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WHEN TO STORE ENERGY IN A STOCHASTIC ENVIRONMENT

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The ability to store energy enables organisms to deal with temporarily harsh and uncertain conditions. Empirical studies have demonstrated that organisms adapted to fluctuating energy availability plastically adjust their storage strategies. So far, however, theoretical studies have investigated general storage strategies only in constant or deterministically varying environments. In this study, we analyze how the ability to store energy influences optimal energy allocation to storage, reproduction, and maintenance in environments in which energy availability varies stochastically. We find that allocation to storage is evolutionarily optimal when environmental energy availability is intermediate and energy stores are not yet too full. In environments with low variability and low predictability of energy availability, it is not optimal to store energy. As environments become more variable or more predictable, energy allocation to storage is increasingly favored. By varying environmental variability, environmental predictability, and the cost of survival, we obtain a variety of different optimal life-history strategies, from highly iteroparous to semelparous, which differ significantly in their storage patterns. Our results demonstrate that in a stochastically varying environment simultaneous allocation to reproduction, maintenance, and storage can be optimal, which contrasts with previous findings obtained for deterministic environments.

KEY WORDS: Life-history evolution, models/simulations, phenotypic plasticity, trade-offs.

Understanding and predicting the evolution of life histories continues to be a central challenge for evolutionary biologists. Organisms acquire energy and allocate it to various functions within their body: these can be divided into reproductive functions and somatic functions, with the latter including growth, maintenance, and energy storage. Allocation studies have traditionally focused on a three-way trade-off among growth, maintenance, and reproduction, with storage as a forth component often being neglected (e.g., Perrin and Sibly 1993; Gurney and Middleton 1996). However, apart from behavioral adaptations, it is mainly energy storage that enables organisms to deal with temporarily harsh conditions

(Derickson 1976; Fitzpatrick 1976; Pond 1981), by using stored energy to buffer their energetic needs against periods of energy shortage (Downer and Matthews 1976; Parnas and Cohen 1976; Calow and Jennings 1977; Calow 1979). Storing energy can also be beneficial when the average amount of energy available per time is insufficient for reproduction (Calow 1979). Next to ensuring maintenance, storage can be advantageous whenever the returns from immediate reproduction are low, but are expected to increase in the future (Pianka 1976; Reznick and Braun 1987; Ruf et al. 2006).

Organisms with semelparous or iteroparous life histories can both benefit from an ability to store energy. The degree of iteroparity, that is the extent of repeated reproduction, is obviously highly variable between species, and reproductive investments can also vary greatly between successive reproductive opportunities

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during an individual's lifetime, depending on its internal state and on ambient environmental conditions (e.g., Happold and Happold 1990; Reznick and Yang 1993; Doughty and Shine 1998; Ruf et al. 2006; Tully and Ferrière 2008). Analogous observations apply to storage. Optimal storage allocations are expected to vary over time when environmental conditions change (Parnas and Cohen 1976; Calow and Jennings 1977; Pond 1981), which is supported by empirical evidence showing that organisms experiencing fluctuations in energy availability can plastically adjust their storage allocation (Perrin et al. 1990; Smith and Davies 1997; Metcalfe et al. 2002). Phenotypically plastic strategies were generally found to be superior to fixed strategies in variable environments, as they allow organisms to adjust to current conditions (e.g., Clark and Harvell 1992; Gabriel and Lynch 1992; Gomulkiewicz and Kirkpatrick 1992; Houston and McNamara 1992; Ernande and Dieckmann 2004; Lind and Johansson 2007). As most organisms live in variable environments, phenotypic plasticity is an essential mechanism to include in studies of energy allocation.

The existing body of theory about optimal storage strategies was developed for constant or deterministically varying environments, such as seasonally changing environments (Cohen and Parnas 1976; Parnas and Cohen 1976; Schaffer et al. 1982; Schaffer 1983; Pugliese 1987; Iwasa and Cohen 1989; Perrin and Sibly 1993; but see Iwasa and Kubo 1997). These models have consistently predicted that organisms should invest either into reproduction or storage (bang-bang strategies; Perrin and Sibly 1993): although they may alternate between these two functions, simultaneous investments have not been predicted to occur. It is not clear, however, how these results extend to stochastically varying environments. A recent theoretical analysis underscored that expectations based on constant or deterministic environments do not provide reliable predictions for life-history evolution in stochastic environments (Tuljapurkar et al. 2009).

Under stochastic conditions, energy stores can be expected to play a central role in buffering unpredictable fluctuations that occur on top of predictable deterministic environmental changes. To our knowledge, optimal storage strategies in stochastically varying environments have not yet been investigated in general life-history models. Here, we use a stochastic dynamic-programming model to analyze how the ability to store energy influences optimal energy allocation to storage, reproduction, and maintenance in a stochastically varying environment. Assuming that organisms can adjust their allocation decisions plastically to the current environmental conditions, we investigate expected evolutionary outcomes in plastic allocation strategies.

Model Description

We consider individuals inhabiting an environment that temporally varies in the amount of energy it provides. An individual exposed to these environmental fluctuations decides repeatedly at ages a from maturation onwards, $a = 0, 1, \ldots, T$, how to allocate the energy currently available to storage, reproduction, and maintenance. The age $a = 0$ refers to the age at maturation. We assume that growth is determinate, so there is no allocation to growth after maturation. At each age a during the lifetime of a particular individual, the environment provides it with a certain amount of energy, $e_{\text{env}}(a)$. In addition, the individual can potentially dispose of energy from its energy stores, $e_{\text{stor}}(a)$. An individual's state at age a is thus characterized by two components: environmental energy availability $e_{\text{env}}(a)$ and stored energy availability $e_{\text{stor}}(a)$. The total amount of energy available to an individual at age a is determined by the sum of these two sources,

$$e(a) = e_{\text{stor}}(a) + e_{\text{env}}(a). \qquad (1)$$

An individual decides how to divide the currently available energy $e(a)$ between storage, s, reproduction, r, and maintenance, m. We define an allocation reaction norm g as a function that maps the three-dimensional state variable $(a, e_{\text{env}}, e_{\text{stor}})$ onto the three-dimensional decision vector (s, r, m),

$$g(a, e_{\text{stor}}, e_{\text{env}}) = (s, r, m). \qquad (2)$$

The reaction norm g hence describes how the allocation decision varies with age, environmental energy availability, and stored energy availability. The three components of the decision vector (s, r, m) satisfy the inequalities $0 \le s, r, m \le 1$ and sum up to 1, $s + r + m = 1$. The allocation decisions can therefore be fully characterized by only two of these three fractions. The absolute amount of energy allocated to storage, e_s, reproduction, e_r, and maintenance, e_m, is jointly determined by the total energy availability and by the decision vector specifying the split, $e_s(a) = s \cdot e(a)$, $e_r(a) = r \cdot e(a)$, and $e_m(a) = m \cdot e(a)$. Consequently, the total amount of energy allocated to the three functions equals what is currently available,

$$e(a) = e_s(a) + e_r(a) + e_m(a). \qquad (3)$$

For the sake of generality and simplicity, we do not assume costs to be associated with energy storage, and we do not restrict the use of energy that has previously been allocated to an organism's stores. Possible restrictions on the future use of stored energy, as well as the scaling of metabolic costs of energy storage, are likely to be species-specific. Therefore, we make the simplifying assumption that all stored energy can be used for any purpose at any time in the future.

