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Seasonality in Offspring Value and Trade-Offs with Growth Explain Capital Breeding

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ABSTRACT: The degree to which reproduction is based on reserves (capital breeding) and/or current acquisition (income breeding) drives extensive variation in organism life histories. In nature, pure income and capital breeding are endpoints of a continuum of diversity whose ultimate drivers are poorly understood. To study the adaptive value of capital and income breeding, we present an annual routine model of the life history of a perennial organism where reproductive value at birth varies seasonally. The model organisms allocate time and resources to growth, reproduction, and storage. Our model predicts that capital breeding is adaptive when timing of birth affects offspring reproductive value. The stronger the seasonality, the more time is dedicated to capital breeding and growth after maturation (indeterminate growth) instead of income breeding. This is because storage and growth are investments in future (residual) reproduction taken at times when offspring value is low. Storage is a short-term investment in offspring through capital breeding; growth is a long-term investment in reproductive potential. Because the modeled production rate increases less than linearly with body size, growth brings diminishing returns for larger organisms, favoring capital breeding. Building storage requires time, which limits growth opportunities, and we show for the first time that in seasonal environments, the degree of capital breeding is tightly linked to body size of indeterminate growers through allocation trade-offs.

Keywords: income breeding, indeterminate growth, annual routine, resource allocation, body size, seasonal environments.

Introduction

The use of energy storage as a part of a reproductive strategy represents an important component of life-history variation (Stearns 1992). The concept of income versus capital breeding was proposed to depict the role of storage in breeding strategies (Drent and Daan 1980). Capital breeders reproduce from reserves gathered before breeding, whereas in income breeders, current acquisition fuels reproduction. Both pure income and pure capital breeding have evolved, but the majority of life forms exist along a continuum of income to capital breeding (e.g., Thomas 1988; Jönsson 1997). Several hypotheses have been proposed to explain the phenomenon and the observed diversity. Adaptive explanations related to conditions during breeding have underlined scarcity and variability of food intake, increased energy demand, and high risk of obtaining food during breeding (Jönsson 1997; Stephens et al. 2009). Some groups have been suggested as predisposed for capital breeding—for example, ectotherms and, in particular, ambush predators or aquatic representatives—because their physiology and/or lifestyle reduces the costs associated with carrying reserves (Bonnet et al. 1998; Varpe et al. 2009). In pinnipeds, a model mammalian group for studies on capital breeding (e.g., Boyd 1998), the physiological efficiencies of storing resources and scaling of production with body size are important for explaining the diversity of strategies (Trillmich and Weissing 2006; Houston et al. 2007). A predominating overarching view is that capital breeding is the better strategy in stochastically fluctuating environments and that income breeding should be favored in predictable environments (Jönsson 1997; Fischer et al. 2011).

Seasonality as a crucial evolutionary driver of capital breeding has emerged recently (Varpe et al. 2009). Capital breeding comes with temporal and spatial freedom relative to income breeding and allows timing of reproduction to be optimized to the time windows that maximize fitness. In marine copepods, in which growth ceases after maturation, the earliest eggs have a disproportionally high contribution to fitness because of seasonality in food availability and predation risk, which in turn promote capital breeding (Varpe et al. 2007, 2009). Seasonal variation in food availability may also promote capital breeding in pinnipeds (Stephens et al. 2014) and explains the diversity of strategies in organisms selected for short generation time

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and determinate growth, with capital breeding and small size expected when the feeding season is short (Sainmont et al. 2014). In this study, we propose an ultimate explanation emerging from consideration of the fundamental life-history trade-off between allocation of resources to growth (including indeterminate growth), reproduction, and storage in a seasonal environment.

Storing resources, essential for capital breeding, requires time, and there is consequently a trade-off between building reserves and other activities. A trade-off with growth is central not only because growth is time and energetically demanding but also because larger size usually means higher fecundity and/or better provisioned offspring (Peters 1983). A large number of invertebrate and vertebrate taxa (e.g., cladocerans, clams, fish, amphibians, and reptiles) as well as many perennial plants are indeterminate growers; that is, they continue to grow and increase their size after maturity, often until the end of life (Heino and Kaitala 1999). Classic theoretical models concerning aseasonal environments predict irreversible switching of allocation from growth to reproduction (Cohen 1971; Ziółko and Kozłowski 1983), and growth after maturation can appear under somewhat specific conditions (Kozłowski and Ziółko 1988; Perrin and Sibly 1993). A fundamental question in life-history evolution is therefore: why does indeterminate growth exist? (Kozłowski and Uchmański 1987; Stearns 1992; Cichoń 1999; Heino and Kaitala 1999; Kozłowski and Teriokhin 1999).

An increase in the mass of productive tissues attained through growth raises future reproductive success (Kozłowski 2006) but comes with the risk of no payback in case of death even long after the investment. By contrast, building storage can boost reproductive rate during the nearest period suitable for breeding. Growth and storage thus contribute to residual reproductive value at different timescales. Growth is a long-term investment in lifetime reproductive potential, whereas storage is a short-term investment in offspring produced in a relatively near future. Indeterminate growth and capital breeding as options of investment in future reproduction are particularly relevant in seasonal environments where offspring recruitment depends on time of birth. Offspring born late in the season are often subjected to increased mortality (Einum and Fleming 2000; Vonesh 2005; Reznick et al. 2006), experience intense cannibalism or competition from early born conspecifics (Kinoshita 1998; Ryan and Plague 2004; Drummond 2006), and have reduced growth rates associated with deterioration of environmental conditions through the season (Varpe et al. 2007; Warner and Shine 2007). For a perennial organism living in a seasonal environment where offspring prospects depend on time of birth, the evolutionary dilemma is the following: what type of action should an adult undertake in periods when the energy balance is positive but offspring production contributes poorly to fitness? If we consider only a trade-off between growth and reproduction, then the answer is to keep spending acquired resources on growth as long as larger size increases future reproductive rate (Ejsmond et al. 2010).

Here, we develop an annual routine model (cf. Houston and McNamara 1999; McNamara and Houston 2008) to analyze optimal resource allocation in perennial organisms that inhabit seasonal environments, where the contribution to fitness by newborns changes with birth date. We focus on trade-offs involved in growth (determinate vs. indeterminate growth) and breeding strategies (capital vs. income) for the first time combined into one life-history framework. We emphasize the time constraint imposed by seasonality on the reproductive value of offspring, often omitted in life-history studies but resulting in a more realistic and richer array of trade-offs and strategies (Barta et al. 2006; Varpe et al. 2007). These aspects allow us to consider jointly optimal body size, degree of indeterminate growth, breeding phenology, and reproductive mode.

The Model

The model considers a perennial organism—such as clams, fish, or reptiles—living in an environment where mortality and food availability change seasonally to an extent that resource acquisition in harsh periods is only sufficient to cover maintenance costs. Seasonality also results in unequal fate of offspring produced at different times of the year, expressed as the reproductive value at birth. The organism maximizes fitness by optimal scheduling of resource allocation into growth, storage, and reproduction. When free to allocate to different sinks, an organism may be a determinate or indeterminate grower (depending on how resources are allocated to growth after maturation) and use stored or currently assimilated energy for reproduction. For simplicity, the storage of the modeled organism can be used only for reproduction (fig. 1). Note that the term "allocation decision" used throughout the article refers to the life-history strategies that the organisms have evolved. The potential strategy-space in our model allows a full continuum from pure income breeding to pure capital breeding, with a range of mixed strategies in-between. In our model presentation and examples, we refer to animals. Our results are, however, relevant also to indeterminately growing plants, but we did not consider annual shrinkage of productive body, which is frequently observed for plants and sometimes in animals.

