Life history adaptations to seasonality

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Abstract

Seasonality creates a template for many natural processes and evolutionary adaptations. Organisms are often faced with an annual cycle consisting of a productive (favorable) and unproductive period. This yearly cycle along with other seasonal variations in abiotic factors and associated biotic interactions form strong selection pressures shaping the scheduling of annual activities and the developmental stages and modes of life through the year. Annual decisions impact trade-offs that involve both current and future reproductive value (RV), and life history theory provides the foundation to understand these linkages between phenology and an organism's full life. Annual routine models further allow for multiple annual decisions to be optimized and predicted with respect to lifetime consequences. Studies of life history adaptations to seasonality are concerned with questions such as: Within the productive season, should growth come first, followed by reproduction, or the other way around? What is the best time to diapause or migrate, and how will this timing impact other life history traits? Should energy reserves be built, to transfer resources from one year to the next, and allow for the spatial and temporal freedom of capital breeding? If offspring value is low during parts of the productive season, what is then the best alternative to reproduction: accumulate stores, grow or wait in safety? To help answer these and other questions, I provide an overview of key theoretical concepts and some of the main life schedules, annual routines, and trade-offs involved. Adaptations to the unproductive period include diapause (dormancy), embryonic resting stages (eggs, seeds), energy reserves, and seasonal migrations. Adaptations to the productive window include rapid growth, high reproductive effort, capital breeding, and reproduction entrained to the annual cycle and with precise timing. Distinct annual routines, large body size, energy storage capacities, and parental care are also adaptations to seasonality. Phenotypic plasticity and state-dependence are important parts of these traits and are adaptations in their own. I give particular attention to timing of breeding and the associated birth-time dependent contributions to fitness. Seasonality in offspring reproductive value impacts the scheduling of growth, storage and reproduction and may create parent-offspring conflicts over breeding timing. A combined offspring and parent value perspective should be adopted more broadly, also because of the management implications. I further argue for strategic but careful use of latitudinal (and altitudinal) gradients, and more attention to the role of seasonally varying predation risk as a selective force.

Introduction

According to Stearns (2000), a biologist should ask at least three questions when studying life history evolution. First, which factors affect survival and reproduction of individuals of different ages, sizes, or states? Second, how are life history traits connected to each other? Third, what are the constraints on how traits can vary? To all these questions we can add seasonality. The annual-cycle component of environmental variability complicates the selection pressures and trade-offs compared to an aseasonal environment. Age, size, or state dependent growth, reproduction, and mortality all vary through the year. Constraints on energy acquisition and on reproduction (e.g. availability of breeding habitat) may also be highly seasonal, allowing for certain activities only at some times of the year. Fundamentally, annual decisions impact trade-offs that involve both current and future reproductive value (RV), which in turn connect phenology with lifetime consequences. Evolution has led to many different solutions to the life history trade-offs that emerge from seasonality, and seasonality therefore leads to biodiversity (e.g. Kozłowski 2006; Mathias and Chesson 2013). Daan and Tinbergen (1997), Houston and McNamara (1999), and Kozlowski (2006) are among those that have highlighted the interactions between life history evolution and seasonality.

The fundamental driver of seasonality is the annual cycle in solar radiation, caused by the earth circling the sun on a tilted axis. A range of derived physical properties follows, including seasonally varying temperatures, day-lengths, snow and sea ice coverage, precipitation, and winds. Marked seasonality is common in high-latitude environments, but also present near the equator for instance through wet and dry seasons and seasonal coastal upwelling. Seasonality is an important selective force, and organisms display evolutionary adaptations to seasonal variation in abiotic and biotic factors (e.g. Alerstam et al. 2003; Conover 1992; Daan et al. 1988; Forrest and Miller-Rushing 2010; Iwasa and Levin 1995; Lack 1950; Williams et al. 2017). Periodic growth and reproduction are the primary life history adaptations to seasonality. Other adaptations include responses to brief windows of opportunity, such as high growth rates or precise timing of breeding, or responses to harsh or unproductive parts of the year, for instance through dormancy, energy storage, or seasonal migrations. Plasticity in timing and allocation decisions (Nylin and Gotthard 1998) in response to internal state or inter-annual variability in environmental conditions, is a further sophistication of these adaptations.

Seasonal biotic interactions both drive and emerge from adaptations to seasonality, with bottom-up as well as top-down forcing selecting for the timing and combination of life history traits that maximize fitness. These interactions lead to complex seasonal interactions across trophic levels (e.g. Both et al. 2009). Life history adaptations to seasonality also impact spatial fluxes at large spatial scales, through migrations combined with pulsed and capital-based reproduction (Varpe et al. 2005), overwintering (Jónasdóttir et al. 2015), and migrants as seasonal food (Giroux et al. 2012; Willson and Womble 2006). Furthermore, climate change impacts several components of abiotic seasonality, with many biological responses that are about altered phenology and energy allocation trade-offs. Our ability to predict the biological responses rests on our understanding of selection pressures, trophic interactions, phenotypic plasticity, timing cues, and life history trade-offs (Gallinat et al. 2015; Post 2013; Réale et al. 2003; Stenseth and Mysterud 2002; Visser and Both 2005; Williams et al. 2017).

This review and perspectives piece consists of three main parts. First, I explain the main theoretical concepts and trade-offs involved, provide examples of life history adaptations to seasonality, and discuss schedules of growth, development, storage, and reproduction observed when environments are seasonal, including the concept of annual routines. Secondly, I focus on timing of breeding and how the prospects of offspring vary seasonally. Birth-time dependent contributions to fitness are particularly important for understanding annual routines. Since the parent versus offspring perspectives on optimal timing can differ, interesting trade-offs arise. Finally, I provide perspectives and possible future directions. These include the potential for parent-offspring conflicts over timing, seasonal top-down selection by predators (and parasites), and strategic but careful use of latitudinal and altitudinal gradients for studies of adaptations to seasonality.

Central life history and phenology concepts

Some concepts of evolutionary ecology, life history theory and phenology should be specified up front. They have been highlighted by others before, particularly in textbooks (Roff 1992; Roff 2002; Stearns 1992), but are worth reviewing here.

Life history trait: property directly related to reproduction and survival (Stearns 1992) and therefore with direct consequences for fitness. Examples: size at maturity, lifespan, and offspring size. A trait is determined by several genes, and forms part of an organism's phenotype.

Life history trade-off: when a fitness benefit obtained through one life history trait means a fitness cost paid through a change in another life history trait (Stearns 1989). Classic life history trade-offs include offspring size versus number, growth versus reproduction, and current reproduction versus future survival.

Life history strategy: is the combination of life history traits of an organism and the age- (and/or stage- or state-) specific reproduction and survival schedule it results in.

Annual routine: an organism's regular schedule of activities or behaviors over the annual cycle (McNamara and Houston 2008).

