

Review



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Seasonal reproductive tactics: annual timing and the capital-to-income breeder continuum

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Tactics of resource use for reproduction are an important feature of life-history strategies. A distinction is made between 'capital' breeders, which finance reproduction using stored energy, and 'income' breeders, which pay for reproduction using concurrent energy intake. In reality, vertebrates use a continuum of capital-to-income tactics, and, for many species, the allocation of capital towards reproduction is a plastic trait. Here, we review how trophic interactions and the timing of life-history events are influenced by tactics of resource use in birds and mammals. We first examine how plasticity in the allocation of capital towards reproduction is linked to phenological flexibility via interactions between endocrine/neuroendocrine control systems and the sensory circuits that detect changes in endogenous state, and environmental cues. We then describe the ecological drivers of reproductive timing in species that vary in the degree to which they finance reproduction using capital. Capital can be used either as a mechanism to facilitate temporal synchrony between energy supply and demand or as a means of lessening the need for synchrony. Within many species, an individual's ability to cope with environmental change may be more tightly linked to plasticity in resource allocation than to absolute position on the capital-to-income breeder continuum.

This article is part of the themed issue 'Wild clocks: integrating chronobiology and ecology to understand timekeeping in free-living animals'.

1. Introduction

How animals acquire, store and use energy or nutrients across their annual cycle is a key component of their life-history strategy and an important determinant of lifetime fitness [1]. As such, there is increasing interest in the degree to which animals use stored energy to fuel reproduction with an emphasis on the division between capital and income breeders [2–8]. Capital breeders use energy stored in advance of the breeding season whereas income breeders finance reproduction using concurrent energy intake. Though often described as a dichotomy, it is widely recognized that capital- and income-breeding reflect endpoints of a continuum that exists in nature [3]. Numerous studies have focused on the intrinsic and extrinsic drivers of capital- and income-breeding strategies with position on the continuum regarded as a species-level trait linked to factors such as body size, mode of locomotion and resource availability [5,8,9]. Here, we examine the physiological and ecological linkages between reproductive timing and position on the capital-to-income breeder continuum (C–I continuum) in birds and mammals. We limit ourselves to homeotherms since they have considerably higher resource requirements, occupy a wider range, including more extreme environments, and potentially have more scope to alter their phenology given their lower

direct temperature dependence. We also focus our review predominantly on birds and mammals that occupy high latitudes, principally because the literature is biased towards these regions and our understanding of the mechanisms controlling reproductive timing in species that inhabit equatorial regions and areas where resource availability is more irregular (e.g. El Niño Southern Oscillation–dominated) is limited.

In the first part of this review, we describe how reproductive timing, the allocation of capital towards reproduction, and fecundity are interconnected through the endocrine/neuroendocrine systems that control the reproductive axis. Links between these control mechanisms and sensory circuits allow individuals to modulate seasonal timing in response to external environmental cues and/or endogenous state. However, these same mechanisms also allow animals to alter their life-history strategies, reducing their fecundity and/or shifting position on the C–I continuum. Importantly, these mechanisms also probably constrain the response of individuals [10], preventing certain physiological and behavioural states from occurring together [11,12] and limiting the range of positions along the C–I continuum that an individual can occupy. As such, we suggest the endocrine/neuroendocrine systems that control reproductive timing and resource allocation are linked to ecological resilience and present likely target pathways for adaptive genetic changes in response to directional environmental change.

Following our discussion of the molecular and physiological mechanisms that underlie phenological plasticity, we consider the ecological drivers of reproductive timing. A central tenet that has emerged in ecology is that many animals time their reproduction to synchronize their annual peak in energy demands with the annual peak in resource availability [13,14]. Importantly, since species within food chains may respond differentially to climate change this may result in phenological uncoupling and disruptions within these food chains, with some species unable to time their periods of high demand with peaks in food availability [15–17]. Although synchrony between supply and demand is undoubtedly important on a coarse time scale across the annual cycle (i.e. across seasons), we examine the ecological drivers of timing and question the assumption that reproduction in most species is timed to synchronize *peaks* in energy supply and demand. Interestingly, the allocation of capital towards reproduction is invoked both as a mechanism to allow animals to adjust their timing so that the peaks in supply and demand are appropriately synchronized [18], and as a mechanism to allow desynchrony between supply and demand [19]. While these contrary hypotheses may apply to different species, we argue that more work is needed to identify the cues and ecological drivers of seasonal timing for species across the C–I continuum. Finally, we examine how individual-optimization results in both flexible timing and variable allocation of capital towards reproduction within populations and even within individuals. We emphasize that the degree to which capital is allocated towards reproduction is plastic in many species and that this plasticity may be more tightly linked with an individual's ability to cope with environmental change than absolute position on the C–I continuum.