Body Architecture and Production Rate

The body of the model organism is divided into two parts: productive tissues (w) and storage (s; for all key model

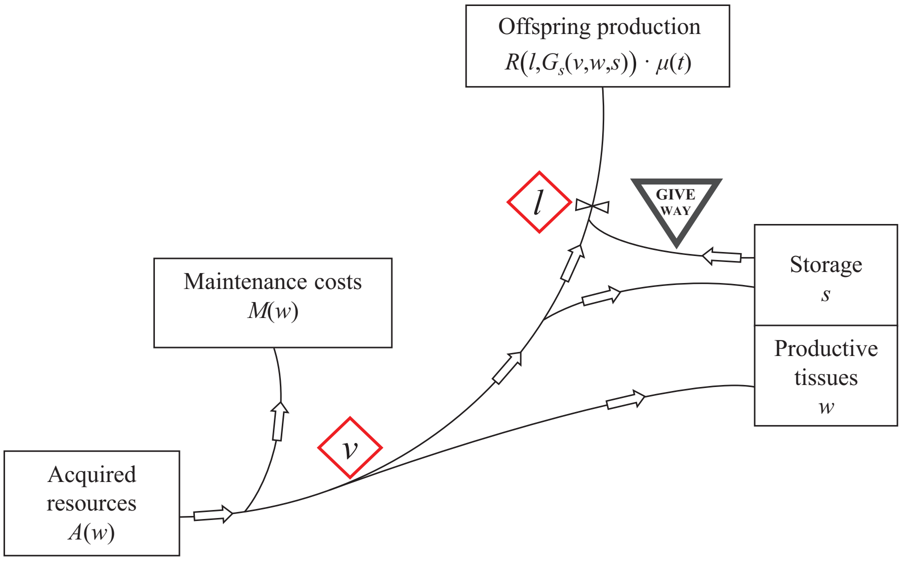

Figure 1: Basic scheme of the allocation components of the annual routine model. A body of the organism consists of two parts: productive tissues w and storage s. Arrows represent direction of energy flow. Decisions about what proportions of resources are allocated to competing functions, v and l (red diamonds), are optimized in each unit of time (days in our model) so that fitness is maximized. Resource acquisition during winter is balanced by maintenance; hence, $A(w) - M(w) = 0$. During summer, the decision v divides surplus resources between growth and two other activities: reproduction and storage. Allocation to storage in a given time unit is possible only if the animal is not utilizing already stored resources for breeding. The rate of offspring production R depends on body size, storage, and decisions v and l. Decision l is a valve that sets the rate of offspring production and therefore also determines the contribution by storage to offspring production. Importantly, mobilization of storage is possible only if all incoming resources are allocated to growth and/or reproduction (indicated by the "give way" sign). The assumption of sequential allocation within a given time unit is purely technical and allowed us to reduce the number of decision parameters considered in the model. The fitness contribution of an offspring produced at a given time of the season is given by $\mu(t)$.

parameters, see table 1). Production rate of an organism $P(w)$ depends on the mass of productive tissues and is given by the allometric function

$$P(w) = a_1 w^{b_1}, \tag{1}$$

where a_1 is a scaling constant set to arbitrary values of 0.2 and b_1 is the allometric exponent set to 0.75 in numerical examples presented below (for graphical presentation, see inset in fig. A1; figs. A1–A5 available online). The results are not affected qualitatively by the assumed value a_1, and allometric exponent b_1 close to 0.75 is well supported by empirical evidence on the scaling of production with body mass (e.g., Peters 1983; Glazier 2005; Sibly and Brown 2009). In general, the conclusions of our model are robust under the assumption that $b_1 < 1$.

Seasonal Variation in Mortality and Assimilation

Years in the model are divided into two seasons: favorable and unfavorable (hereafter, summer and winter). The rate of adult mortality is assumed constant within a season (q_v for summer and q_w for winter). Specific mortality rates can be combined into a yearly survival S_y, partitioned into the summer and winter survivals S_v and S_w, according to

$$S_y = S_v S_w = \exp[-(q_v T_v + q_w T_w)]. \tag{2}$$

The parameters T_v and T_w denote the duration of summer and winter, with each set to 180 days in the numerical examples presented below. In summers, the biomass production is positive, $P(w) > 0$, whereas resource acquisition in winters for simplicity is balanced by maintenance; hence, $P(w) = 0$. Thus, growth, storage, and reproduction are possible only in summers. For the sake of simplicity, and because time devoted to gather storage for maintaining soma in a harsh period can be considered as a part of nonproductive winter (see Giacomini and Shuter 2013), we assumed that storage can be used only for reproduction.

The life cycle of the modeled organism is divided into three consecutive stages: juvenile, immature, and adult. The juvenile period starts at the day of birth and lasts to the end of the first winter. Reproduction and storage are not possible in juvenile organisms. The immature period starts just after the first winter and lasts until the first decision about allocation of resources to offspring production, at which point they become adult.

Table 1: Summary of key parameters

	Interpretation
Model parameters:	
w	Mass of productive tissues
s	Mass of storage
$P(w)$	Production rate
$m_{\mathrm{d}} \in \langle 0, 1.05 \rangle$	Magnitude of size-dependent mortality of juveniles during winter (see fig. 2*B*); the higher the m_d, the stronger the mortality related to size
$Q \in \langle 1, 4 \rangle$	Rate of capital breeding (e.g., for $Q = 2$, organism with unlimited storage is able to reproduce twice as fast as an organisms with no storage); the higher the Q, the faster storage depletion
$K_{\mathrm{f}} \in \langle 0.3, 1 \rangle$	Efficiency of production of offspring tissues from storage
$S_{\mathrm{v}} = 0.8$, $S_{\mathrm{w}} = 0.7$	Probability of surviving summer and winter (immatures and adults)
S_{j}	Probability of surviving to end of first winter (juveniles)
Variables:	
$\mu(t)$	Offspring value defines offspring contribution to fitness according to their date of birth (fitness component calculated through iterative repetition of optimization procedure)
$v \in \langle 0, 1 \rangle$	Decision setting growth rate (optimized in order to maximize fitness)
$l \in \langle 0, 1 \rangle$	Decision setting rates of reproduction and storage (optimized in order to maximize fitness)

Note: Model parameters are given with their range, and variables are free to vary during optimization. Mass of productive tissues, storage, and production rate are given in arbitrary energetic units.