Capital breeding and income breeding: Reproductive strategies that I, together with the role of enegy reserves, return to frequently in this review. Capital breeders produce offspring from stored resources and consequently decouple feeding and reproduction. Income breeders produce offspring from concurrent food intake, with the disadvantage of less temporal and spatial flexibility, but with high efficiency and no inventory costs of carrying stores (Bonnet et al. 1998; Jönsson 1997; Stephens et al. 2009; Varpe et al. 2009).

Reproductive value (RV): the expected rate of transfer of genes to the next generation (Fisher 1930) and a measure of the expected number of offspring an organism will produce throughout its remaining life. RV is a frequently used fitness measure. For a fitness measure looking even further into the future, and thereby capturing the consequences of seasonal offspring value, one can study the RV of the offspring, and the RV of the offspring of the offspring, and so forth, that is, the expected number of descendants left far into the future. This approach combined with dynamic programming has been developed for life history optimization models and models of annual routines (Houston and McNamara 1999) and applied to a range of taxa and questions (e.g. Barta et al. 2008; Ejsmond et al. 2015; Varpe et al. 2007).

Seasonality: Lieth (1974) defines seasonality as "the occurrence of certain obvious biotic and abiotic events or groups of events within a definite limited period or periods of the astronomic (solar, calendar) year". Tonkin et al. (2017) discuss different definitions of seasonality for different purposes as well as the predictability of seasonality.

Phenology: "The study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species" (Lieth 1974), or as defined by the Oxford Dictionary: "The study of cyclic and seasonal natural phenomena, especially in relation to climate and plant and animal life."

The word phenology is increasingly used to mean the actual timing of a particular event within the annual cycle, for example the breeding phenology of a bird.

The Fisher and Williams legacy: Fisher (1930) postulated that enhanced investment of current reproductive effort would decrease the output from future reproduction, and he raised the question of how an organism should divert available resources to growth versus reproduction. Williams (1966) stated the general solution to Fisher's problem: "*expenditures on reproductive processes must be in functional harmony with each other and worth the costs, in relation to the long-range reproductive interest; and the use of somatic processes is favored to the extent that somatic survival, and perhaps growth, are important for future reproduction*" and he formalized it mathematically. Williams coined the term *residual reproductive value* (RRV) for the part of RV that may be realized in the future. His work started a lasting focus on the consequences of current behavioral and life history decisions on future opportunities. In seasonal environments this future opportunity is typically represented by next year's productive season (and the year after that, and so on – depending on life expectancy). Furthermore, in seasonal environments, survival from one breeding season to the next can be demanding and the survival probability sometimes low. A parallel to Williams' discussion of growth is the role of storage in seasonal environments, where storage as well as growth may be seen as investments in future reproduction, but usually at different time-scales. Storage is for capital breeding in relation to the next productive period whereas growth is usually a permanent investment in larger size and therefore higher fecundity or survival (Ejsmond et al. 2015).

Seasonal scheduling of growth, reproduction, and storage

A key challenge in seasonal environments is the limited duration of the favorable time-window when net-growth (or energy gain) is possible (Fig. 1). What is then the best combination of growth, reproduction and energy storage, within the annual cycle and through life? Many life history traits are adaptations to the periodicity of the annual cycle and it is instructive to group them in two main categories: those that have evolved in response to the unproductive season and those that are responses to the windows of opportunity provided by the productive season. Some adaptations, however, such as energy reserves, will form part of both categories, and as for all adaptations be further molded through other abiotic and biotic interactions.

Adaptations to the unproductive part of the year

Two contrasting life history strategies are those spending the unproductive part of the year in an adult or near adult stage, and those spending it as resting egg, seed, or another stage early in ontogeny (Fig. 1). Embryonic diapause as egg or seed is particularly common in annual organisms, such as in many plants, insects, and crustaceans. There are also combinations or midpoints between these extremes. Some species have resting eggs and adults co-occurring during winter, such as in some *Daphnia* (Domis et al. 2007; Lampert et al. 2010). The relative mortality through the unproductive season would then have major impacts on the solution selected for. Other species spend the unproductive period in intermediate developmental stages, for instance as late instar nymphs in some grasshoppers (Landa 1992) or as gradually developing stages of long-lived invertebrates (e.g. Morewood and Ring 1998). The mode of overwintering, as resting egg or adult stage, impacts timing and responsiveness at the return of the productive season. An active stage that can monitor the onset of the productive season directly is more flexible and ready compared with a stage relying on indirect cues (such as photoperiod) and a period of awakening. Winder and Schindler (2004) illustrated these processes in a freshwater system where two zooplankton species were contrasted, a rotifer (*Keratella*) that spends the winter in an active stage and a cladoceran (*Daphnia*) that spends the winter as an resting egg. When the timing of the feeding season (the phytoplankton bloom) advanced, the rotifers were able to follow whereas a mismatch occurred between *Daphnia* resting egg emergence and their food.

Many adaptations to the unproductive (unfavorable) season serve to minimize energy use. These adaptations include diapause, dormancy, hibernation and fasting, as well as reduced metabolism and activity, and are well represented across a broad range of taxa, for instance in moths (Morewood and Ring 1998), crickets (Mousseau and Roff 1989) copepods (Varpe 2012), polar bears (Atkinson and Ramsay 1995), and a range of plants (Bertrand and Castonguay 2003; Galloway 2002; Jonsdottir 2011). The diversity of insect diapause has early on stimulated much theoretical and empirical work, including the long lasting questions about proximate and ultimate drivers of diapause timing (e.g. Cohen 1970; Tauber and Tauber 1976). The annual timing of overwintering, both the start and end, has substantial fitness consequences, and interacts with life history traits such as adult survival, energy storage, and the number of generations per year (Varpe et al. 2009).

Numerous behavioral, physical, and physiological adaptations to harsh winters have also evolved to reduce energy requirements. These are closely linked to life history evolution

because allocation of available energy and the risk involved in acquiring resources are at the core of life history trade-offs. Blix (2016) gives examples of such adaptations in polar mammals and birds, such as fat reserves as insulation in marine mammals, and counter-current heat exchange to prevent heat loss from appendages. In plants (and some animals) we also see considerable reductions in the productive soma (e.g. when trees shed their leaves in the fall) in response to the unproductive season, which takes an extreme form in annual organisms where the parent generation dies and seeds or resting eggs survive until the next productive season.

Energy storage, either internal (Blix 2016) or external (Wauters et al. 1995), is a further adaptation to an unproductive season, and to the uncertain duration of the unproductive season (Fischer et al. 2011). Importantly, gaining reserves trades-off with both growth and current reproduction, and multiple life-history trade-offs emerge because of the links between body size, stores, and winter survival (Biro et al. 2004; Ejsmond et al. 2015). When winters are spent as adults or a near adult form, the capacity to stay in a resting mode may improve with body size due to increased storage capacity and fasting endurance. Hence, seasonality can be a driver of large body size (Lindstedt and Boyce 1985).