We assume that an individual's survival probability increases monotonically with the energy it allocates to maintenance. Specifically, we consider a hyperbolic relationship with a maximum of 1, through which the survival probability $S(e_m(a))$ at age a depends on e_m, and in which the parameter $e_{1/2}$ describes the energy

allocation at which the survival probability reaches $^1/_2$,

$$S(e_m(a)) = \frac{e_m(a)}{e_m(a) + e_{1/2}}. \tag{4}$$

A central component of our model is the stochastically varying environment. To model environmental fluctuations, we construct a stochastic process in discrete time for environmental energy availability e_{env} as the random variable. Because the abundance of resources in nature is often lognormally distributed (Limpert et al. 2001), we assume environmental energy availability e_{env} to follow a lognormal distribution. To model the dynamics of e_{env}, we use an approach derived and explained in detail in Fischer et al. (2009). In short, we choose a multiplicative autoregressive process of order 1 (AR-1) through which environmental energy availability at a given time a depends on environmental energy availability at time $a - 1$ together with a multiplicative noise term. This stochastic process is assumed to be stationary, so the mean and variance of e_{env} do not change over time. We use the coefficient λ of variation of e_{env} (i.e., the ratio between its standard deviation and mean) to measure environmental variability, and we use the autocorrelation time τ of fluctuations in e_{env} to measure environmental predictability. Hence, the two environmental characteristics λ and τ can be varied independently.

Moreover, the dynamics of stored energy have to be specified. All energy an individual allocates to storage at age a will be available for allocation at the next age $a + 1$, in addition to the energy provided by the environment at age $a + 1$, and can be freely allocated to the different functions, including storage. The dynamics of stored energy are thus given by

$$e_{stor}(a + 1) = e(a) \cdot s(a). \tag{5}$$

To maintain a certain level of stored energy, individuals hence have to reallocate it to storage at consecutive ages. By allocating energy to storage, individuals do not gain immediate benefits, but instead increase their potential future reproductive success and/or survival by raising future energy availability.

The aim of our analysis is to determine evolutionarily optimal allocation reaction norms g. For each possible state (a, e_{env}, e_{stor}) of an individual, we want to determine the optimal decision vector (s, r, m) that maximizes the individual's lifetime reproductive success. We solve this optimization problem by applying dynamic programming (Houston and McNamara 1999; Clark and Mangel 2000), a method to optimize sequences of interdependent decisions. Individuals that reproduce repeatedly should adjust their current reproductive investment to their prospects of future reproduction. As current actions thus depend on future actions, it is intuitive to work backwards in time when searching for optimal lifetime strategies. We define evolutionarily optimal allocation reaction norms by maximizing individual fitness measured in terms of lifetime reproductive success R_0. We quantify reproductive suc-

cess by the amount of energy invested into reproduction (rather than translating this energy into the number of offspring). We can thus identify an evolutionarily optimal allocation reaction norm for each age a before some terminal age T and for a given combination of model parameters. For each possible combination of environmental energy availability e_{env} and stored energy availability e_{stor}, we find the optimal allocation strategy at age a by choosing the decision vector (s, r, m) so that the reproductive success R from age a onwards is maximized. The dynamic-programming equation describes $R(e_{env}, e_{stor}, a)$ recursively,

$$R(e_{env}(a), e_{stor}(a), a) = r(a) \cdot e(a) + S(m(a) \cdot e(a))$$
$$\cdot E(R(e_{env}(a + 1), e_{stor}(a + 1), a + 1). \tag{6}$$

$R(e_{env}, e_{stor}, a)$ consists of two additive components: current reproductive success $r(a) \cdot e(a)$ at age a, given by the energy allocated to reproduction at age a, and expected future reproductive success $E(R(e_{env}(a + 1), e_{stor}(a + 1), a + 1))$ from age $a + 1$ onwards, where stored energy availability $e_{stor}(a + 1)$ at age $a + 1$ depends on the storage allocation decision $s(a)$ at age a (eq. 5). Environmental energy availability $e_{env}(a + 1)$ at age $a + 1$ is determined by the stochastic process described above. As the environment varies stochastically, we thus have to take into account all environmental states $e_{env}(a + 1)$ that can possibly succeed the current state $e_{env}(a)$. The considered stochastic process assigns each of these possible future environmental states $e_{env}(a + 1)$ a probability density of occurrence (Fischer et al. 2009). To calculate the expected reproductive success from age $a + 1$ onwards, we therefore have to average over all future environmental states $e_{env}(a + 1)$, weighting each of them with the corresponding probability density of occurrence. Hence, the expected future reproductive success is a weighted integral, with each component being a function of future environmental energy availability, future stored energy availability, and future allocation decisions. This expected future reproductive success is then itself weighted by the survival probability $S(m(a) \cdot e(a))$ from age a to age $a + 1$, which depends on the maintenance investment $m(a)$ at age a (eq. 4) and on the total energy availability $e(a)$ at age a (eq. 1).

The recursive dynamic-programming equation is solved backward in time: starting from a chosen terminal age $a = T$, reproductive success R is maximized iteratively toward younger ages until the maturation age $a = 0$ is reached. Following this procedure, the dynamic-programming algorithm provides the optimal decision vector (s, r, m) for all environmental energy availabilities e_{env}, storage energy availabilities e_{stor}, and ages a, which collectively identify the optimal allocation reaction norm $g(a, e_{stor}, e_{env})$ that maximizes lifetime reproductive success R_0.

Results

In our model, strong backwards convergence (Houston and Mc-Namara 1999, p. 43) holds. This means that in the process of the stepwise backward optimization, the optimal allocation strategy $g(e_{env}, e_{stor}, a)$ converges to an age-independent reaction norm $g(e_{env}, e_{stor})$ that is also independent of the terminal reward $R(e_{env}, e_{stor}, T)$. More precisely, when T is sufficiently large, and for ages a sufficiently before T, the Euclidean distance $|g(e_{env}, e_{stor}, a + 1) - g(e_{env}, e_{stor}, a)|$ becomes smaller than some small threshold, for example, 10^{-5}. Sufficiently before T, the optimal allocation is thus independent of both age and terminal reward.