Juvenile Phase of Life

The prospects of offspring, defined as the reproductive value at birth (i.e., the expected reproduction through current and future offspring production), depend on their day of birth t_{B} because the chance of surviving to adulthood depends on the body mass of the young. Offspring produced early in the season grow for longer, thus attaining larger size at the end of the juvenile period but suffering mortality risk for a longer period than their conspecifics born later (addressed below). The juvenile mortality rate during the first winter has two components: a size-independent mortality rate, for simplicity equal to adult winter mortality q_{w}, and a size-dependent component q_{j}, expressed by

$$q_{\mathrm{j}} = q_{\mathrm{j}}(w_{T_v}(t_{\mathrm{B}})) = m_{\mathrm{d}} \exp\left[-\frac{w_{T_v}(t_{\mathrm{B}})}{n w_{T_v}(1)}\right], \qquad (3)$$

where w_{T_v} is juvenile body mass at the last day of the first summer, as a function of day of birth t_{B}. The scaling parameter n characterizes how fast the survival rate increases with body mass and was set to 0.25 in the examples below, so a juvenile born on the first day of summer survives winter with approximately the same probability as an adult (fig. 2*A*; for details on the role of n, see app. A and fig. A2; app. A available online). By changing m_{d} in equation (3), we manipulated the magnitude of the size-dependent mortality of juveniles in the model (fig. 2*A*). The exponential character of the assumed relationship between the size of juveniles and their survival is supported by empirical evidence (Hutchings 1993) and has been used previously in optimization of allocation strategies under size-dependent mortality (Taborsky et al. 2003). To minimize the number of parameters, we assumed a constant rate of juvenile mortality in summer, equal to the summer mortality of adults, q_{v}. In calculating survival probability for the entire juvenile period, given by equation (4), we take into account that offspring raised early in the season suffered mortality risk longer than their conspecifics born later:

$$S_{\mathrm{j}} = \exp\{-q_{\mathrm{v}}(T_{\mathrm{v}} - t_{\mathrm{B}}) - [q_{\mathrm{w}} T_{\mathrm{w}} + q_{\mathrm{j}}(t_{\mathrm{B}})]\}. \qquad (4)$$

Growth, Storage, and Reproduction in Immature and Adult Organisms

The productive body of the animal changes according to

$$w(t+1) = w(t) + K_{\mathrm{p}}(1 - v)P(w), \qquad (5)$$

where $v \in \langle 0, 1 \rangle$ is an allocation decision (see table 1) where $1 - v$ of available resources will be allocated to growth, and K_{p} denotes the efficiency of conversion of acquired energy into productive body tissues, set to 0.5 in the numerical examples, which fits the empirical estimates for fish (Wieser and Medgyesy 1991). The efficiency of converting acquired resources into body or offspring tissues varies among groups of organisms and types of food, but in our model, K_{p} acted only as a scaling variable and hence did not affect the results qualitatively. The remaining resources can be either stored or allocated directly to reproduction (fig. 1). For simplicity, we assumed that productive tissues cannot shrink and that energy allocated to reproduction is immediately released as offspring. Because we model energy acquisition during summer as constrained only by body mass, we reduced model complexity by assuming that storage can be utilized only for reproduction and not for growth. Furthermore, we did not allow for the simultaneous utilization of storage for reproduction and allocation of current income to storage (which would be inefficient, taking into account costs of building and mobilizing storage). Consequently, when the organism is breeding based on capital, simultaneously ac-

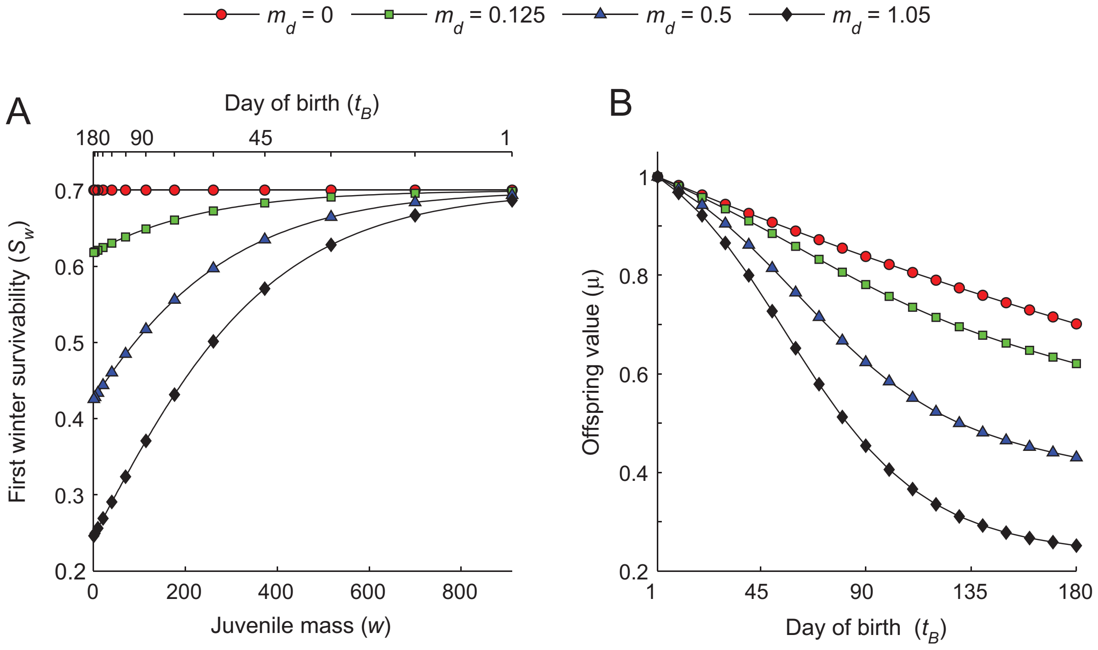

Figure 2: Change in winter mortality of juveniles in relation to model parameters and its effect on offspring value, that is, normalized reproductive value at birth $\mu(t_B)$. *A*, Winter survival of juveniles depends on their body mass (bottom *X*-axis) and therefore indirectly on their date of birth (top *X*-axis). The parameter m_d determines the size-dependent mortality of juveniles, described by equation (4), and thus their winter survival as a function of the day of birth. *B*, Magnitude of the size-dependent mortality influences the offspring value $\mu(t_B)$ determining offspring contribution to fitness. With increasing size-dependent winter mortality of juveniles (expressed by m_d values given in figure), the reproductive value at birth μ decreases more rapidly with day of birth t_B. Winter survival of adults set to $S_w = 0.7$.

quired resources have to be used for income breeding or growth (fig. 1).

Rate of reproduction is an outcome of the allocation decision l (table 1; fig. 1). To avoid unrealistically rapid (in fact, even instantaneous) utilization of the entire storage, we imposed a ceiling G_{max} (eq. [6]) for the amount of energy—the sum of current income and storage—that can be processed by the productive tissues per unit of time:

$$G_{max} = QP(w). \tag{6}$$

For example, if Q equals 2, an organism is capable of allocating resources to reproduction at a rate maximally twice as high as one that covers reproduction only from current income and uses all available resources for reproduction (see table 1). The rate of resource allocation to reproduction may also be limited by the amount of storage s. Thus, the maximum amount of resources G_s that can be allocated to reproduction is given by

$$G_s = \min\begin{cases} G_{max} \\ \\ vP(w) + \dfrac{s}{K_1} \end{cases}, \tag{7}$$

where K_1 is the efficiency of converting storage to reproductive tissues. The allocation decision l (fig. 1) determines the amount of resources for reproduction R according to

$$R = K_p l G_s. \tag{8}$$

Because G_s depends on v (eq. [7]), R is set by both optimized decision parameters v and l, and the combination of v and l consequently determines (1) how an animal allocates incoming resources to storage and/or reproduction and (2) whether the storage is used for reproduction (see also fig. 1). We assumed that reproduction within a given time unit is first based on utilization of current income not allocated to growth, that is, $vP(w)$ (see fig. 1). If an animal allocates to reproduction the amount R lower than $vP(w)$, the rest ($vP(w) - R$) is allocated to storage, and the storage amount will increase by $K_2[vP(w) - R]$, where K_2 is the efficiency of converting current production to storage. Otherwise—that is, when R is higher than $vP(w)$—the difference $R - vP(w)$ must be covered from storage. If there is enough storage, $(1/K_1)[R - vP(w)]$ resources will be taken. If there is not enough storage, the amount of resources going to reproduction will be $vP(w) + s/K_1$, and storage will be depleted.

