



LUND UNIVERSITY

Evolution of multi-stage dormancy in temporally autocorrelated environments.

Olofsson, Helen; Ripa, Jörgen; Lundberg, Per

Published in:
Evolutionary Ecology Research

2005

[Link to publication](#)

Citation for published version (APA):
Olofsson, H., Ripa, J., & Lundberg, P. (2005). Evolution of multi-stage dormancy in temporally autocorrelated environments. *Evolutionary Ecology Research*, 7(8), 1125-1137. <http://www.evolutionary-ecology.com/issues/v07n08/ear1845.pdf>

Total number of authors:
3

General rights

Unless other specific re-use rights are stated the following general rights apply:
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Read more about Creative commons licenses: <https://creativecommons.org/licenses/>

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

Evolution of multi-stage dormancy in temporally autocorrelated environments

Helen Ivarsson,* Jörgen Ripa and Per Lundberg

*Department of Theoretical Ecology, Ecology Building,
Lund University, SE-223 62 Lund, Sweden*

ABSTRACT

Question: Under what circumstances does a capacity for multi-stage dormancy (i.e. dormancy in more than one life-stage) evolve?

Mathematical methods: Optimization in stochastic environments. Results are derived both analytically and by simulations.

Key assumption: There exists some trade-off between resources allocated to reproduction and adult dormant survival. Different shapes of this trade-off are investigated.

Major conclusions: Multi-stage dormancy can evolve in an environment with low serial autocorrelation. However, a slowly changing environment, with high positive autocorrelation, will prevent the evolution of dormancy in several life-stages. In general, a high positive environmental autocorrelation will separate the evolution of life parameters associated with active life from that of parameters associated with dormant life.

Keywords: autocorrelation, dormancy, life-history evolution, stage structure, stochastic environment.

INTRODUCTION

A varying environment is a considerable challenge to most organisms, especially if the local environment fluctuates between inhabitable and uninhabitable conditions. To overcome periods of zero survival probability, the organisms have two major options – to escape in space (i.e. migrate or disperse) or in time by entering resting stages. Both alternatives are most likely costly. Birds that migrate can have substantial energetic and survival costs of the actual movement from one place and they also risk getting worse territories and a delayed start to their breeding by spending time away from the breeding grounds (Alerstam and Hedenström, 1998). Organisms that choose to go through some period of inactivity bear costs associated with preparation of their bodies for substantial physiological challenges, such as alterations of their internal structure and metabolism (Soula and Menu, 2003).

The ecological and evolutionary problems of resting through adverse times have received considerable attention because it is a widespread phenomenon among invertebrates and

* Author to whom all correspondence should be addressed. e-mail: helen.ivarsson@teorekol.lu.se
Consult the copyright statement on the inside front cover for non-commercial copying policies.

plants [insects (Brown and Hodek, 1983; Danks, 1987); plants (Lang, 1996)]. One of the first attempts to analyse the evolutionary mechanisms of dormancy was Cohen's (1966, 1968) model of an annual plant with a variable proportion of new seeds entering a dormant state (i.e. postponing germination by one year). In a constant environment there is no point in postponing germination, but with high enough environmental variability the optimal fraction of dormant seeds becomes non-zero (Cohen, 1966).

Tuljapurkar and Istock (1993) constructed a similar model to that of Cohen, but allowed for stage structure as well as serial autocorrelation of the environment. They arrived at similar conclusions, but showed that stage structure predicts a wider optimum of the optimal diapause fraction. A non-structured model is not sensitive to environmental autocorrelation, whereas a structured model is. A positive autocorrelation decreases the importance of diapause because the environment becomes more predictable with increasing autocorrelation (Tuljapurkar and Istock, 1993). A negatively autocorrelated environment gives the opposite result – the growth rate of the population increases with an increasing fraction of diapausers.

A plant seed cannot predict the weather – it has to choose whether to germinate before the environmental conditions of the upcoming season are known. Other organisms can respond more directly to changing conditions. Tardigrades (an invertebrate phylum) are dependent on a moist environment to sustain an active life. Terrestrial tardigrades, which live predominately in mosses, lichens and leaf litter (Rebecchi *et al.*, 2000), respond immediately to drought by going into a dormant stage called cryptobiosis (Keilin, 1959). This kind of obligate dormancy can be found, for example, in nematodes and rotifers as well. In the tardigrades, all stages from eggs to adults have the capacity to enter cryptobiosis (Kinchin, 1994). When favourable (humid) conditions return, tardigrades return to an active state within a couple of minutes (Crowe and Madin, 1979). It is believed that terrestrial tardigrades have originated from the sea, and cryptobiosis is thought to have evolved among those that lived in the tidal zone, and therefore needed to evolve some sort of protection in the case of becoming stranded and dried out. Jönsson and Järemo (2003) studied what parameters are important for the evolution of cryptobiosis under these conditions. They concluded that investment in cryptobiotic traits should increase with increasing probability of getting stranded and, more importantly, the more fatal a stranding is the more favourable it is to evolve cryptobiosis.