An alternative to deal with the unproductive season in a resting stage is to move to areas more suitable for an active life year round. Seasonal migrations exploit spatiotemporal variation in resources, and sometimes risk. Long-distance seasonal migrations combined with breeding are common in longer-lived animals in particular, and across a range of taxa such as birds, fish, large mammals, and some crustaceans and insects (Alerstam et al. 2003; Milner-Gulland et al. 2011; Quinn and Adams 1996; Varpe et al. 2005). Movement is costly and sometimes more costly for smaller than for larger individuals, such as in fish (Nøttestad et al. 1999). Consequently, long-distance seasonal migrants may also evolve large body sizes. Some organisms combine seasonal migrations with dormancy, such as for copepods that migrate from risky surface waters to the safer deep ocean where visual fish predators cannot forage efficiently (Bagøien et al. 2001; Varpe 2012). Others may reproduce after migration to a non-productive area – possible when reproduction is fueled by reserves gained in the productive habitat. One example is humpback whales migrating long distances from high-latitude feeding grounds to give birth in the oligotrophic waters around the Hawaiian Islands (Darling and McSweeney 1985). Increased offspring survival is then a likely selective force; a form of parental care through spatial movements. Another example is copepods of the genus

Neocalanus which produce eggs at the great depths of their overwintering habitat and let the eggs (the next generation) ascend to the productive surface waters (Miller et al. 1984).

Adaptations to the productive part of the year

Acquisition of resources and rapid transfers of energy and nutrients are key aspects of the productive season. Many activities are involved, particularly the fundamental processes of growth, storage and reproduction (see Fig 2 in Enberg et al. 2012), and the scheduling of these activities and the energy allocation between them has important fitness consequences (Ejsmond et al. 2010; Houston and McNamara 1999; Reznick and Braun 1987; Stearns 1992). Consequently, many questions concerning life-history trade-offs arise, such as: when during the season should offspring be produced, and what should be their size (Bolmgren and Cowan 2008; Einum and Fleming 2000b)? In iteroparous species with indeterminate growth, should the annual growth period follow reproduction or should reproduction follow growth (Ejsmond et al. 2010; Kozlowski and Teriokhin 1999)? And what is the role of energy reserves, a resource for metabolism during the non-growing season, but for some life history strategies also a resource for reproduction (capital breeding) early in or prior to the next breeding season (Jönsson 1997; Stephens et al. 2009; Varpe et al. 2009)?

Growth, storage and reproduction within an annual cycle are often regarded as sequential processes (as displayed in Fig 1). Many different schedules could arise (Fig 1), and the trade-offs and adaptations would differ for annuals and perennials (Perrin and Sibly 1993). Whether small offspring or larger adult forms survive the winter determines how the summer activities can be structured. If starting as a resting egg, growth would come first, followed by reproduction (Fig 1A), sometimes with multiple generations (not shown in Fig 1), whereas overwintering adults could reproduce as soon as conditions are favorable again (Fig 1B-1D). Allocation to growth versus storage is a further trade off. Giacomini and Shuter (2013) analyzed the switching strategy between structural growth and energy storage in fish, and predicted structural growth early in the season, followed by storage for winter survival during the second part of the productive season. This scheme is commonly observed in fishes. If season length was short, storage was prioritized, and growth was reduced. The latter may be compensated by faster growth (see below). Growth and storage must however not necessarily be separated in time. Under some conditions of environmental stochasticity, allocation to reproduction, maintenance and storage has been predicted to co-occur (Fischer et al. 2011).

Seasonal timing of reproduction, often early in the productive part of the year, is a core adaptation to seasonality across a range of taxa (Daan et al. 1988; Edwards and Richardson 2004; Ejsmond et al. 2010; Festa-Bianchet 1988; Olsson and Shine 1997; Reznick et al. 2006; Varpe et al. 2007; Zerbe et al. 2012), with complex links to parent and offspring quality as parents in good quality may be those capable of reproducing early and at the same time produce high quality offspring (Daan and Tinbergen 1997). Furthermore, seasonality may also impact sexual selection, such as degree of protandry, and select for gender specific phenology (Nylin et al. 1993). Conover (1992) evaluates some life history adaptations to seasonality in the context of fish, specifically the Atlantic silverside *Menidia menidia*. In this species, a brief period of reproduction early in the productive season is advantageous. This pattern arises because reaching large size before winter improves winter survival, which in turn lead to faster growth where season length is shorter, such as for the highest latitude habitats (Yamahira and Conover 2002).

The ability to skip reproduction in certain years is a further adaptation, seen for instance in seabirds (Chastel et al. 1995) or fish (Jørgensen et al. 2006), but also reported as absent in cases where it could potentially have provided fitness benefits (Festa-Bianchet 1988). Skipped reproduction can be because of body-condition requirements for breeding that are not fulfilled (Chastel et al. 1995). For indeterminate growers, skipped reproduction allows continued growth, an investment in future reproduction when fecundity increases with body size (Jørgensen et al. 2006). The decision to skip can be taken at different times of the year and at different stages in the reproduction cycle (Rideout et al. 2005), and depend on the internal state of the parent (Olsson 1997). Such state-dependent decisions can be complex and depend not only on the state of the parent, but also the state of the partner and offspring, as shown for chick guarding in the Antarctic petrel (Varpe et al. 2004). One would further expect that offspring born at sub-optimal times of the year would be more easily deserted. For some species, skipped reproduction includes atresia or abortion some way into the reproductive event and re-allocation of resources towards maintenance and survival (Rideout et al. 2005).

Capital breeding provides temporal freedom of reproduction because it is fueled by on board resources. This freedom is highly relevant for seasonal environments and likely a key driver of capital breeding. Seasonality in offspring value (discussed below), can select for capital breeding because stored resources can secure reproduction at the time of year when offspring fitness is highest (Ejsmond et al. 2015) and food potentially lacking (Varpe et al. 2009). If the time of peak offspring fitness is within the productive season, capital breeding

can also boost reproductive rates beyond the levels that income breeding offers. Studies of mosquitofish illustrate how storage can bridge seasons (Reznick et al. 2006; Reznick and Braun 1987). Reproduction in mosquitofish is possible in the fall, but its value is higher in spring. Mosquitofish therefore prioritize storage in the fall and use these reserves for overwintering and subsequent reproduction in spring, a strategy that comes with the risk of winter mortality. Postponing reproduction to the future selects for risk sensitive strategies because the pre-breeding costs of reproduction enter the fitness budget (Jönsson et al. 1995). Similar selection pressures also operate when stores are external, which is the case for hoarding animals (Fletcher et al. 2013). For internal storage, larger body size and capital breeding are expected to co-evolve, as body size determines the amount of stored energy that can be carried (e.g. Sainmont et al. 2014). Finally, benefits of capital breeding include the spatial freedom it provides when combined with seasonal breeding-migrations (see discussion of migrations above).