2. The adaptive value of capital and income breeding strategies

The terms 'capital' and 'income' breeding were originally put forward by Drent & Daan [20] who were interested in

understanding how the investment of endogenous versus exogenous nutrients into eggs influenced decisions on lay date and clutch size in birds. Endogenous nutrients encompass proteins and lipids previously incorporated into maternal tissues that are subsequently broken down for delivery to the egg. The C–I continuum is now considered more generally, encompassing energy allocation throughout reproduction [5], although differences in how capital is defined has led to uncertainty in the applicability of conclusions across systems [7]. While Drent & Daan [20] lamented the lack of a methodology to quantify exogenous versus endogenous inputs, our understanding of the intrinsic and extrinsic factors that influence the evolution of capital- and income-breeding strategies has advanced substantially in the intervening decades, largely owing to the use of stable isotopes to measure nutrient input into eggs/offspring [4,21], as well as to the development of innovative modelling approaches [6,8]. For example, the evolution of capital breeding has been linked to a variety of extrinsic factors, including low/unreliable food availability and spatial separation between foraging and breeding areas especially among migrating species [2,8,20]. Intrinsic factors that influence tactics of resource use are related to morphology and physiology, and include aspects such as body size and the costs of carrying stored reserves. The costs of accumulating and carrying capital vary widely with taxonomic group and mode of locomotion and include demographic costs, which stem from potential increases in mortality, and metabolic costs, which result from increased energy expenditure [6,8,22].

Birds and mammals differ fundamentally in their reproductive physiology and life-history strategies and this has important implications for how they allocate energy and nutrients towards reproduction. Firstly, birds can only provide endogenous nutrients to their young during the relatively short interval of egg development; in contrast, the interval of gestation is comparatively long for a similarly sized mammal and endogenous nutrients can also be supplied throughout lactation. Additionally, flight substantially increases the physiological and ecological costs of endogenous nutrient transport [22] and limits the evolution of large body size in birds. Body size is important because, while the ability to store energy scales linearly with body mass, small-bodied animals have higher mass-specific metabolic rates and, as such, will more rapidly deplete their endogenous energy stores in comparison to larger animals [3]. Although many studies restrict the term 'capital' to endogenous stores, some animals will finance reproduction, in part, using energy or nutrients from exogenous food hoards [2,23]. Use of exogenous capital provides similar ecological benefits while circumventing some of the constraints set by body size and avoiding the energetic costs of transport, although ecological and energetic costs of acquiring and defending hoards can be significant [24].

While higher rates of metabolism can limit the use of endogenous capital for breeding in small endotherms, large mammals may have greater difficulty in synchronizing the peaks in energy supply and demand because of their much longer intervals of gestation [25]. In species where long gestation times shift the mating period into the winter season when conditions are energetically unfavourable, sufficient capital must be accumulated during the summer and fall to cover the energetic costs of the mating season and surviving winter [26]. However, many mammals can delay fertilization or implantation which allows them to uncouple mating from the timing of the reproductive cycle [27]. Additionally, males