For a given parameter combination, the optimal allocation reaction norm g maps the two-dimensional state (e_{env}, e_{stor}) onto the three-dimensional decision vector (s, r, m). To visualize these reaction norms, we present contour plots in which each panel shows the dependence of one allocation dimension (s, r, or m) of the optimal reaction norm on the state (e_{env}, e_{stor}) (Fig. 1A–C). Logarithmically scaled axes are chosen for e_{env} and e_{stor} to visualize allocation decisions across a large range of state space. The region in state space in which allocation to storage is optimal has an angular shape (Fig. 1A): energy is allocated to storage when environmental energy availability is intermediate and energy stores and not yet too full. Accordingly, the optimal allocation to storage is zero for both very low and extremely high environmental energy availability. Our model predicts that allocation either only to maintenance or only to reproduction can be optimal for some states (Fig. 1B–D), whereas allocation only to storage does not occur. This makes sense intuitively because allocation to storage
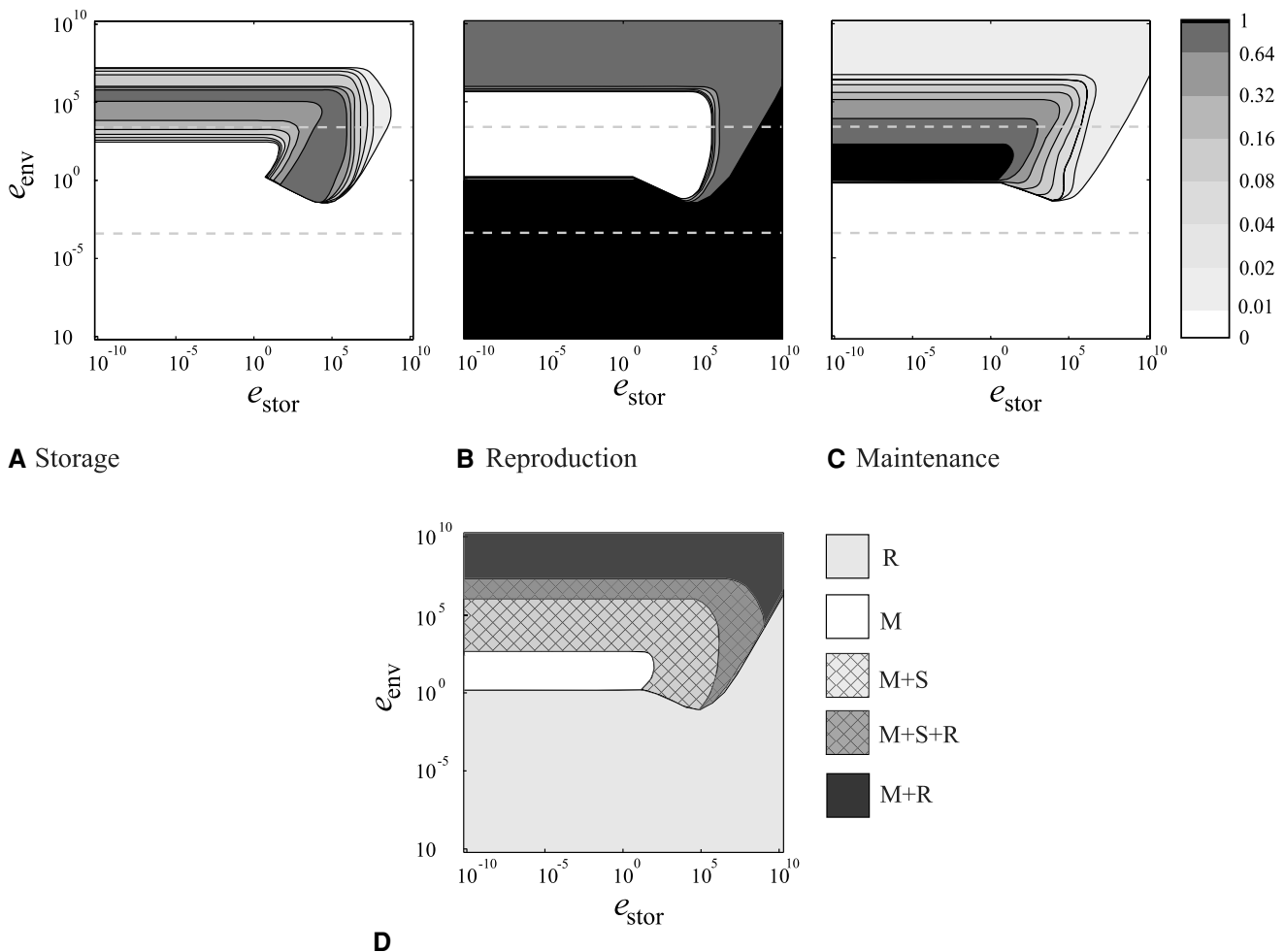