Inspired by the tardigrades, we were interested in how the capacity to diapause can evolve in not just one but several life-stages. A conversion from an active life to cryptobiosis involves total extraction of body water and formation of various compounds (e.g. trehalose) (see, for example, Clegg, 2001 and references therein). Why should an adult invest in an ability to convert to a cryptobiotic stage instead of investing in eggs, which are less complex and presumably more apt to convert to cryptobiosis? Furthermore, how is the evolution of multi-stage dormancy dependent on the type of environmental variation, such as serial autocorrelation?

We construct an age-structured model with two stages (eggs and adults) and two states (active and dormant). We allow for fluctuating weather conditions with different amounts of autocorrelation. For some simplified cases analytical solutions are available, leading to tentative general conclusions, which in turn are confirmed with computer simulations. In the case of very unstable weather both adult and egg dormancy can evolve, but when autocorrelation is high only one of the stages will evolve a capacity for dormancy. Apart from this, we find no consistent patterns of life-history changes with an increasing

environmental autocorrelation. Nevertheless, we find that a strong positive environmental autocorrelation de-couples the evolution of life parameters associated with active states on the one hand and parameters associated with dormant states on the other.

THE MODEL

Consider an organism with two stages – eggs and adults. Both stages are capable of entering dormancy whenever needed. During advantageous conditions (‘good weather’), all dormant states immediately become active. Active eggs mature with probability P_1 and active adults survive with probability P_2 . At the end of a time-step all active adults produce R eggs. Figure 1A depicts the full life-cycle graph corresponding to good conditions. In bad weather conditions, active eggs enter dormancy with probability D_1 and active adults with probability D_3 . Dormant eggs and adults survive as dormant with probabilities D_2 and D_4 , respectively (Fig. 1B).

The weather model

Weather conditions change stochastically from good to bad or vice versa with probability p . Thus, a low p -value means a highly autocorrelated environment with long periods of constant weather conditions, good or bad. A p equal to 1 corresponds to a deterministic environment, alternating between good and bad conditions, with negative environmental autocorrelation. At $p=0.5$ the environment is totally unpredictable – current weather conditions give no clue to future weather conditions. Accordingly, environmental autocorrelation increases from $p = 1$ to $p = 0$. In fact, $1 - 2p$ is the proper expression for the environmental first lag autocorrelation if the conditions ‘good’ and ‘bad’ are given two arbitrary (different) numerical values. In all cases, on average half of the time steps will have good conditions and half of them bad conditions.

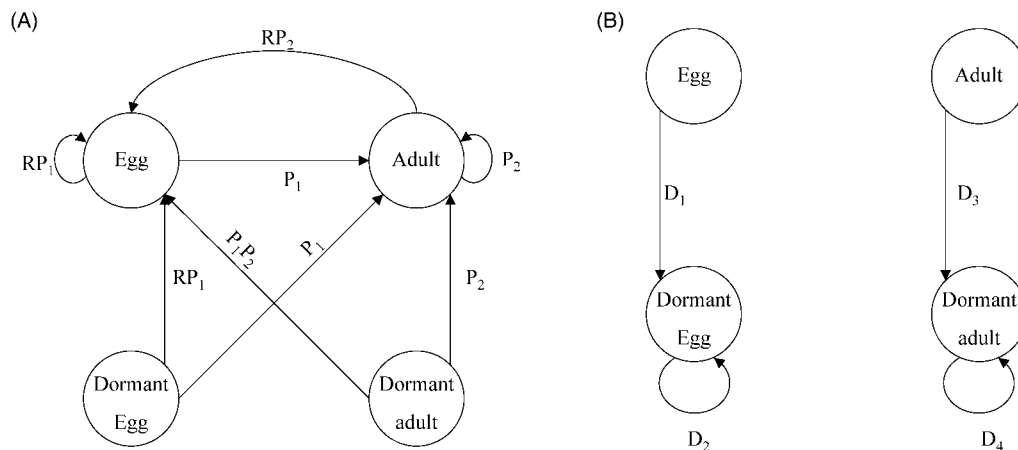


Fig. 1. The life-cycle graph for (A) ‘good’ weather conditions and (B) ‘bad’ weather conditions, respectively.