The number of generations (or broods) per year, is closely linked to seasonality and season length. Direct development and one more generation before overwintering stages are produced is possible when the productive season is long enough (Mousseau and Roff 1989). The trade-off between body size (it takes time to grow large) and number of generations lead to interesting predictions about discontinuous body size distributions along gradients of season length. Adult body size is predicted to become smaller when another generation is fitted into the productive season, but to increase again for an even longer productive season, until yet another generation is optimal. This pattern is referred to as a saw-tooth cline in body size (Roff 1980). These clines and patterns may be complicated by selection pressures causing variability in growth rate. Growth rate often varies with season length, typically with lower growth rate where season length is longest (Gotthard et al. 1994; Yamahira and Conover 2002).

Importantly, the start and end of the productive season is to some degree uncertain, and may vary between years. The evolutionary and ecological importance of stochastic and year-to-year fluctuations in environmental conditions are many, and would lead to the evolution of bet-hedging strategies (e.g. Kivela et al. 2016). Iwasa and Levin (1995) analyzed how the strategies emerging in such cases are compromises between the benefits of breeding early and the risk of failed breeding if begun too early. Similarly, the benefits of being early can depend on differences between years in factors such as food availability or population density (Williams et al. 2014).

Annual routines

Adaptations to the productive and unproductive part of the year must be viewed together. To predict whether an activity (such as breeding) should be performed, we must understand associated trade-offs and how natural selection shapes the full schedule of activities over the annual cycle. The concept of annual routines, the regular schedules of activities over the annual cycle, and models of optimal annual routines capture these challenges (Houston and McNamara 1999; McNamara and Houston 2008). Annual routines are shaped by the many interactions between activities and traits (such as body size and number of generations) and whether they can be performed at the same time or not (such as breeding and feather molt, see below). Finally, the adaptations are shaped by how the timing of one activity influences the optimal timing of other activities, and how one activity, through its influence on state (such as energy reserves), has delayed consequences and determines the options available later in the annual cycle or later in life (see also Fig 1 in Varpe 2012). Effects of current behavior on future state can for instance result in delayed mortality, such as mortality during winter if breeding efforts were large during the productive season. These properties have important applied value because interactions between anthropogenic stressors (e.g. harvesting or pollution) have direct as well as delayed consequences. A change in one component of the annual routine, such as a plastic or evolutionary response to environmental change, is likely to lead to changes of other aspects of the annual routine and at other times of the year. Seasonality hence adds complexity to the responses of organisms to environmental stressors and change.

Traditionally, one seasonal decision was studied at a time, but for models of optimal annual routines multiple decisions can be optimized and predicted (Houston and McNamara 1999), for instance decisions about when to breed and when to migrate, and whether to desert a brood that is already produced (McNamara et al. 1998). Annual routine problems deal with allocation decisions and require life history theory and a fitness perspective to be solved. Long term fitness considerations are ideally needed as optimization criteria. That is, alternative actions must be evaluated in terms of their current as well as future fitness consequences (Williams 1966), and with the reproductive value of offspring accounted for (Fig. 2). This approach is elegantly incorporated in optimality modelling which uses dynamic programming to find optimal state-dependent strategies by maximizing the number of descendants left far into the future (McNamara 1991; McNamara and Houston 1996). Models of optimal annual routines often include individual state variables which allow optimal

behaviours or energy allocation to depend not only on time of year but also on individual state. Annual routine models are synonymous with life cycle models in the case of annual organisms, but can also predict shorter (Fiksen and Carlotti 1998; McNamara et al. 2004) and longer (Ejsmond et al. 2015; McNamara et al. 2004) generation times. Seasonality in offspring reproductive value is important for understanding the evolution of annual routines. Earlier models of breeding timing have typically assumed a given seasonality in offspring value (Daan and Tinbergen 1997; Rowe et al. 1994). In full annual routine models, the seasonality in offspring value emerges, together with the reproductive value of any modelled stage (and state) in the life cycle (McNamara et al. 2004; Varpe et al. 2007). This is a powerful approach for understanding how timing of reproduction impacts the costs and benefits of both offspring and parent.

Some examples illustrate the logic and power of annual routine models and reasoning. 1) Galloway and Burgess (2012) performed artificial selection on early- and late-flowering in *Campanulastrum americanum* and studied the accompanying life history changes. Evolution of timing of flowering led to changes in the phenology of other reproductive traits, including whether an annual or biannual pathway was followed. The experiment took place in two light environments. For the understorey, plants delayed flowering but associated traits changed including faster flower deployment and maturation of fruits. 2) Varpe et al. (2009) modelled copepod annual routines and found that birth time had significant impacts on the optimal solution. In environments favoring capital breeding prior to the feeding season (as in Fig 1c), late born young not able to reach a stage capable of capital breeding within one year opted for a 2-year life cycle to allow for energy storage and the premium of capital breeding the year after. Hence, a longer life with survival through two winters instead of a one year life cycle with income breeding only. 3) Barta et al. (2006) modelled breeding and feather molt strategies in birds. Both activities are energetically demanding and can therefore not be performed simultaneously. Different degrees of seasonality in food availability selected for different molting schedules. In highly seasonal environments, birds were predicted to first breed and then molt, within the same productive period. In less seasonal environments, breeding effort was reduced and survival increased, a pattern also observed when comparing tropical with higher latitude birds. The molt strategies also changed. The birds were either predicted to combine breeding with molting of some of the feathers, or alternated between breeding in one year and molting feathers in the other. Barta et al. (2008) increased the complexity of the question by adding seasonal migration to the model. Observed molting

patterns in relation to migrations are highly variable (Lank et al. 2003), and Barta et al. (2008) found that the seasonality in food and the spatial variability caused by distinct summer and winter habitats were influential in shaping when during the annual cycle molting took place, such as a winter molt for long-distance migrants.

For further discussions of opportunities, limitations, and challenges with optimal annual routine models, see (Barta 2016; Fero et al. 2008; McNamara and Houston 2008; Varpe 2012).

Seasonality in offspring value

Offspring born at different times of the year have different future prospects (Table 1), with considerable differences even within relatively short breeding windows. A common seasonality in the reproductive value (RV) of offspring is an early peak followed by declining RV (Table 1, Fig 2A and 2B), which includes costs for those born too early (Nilsson 1994). Seasonality in offspring RV can emerge from optimal annual routine models. Barta et al. (2006) predicted an early peak in RV of fledglings, mostly because of lower survival the later born. Seasonality in food availability was the environmental driver. A zooplankton model predicted the RV of copepod eggs to peak early in the season, and even prior to the feeding season because the first developmental stages are non-feeding and develop based on energy reserves from the mother. Seasonality in food availability and predation risk were the environmental drivers, and the main fitness benefits of early breeding were lower predation risk early and more time for the offspring to develop to a favorable and near-adult overwintering stage (Varpe et al. 2007). Reaching such a critical developmental stage or state before the end of the productive season (Landa 1992), or to be larger or better prepared (e.g. more reserves) when the unproductive season starts, is a common driver of early birth (Table 1). Increased competitive capacities of early young is a further advantage, sometimes also resulting in cannibalism on late young by those born earlier, as argued to be part of the trade-offs on birth timing for the pierid butterfly (Kinoshita 1998).