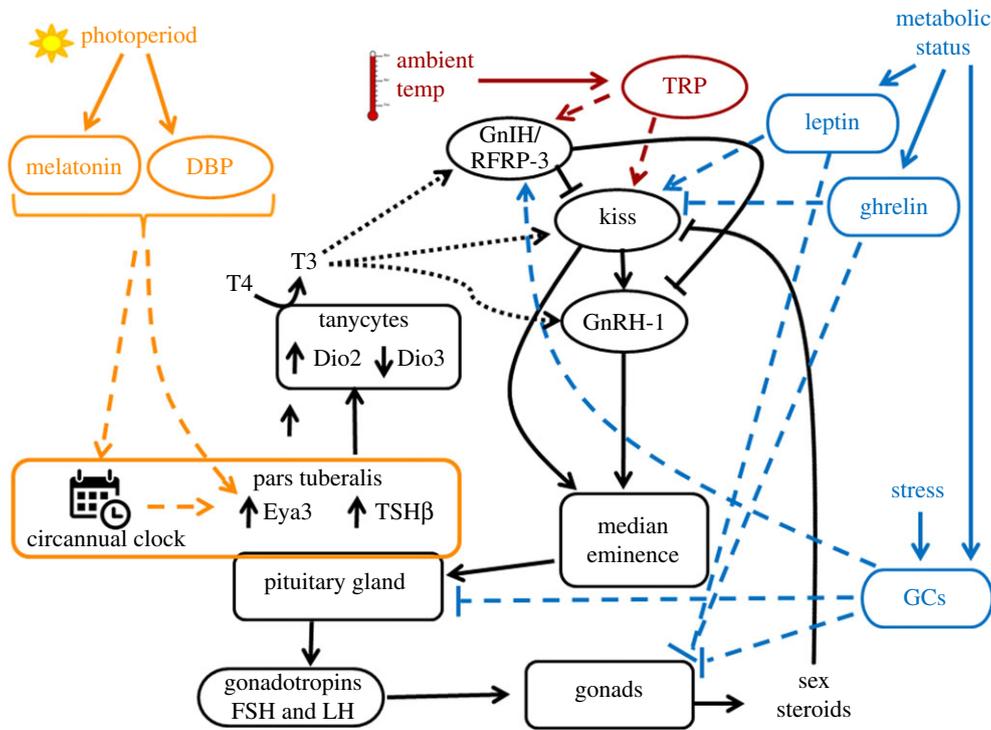


Figure 1. Current view of the mechanisms responsible for activation and modulation of the reproductive axis in birds and mammals. Changes in photoperiod or the circannual clock activate the hypothalamus-pituitary-gonadal axis via the EYA3-TSH-Dio-T3 pathway. In mammals, this occurs via the melatonin signal whereas deep brain photoreceptors (DBP) also play a role in birds. Metabolic state influences timing via effects of glucocorticoids (GCs), leptin and ghrelin on the RF-amides kisspeptin (KISS), and GnIH; reproductive inhibition in response to these signals is also probably occurring at the level of the gonads. Dashed black arrows from T3 indicate multiple pathways that may vary across taxa. The KISS signalling pathway, for example, appears to be non-functional in birds. Ambient temperature is also hypothesized to influence timing via transient receptor potential (TRP) thermoreceptors. Solid coloured arrows indicate effects of physical cues (photoperiod—orange; temperature—red) or metabolic cues (blue) on hormones/neurons that in turn influence the reproductive axis (via connections shown in dashed lines). GnRH-II (not shown) also appears to have a neuromodulatory role in affecting feeding and reproduction.

and females differ in how and when energy is allocated to reproduction, which drives sex-differences in capital- and income-breeding strategies, particularly in species that lack male parental care [7]. When considering the reproductive investment of males, it is particularly important to consider investment beyond nutrients allocated directly to offspring, such as energy directed towards intraspecific competition for mates [7,28]. For simplicity, we will only consider female reproductive tactics in this review, although sex certainly factors into C–I differences among individuals.

3. Molecular control of reproductive timing

Although many details of the mechanisms that underlie the transitions between seasonally recurring life-cycle events remain unclear, our general understanding of seasonal activation of the reproductive axis has advanced markedly in the past decade. This has involved delineation of the pathways through which annual changes in photoperiod signal the neuroendocrine circuits that drive seasonal reproductive cycles in many temperate zone vertebrates (figure 1). In most mammals, this includes a key timing hormone, melatonin, which is secreted from the pineal gland during darkness. A crucial site of action for melatonin is the pars tuberalis (PT) of the pituitary where it interacts with a circadian-based timing mechanism that drives the reproductive axis via action on thyroid hormone (TH) metabolism in adjacent hypothalamic cells [29]. In birds, the melatonin system is redundant to some degree, as deep brain photoreceptors can directly

transduce the long day signal [30]. In photoperiodic birds and mammals, reproductive competence is initiated by photoperiod-dependent changes in the expression of deiodinase enzymes (DIO2 and DIO3) in tanycytes of the hypothalamus, which, in turn, increase intra-hypothalamic bioavailability of triiodothyronine (T3) [31,32], the most biologically active form of TH. The expression of deiodinases in tanycytes is controlled by thyroid stimulating hormone (TSH), synthesized and secreted by cells called thyrotrophs within the PT [33]. As a modulator of seasonal reproductive competence, T3 regulates gonadotropin releasing hormone (GnRH-I) neurons, possibly through the RF-amide related proteins, kisspeptin (KISS) and gonadotropin inhibiting hormone (GnIH; also known as RFRP-3) [34]. A functional KISS system, however, does not seem to exist in birds [35]. Further, in addition to the hypothalamic form of GnRH (GnRH-I), a midbrain form exists (GnRH-II) that does not play a major role in pituitary regulation but appears to act as a signal of energetic state, permitting breeding to occur only when sufficient energy reserves are available [36,37].

It is now clear that the specialized PT thyrotrophs are key to governing seasonal timing in several vertebrate lineages, driving photoperiodic activation of TH-converting circuits and gonadotrophins [29,33]. However, reproductive state is not simply driven by photoperiod as animals can become photorefractory; long-day breeding rodents become refractory to the suppressive effects of short days whereas birds become refractory to the stimulatory effect of long days [38]. Further, some species exhibit seasonal cycles of behaviour and physiology (e.g. reproduction, moult, appetite and fattening, and

migration or hibernation) that are predominantly controlled by an endogenous circannual clock that is entrained by, but not dependent on, changes in photoperiod [39,40]. In these species, circannual rhythms persist under constant environmental conditions (including continuous light or dark) for the lifetime of the animal with a free-running period that deviates slightly from 12 months [40,41]. Although photoperiodic species differ fundamentally from circannual species in that they fail to exhibit persistent approximately 12 month rhythms under constant photoperiod, much of the molecular machinery that underlies seasonal timing in these groups is probably shared [42]. In fact, some species that are typically regarded as photoperiodic, such as the European starling (*Sturnus vulgaris*), will display components of circannual rhythms of physiology and behaviour when maintained on exactly 12 h light : 12 h dark photoperiod [43]. In strongly circannual species, however, the timing of annually recurring life-cycle events is controlled by the circannual clock itself; in these species, changes in photoperiod entrain the circannual clock but changes in day-length do not immediately trigger the onset or termination of seasonal physiologies and behaviours, such as hibernation and reproduction [41]. In these species, the PT thyrotrophs are strong candidates for independently driving circannual rhythms in the absence of a photoperiodic signal [29]. In contrast to 'photoperiodic' and 'circannual' breeders, many species are classified as 'opportunistic' breeders, with reproduction occurring whenever conditions are favourable, regardless of interval or periodicity [44]. These species will maintain a partially activated reproductive axis allowing them to rapidly respond to unpredictable environmental changes that can alter resource availability. However, despite their designation as opportunistic breeders, these species often exhibit sensitivity to long days [45], though long days alone may be insufficient to drive reproductive development [46,47].