Fitness

The model consists of two Leslie matrices, each corresponding to one of the life-cycle graphs in Figs. 1A and B, respectively. In other words, the growth of the population proceeds according to:

$$\begin{cases} \mathbf{N}_{t+1} = \mathbf{GN}_t & \text{if weather at time } t \text{ is 'good'} \\ \mathbf{N}_{t+1} = \mathbf{BN}_t & \text{if weather at time } t \text{ is 'bad'} \end{cases} \quad (1)$$

where \mathbf{N}_t is a column vector of abundances within the four different states: active egg, dormant egg, active adult and dormant adult. The two Leslie matrices \mathbf{G} and \mathbf{B} are defined as follows:

$$\mathbf{G} = \begin{bmatrix} P_1R & P_1R & P_2R & P_2R \\ 0 & 0 & 0 & 0 \\ P_1 & P_1 & P_2 & P_2 \\ 0 & 0 & 0 & 0 \end{bmatrix} \quad \mathbf{B} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ D_1D_2 & D_2 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & D_3D_4 & D_4 \end{bmatrix} \quad (2)$$

The fitness of a given set of life-history parameters is defined (following Caswell, 2001) as the long-term mean log growth rate:

$$r = \lim_{t \rightarrow \infty} \frac{\log(N_t) - \log(N_0)}{t} \quad (3)$$

where N_t is total population size at time t .

ANALYTICAL EXAMINATION OF THE MODEL

The full stochastic version of our model is difficult to study analytically, because a single stable age structure, with an accompanying growth rate, is impossible to define. The stable age structure of good conditions differs from that of bad conditions, and every period of good or bad conditions starts with a population that differs from the corresponding stable age structure. However, during good conditions it only takes a single time step to establish the stable age structure that has the ratio R between active eggs and active adults (there are no individuals in dormant states during good conditions) and a corresponding growth rate $P_1R + P_2$. Thus, every period of bad conditions starts with a ratio R between eggs and adults, no matter the length of the preceding period of good conditions. This fact can be used to calculate the long-term fitness of an arbitrary strategy for some special cases of weather changes.

First, consider the case of deterministic alternations, $p = 1$, which corresponds to a negative environmental autocorrelation ($1 - 2p = -1$). Every second time step is good and every other one is bad. After each time step of good conditions, there are R as many eggs as there are adults. During the subsequent time step of bad conditions, a proportion D_1D_2 of the eggs survive and a proportion D_3D_4 of the adults survive. The ensuing time step of good conditions renders in total $R(P_1RD_1D_2 + P_2D_3D_4)$ eggs and $P_1RD_1D_2 + P_2D_3D_4$ adults (relative to the initial population size). Thus, the original age structure is re-established and

the population has grown with a factor $(P_1RD_1D_2 + P_2D_3D_4)$ during the two time steps. The geometric mean growth rate becomes:

$$\lambda = (P_1RD_1D_2 + P_2D_3D_4)^{1/2} \tag{4}$$

The analysis above is readily extended to a deterministically alternating weather of k time steps of good conditions and k time steps of bad conditions, which gives a mean growth rate:

$$\lambda = (P_1R + P_2)^{\frac{k-1}{2k}} (P_1RD_1D_2^k + P_2D_3D_4^k)^{\frac{1}{2k}} \tag{5}$$

Equation (5) is based on a deterministic weather scenario, but might be used as an approximate fitness expression for stochastic weather conditions where the mean length of a period of good or bad conditions is equal to k . The expression gives exactly equation (4) when $k = 1$, but should also be valid when p is low. That is, when periods of the same weather conditions have a long mean length, the stable age structures of both conditions are allowed to establish fully and the number of transitions from one to the other is minimal. In the limit when period length k approaches infinity, the expression in (5) becomes:

$$\begin{cases} \lambda = (P_1R + P_2)^{1/2} D_4^{1/2} & \text{if } D_4 > D_2 \\ \lambda = (P_1R + P_2)^{1/2} D_2^{1/2} & \text{if } D_2 > D_4 \end{cases} \tag{6}$$

Although we have not proven it, we have good reasons to believe equation (6) is an accurate fitness expression for the case when p approaches zero in the original, stochastic model (see simulations below).

We will use the analytical results above to discuss the differences between evolution of dormancy in a negatively autocorrelated environment ($p = 1$, equation 4) and evolution in a strongly positively autocorrelated environment ($p \rightarrow 0$, equation 6).