The reproductive strategies of parents have co-evolved with the seasonality in offspring value, and parents also adjust their own life history decisions in accordance with time of the season and the prospects of the young. In grasshoppers, where offspring value peaks early, it was found that females that matured late in the season started to reproduce sooner after maturation and at a higher rate (Landa 1992). One indication of seasonality in offspring fitness is when mothers do not reproduce at times of the productive seasons when

food is still abundant. This has been observed and interpreted as a consequence of offspring value having dropped to low levels at that time of the season (Conover 1992; Reznick and Braun 1987). A useful question is therefore; when should an individual *not* reproduce (even if possible) and what is the best thing to do instead? Energy storage in preparation for the next breeding season is one solution (Conover 1992; Ejsmond et al. 2015; Reznick and Braun 1987). Alternatively, the time between reproduction and preparation for the future may be spent resting and in a mode of low activity. This is the case for red squirrels who reproduce early in the season, then are relatively inactive (low energy expenditure) during summer, before being very active while hoarding in the fall when their main food is most abundant (Fletcher et al. 2012). In contrast to iteroparous organisms, annual organisms (or those longer lived but semelparous) would, once reproduction is started, continue to breed until death and therefore more likely produce some offspring of low value (Varpe et al. 2009). In copepods there is empirical evidence for time points when iteroparous species switch from reproduction to preparation for the future, whereas semelparous species keep reproducing (Swalethorp et al. 2011).

It is difficult to separate the date effect from a parent (and offspring) quality effect (Daan and Tinbergen 1997; Olsson and Shine 1997; Verhulst and Nilsson 2008). Early born offspring may be born by high quality parents and therefore also be of high quality, for instance starting life at a larger size or with more reserves. Experiments have manipulated timing with the aim to tease apart the causes behind seasonality in offspring fitness and the realized breeding times of the parents (Brinkhof et al. 2002; Einum and Fleming 2000b). Verhulst and Nilsson (2008) have reviewed studies that manipulated timing of breeding in birds and conclude that both quality and timing seems to underlie a seasonal decline in reproductive success. Ideally, one should also aim to break down the offspring fitness components by analyzing how survival and fecundity at different parts in life are impacted by breeding timing. Schultz (1993) was able to analyze this for a viviparous teleost fish (*Micrometrus minimus*) and concluded that selection for birth date was stabilizing. Others have found evidence for directional selection for earlier breeding (e.g. Svensson 1997).

Ejsmond et al. (2015) analyzed the switch from reproduction to growth and storage, the two main alternative activities to reproduction. The model predicted that capital breeding, which requires storage, was adaptive when timing of birth affected offspring reproductive value. If seasonality was strong, more time was used for capital breeding and growth after first reproduction and less for income breeding. Growth and storage are both investments in

future reproduction and favored in the part of the growth season when offspring value is low. Storage is an investment in the relatively near future, through capital breeding in the next breeding season, whereas growth is a long-term investment in a lasting and increased reproductive potential. Furthermore, as larger body size was modelled to give diminishing returns through fecundity, capital breeding was favored over growth. Consequently, capital breeding could be explained by seasonality in offspring value and trade-offs with growth.

For management of populations, it is important to understand recruitment as units of reproductive value, not simply in terms of the number of offspring. Knowing the approximate reproductive value of an individual has consequences for how we should interpret data and how harvested stocks should be managed. Times of the year when only a few offspring are born may seem unimportant from a management point of view, but their reproductive value may be highest and their contribution to the next generation therefore relatively large (Varpe et al. 2007). Similarly, when reproduction extends beyond the main breeding window, late births may be misinterpreted to be of adaptive value, unless the future prospects of those young are investigated (Festa-Bianchet 1988).

Perspectives

Parent-offspring conflict over timing

Parent-offspring conflicts over parental care are well known (Godfray 1995; Trivers 1974). There are also parent-offspring conflicts over reproduction timing. The best time to be born may not be the best time for the parents to produce young. Parents may be physically constrained and therefore not able to produce young at the time of peak offspring value. Such a case would not be a real conflict, as the parents lack the temporal freedom needed. However, if the parents are able to produce offspring at the time of peak offspring value but still reproduce at other times of the year, a conflict can be argued. The trade-offs from the parent perspective are about investment in current reproduction versus future survival and reproduction and about timing of offspring production versus fecundity (Daan et al. 1990; Daan and Tinbergen 1997). The interest of the offspring is a best possible starting point, but is the offspring able to influence the outcome? It would require the offspring to have information about timing. I am not aware of studies documenting that offspring engage in this conflict by impacting parent decisions about timing, but one may imagine such processes, analogous to evolution of begging behaviors of offspring to obtain parental care.

Based on long term observations of kestrels, Daan et al. (1990) quantified the reproductive value of parents as well as offspring. Parents would more easily obtain food for their young some time into the breeding season, but because offspring value was highest early, there is an incentive to shift reproduction to earlier dates. Daan et al. (1990) further focused on the "family planning" component that includes how many young to produce. Depending on the food availability, particular combinations of clutch size and laying dates were predicted to maximize total reproductive value. From a single offspring perspective however, it would have benefitted from being produced earlier. Such interactions between clutch size and timing have received much attention in bird studies (Verhulst and Nilsson 2008). In species that can produce a second clutch within the same breeding season, a first clutch would be earlier than if a single clutch was produced (Tinbergen and Daan 1990).

Parents in some taxa produce many offspring and over a longer seasonal window despite a narrow part of this window allowing maximum offspring value (Varpe et al. 2007). In a model of optimal annual routines in copepods (Varpe et al. 2007), the bulk of egg production occurred at times of medium to low offspring value. This mismatch occurred because the parent gains more from producing many offspring of lower value compared with few offspring of maximum value. The issue of capital versus income breeding was involved in this tension (Varpe et al. 2009). Capital breeding allowed few offspring but of peak value, and income breeding allowed many offspring but of lower value. It usually paid to delay the capital breeding contribution and connect it with the window for income breeding. Varpe et al. (2007) termed this parent-offspring conflict an "internal life history mismatch".