We contend that much of the circuitry controlling reproductive timing is probably shared among photoperiodic, circannual and opportunistic breeders. That is to say, we argue the distinctions between these groups are not clear cut, and the mechanisms that underlie photorefractoriness are probably homologous with those that drive transitions between states in circannual breeders. Equally important, however, is that whether and when reproduction is activated each year is variable and sensitive to the age, metabolic state and endogenous fuel stores of the organism. This variability stems from 'noise', which is due to effects of weak or interfering signals (cues) or weak transduction and integration of signals, and from 'plasticity' (or phenotypic flexibility; *sensu* [48]), which entails reversible phenotypic variation in response to changes in environmental conditions or physiological state. Evidence to date suggests some of this plasticity occurs at the level of the RF-amides that regulate the release of GnRH-I, as well as at the gonads themselves. The adipose-derived hormone leptin, for example, has permissive effects on the onset of female puberty that appear to be principally mediated through hypothalamic KISS expression [49]. The gut-derived hormone ghrelin, which plays key roles in metabolism and energy homeostasis [50], acts in an opposing manner to leptin as a signal for energy insufficiency, suppressing KISS expression in discrete nuclei of the hypothalamus [49,51]. Both leptin and ghrelin also appear to influence reproductive state through direct effects on the gonads [49,52]. GnIH also plays a critical role in fine-tuning the timing of seasonal breeding by relaying information on metabolic state to reproductive and motivational circuits [53].

GnIH neurons are activated by food restriction, and the infusion of GnIH inhibits sexual motivation [54]. The inhibitory effects of stress on reproductive function are also likely to be mediated by GnIH, as stress hormones (glucocorticoids) can directly induce GnIH transcription [55]. GnIH is also expressed in the gonads, where it may play a role in the local inhibition of sex steroid secretion in response to stress [56]. Relative levels of leptin, ghrelin and GnIH therefore could reflect an organism's state of adiposity and rates of food intake and energy expenditure, and therefore its acute capacity to fuel reproduction on a capital versus income basis. However, we do not yet understand the mechanisms through which exogenous capital (i.e. a food hoard) influences reproductive timing, though we speculate this could occur via direct effects of neurobiological reward systems on the RF-amides that stimulate or inhibit reproduction.

Our understanding of the mechanisms that underlie seasonal timing at different phases of the annual life cycle lags behind progress made in defining the neuroendocrine circuits that trigger activation of the reproductive axis. For example, while nearly 100 mammals in seven different orders are known to undergo delayed implantation affecting timing of birth, we are only beginning to understand the molecular mechanisms that underlie this process [27]. In large mammals, adjusting the length of gestation is an important mechanism for altering the timing of birth, though the mechanisms and limitations underlying this are unclear. Adjustment of gestational length appears to be particularly important in ungulates where it is assumed that high food availability towards the end of gestation facilitates faster growth of the fetus during the phase of rapid fetal growth and thus advances parturition date [57,58]. This flexibility in gestation duration is particularly impressive in bison (*Bison bison*), which, when in good body condition, can shorten gestation length by as much as 15 days as a means of synchronizing parturition within a herd [59]. Similarly, there are hints for such flexibility in the red deer (*Cervus elaphus*), where parturition dates advance faster in response to environmental conditions than does female oestrus [60]. A possible explanation for this effect of income in this 'capital' breeder can be found when reanalysing heart rate data from Turbill *et al.* [61]. Heart rate indicates female red deer under food restriction lower their metabolism more during winter to save energy and also delay the typical spring increase in metabolism by several days compared to females under ad libitum conditions [61] (figure 2); this delayed increase in metabolism caused by low food availability may depress rates of fetal growth and thus lengthen the duration of gestation and delay parturition. Thus, while species that fall towards the capital end of the C–I continuum are sometimes regarded as buffered from conditions during the interval of peak energy demand (see below), evidence from ungulates suggests that these animals will still adjust their gestation length in order to match energy supply and demand during lactation and/or reduce the risk of predation to their young by maintaining synchrony with other females [58,60].