In the case of negative autocorrelation (equation 4), fitness is composed of two terms, one related to reproduction and survival of eggs ($P_1RD_1D_2$) and the other related to adult survival ($P_2D_3D_4$). All life-history parameters have a positive contribution to fitness. The optimal set of parameters therefore depends on which trade-offs between parameters are active. Given the structure of the fitness function (equation 4), there are in principle two different scenarios. There is either a trade-off between two parameters within the same term or a trade-off between parameters included in different terms. The first case corresponds to a trade-off between parameters involved in reproduction and egg survival or between parameters of adult survival. The second case arises if there is a trade-off between reproduction and egg survival on the one hand and adult survival on the other.

Figure 2A shows contour lines of fitness (equation 4) as a function of two parameters: probability to survive in the dormant state as adult (D_4) and probability to survive as adult (P_2). Since these two parameters are part of the same term, the fitness contour lines ($(P_1RD_1D_2 + P_2D_3D_4)^{1/2} = \text{constant}$) will be hyperbolic with the exact shape determined by the other parameters (see Table 1 for the values used in our calculations). We have also included three possible trade-off curves. As a consequence of the shape of the fitness landscape, the optimal strategy will be intermediate, regardless of the exact shape of the trade-off (Fig. 2A). In a negatively autocorrelated environment, maximal fitness is obtained when the adults divide their resources between both survival in the dormant state and survival as active. See Table 2 for a summary of all analytical results.

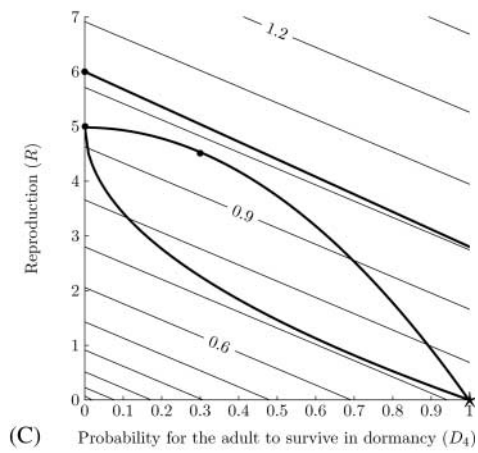
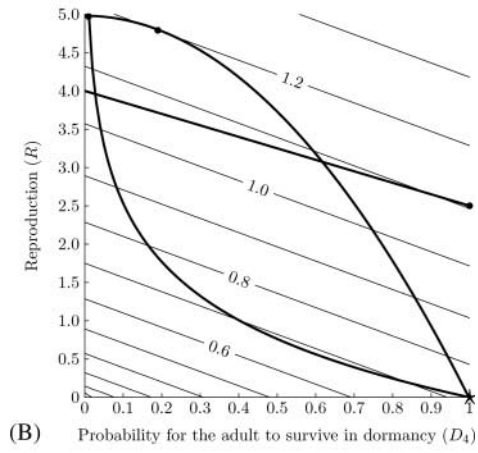
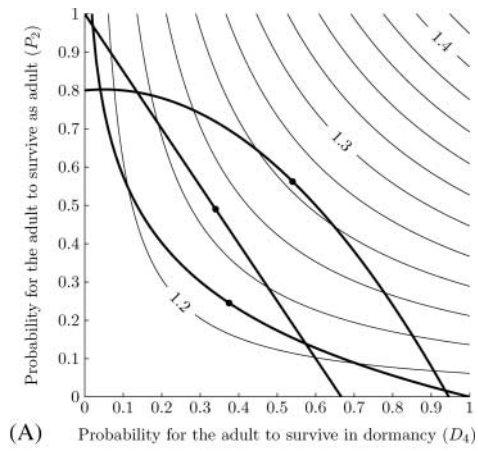


Table 1. The parameter values used in the model

Parameter	Meaning	Value
P_1	Probability of surviving from egg to adult	0.5
R^*	The number of eggs produced per adult	0–5 (5)
D_1	Probability of the egg entering dormancy successfully	0.7
D_3	Probability of the adult entering dormancy successfully	0.65
D_2	Probability of the egg surviving as dormant	0.8
D_4^*	Probability of the adult surviving as dormant	0–1
P_2^*	Probability of surviving as an adult in an active state	0–1 (0.8)

* The parameter is involved in a trade-off and the value within parentheses indicates the parameter value when it is not involved in any trade-off.