Analyses of selection on maternal versus offspring fitness are central for predicting life history adaptations to seasonality (Rowe et al. 1994); analog to its relevance for other life history trade-offs, such as between offspring number and size (Einum and Fleming 2000a). A combined offspring and parent value perspective (Daan et al. 1990; McNamara et al. 2004; Rowe et al. 1994) should be adopted more broadly in ecology. It has important implications for how we understand life history evolution, temporal match and mismatch processes, and the timing responses of organisms to environmental change.

Seasonality in predation risk

Predators and the temporal and spatial landscapes of risk are major selective forces. Studies of adaptations to seasonality are however dominated by bottom-up processes because the seasonality of the physical environment (sometimes through absolute constraints on breeding)

and the seasonality of food have major impacts (Cushing 1990; Daan et al. 1988; Immelmann 1971; Table 1). It would be instructive to lay out in which cases seasonality in risk contributes as a driver of life history diversity. Such an effort would connect selection on phenology and annual routines with the well acknowledged overall role of risk and survival probabilities for life history diversity. Reproductive effort models have mortality at the core and predict how life history traits such as age-specific reproduction, age at maturation, and body size should change with increased or decreased mortality (Michod 1979; Roff 1981). It is well known that increased predation risk selects for traits such as earlier maturation and smaller body size (Reznick et al. 1990). Analyses of background mortality (mortality independent of the organism's state or behavior) in an annual routine model predicted among other things that reproductive effort increased as mortality increased (McNamara et al. 2004). Furthermore, McNamara et al. (2004) found that increased mortality led to breeding earlier in the season or even that entrainment of breeding to the annual cycle broke down in high-mortality environments. Finally, from a plasticity perspective, when organisms are under time constraints, such as late in the season, we would expect them to take more risk to reach a critical stage or condition (Ludwig and Rowe 1990). Here, however, I am concerned with the seasonality in predation risk, through seasonality in predator abundance or efficiency, and its impacts on life history traits and annual routines.

Some studies suggest seasonal selection pressures caused by predators or parasites. The brief and early growth spells of the wooly caterpillar *Gynaephora groenlandica* and its entry into diapause while there is still a substantial part of the productive season left, is likely because of the high risk of parasitoids late in the growth season (Morewood and Ring 1998). Similarly, the oceanic copepod *Calanus finmarchicus* enters diapause after the first generation despite ample food, perhaps because migratory fish predators enter the system during the copepods' feeding season (Kaartvedt 2000). Similar anti-predator responses in zooplankton are common in freshwater studies, including direct responses to fish chemicals (Pijanowska and Stolpe 1996). There are particular reasons to study the selection pressures caused by predators that depend on light to see their prey, such as fish (Varpe and Fiksen 2010), because light regimes are highly seasonal, particularly so at high-latitudes. Studies of predators that themselves need to avoid light, such as bats (Duverge et al. 2000), are equally interesting from the perspective of a mechanistically based and seasonal top-down selection.

Terrestrial herbivores may also have seasonally varying impacts on their plant food. Date of flowering is one trait that can be impacted by herbivores. Higher seed survival if

produced prior to or after peaks in flowering time indicates reduced impacts by herbivores at the shoulders of the flowering distribution (Albrectsen 2000; Freeman et al. 2003). Such patterns could lead to selection for early or late flowering, or for longer periods of flowering (Elzinga et al. 2007). Seasonal plant growth may in turn impact higher trophic levels, not only as food, but also in shaping arenas for predator-prey interactions. The efficiency of lions hunting giraffe calves was suggested to vary over the season due to reduced stalking cover during the dry season, possibly contributing to the higher survival of calves during the dry season (Lee et al. 2017).

Sometimes organisms prioritize safety (e.g. enters diapause) while there is still considerable food left within the productive window. This is a strong indicator of top-down selection on phenology and annual routine. Such responses to predators should have life history consequences such as smaller size, less reserves or fewer generations per year, and may even select for semelparity where the parent generation reproduces prior to peak risk, and then let offspring (typically vulnerable to other predators) pass through the risky window. Capital breeding can be one response to seasonality in predation risk (Varpe et al. 2009) as it offers a mechanism for shifting offspring production to safer times or places.

Synchronization of breeding timing, which allows for predator swamping (Ims 1990), is another timing response to predation risk, but it does not require seasonality in risk. In seasonal environments where reproduction is already somewhat synchronized to bottom up drivers, even stronger synchronization for predator swamping may however more easily evolve. Synchronized reproduction of some birds and plants may illustrate the predator swamping strategy (Burr et al. 2016; Findlay and Cooke 1982; Hatchwell 1991; Janzen 1971).

Interesting top-down oriented phenology questions can be asked. One question is how migration timing may impact the spatial and temporal distribution of predators? McKinnon et al. (2010) provided evidence for lower mortality of bird eggs the higher the latitude and suggested it as a driver of Arctic breeding migrations. Would the timing of their migrations also be impacted by risk and therefore not possible to predict through knowledge of the resource availability only? Lank et al. (2003) provide strong evidence for the selective importance of avian predators in shaping the migration timing of shorebirds, including strategies for departing both before or after the peak in predation risk by falcons. Another question is to what extent timing is flexible and a direct response to predator presence? Such plasticity was observed for the reed frog where developing stages hatch earlier if predation is severe (Vonesh 2005). Similarly, some ground nesting birds breeding on Arctic islands will

for instance delay egg laying if there is an ice-bridge between the island and the mainland, because the ice-bridge allows the Arctic fox to enter (Chaulk and Mahoney 2012). In years of high risk, one could expect skipped breeding, particularly if predators are abundant at the time when decisions about reproduction are made. Similarly to the success of investigating life history adaptations to seasonality along clines of seasonality in resources or temperature (Conover 1992), one should establish studies along clines that include seasonality in risk. Candidate organisms and systems could be visually searching predators, such as fish in lakes and oceans (e.g. Brooks and Dodson 1965; Varpe et al. 2015).

Macrophenology and latitudinal gradients as arenas for comparative work

Comparative studies across latitudes, often of the same species, are much used for investigations of how seasonality shapes life history and phenology (Aguilar-Kirigin and Naya 2013; Burr et al. 2016; Conover 1992; Mousseau and Roff 1989; Nylin et al. 1993). The design rests on the assumption that the environmental drivers of interest are more seasonal the higher the latitude. This certainly holds true for irradiance, generating latitudinal gradients in the light regime, and often also for derived physical and biological properties such as primary production (Winder and Cloern 2010). However, for some derived physical properties, such as temperature, precipitation, and sea ice, latitude *per see* is not always a good proxy. Increasing seasonality with latitude is for instance not the case for the temperature of the ocean, which at high latitude varies relatively little over the year compared with mid-latitude regions with pronounced summer warming and winter cooling (Mackas et al. 2012). Regional variability can also be considerable such as for the southern extent of sea ice in the Arctic, particularly clear if comparing the Atlantic and Pacific sector (Langbehn and Varpe 2017). Latitude may in such cases be a poor proxy for the seasonality of environmental conditions and a poor predictor of life history variability (e.g. Daase et al. 2013). Importantly, there are also profound annual cycles in lower-latitude environments, such as alternating rainy and dry seasons of the tropics or the upwelling periods of sub-tropical coastal systems, to which annual routine and life history adaptations are observed (Brown and Shine 2006; Lowe-McConnell 1979; Peterson 1998; Sinclair et al. 2000; Watling and Donnelly 2002). Williams et al. (2017) suggest increased attention to how temporal ecological interactions in tropical systems are changing.