Figure 1. Representative illustration of an evolutionarily optimal allocation strategy. Contour plots show the dependence on environmental energy availability e_{env} and stored energy availability e_{stor} of optimal (A) storage investment s, (B) reproductive investment r, and (C) maintenance investment m. Note that vertical and horizontal axes are scaled logarithmically. Dashed gray lines show the 95% confidence intervals for environmental energy availability. Contour lines show allocation fractions of 0, 0.01, 0.02, 0.04, 0.08, 0.16, 0.32, 0.64, and 1. (D) Division of the state space (e_{env}, e_{stor}) into five regions according to qualitative patterns of optimal energy allocation: S = allocation to storage, M = allocation to maintenance, and R = allocation to reproduction. Parameters: $\lambda = 50$, $\tau = 50$, and $e_{1/2} = 50$.
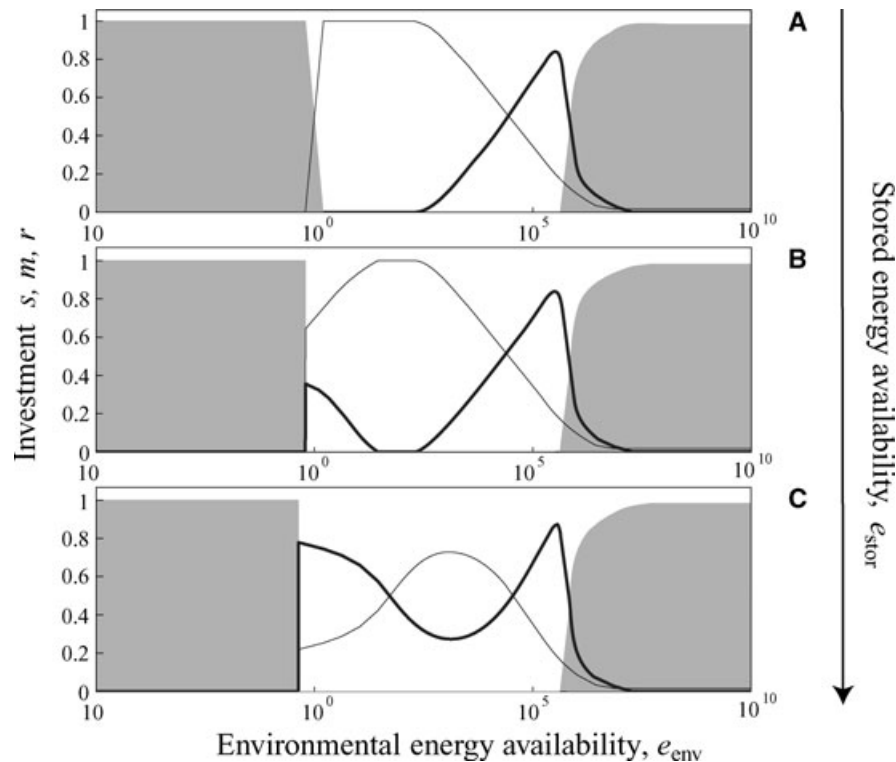
Figure 2. Evolutionarily optimal allocation strategies for three constant levels of stored energy, e_{stor}, describing the dependence on environmental energy availability e_{env} of optimal storage investment s (thick black lines), optimal maintenance investment m (thin black lines), and optimal reproductive investment r (upper edges of gray areas). The three constant levels of e_{stor} (top panel: $e_{stor} = 3.6 \times 10^{-7}$; middle panel: $e_{stor} = 5.1 \times 10^2$; bottom panel: $e_{stor} = 1.6 \times 10^5$) are chosen such that figure figure shows three vertical cuts through the optimal energy-allocation reaction norm depicted in Figure 1. Other parameters: $\lambda = 50$, $\tau = 50$, and $e_{1/2} = 50$.

alone would imply zero investment to maintenance. This would mean that organisms die right after making this allocation decision without gaining any fitness benefits from this allocation. Investing only in maintenance is optimal at intermediate levels of e_{env} and at zero to intermediate levels of e_{stor} (Fig. 1C, D), whereas investing only in reproduction is optimal when e_{env} is low. The region in which optimal allocation is only to reproduction first decreases with increasing e_{stor} (black region in Fig. 1C). Unexpectedly, for large values of e_{stor} this region expands again, so investing into reproduction alone becomes optimal at high levels of e_{env} for extraordinarily high e_{stor}. At these exceptionally high energy-availability levels, total expected future reproductive success is lower than what can be gained from a single full investment into reproduction (Fig. 1B, D). That a terminal investment strategy can here be superior is possible only because reproductive investment is not limited in our model. At intermediate levels of both e_{env} and e_{stor}, mixed allocation to maintenance and storage is optimal (Fig. 1A, C, D). When e_{env} or e_{stor} are further increased, simultaneous allocation to all three components becomes optimal (Fig. 1D, gray area). Mixed allocation to maintenance and reproduction, without any allocation to storage, is optimal for extraordinarily high levels of e_{env}.

Figure 2 shows the dependence of the three components of the optimal allocation strategy for three fixed levels of stored energy availability. Figure 2 hence represents three slices obtained from vertical cuts through the narrow part (Fig. 2, top panel) and the wide part (Fig. 2, middle and bottom panel) of the angular region in Figure 1A. The reproductive component r of the allocation reaction norm has a distinctive U-shape, which extends a finding that has already been reported in an earlier study (Fischer et al. 2009). When environmental energy availability is close to zero, the optimal reproductive investment r equals 1. Surprisingly, this "terminal investment" effect occurs irrespective of the considered constant level of e_{stor} (Fig. 1B, black area). This is the region in state space in which environmental energy availability is so low that survival is almost impossible. Hence, it is optimal to fully invest into reproduction, although this implies death after reproducing. At a certain threshold of e_{env}, survival becomes likely and the benefits expected from future reproduction then outweigh those from immediate reproduction. Beyond this threshold, reproductive investment rapidly decreases to a minimum and can even become zero (Fig. 2A, B). With environmental energy availability increasing, allocation to reproduction occurs again and asymptotically converges to 1. The U-shape of the reproductive allocation
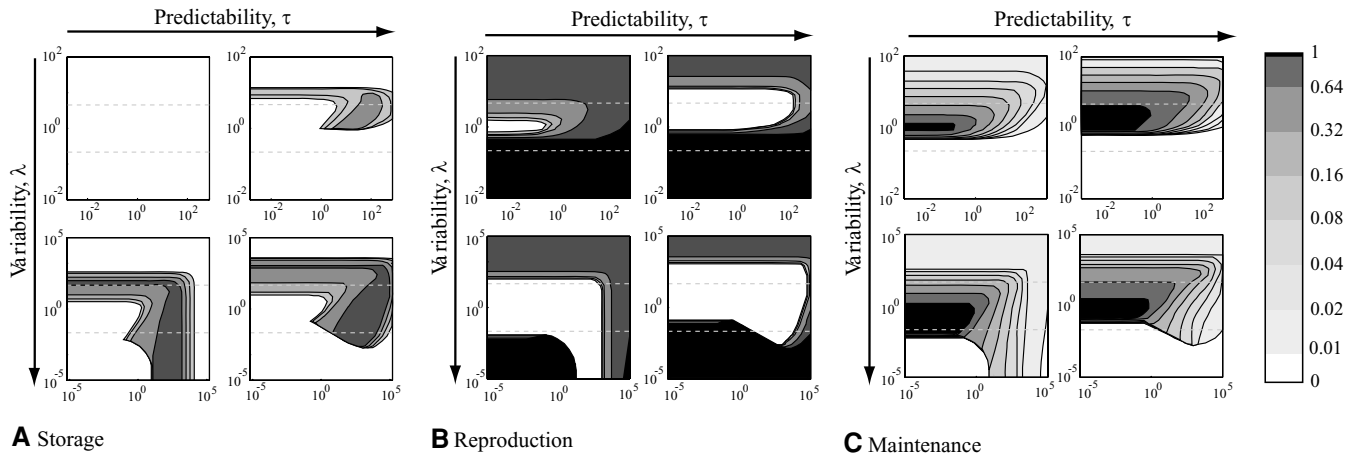
Figure 3. Evolutionarily optimal allocation strategies, describing the dependence on energy availability e_{env} (vertical axes) and e_{stor} (horizontal axes) of optimal (A) storage investment s, (B) reproductive investment r, and (C) maintenance investment m in four stochastic sample environments that differ in terms of environmental variability and predictability. Dashed gray lines show the 95% confidence intervals for environmental energy availability. In (A), (B), and (C), environmental variability is larger in the bottom row ($\lambda = 25$) than in the top row ($\lambda = 1$), whereas environmental predictability is larger in the right column ($\tau = 125$) than in the left column ($\tau = 5$). Contour lines show allocation fractions of 0, 0.01, 0.02, 0.04, 0.08, 0.16, 0.32, 0.64, and 1. Other parameter: $e_{1/2} = 1$.

component r remains irrespective of the other two allocation components m and s.