Table 2. Summary of the analytical results showing the type of fitness landscape associated with different trade-offs between life-history parameters

A trade-off between any of the traits:	Negative environmental autocorrelation			A trade-off between any of the traits:	Positive environmental autocorrelation		
	Concave	Convex	Linear		Concave	Convex	Linear
P_2, D_3 or D_4	1	1	1	P_1 and R	1	1	1
R, P_1, D_1 or D_2	1	1	1	$(P_1$ or $R)$ and P_2	2	2	2
$(D_4, D_3$ or $P_2)$ and $(R, P_1, D_1$ or $D_2)$	1	2	3	$(R, P_1$ or $P_2)$ and $(D_2$ or $D_4)$	3	3	2

Note: The left-hand columns are based on equation (4) and the right-hand columns are based on equation (6). P_1 and P_2 are survival of active eggs and active adults, respectively. R is the per capita reproduction. In bad weather conditions, active eggs and active adults enter dormancy with probabilities D_1 and D_3 , respectively. Finally, D_2 and D_4 represent dormant survival of eggs and adults, respectively (cf. Table 1, Figs. 1A, B).

1 = Resources are allocated to both traits, an intermediate optimum. 2 = Both extremes are local optima. 3 = One of the extremes is an optimum; which one depends on the parameter values.

In Figs. 2B and 2C we consider trade-offs between adult dormant survival (D_4) and reproduction (R). R is a member of the first term and D_4 a part of the second term in the fitness expression (equation 4) and fitness will therefore be constant along straight lines, the slope of the lines depending on the value of the other parameters. The difference between Fig. 2B and Fig. 2C is that D_2 equals 0.8 in B and 0.5 in C. Again, we have plotted three possible trade-off curves. In the case of a linear trade-off, maximal fitness will be reached

Fig. 2. Contour lines of the fitness landscape in a negatively autocorrelated environment (equation 4). The bold lines illustrate three possible trade-off curves: a linear, a convex and a concave trade-off. Solid circles denote global fitness maxima and stars indicate local fitness maxima. (A) Fitness as a function of adult dormant survival (D_4) and adult active survival (P_2). (B) and (C) Fitness as a function of adult dormant survival (D_4) and per capita reproduction (R). Parameter values according to Table 1, except in (C) $D_2 = 0.5$.

either when adults allocate all of their resources to surviving dormancy (Fig. 2B) or to reproduction (Fig. 2C). The difference in the results depends on the slope of the trade-off line and the slope of the fitness landscape. With a linear fitness landscape like this, only a (at least locally) concave trade-off will yield an intermediate solution. A convex trade-off gives local optima at the two endpoints, with a fitness minimum in between (Figs. 2B, C). A gradual evolution will lead to one of the extreme solutions – which one depends on initial conditions. In conclusion, dependent on both the shape and the slope of the trade-off line, both ‘r’ (high reproduction, low survival) and ‘K’ (high survival, low reproduction) strategists can evolve.

When the environment is heavily positively autocorrelated, fitness is given by equation (6). The parameters D_1 and D_3 (i.e. the probabilities for entering dormancy for eggs and adults respectively) are absent from the fitness expression. This is intuitively clear since the weather is stable and individuals enter dormancy relatively rarely. The other parameters are separated into two factors – one composed of parameters associated with active states ($P_1R + P_2$) and the other is a function of the two dormant survival rates ($\max(D_2, D_4)$). Consequently, fitness in the active states, in good weather, is independent of the life history as dormant and vice versa. As long as there is no trade-off between parameters from the two different states, the optimal strategy as active will be independent of the optimal strategy as dormant.

Trade-offs between parameters associated with active states (P_1 , P_2 , and R) give situations similar to those described above. The shape of the fitness landscapes will depend on whether the two parameters belong to the same or different terms of the expression $P_1R + P_2$ (equation 6). On the other hand, trade-offs between one of the dormant survival parameters (D_2 or D_4) and an active state parameter give different types of fitness landscapes. In Fig. 3A we show some possible trade-offs between D_4 (adult dormant survival) and R (reproduction). The fitness contour lines are horizontal lines until D_4 is larger than D_2 (egg dormant survival) and from that point the curves will have the shape of $(P_1R + P_2)D_4 = \text{constant}$. The linear trade-off has one local optimum (marked by a star) and one global optimum (marked with a dot), separated by a fitness valley. The fitness minimum is at the point where adult dormant survival (D_4) is exactly equal to egg dormant survival (D_2). Again, initial conditions will determine whether evolution will result in low reproduction and high adult dormant survival (the local optimum) or high reproduction and no adult dormant survival (the global optimum). It is, however, more likely that a capacity for dormancy first arises in a simpler stage than in the adult stage, such that initial conditions are probably to the left of the fitness minimum and a species will evolve to invest resources in reproduction instead of adult dormant survival. The same line of reasoning applies to the convex trade-off in Fig. 3A, whereas the concave trade-off only has a single optimum at maximal reproduction. It follows in all cases that resources should be invested in reproduction instead of adult survival. In fact, a corresponding result applies to the case of a trade-off between any of the active survival parameters (P_1 and P_2) and adult dormant survival (D_4). As long as egg dormancy evolves first, a gradual evolution cannot result in adult dormancy in heavily autocorrelated environments.