Because our aim was to focus on trade-offs involved in the origin of indeterminate growth and capital breeding and not to consider the details of the physiological processes, the results are analyzed with reference to one coefficient $K_f = K_1K_2$ describing the combined effect of both efficiencies K_1 and K_2 (see table 1). K_f defines the final efficiency of offspring tissue production from storage. Livestock energy budgets suggest that the total efficiency of fat conversion can reach very high levels, even close to 1 (e.g., Noblet and Etienne 1987). While in "Results" we show outcomes for a broad range of K_f values, in most of the numerical examples we assumed $K_f = 0.9$, which means that 10% of acquired and then stored resources will be lost through dissipation before being used for reproduction.

Fitness Measure

The optimal lifetime allocation pattern was found through maximization of fitness F, given by

$$F = S_j(t_B)\sum_{i=1}^{\infty}\left[\int_{t=0}^{T_v} R(i,t)L(i,t)\mu(t)dt\right], \qquad (9)$$

where reproduction rate R (see eq. [8]) depends—directly and indirectly through mass of productive tissues—on optimized decision parameters v and l (see table 1; eqq. [5], [8]). The organisms were able to reproduce after the first winter, that is, after surviving the juvenile period. The probability of surviving to the end of the first winter S_j depends on birth date (see eq. [4]), and thus S_j is before the summation sign in equation (9). Energy allocated to reproduction R is weighted by $L(i,t)$, which is the probability of surviving from the beginning of the second year of life (the first year with potential for reproduction) to day t in the ith year. Resources allocated to reproduction R are also weighted by $\mu(t)$, the relative offspring value (see below).

Offspring Value

The offspring value μ is equivalent to the normalized reproductive value at birth (see also table 1). The function $\mu(t)$ defines how offspring contribution to fitness depends on birth date and thus depends on time when offspring is produced. In the model, offspring reproductive value is the outcome of an optimization procedure and emerges from maximizing the number of descendants left far into the future through iterative repetition of the optimization (McNamara 1991; Houston and McNamara 1999). Initially, arbitrary values are assigned to $\mu(t_B)$ (e.g., a constant value 1) for all t_B. Then, vectors of optimal allocation decisions that characterize the life history of an organism born on day t_B are calculated through optimization, together with corresponding fitness values $F(t_B)$. Using these values, offspring value used in the next optimization round $\mu'(t_B)$ is calculated according to $\mu'(t_B) = F(t_B)/\max[F(t_B)]$, and the procedure is repeated until reaching an asymptotic limit or, more precisely, when $\mu'(t_B)$ satisfies the condition $\max\{|\mu(t_B) - \mu'(t_B)|\} < \varepsilon$, where ε match assumed numerical accuracy (for details, see app. A). This approach has been applied successfully in previous work on timing of birth in seasonal environments (McNamara et al. 2004; Varpe et al. 2007; Walczyńska et al. 2010).

The fitness measure (eq. [9]) is valid under two assumptions. First, offspring size is not considered to evolve, and a constant amount of resources is required to produce a single offspring. Also, population size is constant and regulated by density-dependent juvenile survival or dispersal, which is likely the case for perennial organisms (Kozłowski 1993; Mylius and Diekmann 1995; Brommer 2000). To find the set of allocation decisions $v(i,t)$ and $l(i,t)$ maximizing fitness, we applied dynamic programming (Houston and McNamara 1999; Clark and Mangel 2000). All calculations were performed with MATLAB 7.9 (Mathworks, Natick, MA). MATLAB code of the dynamic optimization program used to obtain optimal life histories presented in this article is available online.

Because juveniles and adults differed in mortality rate only during winters, summer survival does not affect qualitatively the seasonality in offspring value. As a result, the rate of summer mortality q_v did not affect conclusions on the reproductive strategy in our model. To keep our report concise, we present results only for a summer mortality level set to $S_v = 0.8$.

Results

High Mortality of Late Borns Drives the Reproduce-First Grow-Later Tactic

Let us first consider an obligatory income breeder, that is, an animal unable to store energy for reproduction. This consideration corresponds to setting the efficiency of energy storage and mobilization K_f to 0. The allocation dilemma is then reduced to how growth and reproduction should be scheduled during the vegetative seasons. The optimal strategy is given by the switching curve, which is the outcome of the optimization process (e.g., fig. 3*A*, 3*B*). The switching curve divides the body size versus age plane into two parts. To maximize fitness, an organism should allocate to growth if its body mass at a given age is below the curve and switch to reproductive allocation if above. Because offspring produced early grow longer and thus reach the switching curve earlier than conspecifics produced late in the summer, the optimal allocation strategy depends on the day of birth t_B (see fig. A1). If the offspring reproductive value is indepen-

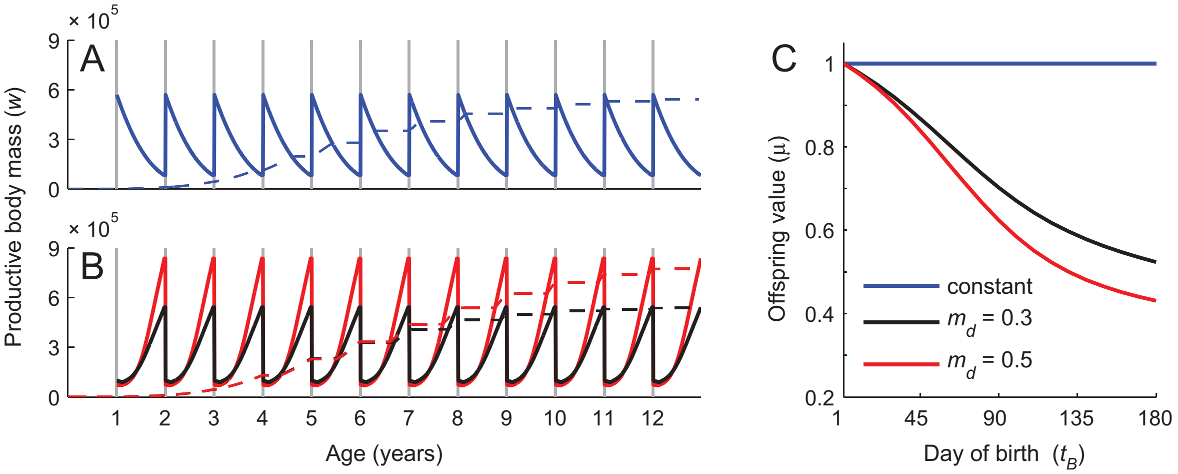

Figure 3: *A*, *B*, Optimal allocation strategies of an obligatory income breeder. Switching curve is the outcome of optimization (solid lines) and growth trajectory (dashed lines) for cases when offspring value is time independent (*A*) or when it decreases through summer (*B*). To maximize fitness, either an organism keeps growing if its body size is below the switching curve or it reproduces. The shapes of the switching curve and growth trajectory depend on the reproductive value at birth $\mu(t_B)$ depicted in *C* (lines correspond to switching curves in *A* and *B*). Because respiration balances assimilation in winter, body size does not change, and winters are compressed to vertical lines. For readability, the first 12 years are displayed, and growth curves represent trajectories for an organism produced on the first day of summer ($t_B = 1$). Other model parameters: $K_f = 0$, $S_w = 0.7$.