The sharp decrease from full reproduction to no reproduction corresponds to a sudden increase in allocation to maintenance. In Figure 2A, at a relatively low level of e_{stor}, this transition is steep but continuous. Simultaneously, allocation to maintenance increases rapidly from zero. For a higher level of e_{stor}, this transition becomes discontinuous (Fig. 2B). As the state reaches the bifurcation point, reproductive investment drops to zero, and investments into maintenance and storage both jump to considerable levels. With increasing e_{env}, maintenance investment increases further until it reaches a maximum (Fig. 2B, C) and finally decreases again as e_{env} is further increased. Note that although the maintenance investment m is a relative measure, the absolute amount of energy invested into maintenance increases monotonically from the transition onwards with growing e_{env} (results not shown). Optimal storage investment follows a more variable pattern. Depending on the level of e_{stor}, s exhibits either one (Fig. 2A) or two (Fig. 2B, C) local maxima. Between these two maxima, storage can even be skipped (Fig. 2B). At very high levels of e_{env}, storage investment s decreases again until it becomes zero. Storage allocation is here outcompeted by the extraordinarily large benefits that can be gained from high reproductive investment at such exceptionally high energy levels.

Depending on the characteristics of the environment, it is not always optimal to store energy. In an environment with low variability and low predictability, organisms should split their available energy only between reproduction and maintenance, regardless of current energy availability (upper left panels of Fig. 3A–C). Allocation to storage becomes optimal for an in-

creasing range of environmental states when environments become more variable and/or more predictable (Fig. 3A).

The fraction of energy allocated to storage rises as τ or λ increases (Figs. 3A and 4). In particular, increasing environmental predictability τ results in a shift, toward higher levels of e_{env}, of the region in which optimal storage allocation is positive (Figs. 3A and 4). The vertical branch of the angular region broadens toward lower levels of e_{stor} until a bifurcation appears beyond which no storage occurs. With increasing environmental variability λ, storage generally becomes optimal for a wider region in state space, and the vertical branch of the angular region stretches toward lower levels of e_{env}.

When increasing the parameter $e_{1/2}$ (i.e., the energy allocation to maintenance at which survival reaches $^1/_2$), storage is optimal only for higher levels of variability and predictability (results not shown). For higher $e_{1/2}$, survival becomes increasingly unlikely (eq. 2), so that the potential fitness benefits of future reproduction are diminished and storage thus becomes less beneficial.

In an entirely unpredictable environment ($\tau = 0$), it is irrelevant for optimal allocation decisions whether the energy is provided by the current environment or whether it comes from the energy stores, as storing energy in our model is cost-free. Optimal strategies for the same amount of total available energy e are equivalent, and thus strategies are reflection symmetric with respect to the state space's diagonal $e_{stor} = e_{env}$ (Fig. 4A). This symmetry is broken in predictable environments, for which expected future energy availability depends on the present conditions (Fig. 4B–E). The loss of symmetry is also visible in the corresponding fractions of reproductive allocation and
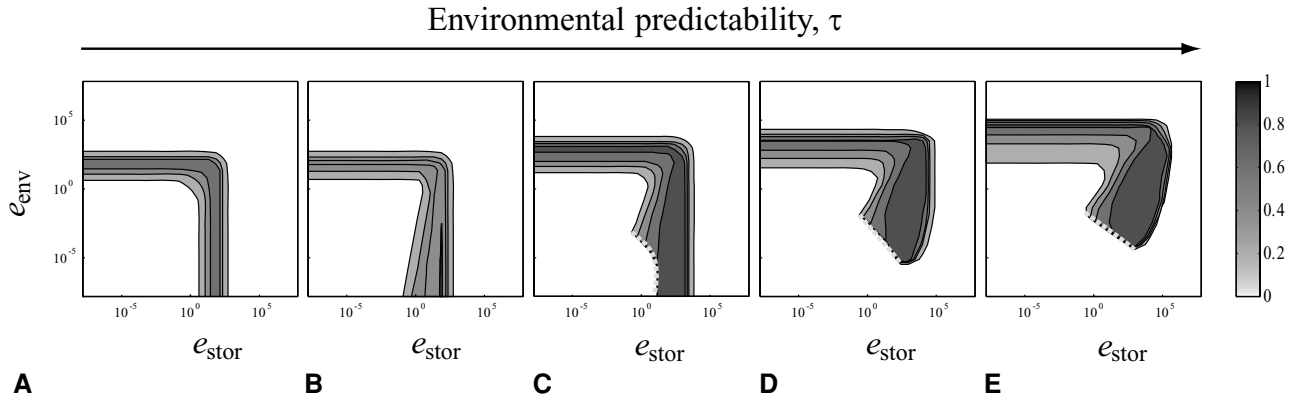
Figure 4. Loss of state-space symmetry of evolutionarily optimal allocation strategies. Departures from the reflection symmetry with respect to the diagonal $e_{env} = e_{stor}$ in state space gradually increase as environmental predictability τ grows (from left to right: $\tau = 0$, 1, 5, 25, and 125). Dashed gray lines depict the locations in state space of discontinuous bifurcations in investments described by the evolutionarily optimal allocation strategy. Contour lines show allocation fractions of 0, 0.2, 0.4, 0.6, 0.8, and 1. Other parameters: $\lambda = 20$ and $e_{1/2} = 1$.

maintenance allocation (results not shown). For low environmental predictability τ, the storage strategy is still close to symmetric (Fig. 4B). As the environment becomes more predictable, the vertical branch of the angular region broadens toward lower levels of e_{stor} due to increasing selection for allocating energy to storage already at lower levels of e_{stor}. At very low total energy availability, however, an opposing selection pressure determines optimal allocation to storage. Prospects for future reproduction are expected to be very low and a "terminal investment" strategy of full reproduction is favored by selection. Owing to these two antagonistic selective forces, the fitness function R_0 possesses two alternative local optima (Fig. 5). When these two fitness maxima are similarly high, a merely slight change of energy availability

causes the global maximum to switch its position from one local maximum to the other (Fig. 5). At the location of these discontinuous switches between maxima, a cusp bifurcation appears in state space (Fig. 4C–E, dashed gray lines).