In Fig. 3A, all trade-off curves had a global optimum at maximum reproduction. This is of course not always the case. In Fig. 3B, D_2 is lowered to 0.5 (compared to 0.8 in Fig. 3A) and the slope of the linear trade-off is slightly different, which gives a global optimum when all resources are invested in survival during adult dormancy (D_4). In addition, the concave trade-off has a local, intermediate optimum.

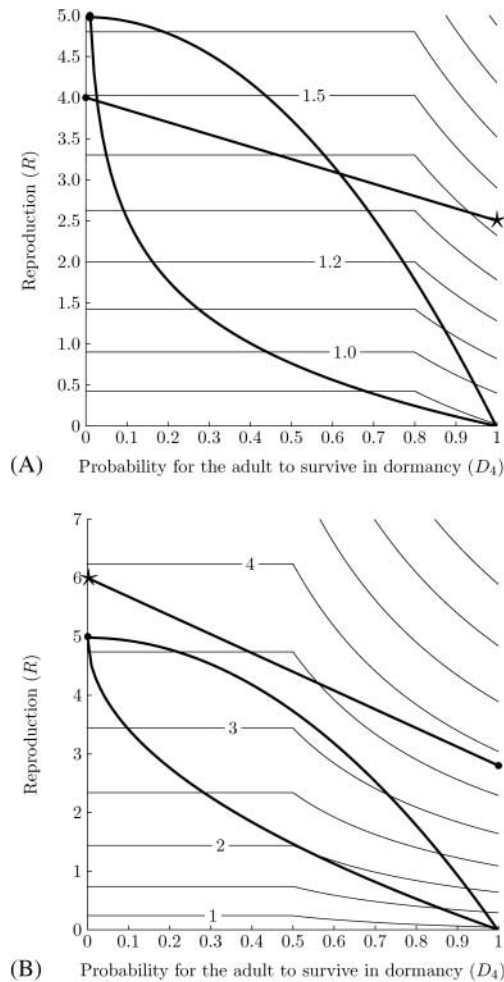


Fig. 3. Contour lines of the fitness landscape in a positively autocorrelated environment (equation 6), depicted as a function of adult dormant survival (D_4) and per capita reproduction (R). The bold lines illustrate three possible trade-off curves: a linear, a convex and a concave trade-off. Solid circles denote global fitness maxima and stars indicate local fitness maxima. Parameter values according to Table 1, except in (B) $D_2 = 0.5$.

SIMULATION

The analytical results above only apply to the extreme cases of a deterministically alternating environment ($p = 1$) or an environment with infinite periods of good and bad weather conditions ($p = 0$). To evaluate anything in between, we rely on computer simulations. The growth of the population was simulated for 10,000 time-steps according to equations (1) and (2). Fitness was calculated according to equation (3), discarding the first 1000 time-steps. Below, we examine the optimal life history given different trade-offs and life-history parameters.

First, we investigate two linear trade-offs between adult dormant survival (D_4) and reproduction (R):

$$R = -1.5D_4 + 4 \quad (7a)$$

which corresponds to the straight line in Figs. 2B and 3A and

$$R = -3.2D_4 + 6 \quad (7b)$$

which corresponds to the linear trade-off in Figs. 2C and 3B. The value of adult dormant survival (D_4) resulting in maximal fitness is plotted in Fig. 4. In the first case (equation 7a), the optimal strategy changes from full investment in adult dormant survival ($D_4 = 1$) to no investment in adult dormancy ($D_4 = 0$) as the environmental autocorrelation increases from -1 to 1 (solid line). In the other case, the pattern is reversed (equation 7b, dashed line). In conclusion, a small difference in the slope of the trade-off line and a difference in the probability for eggs to survive dormancy (D_2) results in opposite predictions in terms of how an organism should respond to increased environmental autocorrelation. Note that both scenarios predict a threshold value of autocorrelation where the optimal life history changes from one extreme to the other. We stress that reproduction never goes to zero, even at maximum investment in adult dormant survival (equations 7a,b). Also note that the simulation results confirm our analytical results above (at the two endpoints).

When the autocorrelation is around zero (i.e. totally unpredictable weather), both trade-offs predict that allocating all resources to reproduction will maximize fitness. However, we refrain from drawing any general conclusions about the optimal life history in a totally unpredictable environment, since the threshold autocorrelation, where the optimal strategy shifts from one extreme to the other, probably is both parameter and model dependent.

