of communities*: 16–50. Harward University Press, Cambridge, Massaschusetts.
Meszéna, G., Gyllenberg, M., Jacobs, F. J. & Metz, J. A. J. 2005: Link between population dynamics and dynamics of Darwinian evolution. — *Physical Review Letters* 95, 078105, doi:10.1103/PhysRevLett.95.078105.
Meszéna, G., Gyllenberg, M., Psztor, L. & Metz, J. A. J. 2006: Competitive exclusion and limiting similarity: a unified theory. — *Theoretical Population Biology* 69: 68–87.
Meszéna, G. & Metz, J. A. J. 1999: *Species diversity and population regulation: the importance of environmental feedback dimensionality*. — Interim Report IR-99-045, International Institute for Applied Systems Analysis, Laxenburg, Austria.
Metz, J. A. J., Mylius, S. & Diekmann, O. 2008: When does evolution optimise? — *Evol. Ecol. Research* 10: 629–654.
Metz, J. A. J., Stankova, K. & Johansson, J. 2016: The canonical equation of adaptive dynamics for life histories: from fitness-returns to selection gradients and Pontryagin's maximum principle. — *Journal of Mathematical Biology* 72: 1125–1152.
Parvinen, K., Dieckmann, U. & Heino, M. 2006: Function-valued adaptive dynamics and the calculus of variations. — *Journal of Mathematical Biology* 52: 1–26.
Parvinen, K., Heino, M. & Dieckmann, U. 2013: Function-valued adaptive dynamics and optimal control theory. — *Journal of Mathematical Biology* 67: 509–533.
Nicholson, A. J. & Bailey, V. A. 1935: The balance of animal populations. Part I. — *Journal of Zoology* 3: 551–598.
Ricker, W. E. 1958: *Handbook of computations for biological statistics of fish populations*. — Fisheries Research Board of Canada, Ottawa.
Ripa, J. & Dieckmann, U. 2013: Mutant invasions and adaptive dynamics in variable environments. — *Evolution* 67: 1279–1290.
Roughgarden, J. 1976: Resource partitioning among competing species — a coevolutionary approach. *Theoretical Population Biology* 9: 388–424.
Stearns, S. C. 1992: *The evolution of life histories*. — Oxford University Press, Oxford.

Appendix

Predator–prey model

We derive a discrete predator-prey model, which is a variant of the Nicholson-Bailey model with density-dependent prey dynamics and a long-lived predator. The prey individuals live for at most one season and those who escape predation reproduce at the end of the season and then die. Predators do not die during the season, but at the end of the season a fraction F survive and reproduce.

The prey appear in two competing types the densities of which are denoted by x and y. The predator density is z.

Predators attack type x prey with a rate α_x and type y prey with a rate α_y. We assume that

$$\alpha_x = \alpha\gamma_x, \text{ and } \alpha_y = \alpha\gamma_y. \tag{30}$$

where α is a property of the predator (its general predation activity), whereas the type specific parameter γ measures the vulnerability of the prey to predation. Assuming a linear (Holling type I) functional response we arrive at the following system of ordinary differential equations describing the dynamics during the season:

$$\dot{x} = -\alpha\gamma_x xz, \text{ and } \dot{y} = -\alpha\gamma_y yz. \tag{31}$$

The solution to Eq. 31 is given by $x(t) = \exp(-\alpha\gamma_x z_0 t)x_0$, $y(t) = \exp(-\alpha\gamma_y z_0 t)y_0$, $0 \le t \le T$, where x_0, y_0 and z_0 are the initial densities of prey and predators, and T is the length of the season.

We introduce the new parameter $a = \alpha T$. The number of prey eaten during the season is given by $(1 - \exp(-\gamma_x az_0))x_0 + (1 - \exp(-\gamma_y az_0))y_0$, and of these $F((1 - \exp(-\gamma_x az_0))x_0 + (1 - \exp(-\gamma_y az_0))y_0)$ have been digested by predators that survive from the foraging season to reproduction. We assume that a fraction m of this prey mass is transformed into new predators at the end of the season.

Finally we assume that the recruitment of prey follows the Ricker model, that is, the prey individuals which survived predation produce $\beta\exp(-k(x + y))$ offspring on average, again with k and β type specific.

To simplify the model we take $\gamma_x = k_x$, and $\gamma_y = k_y$ and arrive at the following discrete model

$$x_{n+1} = x_n\beta_x\exp(-k_x(x_n + y_n + az_n)), \tag{32}$$
$$y_{n+1} = y_n\beta_y\exp(-k_y(x_n + y_n + az_n)), \tag{33}$$
$$z_{n+1} = mF\big((1 - \exp(-k_x az_n))x_n + (1 - \exp(-k_y az_n))y_n\big) + Fz_n. \tag{34}$$

Observe that Eqs. 32 and 33 are of types as Eqs. 1 and 2 with per-capita recruitment of Ricker type as Eq. 3 and environmental interaction variable $I = x + y + az$.

The term az can be interpreted as the predation pressure each prey individual is subject to.

Remark: A perhaps more realistic model for the within season dynamics would allow predators to die during the season. In that case the predator density z in Eq. 31 would not be constant but the solution a differential equation, say

$$\dot{z} = -\delta z. \tag{35}$$

Equation 31 augmented by Eq. 35 can still be solved in closed form, but the difference is that then the amount

$$\int_0^T \alpha\gamma_x x(t)\,dt + \int_0^T \alpha\gamma_y y(t)\,dt$$

of prey consumed during the season could not be evaluated using elementary functions but would involve the exponential integral Ei. The resulting discrete dynamical system could of course still be treated numerically and the results would be qualitatively the same as for the simpler model that we chose.