We also analyzed the life histories resulting from the optimal allocation strategies derived above. Because we did not want to predefine the life spans of the simulated organisms, we based this analysis on the age-independent allocation strategies. We simulated individuals allocating energy according to the optimal strategy in four different sample environments (Fig. 6). These parameter combinations were selected to represent the variety of resulting life histories that emerge by varying λ, τ, and $e_{1/2}$. An environment with low variability λ, low predictability τ, and low
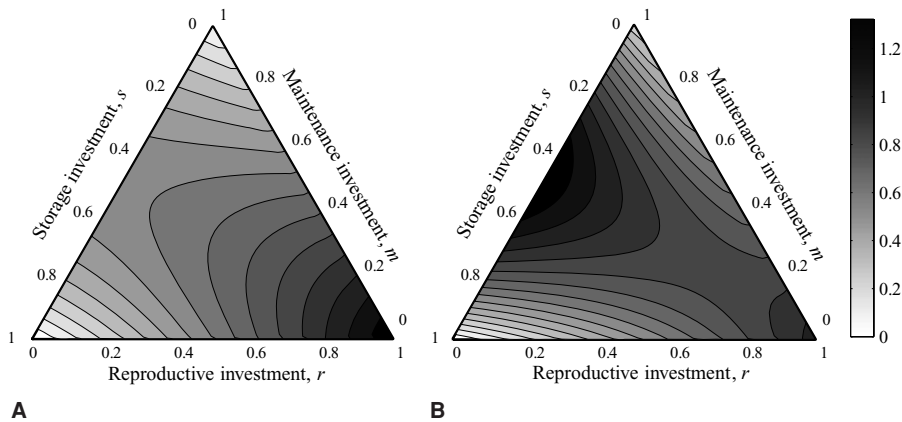

Figure 5. Dependence of expected lifetime reproductive success R_0 on investments (s, r, m) for two different levels of environmental energy availability e_{env}, illustrating the cause of discontinuous bifurcations in evolutionarily optimal investments. The corners of the triangle correspond to full investments into a single function ($s = 1$, $r = 1$, or $m = 1$). (A) The global maximum of R_0 is located at $s = 0$, $r = 1$, and $m = 0$. (B) A slight increase in environmental energy availability e_{env} raises the local maximum at $s = 0.49$, $r = 0$, and $m = 0.51$, so that it becomes the global maximum, thus resulting in a switch of evolutionarily optimal investments. Parameters: (A) $e_{env} = 1.9 \cdot 10^{-5}$ and $e_{stor} = 1.2$; (B) $e_{env} = 5.4 \cdot 10^{-5}$ and $e_{stor} = 1.2$.
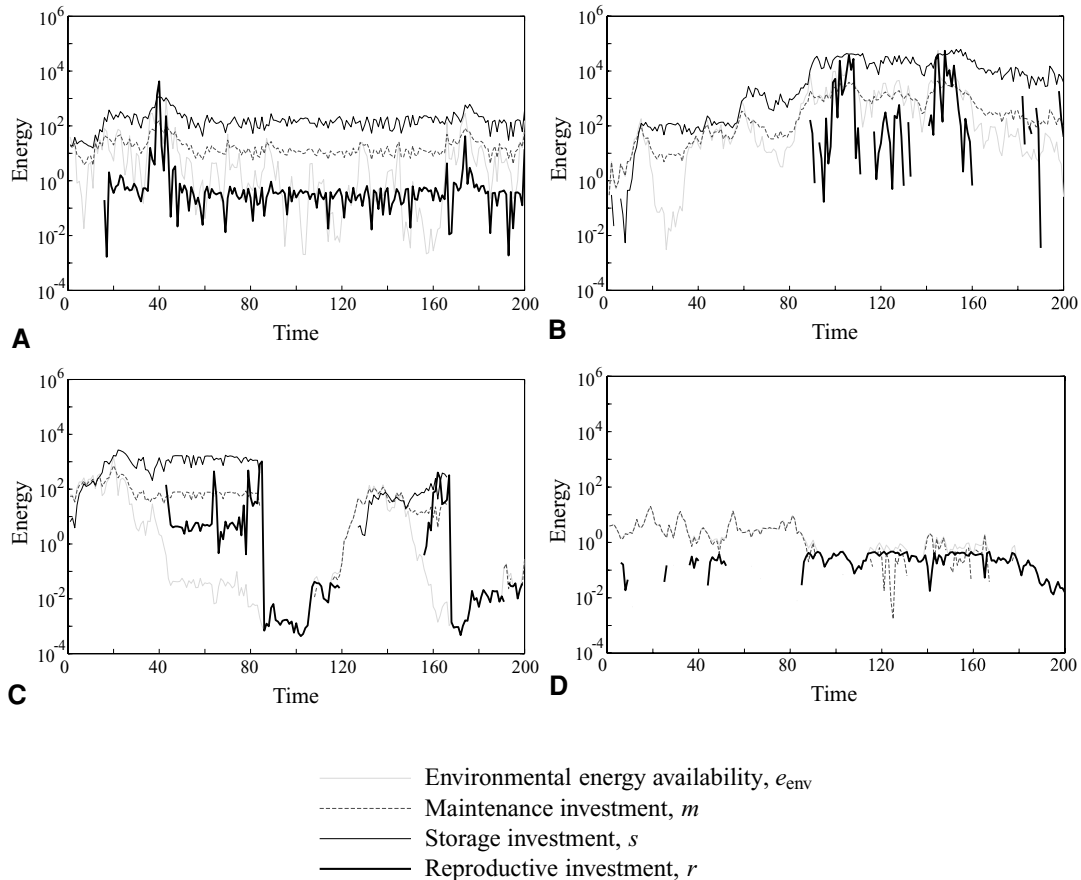
Figure 6. Examples of life histories resulting from evolutionarily optimal allocation strategies in four stochastic sample environments that differ in terms of environmental variability, environmental predictability, and the cost of survival. Each panel shows a sample time series of energy levels for an individual allocating energy according to the allocation strategy that is evolutionarily optimal in the respective environment: environmental energy availability e_{env} (gray lines), maintenance investment m (dashed black lines), storage investment s (thin black lines), and reproductive investment r (thick black lines). Note that vertical axes are scaled logarithmically. Parameters: (A) $\lambda = 20$, $\tau = 5$, and $e_{1/2} = 1$; (B) $\lambda = 40$, $\tau = 25$, and $e_{1/2} = 1$; (C) $\lambda = 20$, $\tau = 25$, and $e_{1/2} = 5$; (D) $\lambda = 40$, $\tau = 125$, and $e_{1/2} = 125$.