Next, we studied a possible trade-off between the probability to survive adult dormancy (D_4) and the probability to survive as an active adult (P_2). Those two parameters are part of the same term in equation (4), which predicts that in a rapidly changing environment there

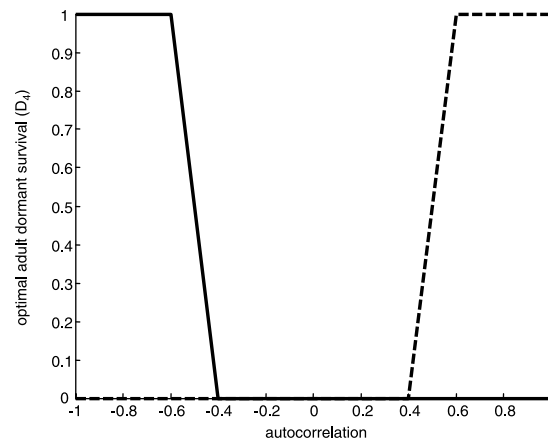


Fig. 4. Optimal adult survival as a function of environmental autocorrelation, given a linear trade-off between adult dormant survival (D_4) and per capita reproduction (R) according to equation (7a) (solid line) or equation (7b) (dashed line) in the text. Other parameters are taken from Table 1, except for the second trade-off (dashed line), where $D_2 = 0.5$.

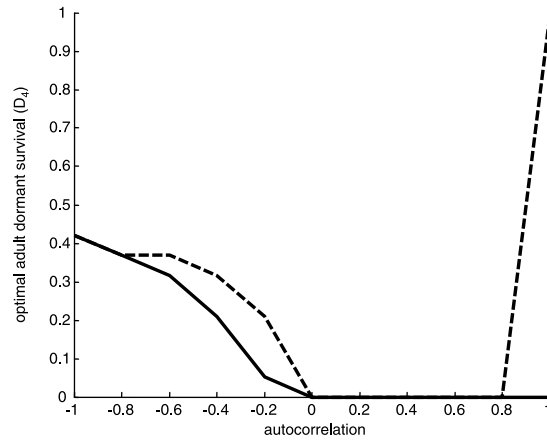


Fig. 5. Optimal adult survival as a function of environmental autocorrelation, given a linear trade-off between adult active survival (P_2) and adult dormant survival (D_4): $P_2 = -1.1D_4 + 0.9$. Other parameter values according to Table 1, except dashed line: $D_2 = 0.6$.

should be an intermediate solution where resources are allocated to both life-history terms. In the case of a positively autocorrelated environment, equation (6) predicts an all or nothing solution, at least with a linear trade-off (cf. Figs. 3A and B). Figure 5 depicts the optimal value of D_4 for two slightly different sets of parameters, as a function of environmental autocorrelation. The two endpoints are still well predicted by equations (4) and (6), but in between one of the relationships is far from monotonic (dashed line). This shows that the optimal response to a variable environment is not always a monotone function of environmental autocorrelation. It also underscores that simulations are necessary to predict the optimal life history, except in the simplified, extreme cases.

DISCUSSION

In this paper we have modelled an organism with two stages (eggs and adults) and two states (active and dormant). We were especially interested in optimal adult investment in different life-history parameters such as dormancy, reproduction and survival. We conclude that the evolution of adult dormancy depends on a wide range of factors, such as other life-history parameters, trade-offs between these parameters and the autocorrelation in the environment. More precisely, we found that the amount of environmental autocorrelation determines the connection between life-history parameters of the two states, active and dormant.

In fairly stable weather conditions with high autocorrelation, the evolution of dormant survival of eggs and adults is decoupled from the parameters of active states. Since long-term fitness in this case is a function of the largest dormant survival, organisms will invest in survival of either eggs or adults, never both. Which one depends on which life-stage initially gave the organism the greater probability to survive a period of dormancy (see equation 6). Evolution will favour an increased dormant survival of the life-stage that already has the greatest dormant survival, even if small. At the same time, there is no fitness benefit in increasing an already inferior dormant survival. Since eggs are less differentiated

than adults, it should be easier to convert an egg to a dormant state than an adult. Thus, we predict that organisms in highly autocorrelated environments, with several generations between shifts in environmental conditions, will only develop a capacity for dormancy in the simplest, least differentiated life-stage.