High-latitude and polar environments can offer unique laboratories for studies of how seasonality shapes evolutionary adaptations and ecological dynamics. These regions have rapid shifts between the productive and unproductive part of the year, and the usually severe

winter conditions (snow cover, sea ice or darkness), lead to marked selection gradients and limits for the possible annual routines. Constraints through brief productive seasons and harsh and/or long winter conditions are often pointed to as drivers of life history strategies of high-latitude organisms (Alerstam et al. 2003; Bronson 1985; Danks 2004; Langvatn et al. 2004). Consequently, high-latitude ecosystems typically have species that either move away or are inactive during the unproductive season (but see Berge et al. 2015). At lower latitudes there are more likely fluctuating species compositions throughout the year, as other forms may thrive during the alternating conditions, such as for stream invertebrate communities during dry and wet periods (Tonkin et al. 2017) or pelagic communities during spring- and autumn-bloom conditions (Edwards and Richardson 2004). To what extent harsh and seasonal conditions reduce the interaction between organisms (e.g. Chesson and Huntly 1997) is a research question where diversity along latitudinal gradients can offer valuable comparisons, with implications for our ability to disentangle the relative role of the abiotic environment and species interactions in shaping phenology.

Studies along latitudinal gradients have been influential in disentangling seasonality from other drivers (Conover 1992; Mousseau and Roff 1989) and should continue to form a central part of evolutionary phenology. Common garden experiments can be valuable in this respect, with organisms from environments with different seasonality brought to a common one, as successfully done for studies of growth rates in fish (Conover and Present 1990; Yamahira and Conover 2002). Finally, altitude also offers gradients in season length, and work along altitudinal gradients is successfully used for studies of life history evolution, such as the trade-off between fecundity and parental care (Badyaev and Ghalambor 2001). It seems rewarding to combine altitudinal and latitudinal gradients (or other spatial contrasts) for studies of adaptations to seasonality (cf. Chown and Klok 2003; Körner 2000). Studies of phenological variability over large spatial scales could be called macrophenology, analog for instance to the field of macrophysiology (Chown and Gaston 2016).

Concluding remarks

We have at all times acknowledged seasons. Vivaldi's musical conception of seasonality in The Four Seasons (*Le quattro stagioni*) is a splendid artistic reminder. We relate actively to our seasonal environments, and our evolution and adaptations are shaped by seasonality (e.g. Bronson 1995). A seasonal perspective is also central to several disciplines beyond the natural sciences, for instance economics (Hylleberg 1992). The large interest in phenology and the many links to our culture are impressive. Knowledge about seasonal biological interactions

has for instance been fundamental for successful agricultural practices. Seasonality is also deeply linked with evolution and macroecological patterns, and the extent that seasonality leads to speciation should be a rewarding direction for more work (Kivela et al. 2013).

The overall seasonality in solar radiation is not impacted by global warming; the axial tilt (obliquity) of the earth (currently about 23.5°) remains the same although it varies over much longer time scales (Zachos et al. 2001). Climate change does however influence other seasonal properties, such as temperature dependent onsets and endpoints of seasonal time windows, or the seasonality of physical properties such as sea ice or snow cover, rainfall, water mixing in lakes, or currents in the ocean. Organisms respond to these changes, with phenology and life history responses forming a central part (e.g. Thackeray et al. 2016). Many ecosystems are substantially changed, partly through mismatches between trophic interactions, but also through new matches. Changing distributions of organisms further modify biological interactions linking spatial and temporal processes. Many selection pressures on adaptations to seasonality are consequently under rapid change. Life history theory equips us to study these changes and to advise on their implications.

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Figure and table legends

Table 1. Examples of empirical studies documenting seasonality in the reproductive value (RV) of offspring, or fitness components that are part of RV, with a description of the shape and the main selective pressures involved. Our main interest is in the effects of date on single offspring, not in the value of a clutch or group of offspring. Only bird, fish and mammal examples are included here, but see the main text for more examples, including insects (Landa 1992) and reptiles (Olsson and Shine 1997), and for model predictions of seasonality in offspring value. For additional bird examples, see (Daan et al. 1988; Verhulst and Nilsson 2008).

Species name and reference	Description of seasonality in offspring RV	Seasonal selection pressures
Kestrel - *Falco tinnunculus* (Daan et al. 1990)	RV of a single egg declined from ~ 1.3 to 0.3 for laying dates from late March to early June, with RV rather stable for the first month.	Seasonality, and inter-annual variation, in the main food supply, the voles. Juvenile survival in the nest and after fledging declined as season progressed. Early born may be better competitors.
Blue tit - *Parus caeruleus* (Svensson 1997)	Post-fledging survival declined with hatching date (in two of three years). Experiments where the first clutch was removed (triggering relaying) supported a causal effect of date.	Seasonality in food availability. Better competitive abilities of early fledglings.
Atlantic salmon - *Salmo salar* (Einum and Fleming 2000b)	Offspring survival declined the later the emergence from gravel nests. Manipulation of fertilization timing allowed causality to be determined. Timing interacted with size at emergence.	Competition among juveniles with at least two possible effects. 1) Increased starvation if late emergence; or 2) selective predation on late-emerging juveniles because fish that emerged late are displaced downstream to higher predator densities.

Mosquitofish - *Gambusia affinis* (Reznick et al. 2006)	Earlier age at maturity for early born offspring leading to higher probability of survival to maturity. Early young can reproduce in the year they are born.	Seasonal decline in food availability. For the same species, in more temperate environments, the winter mortality was also higher for smaller (i.e. typically late born) individuals (Reznick and Braun 1987).
Dwarf perch - *Micrometrus minimus* (Schultz 1993)	RV highest for those born in the middle of the season. Early born females had higher reproductive success during first reproduction. Early and late born individuals were less likely to survive. Stabilizing selection was concluded.	Longer growth season allowed for larger size, beneficial since fecundity increases with body size. Low temperatures and low food availability impacted early survival selecting against early birth. Low winter survival selected against late birth.
Giraffe - *Giraffa camelopardalis* (Lee et al. 2017)	Calves born during the dry season had higher survival compared to other seasons. Calves are born all year round.	Food quality for mothers (capital breeding) and young, through impacts by the rainy and dry season. Possibly lower predation risk during the dry season due to reduced stalking cover for lions.
Bighorn sheep - *Ovis canadensis* (Festa-Bianchet 1988)	Late born lambs (June and July) had lower survival (to half a year or one year of age) compared to the bulk of lambs that were born earlier (May). Note the characteristic positive skew of the breeding time distribution.	Food availability and quality, for offspring as well as mother (milk production).