$e_{1/2}$ (with the latter implying that survival is not costly in terms of investments required into maintenance), selects for a typical iteroparous life history (Fig. 6A). After creating a moderate storage deposit, the individual starts to reproduce and continues to do so until the end of its lifetime. Increasing both variability and predictability produces a life history in which reproduction requires favorable environmental conditions in addition to sufficiently filled energy stores; otherwise, reproduction is skipped (Fig. 6B). If survival is costly (high $e_{1/2}$), so that survival becomes harder, it becomes more likely that individuals are best off by making a "terminal investment" when environmental conditions are harsh (Fig. 6C). Note that the shown time series continue even after a "terminal investment" event: when an individual dies before the end of the simulated time series, it is immediately replaced with a new individual, so as to keep the lengths of the shown time series equal for all examples in Figure 6. The two example time series involving terminal investment events (Fig. 6C, D) hence do

not illustrate the life history of single organisms. Instead, each of them corresponds to the life histories of several organisms. Semelparous life histories (in which a single reproductive event is followed by the death of the reproducing individual) are expressed in those parts of the time series in Figure 6C, D in which a series of "terminal investment" events occurs. These are the sections where the reproductive investment time series (thick black line) is the only visible line, as it coincides with environmental energy availability (Fig. 6C, D). Finally, when survival is very costly (Fig. 6D), storage can essentially no longer be afforded, which means that storage allocation only occurs for energy levels that are so high that they are virtually never reached in this environment.

Discussion
We have introduced and analyzed an energy-allocation model in which organisms can allocate available energy to maintenance,

reproduction, and storage. To our knowledge, our study is the first to provide a general analysis of storage strategies when environmental energy availability varies stochastically. Optimal storage allocation under these conditions differs qualitatively from optimal allocation strategies obtained from models in deterministic environments. In stochastic environments, simultaneous allocation to reproduction, maintenance, and storage can be optimal under some conditions, whereas this has never been found for deterministic environments (Perrin and Sibly 1993). Furthermore, we have shown that optimal allocations among different functions can switch rapidly or even discontinuously when energy availability changes only slightly. Our results show how properties of a stochastic environment critically influence whether organisms should be semelparous or whether, and to which degree, iteroparity is expected to evolve.

Our model illustrates that in almost constant environments it is often not optimal to store energy, which agrees with previous model results (Perrin and Sibly 1993; Kooi and Troost 2006). The evolution of energy storage requires at least some extent of either deterministic or stochastic environmental variability. Almost all organisms are physiologically able to store energy in some form, and life histories without any storage seem to be rare (Pond 1981). It is theoretically well understood that in deterministic environments organisms should only store energy if (1) reproductive success is expected to be higher in the future (e.g., Schaffer et al. 1982; Chiariello and Roughgarden 1984), (2) energy availability exceeds physiological thresholds of maximal reproductive investment (e.g., Kozlowski and Ziolko 1988), or (3) organisms have to prepare for periods of energy limitation (e.g., Cohen and Parnas 1976). A strategy of maintaining a baseline storage level even during periods of high and reliable food availability would not be adaptive in a fully predictable deterministic environment. In most environments, however, environmental variation is not exclusively deterministic (Tuljapurkar et al. 2009). We propose that storage strategies have evolved to buffer both predictable deterministic and unpredictable stochastic environmental changes, and consequently we incorporated both sources of variation in the formal description of environmental dynamics analyzed here.

Our findings demonstrate that results on energy allocation derived for constant or deterministic environments cannot provide reliable predictions for stochastic environments. This is in line with recent findings by Tuljapurkar et al. (2009) showing that optimal life histories are expected to differ substantially between stochastic and constant environments. In their study, Tuljapurkar et al. developed a framework for analyzing general life-history strategies in stochastic environments. They compared the fitness of a particular life history in a constant environment with the fitness the same strategy has in a stochastic environment, using an age-structured population model and suitable fitness measures for both settings. Their analysis revealed that for a particular life his-

tory, fitness in a stochastic environment is not equal to, but often substantially higher or lower than, the fitness in a constant environment. They suggest that the degree of iteroparity, the generation time, as well as within-year variances, within-year correlations, and between-year correlations of survival and fertility matter for a life-history strategy's success in a stochastically fluctuating environment. Our approach differs from their study by modeling the stochastic environment explicitly and by not making any a priori assumptions about the variability of, or correlation between, changes in survival and fecundity. Instead, in our analysis these features emerge as properties of the optimal allocation strategy. As energy allocation is not made explicit by Tuljapurkar et al., they do not consider or discuss energy storage. Making environmental dynamics explicit allows us to search for the optimal life history in any particular stochastic environment, without having to test the relative successes of an example set of life histories in different environments, as done by Tuljapurkar et al. (2009). Additionally, our approach accounts for phenotypic plasticity in energy allocation. Plastic responses to changing environmental conditions, as described by an optimal allocation strategy, imply that investments into reproduction and survival may be correlated for some environmental states, but not for others, a realistic feature that Tuljapurkar et al.'s framework is not designed to capture.

A variety of earlier studies have examined optimal storage strategies in deterministically varying environments. The classical view used to be that organisms should store only when there is a surplus of energy available at a given time (e.g., Wilkinson 1959; Cook 1963). This perspective has been revised, and it has been demonstrated that in deterministically varying environments energy storage can be beneficial, and thus can evolve, not only when there is a surplus of energy (Parnas and Cohen 1976; Kooi and Troost 2006), but also whenever it is likely that stored energy is needed in the future. So far, studies concluded that energy could be allocated to storage or reproduction in addition to maintenance, but not to both simultaneously (Perrin and Sibly 1993). However, all these earlier results stem from analyses in deterministic environments. Perrin and Sibly (1993) suggested in their review that an intermediate allocation to storage might be optimal in stochastic environments. Here, we have shown that this qualitative anticipation was correct: simultaneous allocation to maintenance, reproduction, and storage can be optimal under stochastically fluctuating environmental conditions.

Dynamic state variable models have been used before to model energy storage in the special case of foraging under predation. In a series of papers, McNamara, Houston, and colleagues studied optimal foraging decisions and resulting optimal energy-reserve levels in birds (McNamara and Houston 1990; Houston and McNamara 1993; Houston et al. 1993; Bednekoff and Houston 1994; reviewed by Brodin and Clark 2007). In line with our findings, these models predict intermediate levels of