dent of birth date, the optimal strategy of a perennial organism in a seasonal environment is to use the first part of the vegetative season to grow and to reproduce late but before winter (fig. 3*A*; see also Kozłowski and Teriokhin 1999). However, in our model, winter survival of juveniles depends on body mass (see eq. [3]; fig. 2*A*). The early born offspring have more time to grow before first winter, and the reproductive value of juveniles μ therefore decreases with their birth date t_B (fig. 2*B*). The decrease defines the strength of the size dependence of winter mortality and is steeper for large values of m_d (cf. fig. 2*A*, 2*B*). Consequently, the optimal strategy is to switch to reproduction early, when the reproductive value of juveniles is relatively high, followed by growth, which is an investment in future reproduction (fig. 3*B*). The higher m_d—corresponding to steeper decrease in offspring reproductive value $\mu(t_B)$—the more pronounced the tendency to grow after maturation (compare red and black switching curves in fig. 3*B*).

Strong Seasonality in Offspring Reproductive Value Promotes Capital Breeding

By setting $K_f > 0$, we allow the model organism to store energy for future reproduction, and the growth trajectory must be drawn in the three-dimensional space of body mass w, current level of storage s, and age t. Consequently, the optimal strategy is now described by a three-dimensional switching surface, which is an outcome of the optimization process (e.g., see fig. A3). Each time the trajectory for productive mass, storage, and age of an organism crosses the surface from the bottom up, the organism stops allocating to growth and rather allocates to storage and/or reproduction (fig. 1).

As stated previously, a sharp decline in offspring value with date of birth (fig. 3*C*) favors an obligatory income breeder ($K_f = 0$) to start a summer with reproduction and then grow for the remaining time of that summer (fig. 3*B*). Organisms able to build storage also start a summer with reproduction and grow afterward when offspring value declines, but now the end of summer is dedicated to gathering stores for future reproduction (fig. 4*A*).

The following year, storage is utilized to increase the rate of offspring production above the level allowed through income breeding. The lifetime allocation strategy illustrated in figure 4*A* is then to grow only in the first year, grow during most of the second season, and store reserves at the end of the season. From year 3 onward, the optimal strategy is to (1) first reproduce from both capital and income; (2) after storage is used, reproduce from current income; (3) stop reproduction and invest in productive soma by growing (indeterminate growth); and (4) store energy, which will again be used to boost reproduction rate in the early part of the next summer.

The degree of capital breeding increases with the seasonality in offspring value. With the increase in m_d, the offspring value decreases more and more steeply with date of birth (see insets in fig. 4*B*). As a result, storing energy

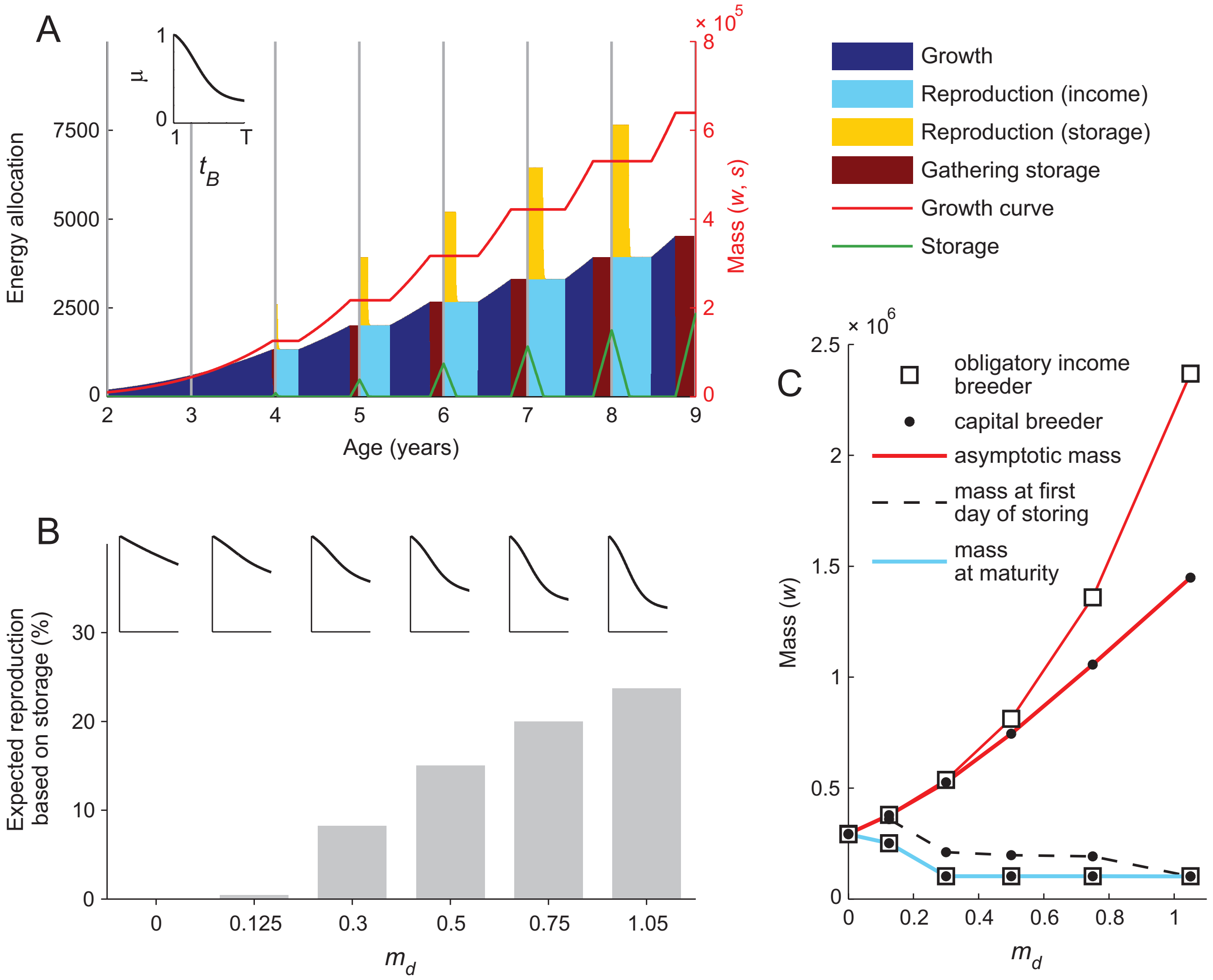

Figure 4: *A*, Growth trajectory and allocation of energy to different sinks for strong size dependence of juvenile mortality in winter ($m_d = 1.05$). The reproductive value at birth $\mu(t_B)$ is illustrated in the inset. Because respiration balances assimilation in winter, body size does not change, and winters are compressed to vertical lines. For legibility, only the eight initial years are displayed. *B*, Gray bars show the percentage of reproduction covered from reserves as a function of the size dependence of juvenile winter mortality (higher values of m_d lead to stronger dependence of the offspring value $\mu(t_B)$ on the day of birth; insets). Because the model organisms have positive energy balance during summer, capital breeding was always accompanied by income breeding. *C*, Asymptotic body mass, mass at maturity, and productive mass at first day of storing reserves for an obligatory income breeder and an animal that is able to choose the mode of reproduction. Note the difference in asymptotic size of obligatory income breeders and capital breeders. Other model parameters: $K_f = 0.9$, $Q = 2$, $S_w = 0.7$.

for future reproduction starts to be profitable, and optimal breeding changes from pure income breeding—optimal under flat offspring value (weak size dependence of juvenile survival, low m_d)—to a strategy where rate of offspring production relies considerably on stored resources (fig. 4*B*).