Fig 1

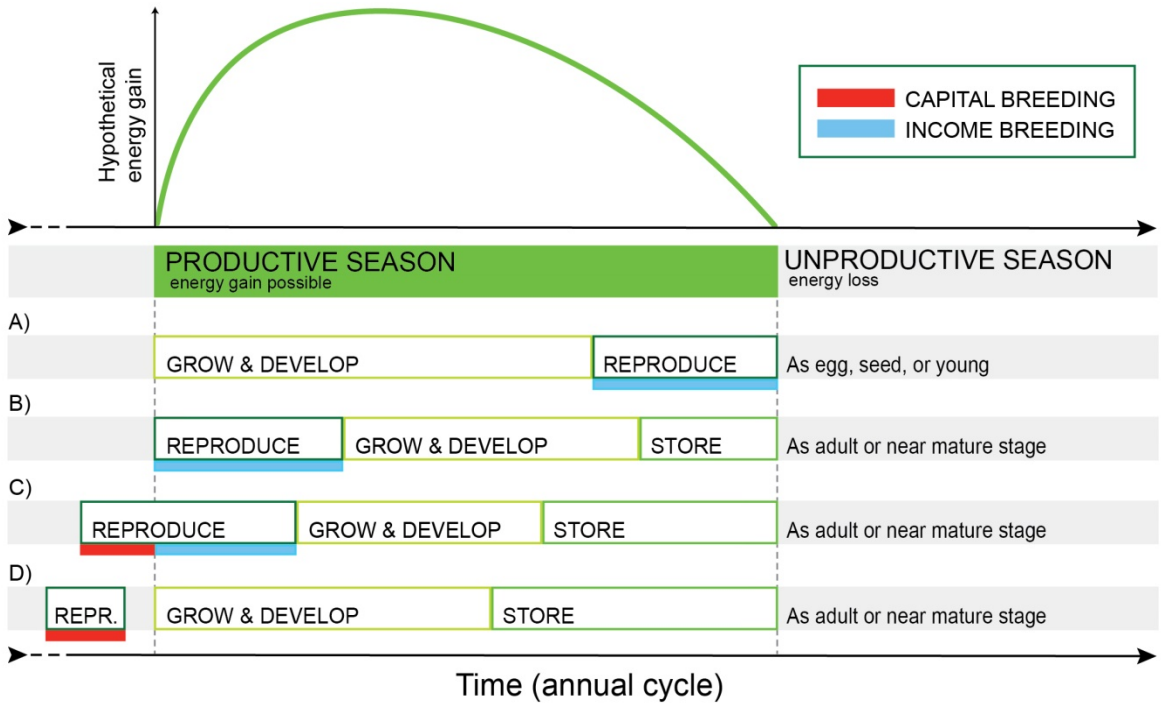

Fig. 1 Alternative schedules of growth, storage and reproduction in seasonal environments, including the variability that capital versus income breeding can generate. One year is shown, but the logic can be extended to a multi-year scale and lifespan. Only some main schedules are shown, others clearly exist. The assumed environment consists of a productive season (spring/summer/fall) and an unproductive season (winter). Several seasonal properties can modify the realized seasonality in energy gain, including food quality, risk, temperature, and varying maintenance and acquisition costs. In nature, transitions between the productive and unproductive season vary in abruptness and predictability, but are made distinct here. The stage surviving the unproductive season takes two main forms, as embryonic diapause (A) or as adult or near mature individuals (B, C, D). Reproduction can be at the end of the feeding season (A) at the start of (B, C) or before (D) the feeding season. Capital breeding can be directly prior to the income breeding (C), and even co-occur with income breeding (not shown), or before the productive window (D), with (not shown) or without income breeding later in the season.

Fig 2

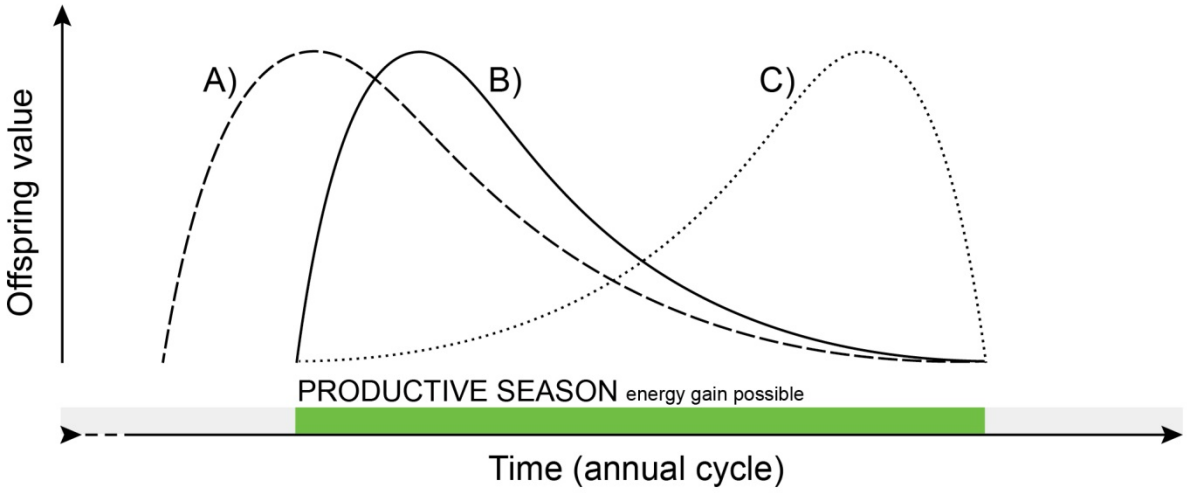

Fig 2. Three hypothetical curves of seasonally dependent offspring value, i.e. the reproductive value of young at birth as a function of time of year. The time-windows of the productive and the unproductive (light grey) season are outlined along the time axis. Two main types are illustrated; *early is better* scenarios (A and B), as observed across a range of taxa (Table 1), and a *late is better* scenario (C), likely beneficial when the newborn offspring is the overwintering stage. The early is better scenarios are differentiated into two types. A) Offspring value peaks prior to or at the onset of the productive season. This would require mothers to draw on reserves gathered the previous season, i.e. a capital breeder solution, and young would have to be fed by parents (lactation in mammals) or rely on reserves transferred to the egg (common in many fish and zooplankton species) until the feeding season starts. B) Offspring value peaks early, but while there is food around for offspring as well as parents, which allows for income breeding and immediate feeding by the young. Finally, other offspring value curves could also arise, for instance bimodal curves with beneficial conditions early and late.

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