stored energy that optimally balance mortality risks. How do the key assumptions of their framework compare to our approach? To answer this question, we need to consider the following three points. (1) An essential difference between the two approaches is that in the models by McNamara, Houston, and colleagues the predation-starvation trade-off is assumed to be a key factor for determining energy-storage strategies. In particular, predation risk is assumed to increase with stored energy, which creates an incentive for birds to reduce their energy reserves. Although this assumption is empirically well supported for small birds with risky foraging strategies (e.g., Lima 1986; Ekman and Hake 1990; but see Lilliendahl 1998), it is not evident in flightless animals (Brodin and Clark 2007). For the sake of generality, predation risk or foraging behavior are thus not made explicit in our model. Nevertheless, allocating energy to storage reduces survival also in our model, as it diverts energy from other functions, including maintenance. (2) In the models by McNamara, Houston, and colleagues, survival is assumed to depend directly on the amount of stored energy. Birds die of starvation when their energy reserves drop below a threshold. In our model, by contrast, survival is determined by the allocation of energy to maintenance. In this regard, our model is more general, because it allows organisms to survive not only by using their energy stores, but also by channeling available energy directly to maintenance, even when their energy stores are used up. (3) A third crucial difference concerns the fitness implications of different storage strategies. In the models by McNamara, Houston, and colleagues, optimal energy storage is determined by minimizing mortality risk (so that reproductive investment is excluded from the analysis; McNamara and Houston 1990) or the considered life history is a priori assumed to be semelparous (so that organisms may reproduce only once, either at a certain time or in a certain state; Houston et al. 1993). In our approach, in contrast, reproductive investment is completely flexible. This enables us to analyze not only which storage strategies, but also which associated life histories are expected to evolve in different environments.

In a previous study, we identified a characteristic U-shaped variation of reproductive allocation with increasing energy availability (Fischer et al. 2009). This pattern remains largely unchanged when including the additional option of energy storage. In contrast to our previous study, however, environmental predictability can affect allocation decisions in an unexpected way when storage opportunities are added. The switch from full reproductive investment to investment into storage and maintenance, which occurs for increasing energy availability, can become discontinuous when environmental predictability is high. Biologically it might not be all that relevant whether this switch happens fast and continuously or discontinuously, but it needs to be highlighted that in both cases minor changes in environmental energy availability or in stored energy availability may lead to abrupt

(and, over a wider range of energy availabilities, nonmonotonic) changes in the optimal allocation strategy.

An obvious but important result of our model is that for low energy availability, organisms secure their maintenance before investing into storage or reproduction. In contrast to most previous allocation models (e.g., Kooijman 1986; McCauley et al. 1990), we did not make the assumption that maintenance needs must always be fulfilled before energy can be spent on other functions. Therefore, this pattern is not a model assumption but instead emerges as a result of our analysis. Interestingly, this strategy is not always optimal, however. The full flexibility of allocation strategies implemented in our model allows the individual to channel all available energy to reproduction when energy availability is very low, rather than forcing it to fuel maintenance when survival is almost impossible. This results in the emergence of a terminal-investment strategy when organisms are close to starvation.

When optimizing reproductive success in environments that vary in predictability, variability, and in the cost of survival, a broad range of different life-history strategies emerges, ranging from semelparous life histories to those with various degrees of iteroparity. It therefore seems that the influence of stochastically varying environments is key to understanding the evolution of reproductive life-history strategies. Selection for iteroparous versus semelparous life histories has been the subject of many earlier theoretical studies (e.g., Gadgil and Bossert 1970; Schaffer 1974; Charlesworth 1994; Roff 2002). Life-history theory predicts that iteroparity is favored by selection when survival chances from one reproductive event to the next are high and when the fecundity per reproductive event is low due to external or internal constraints. Increasingly iteroparous strategies are predicted to experience a selective advantage in increasingly variable environments (Murphy 1968; Schaffer 1974). In agreement with these classical insights, we found that a high likelihood of survival is crucial for iteroparity to evolve, but that, in contrast to earlier results, limited fecundity per reproductive event is not a necessary condition for iteroparity to evolve in stochastic environments. Rather, the stochasticity of the environment itself may suffice, under conditions of high adult survival, for iteroparity to evolve. In line with our results, earlier studies found that semelparity is particularly common in unstable, temporary habitats in which adult survival chances from one year to the next are low (Charlesworth 1994; Roff 2002).

To keep our model general and tractable, we made several simplifying assumptions that could be relaxed in future studies. First, energy storage might burden an organism with costs resulting from an increased body mass that needs to be maintained; likewise, mobilization and reallocation of stored energy can be costly (Pond 1981; Bonnet et al. 1998). These costs are likely to vary among species (Pond 1981). In ectothermic animals, for

example, energetic costs associated with the maintenance and utilization of body reserves are lower than in mammals and birds, as fat bodies impede heat flow (Jönsson 1997; Bonnet et al. 1998; Shine 2005). Furthermore, an organism with large energy reserves may suffer from an increased risk of predation, for example, if an increased body mass implies reduced mobility. Such a cost must again be expected to vary greatly among species (e.g., aerial species need to be lightweight, whereas aquatic species can carry relatively large fat stores at much lower costs). Alternatively, establishing large energy reserves may require particularly risky foraging strategies, which could also contribute to a higher predation probability (Lima 1986; Houston and McNamara 1990; Houston et al. 1993). In our model, we assumed that energy storage and mobilization are cost-free. Although storage costs will most likely reduce the total amount of energy stored, they are unlikely to change the qualitative allocation pattern across energy-availability states. Second, the amount of exploitable energy available to an organism might not only be limited by what is provided by the environment, but also by the organism's phenotype, for example, by its foraging potential, gut capacity, or physiology (Ricklefs 1991; Weiner 1992; Kersten and Visser 1996; Ricklefs and Wikelski 2002). Such thresholds exist for most organisms and differ greatly between species (Ricklefs 1991; Weiner 1992; Suarez 1996). For the sake of generality, we did not introduce any such species-specific traits or thresholds. Third, our model focuses on energy allocation after maturation and describes organisms with determinate growth. It would certainly be an interesting extension of our approach to investigate size-dependent storage, to model storage allocation during the juvenile period, or to consider organisms with indeterminate growth. In all of these more complicated models, allocation to growth would have to be added to the allocations to storage, maintenance, and reproduction as a fourth decision variable. It is likely that such an extension would cause the optimal allocation reaction norm to become dependent on age. Fourth, we measured reproductive success in terms of energy, rather than trying to translate energy invested into reproduction into a resultant number of offspring. Accordingly, even small quantities of energy invested into reproduction increase an organism's reproductive success. This approach has the advantage that it avoids having to consider a particular, species-specific minimum investment threshold (e.g., a minimum egg size) that has to be allocated to allow for the onset of reproduction (Erikstad et al. 1998). More complex counterparts of these three specific simplifying assumptions could be incorporated in future analyses.

We conclude that in stochastically varying environments, unexpected storage allocation strategies might occur that differ significantly from optimal storage strategies in deterministic environments. In particular, simultaneous allocation to maintenance, reproduction, and storage can become optimal in a stochastically varying environment, and optimal allocation strategies can change

rapidly or even discontinuously in response to very small changes in energy availability. Our results furthermore highlight that environmental stochasticity has a crucial influence on the degree of iteroparity in life-history strategies, which deserves to be investigated in more detail in future work.

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