In the case of very unstable weather conditions (low autocorrelation), however, the parameters belonging to active life and dormancy are intermingled – the evolution of one set of parameters directly affects the evolution of the other. In this case there is potential for both adult and egg dormancy to evolve simultaneously. If there is no trade-off between the two, fitness increases when investing resources in both. Thus, we conclude that the ability to survive as dormant in multiple life-stages, such as is the case of the tardigrades, requires unstable weather conditions. Indeed, tardigrades live in very ephemeral habitats, where they can be desiccated and rehydrated daily (Crowe and Higgins, 1967).

Our result parallels that of Tuljapurkar and Istock (1993), who concluded that the optimal fraction that goes into dormancy increases with increasingly negative autocorrelation. We specifically studied the evolution of adult dormancy, but nevertheless found that adult dormancy is unlikely for high positive autocorrelation.

Brown and Venable (1986) found a ‘seed-bank threshold’ in the environment – as the environment deteriorates, there is a point where plants benefit from changing from specializing in non-seed-banker traits to seed-banker traits. We found a similar threshold in many of our simulation studies – at a certain environmental autocorrelation, the optimal strategy switches from no investment to full investment into dormant survival. We also found exceptions. In quickly changing environments (i.e. those with low autocorrelation), it is often best to divide resources between survival as dormant and survival as active (equation 4 and Fig. 5).

When there is a trade-off between dormancy and reproduction, the optimal life-history changes from a typical ‘K’ to an ‘r’ strategist or from an ‘r’ to a ‘K’ strategist as the autocorrelation increases, all depending on the values of other life parameters (Fig. 4). In general, we found no consistent pattern of life-history changes as the autocorrelation of the environment increases, except for the decreased likelihood of the evolution of adult capacity for dormancy.

To our knowledge, this is the first attempt to explain how the capacity to survive in a dormant state can evolve in several life-stages. We have used an admittedly simple model to highlight one important factor – environmental autocorrelation – but look forward to further examination of the topic.

ACKNOWLEDGEMENT

J.R. is supported by grants from the Swedish Research Council.

REFERENCES

- Alerstam, T. and Hedenström, A. 1998. The development of bird migration theory. *J. Avian Biol.*, **29**: 343–369.
- Brown, J.S. and Venable, D.L. 1986. Evolutionary ecology of seed-bank annuals in temporally varying environments. *Am. Nat.*, **127**: 31–47.
- Brown, V.K. and Hodek, I., eds. 1983. *Diapause and Life Cycle Strategies in Insects*. The Hague: Dr W. Junk Publishers.

- Caswell, H. 2001. *Matrix Population Models*, 2nd edn. Sunderland, MA: Sinauer Associates.
- Clegg, J.S. 2001. Cryptobiosis – a peculiar state of biological organization. *Comp. Biochem. Physiol. B*, **128**: 613–624.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.*, **12**: 119–129.
- Cohen, D. 1968. A general model of optimal reproduction in a randomly varying environment. *J. Ecol.*, **56**: 219–228.
- Crowe, J.H. and Higgins, R.P. 1967. The revival of *Macrobiotus areolatus* Murray (Tardigrada) from the cryptobiotic state. *Trans. Am. Micros. Soc.*, **86**: 286–294.
- Crowe, J.H. and Madin, K.A. 1974. Anhydrobiosis in tardigrades and nematodes. *Trans. Am. Micros. Soc.*, **93**: 513–524.
- Danks, H.V. 1987. *Insect Dormancy: An Ecological Perspective*. Ottawa: Biological Survey of Canada, National Museum of Natural Science.
- Jönsson, K.I. and Järemo, J. 2003. A model of evolution of cryptobiosis. *Ann. Zool. Fenn.*, **40**: 331–340.
- Keilin, F.R.S. 1959. The Leeuwenhoek Lecture. The problem of anabiosis or latent life: history and current concept. *Proc. R. Soc. Lond. B*, **150**: 149–191.
- Kinchin, I.M. 1994. *The Biology of Tardigrades*. London: Portland Press.
- Lang, G.A., ed. 1996. *Plant Dormancy: Physiology, Biochemistry and Molecular Biology*. Wallingford, UK: CAB International.
- Rebecchi, L., Guidi, A. and Bertolani, R. 2000. Tardigrada. In *Reproductive Biology of Invertebrates: Progress in Male Gamete Ultrastructure and Phylogeny IX, Part B* (B.G.M. Jamieson, ed.), pp. 267–291. Chichester: Wiley.
- Soula, B. and Menu, F. 2003. Variability in diapause duration in chestnut weevil: mixed ESS, genetic polymorphism or bet-hedging? *Oikos*, **100**: 574–580.
- Tuljapurkar, S. and Istock, C. 1993. Environmental uncertainty and variable diapause. *J. Theor. Biol.*, **43**: 251–280.