Our intention was to model a case commonly observed in nature, that is, offspring born early being more valuable than those born late. However, one could imagine an alternative scenario in which offspring value increases toward the end of the summer. Under such an assumption, the conclusion presented here does not change, and high degree of seasonality in offspring value translates to high degree of capital breeding and indeterminate growth (see fig. A4).

Capital Breeding Trades Off with Size Attained by an Indeterminate Grower

The time constraint imposed by the duration of the summer is an important aspect of our annual routine model. If we consider the allocation strategy of a capital breeder, then storing energy is a time and resource-consuming process that trades off with growth (see the larger asymptotic size for an obligatory income breeder in fig. 4*C*).

The efficiency of energy conversion associated with gathering and mobilization processes, described by K_f, strongly affects the tendencies for capital breeding (cf. fig. 5*A*, 5*B*). Whereas a decrease in K_f should move the optimal strategy toward more income, it also drives the increase in asymptotic body size (fig. 5*D*). As capital breeding becomes less and less profitable, the lower efficiency of storing (when K_f is low, a large fraction of stored resource is lost) the tendency for an alternative investment in future reproductive success—that is, growth—increases. Under low K_f, the model organism therefore allocates more time and resources to growth. The change in the rate of storage mobilization Q—which in the model is a bottleneck for the rate of capital breeding—also affects the allocation strategy (cf. fig. 5*A*, 5*C*). As Q increases, the rate of reproduction increases, and more juveniles can be released close to the beginning of summer, when the offspring value is high. To meet the high energy demand for reproduction in early summer, organisms have to use more time for building up storage and have less time for growth. Hence, with the increase in Q, the optimal asymptotic size decreases (fig. 5*E*).

In most cases, size at maturity, in contrast to asymptotic size, was the same for capital and obligatory income breeders,

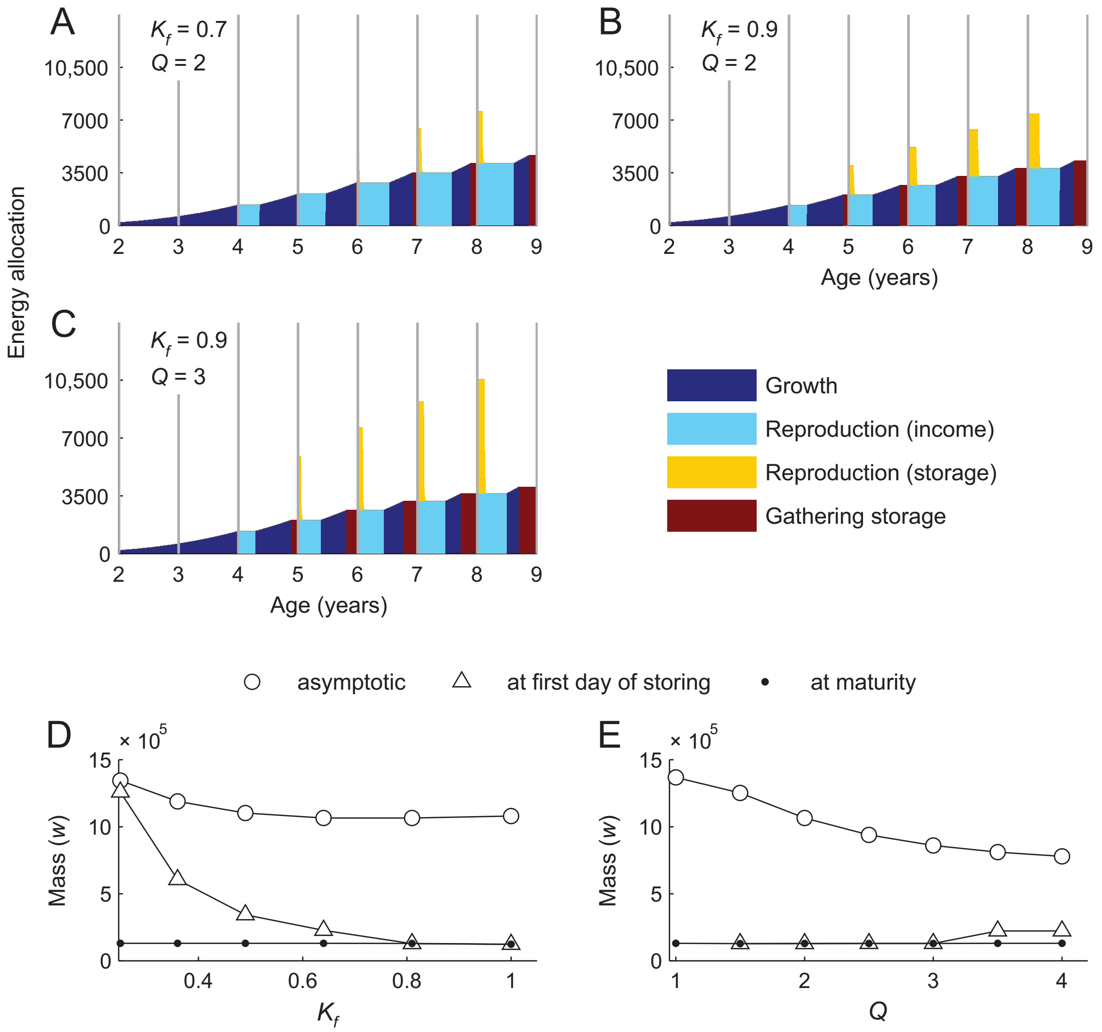

Figure 5: Optimal energy allocation and mass w under constraints on the rate of capital breeding and strong size dependence of juvenile mortality rate in winter ($m_d = 0.75$). *A–C*, Allocation of energy to different sinks. The optimal strategy of energy allocation differs with respect to the efficiency of conversion of storage into offspring tissues K_f (*A* vs. *B*) and the rate of utilization of stored resources Q (*A* vs. *C*). Because respiration balances assimilation in winter, body size does not change, and winters are represented by vertical lines. *D*, *E*, Optimal size w: at maturation, first day of gathering storage and asymptotic under various efficiency of capital breeding K_f (*D*) and coefficient Q describing the rate of offspring production with storage (*E*). Note that the organisms grow less after maturation when K_f or Q increases. Other model parameters: $S_w = 0.7$ and $Q = 2$ (*D*), $K_f = 0.9$ (*E*). For legibility, only the eight initial years are displayed.

no matter whether we change K_f or Q (fig. 5*D*, 5*E*) or m_d (fig. 4*C*). It means that covering reproductive demands from reserves trades off with the degree of indeterminate growth, which means that capital breeders grow less after maturation. In terms of fitness maximization, it may be better to partly sacrifice the long-term investment of enlarged productive body and rather obtain storage, which can be used in the next summer for production of high-quality descendants, that is, early born offspring.