4. Ecological drivers of reproductive timing

Birds and mammals have evolved a variety of life-history strategies in response to seasonality and other periodic environmental variations. These strategies involve partitioning energetically or nutritionally demanding processes into distinct time periods with demanding episodes during reproduction

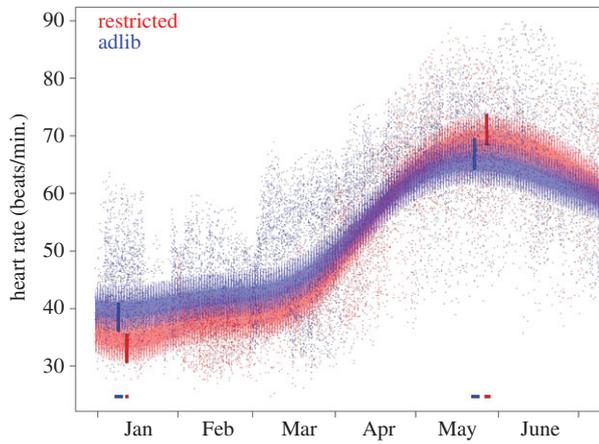


Figure 2. Increase of heart rate from winter to summer and modulation by food availability in adult female red deer ($n = 15$). Plotted are hourly means of heart rate of individuals with unrestricted (blue) or restricted access to food (red, for methodological details see [61]). Shaded belts indicate 95% confidence limits (CI) of smooths fitted to seasonal changes by general additive mixed modelling (R-package 'mcgv'), including a cosinor term accounting for within-day variation and individual cosinor fits as random factor accounting for repeated measurements. To correct for temporal correlation detected in the residual error term of the model, we included an auto-regressive correlation structure ('corARMA' from R-package nlme). Horizontal bars indicate 95% CI of the timing of troughs and peaks, vertical bars 95% CI of trough and peak heart rates. CIs were determined from respective distributions produced by simulating 10 000 replicates of model coefficient vectors from the posterior using 'mvrnorm' from R-package MASS. Data shown are from [61], with additional analyses to identify temporal differences between groups in the seasonal peaks and troughs of heart rates.

typically, though not exclusively, occurring when food is more readily available [11]. In the previous section, we described the mechanisms that allow animals to appropriately time reproduction in seasonal and/or unpredictable environments. An important parallel issue involves understanding the ecological drivers of reproductive timing and how the use of capital influences relationships between linked trophic levels. In seasonal environments, it is often argued that recruitment is maximized if the most energetically expensive phase of the breeding season coincides with the peak in energy availability at the immediate lower trophic level [15]; if there is a mismatch between energy supply and demand, survival and recruitment will be reduced [16]. In recent years, trophic match/mismatch has been increasingly discussed in the context of rapid climate change, which is leading to phenological shifts for many species distributed widely across taxonomic groups and ecosystems [14,16,62]. Many studies now report that climate-driven mismatches between energy supply and demand are becoming more common, and, in some cases, these mismatches are having negative impacts on the survival and recruitment of offspring [63–65]. Because the phenological response to changing climate and seasonality can be different at each trophic level, it is argued that current levels of flexibility in the timing of life-history events may no longer be adaptive for many species [15,64,66,67]. In other words, the timing of the pulse in resource availability has shifted relative to the photoperiodic signal, and the endocrine/neuroendocrine mechanisms controlling plasticity in higher trophic levels do not appropriately account for this shift. Assessing whether a climate-driven mismatch is occurring is difficult, however, as one must track phenology across multiple trophic levels to determine whether the

observed shift matches that of the lower trophic level [15]. Moreover, fitness consequences and selection pressure may vary greatly depending on how the relationship between cue and optimal timing are specifically affected by environmental changes [68]. Finally, observed shifts in timing that are not as strong as the shift in the perceived optimal timing may only appear as maladaptive, whereas in fact these could be highly adaptive and the result of trade-offs between competing demands [69,70].

Although many animals are thought to use environmental cues to time their reproduction in an attempt to match the timing of peak energy demands with the seasonal peak in resource availability [15,16,63], the idea that reproductive timing is dictated by the simple need to match the *peaks* in energy supply and demand is probably an oversimplification for many species. For example, in some cases top-down regulation can be more important than bottom-up control such that prey species increase the survival and recruitment of their young by timing reproduction to increase asynchrony with predator populations [71]. For species breeding at high latitudes, reproductive timing may be dictated primarily by conditions in spring rather than by attempts to match supply and demand [72,73]. For example, while seabirds and insectivorous songbirds are two groups that are generally thought to time breeding such that chick-rearing coincides with the seasonal pulse of food availability [16,64], Shultz *et al.* [74] and Dunn *et al.* [75] found that, for some representatives of these groups, the onset of egg-laying is more closely tied to resource availability during the pre-laying period rather than to the timing of the seasonal peak in energy supply. This may occur, at least in part, because conditions during egg-laying are not predictive of conditions later in the year during peak energy demand. However, smaller animals with higher metabolic rates will also have less capacity for storing energy and nutrients for egg-laying and are therefore more likely to face a nutritional bottleneck upon arrival at their breeding sites in spring, particularly in polar environments [73]. In some non-migratory small mammals and birds, nutritional bottlenecks can be avoided by relying on food caches [24,76]. Although large mammals can potentially use endogenous stores to decrease their sensitivity to nutritional bottlenecks, implantation takes place long before the most energetically expensive period of lactation, which may make it more difficult to time parturition to match the seasonal peak in resource availability (but see [58,59,77]).