Storing Reserves for Future Reproduction Increases with Size

In all studied cases in which storing resources for future reproduction was optimal, the tendency for capital breeding increased with size and therefore with age (e.g., figs. 4*A*, 5*A*–5*C*). Because the production rate increases with size slower than linearly, growth brings diminishing returns for fecundity. Thus, as an organism becomes older and larger, it gains more from short-term investments in future reproduction (storage) than from the long-term investments in future reproduction through growth in body size. In effect, time spent on growth declines with age, whereas more offspring are produced from capital. Ultimately, the proportion of offspring produced from income becomes smaller with age (e.g., figs. 4*A*, 5*A*–5*C*).

Discussion

Our annual routine model considers optimal energy allocation between growth, reproduction, and storage in perennials living in a seasonal environment. The model organism makes a long-term investment by enlarging productive soma, allowing for an enhanced rate of future reproduction. By contrast, gathering of reserves should be seen as a short-term investment in future success, here used to boost reproduction in periods with high offspring value in the next summer. We found that the degree of both capital breeding and indeterminate growth was driven by the seasonal changes in the reproductive value of offspring (see fig. 4*C*). The stronger the seasonality, the more capital breeding, and the more investment in indeterminate growth and storage at times of the season with low offspring reproductive value. Our work not only shows an extensive variation of breeding strategies along an income-capital breeding gradient but also reveals a trade-off between the structural size attained by organisms and the degree of capital breeding (for a brief summary of the main predictions, see table 2). The trade-off arises because the duration of the vegetative period constrains the amount of acquired resources and the net energy gain that could be allocated to growth or stored in reserves. In contrast to the great majority of life-history theory, we explicitly consider the seasonal variation in offspring reproductive value; in our model, this variation emerges from basic assumptions, here size dependence of the juvenile mortality rate in winter. This approach is particularly relevant for life-history considerations on phenology and particularly optimal timing of breeding (McNamara and Houston 2008).

Table 2: Brief summary of the main model predictions

Statement	Capital breeding	Indeterminate growth
Offspring prospects depend on birth date	+	+
High rate and/or efficiency of storage-based reproduction[a]	+	−
High costs of storage[a]	−	+

Note: Symbols indicate the expected response in the degree of indeterminate growth and capital breeding.

[a] Seasonality of reproductive value at birth does not change.

Whereas reproductive strategies in the model represent a continuum of income to capital breeding, it does not predict pure capital breeding (reproduction covered with reserves only). Our model concerns organisms with positive resource assimilation during the vegetative season, and the energy not used for storage or reproduction has to be allocated to growth. Hence, during periods with capital breeding (high offspring value), the model organism always contributed to reproduction with income breeding as well (e.g., figs. 4*A*, 5*A*–5*C*). Thus, our model does not concern cases when breeding occurs before the feeding season, such as for some marine copepods (Varpe 2012). However, in the majority of species regarded in the past as pure capital breeders, the reproductive success relies to some extent on current income (Meijer and Drent 1999; Bonnet et al. 2001; Lourdais et al. 2003; Senechal et al. 2011).

Seasonality in Offspring Value Drives the Evolution of Capital Breeding

Our model predicts capital breeding to increase reproductive output at a time of year when offspring value is high, also predicted by Varpe et al. (2009) and Stephens et al. (2014). There are numerous examples of aquatic and terrestrial environments where capital breeding is likely to be advantageous because of strong seasonality in offspring prospects. For instance, copepods experience strong seasonality in their food source—with a clear distinction between summer and winter, as in our model—and reproduce early or ahead of the peak in primary production (e.g., Daase et al. 2013) and rely on their offspring reaching a minimum developmental stage and condition in order to overwinter successfully (Conover 1988; Varpe 2012; Sainmont et al. 2014). In several of these species, either capital breeding co-occurs with income breeding (as our results show) or capital breeding takes place before the feeding season (an option not included in our model). A copepod life-history model predicted capital breeding as a strategy to target seasonal windows of high offspring value (Varpe et al. 2009). Copepods may be perennial, but they are not indeterminate growers (their adult stages are not observed to molt to allow an increase in structural size), and hence they do not display the full diversity of our model.

Capital breeding is frequently observed in fish, with the classic examples of migratory herrings (*Clupea* sp.; Varpe et al. 2005). Utilization of stores for reproduction in iteroparous fish is driven by oocyte development and ovarian organization (Murua and Saborido-Rey 2003; McBride et al. 2015). Income breeding prevails in species with asynchronous egg development and indeterminate fecundity, which means that unyolked oocytes mature continuously and are released during one spawning season. Capital breeding, by contrast, is found in species with synchronous egg development, determined fecundity, and group-synchronous breeding (Murua and Saborido-Rey 2003; McBride et al. 2015). The origin of these reproductive tactics is debated in fisheries science (Jager et al. 2008; Ganias 2013). Recent evidence suggests that oocyte production during spawning also occurs in species with determinate fecundity, and these new cohorts of oocytes are released during the following spawning season (for references, see Ganias 2013). We can imagine a shift in climatic conditions that leads to a prolonged period of suitable conditions for spawning and can then expect capital breeding to occur at the beginning of the spawning season, with the production of later eggs from current income. Our model predicts such a pattern. The horse mackerel (*Trachurus trachurus*) was thought to be a pure income breeder with asynchronous oocyte development. However, it adopts a mixed reproduction strategy, with capital breeding boosting early reproduction and incoming resources being used for egg production later in a season (Van Damme et al. 2014).

The primary question is whether the degree of capital breeding relates to the degree of seasonality in offspring value. In fish, reproduction often occurs just after a nonproductive winter and is fueled at least to some extent from stored lipid reserves (Marshall et al. 1999; Jørgensen and Fiksen 2006). An extensive number of empirical studies suggest that in many cases, the selection pressure for early offspring is strong (for a review, see Wright and Trippel 2009). However, to identify the benefits of capital breeding for a particular species, we would like to see estimates of the degree of seasonality in offspring fitness across fish species, with links to adopted breeding strategy. This is a difficult task. Even the degree of capital breeding can be difficult to estimate (Varpe et al. 2009). However, there are good examples of a strong relationship between building up reserves for reproduction and the timing of offspring production (Reznick and Braun 1987; Reznick et al. 2006).

Why Does Indeterminate Growth Exist?

In this model, under strong seasonality in offspring value, capital breeding always co-occurs with indeterminate growth. However, determinate growth has not evolved in many organisms, such as the majority of insects, birds, and mammals. One potential explanation for determinate growth is developmental or design constraints, such as in holometabolous insects or copepods that do not molt after maturation. Birds also likely fall within this group, with their fine-tuned morphology and physiology necessary for flight. Another explanation is low life expectancy, which translates to low profit of investment in productive body and instead resources can be stored and used for reproduction in the next period with high offspring value. This is most likely why short-lived but still potentially indeterminate growers, with a pronounced degree of capital breeding, typically do not grow after maturation (e.g., Reznick and Braun 1987; Poizat et al. 1999; Reznick et al. 2006).

If we consider the growth-reproduction trade-off in perennial organisms in which offspring prospects depend on time of birth, we can expect growth at times when reproduction contributes poorly to fitness, as long as larger size leads to higher fecundity (Ejsmond et al. 2010). As shown in our model, the tendency for indeterminate growth is strong even when the organism can gain stores. Thus, the fundamental question in life-history evolution "Why does indeterminate growth exist?" (Kozłowski and Uchmański 1987; Stearns 1992; Cichoń 1999; Heino and Kaitala 1999; Kozłowski and Teriokhin 1999) should instead be asked as "Why does indeterminate growth so often not exist?" This would stimulate research explaining why there is so little growth after maturation in organisms with breeding phenology driven by the strong seasonality of offspring value. The most intriguing example is mammals, regarded as a classic example of determinate growth. However, recent analysis of bone growth in ruminants by Kohler et al. (2012) shows close similarities between growth patterns observed in mammals and cold-blooded indeterminate growers, which suggests that the lack of growth observed in adult mammals is likely not a constraint (Padian 2012).

Capital Breeding and Indeterminate Growth: Patterns in Nature

When offspring value is seasonal, a mother faces an unavoidable dilemma: how to spend the time when production of offspring contributes poorly to fitness. The stronger the seasonality in offspring prospects, the more acute is the dilemma. When not breeding, an organism can store resources to increase short-term future reproduction or grow in size to increase future reproductive capacity, which is a long-term investment. According to our results, both these tendencies increase when seasonality in offspring prospects increases (fig. 4*B*, 4*C*). Indeed, intriguing patterns can be found among indeterminate growers that breed with short, intensive seasonal peaks, which suggest strong seasonality in offspring value. Small hermit crab species breed more or less continually throughout the year, whereas larger species tend to limit their reproduction to well-defined periods (Carlon and Ebersole 1995; Turra and Leite 2000; Wada et al. 2000). Similarly, in marine fish, income breeders with a protracted spawning period are small pelagic species, whereas capital breeding fishes with more restricted duration of spawning are demersal species inhabiting cold regions (Murua and Saborido-Rey 2003). There are also examples of closely related species or even intraspecific tendencies showing that capital breeding and indeterminate growth correlate negatively with the duration of the reproductive period (Llompart et al. 2013; van der Hammen et al. 2013). The comparison of reproductive strategies with regard to the seasonal cycle of energy stores and allocation to growth in two species of flatfishes, turbot (*Scophthalmus maximus*) and brill (*Scophthalmus rhombus*), show that turbot attain larger asymptotic size and adopt capital breeding. Turbot spawn within a shorter period of the season than brill, which attain smaller asymptotic size and have a protracted spawning period based primarily on income breeding (van der Hammen et al. 2013). In the marine pejerrey (*Odontesthes argentinensis*), fish in temperate populations (where seasonality is more pronounced) have a much shorter spawning period and attain larger asymptotic size than conspecifics from tropical areas (Llompart et al. 2013).

One of the most pervasive patterns in biogeography is a positive relationship between animal size and latitude, often called Bergman's rule (Atkinson 1994; Meiri and Dayan 2003; Angilletta 2009). This consistent clinal pattern has fueled speculation and debate on its evolutionary origin (Angilletta and Dunham 2003; Blanckenhorn and Demont 2004; Wilson 2009). Conover (1992) hypothesized that organisms at high latitudes are selected to reproduce within brief periods early in the summer, which increases the likelihood of winter survival among offspring. The role of offspring value in the origin of geographical patterns of body size was also postulated by Ejsmond et al. (2010), but the model assumed unrealistically that no allocation alternatives were available in addition to growth and immediate reproduction. The model presented here considers an alternative sink—the capital—and predicts that high-latitude perennials that face rapid seasonal change in offspring prospects should rely more on capital breeding combined with indeterminate growth than their counterparts from low latitudes. Thus, this strategy ultimately produces large perennials at high latitudes and small perennials at low latitudes.

Trade-Off between Capital Breeding and Indeterminate Growth

Our model predicts that when the efficiency of converting stored reserves into offspring tissues is high or the rate of storage utilization increases, organisms attain smaller asymptotic size because of a decreasing tendency of continuing growth after maturation (fig. 5*D*, 5*E*). When these costs increase, there is not only a lower tendency to store reserves but also a greater tendency to grow after maturation (results in app. A and fig. A5). These results are driven by the duration of the postbreeding period that constrains the amount of resources allocated to growth or storage, which imposes a trade-off between the degree of capital breeding and indeterminate growth (see also Bunnell and Marschall 2003).

Testing the existence of trade-off between capital breeding and indeterminate growth is difficult because we must compare strategies optimal at the same dynamics of offspring value within a season. Otherwise, we are not able to separate the effects of seasonality in offspring prospects—which influences both capital breeding and indeterminate growth—from the store-grow trade-off. Despite this difficulty, there is empirical evidence indicating a trade-off between growth and storage for capital breeding. Some migratory and capital breeding fishes grow more intensively in years with skipped spawning (Holmgren 2003; Jørgensen et al. 2006). Wada et al. (2007) studied four species of *Pagurus* hermit crabs, in which molting is obligatory for future growth but not for egg fertilization. They showed that females that molt just before copulation have a more prolonged interval between reproductive events and invest more in enlarging the body at the expense of allocation to reproduction (Wada et al. 2007, 2008). The fact that the decision on prenuptial molt is taken before breeding suggests that the relation between the investment in productive soma and reproductive potential is determined by internal reserves. Another example comes from krill (*Euphausia*), an abundant group of large and relatively long-lived marine crustaceans. Adult krill display multiple molts (Buchholz 1985; Tarling and Cuzin-Roudy 2008) and are indeterminate growers (Siegel 1987). It is believed that capital breeding krill spawning in early spring, such as *Thysanoessa inermis* and *Thysanoessa rashi*, accumulate lipids during summer—reaching between 30% and 60% of dry weight—at the expense of investing in productive soma (Pinchuk and Coyle 2008).

Body Size Affects Tendency to Rely on Stored Reserves during Reproduction

Our model predicts that the degree of capital breeding increases with body size. Because production rate scales slower than linearly with body size, larger organisms are expected to gain relatively less in the future by growing. As age often correlates with size, the tendency to breed from capital also increases with age. There are examples of an increasing component of capital breeding in older and/or larger animals. For example, in the montane lizard (*Sceloporus scalaris*), smaller yearling females are purely income breeders, whereas older and larger females store reserves for reproduction (Ballinger and Congdon 1981). Indirect evidence can be found in cod, a batch spawner with considerable component of capital breeding, where older and thus slower growing females produce more eggs per unit of mass and have prolonged periods of spawning within a season (Marteinsdottir and Begg 2002). This pattern is also observed between species. Larger species of pinnipeds are characterized by a higher tendency for capital breeding (Boyd 1998; Trillmich and Weissing 2006).

Life-history theory has advanced our understanding of the evolution of the diverse strategies of breeding and growth observed in nature (Stearns 1992; Kozłowski 2006). By considering the links between offspring prospects, timing of offspring production, and accumulation of reserves for future reproduction, our model explains a large part of this diversity. It also provides an interesting perspective for future studies of biological transitions driven by environmental changes. Global climate change will affect not only mean environmental characteristics but also key characteristics of seasonal environments, such as thermal variance, precipitation level, and season length (Kingsolver et al. 2013; Clark et al. 2014). Additional work that accounts for these changes conducted within the framework of life-history evolution may improve our ability to make predictions about shifting selection pressures with climate change.

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