There are other reasons for a lack of synchrony between reproductive timing and timing of resource availability. Early breeders tend to have higher reproductive success and produce more recruits into the population [5,78–80], but see [81]. Although this is partly because higher-quality individuals breed earlier in the season, the main advantage of early breeding is that it extends the length of the reproductive season providing (i) opportunities to renest if the first litter/clutch is lost to predation or inclement weather [82], (ii) opportunities to produce multiple litters/clutches during the year [82,83], and (iii) increased time for juveniles to develop, grow and fatten prior to hibernation, migration or overwintering [78,80]. Recently, it has been argued that decreased double brooding in great tits (*Parus major*) is an indication of climate-induced mismatch [84]. Although this is a mismatch of sorts, it is not driven by a lack of synchrony between the *peaks* in supply and demand; instead, animals may be breeding too late to take advantage of the tail end of the pulse in food availability.

Thus, when considering trophic mismatch, it is also important to identify the temporal scale at which matching occurs.

Despite the relatively widespread use of capital as a source of energy for reproduction, relatively few studies have considered how position on the C–I continuum influences synchrony in timing across trophic levels. Two contrary ideas are present in the literature. The first is that, regardless of whether it is stored endogenously as fat or exogenously in a food hoard, capital acts to extend the energetic benefits of a resource pulse, thus lessening the need to couple supply and demand [19,82]. Kerby & Post [19] argue that capital breeders may be less sensitive to trophic mismatch and therefore are buffered from climate-induced changes in the relationships between physical cues and ecological processes. In support of this, they found that income-breeding caribou are sensitive to synchrony between peaks in supply and demand, whereas sympatric muskox (*Ovibos moschatus*), which fall much closer to the capital end of the continuum, are relatively unaffected by trophic mismatch [19]. The second argument made for how the use of capital influences reproductive timing is that mixed-strategy (i.e. partial-capital) breeders use capital early in the breeding season as a mechanism to facilitate better synchrony between peaks in energy supply and demand later in the reproductive cycle [60]. For example, some ungulates that are generally regarded as being on the capital end of the spectrum, such as red deer and mountain goats (*Oreamnos americanus*), use capital in the lead-up to parturition, which is thought to be timed such that lactation coincides with green-up [58,60,77].

5. Carry-over effects

In our discussion thus far, we have generally considered reproductive timing independently of other life-history stages, yet the sequential nature of integrated biological systems means that the environment and/or physiological state of an organism during one life-history stage can influence individual performance during subsequent stages, a phenomenon known as a ‘carry-over effect’ (reviewed by [85]). Migrants are generally perceived as being more susceptible to carry-over effects and climate change–induced mismatches between linked trophic levels because they initiate their spring migration at distant wintering sites and therefore may be less able to adjust timing to local conditions at their breeding grounds [86]. For example, mismatches between arrival dates at the breeding grounds, which have not changed or changed insufficiently, and the peak in food availability, which are advancing due to warming spring temperatures, have been observed in pied flycatchers, *Ficedula hypoleuca*, and this has led to a 90% decline in abundance of some populations [64] (but see [65]). Further, in a study of 100 European migrant bird species, Møller *et al.* [87] found that species that have not exhibited a phenological response to climate change are more likely to be in population declines compared to species that have advanced their spring migration.

Whereas small migratory birds are typically reliant on capital only to fuel migration (but see [88]), many larger migrants are capital or mixed-strategy breeders [4,5,21]. High-latitude–breeding migratory waterfowl by and large track a successively delayed spring flush of plants on their way from the wintering grounds in the temperate zone to their Arctic breeding grounds, leading to the expression that they ‘surf the green wave’ [89]. Surfing the green wave has also

been observed in ungulates, although interspecific variability was found in whether animals surfed the leading edge, trailing edge or crest of the wave [90]. Exceptions do exist, however, with some waterbirds overtaking the green wave, arriving early at the breeding site prior to the spring flush of plants [18,91]. By accumulating body stores along the flyway, these animals can use a partial capital-breeding strategy to initiate reproduction prior to spring green-up such that the peak in nutrient availability occurs during offspring development [18]. Interestingly, inter- and intra-specific comparisons in waterfowl reveal that more northern populations will reduce time between arrival and egg-laying and incorporate more capital into their breeding attempts [5]; initiating breeding as soon as possible is thought to be an adaptation to the short growing season in the Arctic [5,73]. In years with late springs, waterbirds will decrease the interval between arrival and laying the first egg by investing more capital into their clutch [5]. However, it is important to note that much of this capital may be acquired in relatively close proximity to the breeding grounds as birds congregate near the edge of ice melt and fatten in preparation for breeding [5].

Carry-over effects may also be important for hibernators, which survive seasons with low resource availability by suppressing metabolism and relying on accrued capital. In large hibernators, such as bears, reproduction and hibernation overlap, and capital must be used to fuel self-maintenance and the early stages of lactation; the rate of mass-loss for denning in lactating females relative to non-lactating females is 45% higher for black bears (*Ursus americanus*) and 95% higher for grizzly bears (*U. arctos*) [92]. In small hibernators, reproduction and hibernation typically do not overlap [40], though daily torpor during incubation, brooding, pregnancy or lactation occurs in a variety of birds and mammals [93]. Most small female mammals rely on capital to fuel hibernation and income to fuel reproduction although this strategy appears to be flexible as females (and males) may use ‘leftover’ capital during breeding depending on body condition and the timing of spring. The most extreme example of this occurs in some female bats, which will emerge in spring with large enough fat stores for initiation and support of early pregnancy [94]. Similarly, female Arctic ground squirrels (*Urocitellus parryii*) will continue to use capital and lose body mass during the first two weeks of gestation [95]. However, in years with early spring and snow melt, females will immediately begin accruing body mass, indicating the use of capital is probably plastic [96]. The situation in more temperate Columbian ground squirrels (*U. columbianus*) is somewhat different, however, as females that emerge from hibernation in good body condition do not lose mass but are able to invest more income into their litters, rather than their own maintenance, compared to females in poor condition [97].

6. Individual optimization

Early researchers studying the timing of reproduction in birds postulated that if phenology has a genetic basis, then selection would lead to early and late breeders producing fewer recruits compared to average breeders [98]. However, population studies revealed that individuals that breed earlier often produce more offspring compared to individuals that begin laying eggs later in the season [78,79]. This discrepancy has been reconciled with optimal-timing theory, which postulates that the phenotypic adjustment of laying date to

food conditions is an optimization problem with different solutions for individuals in different physiological states [79,80]. It should be noted that while we use the term optimal throughout this paper, we recognize that evolution does not produce perfect designs but instead selects for genetically based traits that, on average, lead to higher fitness. Despite this important qualification, we argue that approaches that use an optimization framework can yield important insights and predictions with respect to understanding life-history trade-offs [68].

Variability in physiological state among individuals reflects different genotypes, differences in environmental conditions experienced throughout their lives, and gene–environment interactions. Within a population, individual optimization models predict that variability in reproductive timing, as well as clutch size, can occur due to variation in the vitality and/or body stores of an animal [86,99,100]. That is to say, seasonal timing can be viewed as a variable trait that is influenced not just by external factors, but also in response to the physiological state, such as the endogenous stores, of the organism; this concept is well supported by studies examining the molecular drivers of phenological plasticity (see §3). However, while reproductive timing is typically viewed as a plastic trait, position on the C–I breeder continuum is often thought of as a species-level trait. We argue that for species that do not occupy the endpoints of the continuum, use of capital is often highly plastic, intrinsically linked to reproductive timing and an important component of resilience to environmental change. A graphical representation of a simple conceptual model that allows for individual optimization with advancing springs under climate change in a mixed-income breeder is shown in figure 3, where individuals low in body stores breed later, allowing them to reduce their reliance on capital, instead taking advantage of the seasonal increase in resource availability (figure 3*a*). Although individuals are maximizing their reproductive output by adjusting phenology and reliance on capital in response to their own body stores, individuals that have lower body stores and breed later will produce fewer young, on average, owing to reduced opportunities to produce secondary clutches/litters and/or lower recruitment of young born later in the year. This conceptual model assumes there is genetic variation in the mechanisms that underlie phenological plasticity but that stabilizing selection maintains an appropriate plastic response and optimal timing for an animal with a given amount of body stores (indicated by the bell-shaped curves in figure 3*a*). As climate change drives warming conditions and earlier springs, the seasonal pulse in food availability advances and individuals will plastically advance their timing in response (figure 3*b*); at this stage, weak selection may be occurring though it may be difficult to detect. As warming continues, limits to physiological plasticity in reproductive timing result in individuals breeding later than is optimal (figure 3*c*).

In our conceptual model we have assumed that (i) natural selection favours early breeders, and (ii) there is a heritable component to timing. However, micro-evolution will not occur unless selection is acting on the heritable component of the trait [101,102], which is not the case if individuals are optimizing their timing based on their own body stores (figure 3*a*). Despite individual optimization, evolution may be occurring if the difference in body stores among individuals has an underlying genetic basis. For example, a polymorphism that provides resistance to disease could influence phenology by

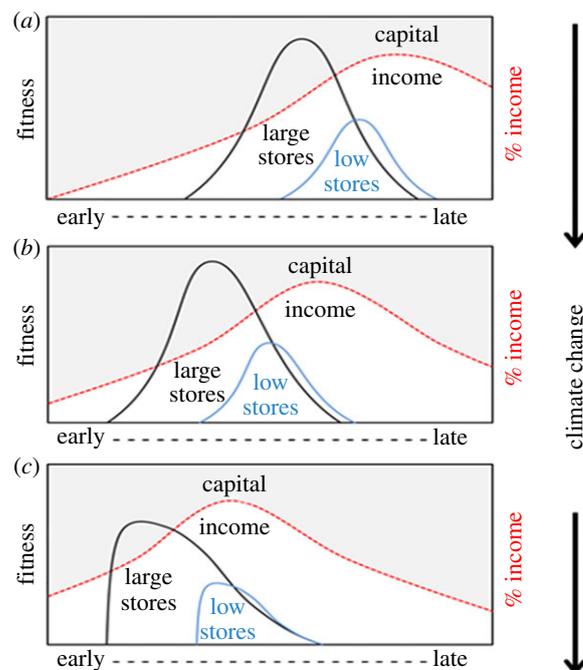


Figure 3. Conceptual model illustrating how individual optimization influences the trade-off between reproductive timing and use of capital in a mixed-strategy breeder. (*a*) Optimal timing is earlier for an animal with large body stores (black line) versus low body stores (blue line); individuals with low body stores delay breeding in order to take advantage of the seasonal peak in resource availability; the percentage of energy allocated towards reproduction that can come from income is represented by the dashed red line (i.e. % income increases with the seasonal increase in resource availability and then begins to fall after the resource peak). Breeding earlier requires a greater investment of capital (grey shaded area above dashed red line) relative to income (non-shaded area below dashed red line) for successful reproduction. (*b*) Under warming conditions and earlier springs, animals respond plastically to their environment and advance the onset of the breeding season; stabilizing selection maintains an appropriate plastic response and optimal timing for a given physiological condition. (*c*) Under continued warming, the timing of reproduction fails to advance sufficiently to maintain synchrony with phenological shifts occurring at lower trophic levels and mismatches occur such that selection acts on the mechanisms that control timing and/or the sensitivity of these mechanisms to environmental cues.

affecting physiological state (e.g. defence against disease at the expense of body stores), shifting individuals lacking the polymorphism towards later breeding and an increased reliance on income to fuel reproduction. In this case, selection would be acting on the phenotypic trait (phenology) and the underlying genetic component that influences timing (the polymorphism that confers disease resistance), yet not on the genes that directly control timing. Under climate change, we anticipate that limits to physiological plasticity will be exceeded and timing will no longer be optimized (figure 3*c*). Assuming constraints in plasticity arise from control mechanisms [10], long-term directional environmental change, including climate change, might act on genetic variation in the endocrine/neuroendocrine systems that underlie state-dependent plasticity in seasonal timing. Although climate can undoubtedly act as a strong selective force, evidence of genetic change in phenology in response to anthropogenic change is lacking for birds and mammals [103,104] (figure 3*c*).

The presented concept is supported by a few studies showing considerable among year variation in capital use within

populations in response to differential climatic conditions [105] as well as among-individual variation in capital use in relation to the timing of breeding [106,107]. A particularly good example of plasticity in the use of capital comes from common eiders (*Somateria mollissima*), a mixed-strategy breeder. Individuals that are in poorer body condition delay breeding and, based on stable isotope data, incorporate more nutrients from local sources (i.e. income) into their eggs [21,108]. However, in some years, individuals that are in particularly poor condition may delay breeding and reduce their clutch size such that they invest more capital into each egg, but less into the total clutch [109]. Similarly, food-caching gray jays (*Perisoreus canadensis*) will advance reproduction and increase clutch size when provided with supplemental food to cache prior to the breeding season [76]. Red squirrels (*Tamiasciurus hudsonicus*) breeding in the boreal forests of North America provide another example of a food-hoarding species that delays reproduction when capital is low. These squirrels get most of their nutrition from the cones of white spruce (*Picea glauca*), a masting species that intermittently produces large cone crops synchronously across vast geographical areas [110]. However, because white spruce cones mature in the late summer, they are not available for consumption during spring reproduction [82] and instead squirrels clip and hoard cones in the early fall, before the cones open and the seed is dispersed [23]. Reproductive timing is not related to spring conditions or food supply in the current year; instead, red squirrels delay reproduction following years with low cone production to time peak reproductive demands to be late enough to coincide with the seasonal pulse in alternate (i.e. not cones) sources of income (figure 4) [23,82]. Thus, in this system there appears to be a trade-off between reproductive timing and use of capital: individuals without sufficient capital can delay reproduction and shift towards greater use of income, but they do so at the cost of producing fewer recruits [82].

7. Between litter shifts in resource allocation

Thus far, we have focused on variability in the use of capital within and across populations. However, the possibility also exists for individuals to shift their reliance on capital from one reproductive bout to the next within the same year. Among insects, for example, there are species such as the flesh fly, *Sarcophaga crassipalpis*, that systematically shift from partly capital- to entirely income-based investment between the first and subsequent clutches [111]. Although this may occur in larger birds that lay repeat clutches after nest failure, it is unlikely to occur in small birds that lay multiple clutches because they rely mostly on income to fuel reproduction. Among mammals, evidence for such a routine seasonal alteration from capital-aided to pure income breeding seems rare. A notable exception, however, is the European brown hare (*Lepus europaeus*). Brown hares typically have 3 (up to 5) litters per year with an average litter size of 2–3 young [112]. In Europe, the breeding season lasts from January to October and litter size peaks in summer (approx. 2.5 young per litter), while only 1–2 young per litter are born early in the season (Jan–Mar; [113]). This lower litter size at breeding onset has been attributed to the fact that young born early in the season are costly. They are exposed to low ambient temperatures, entirely lack burrows or nests, and hence have high energetic costs of thermoregulation [113]. Although hares are

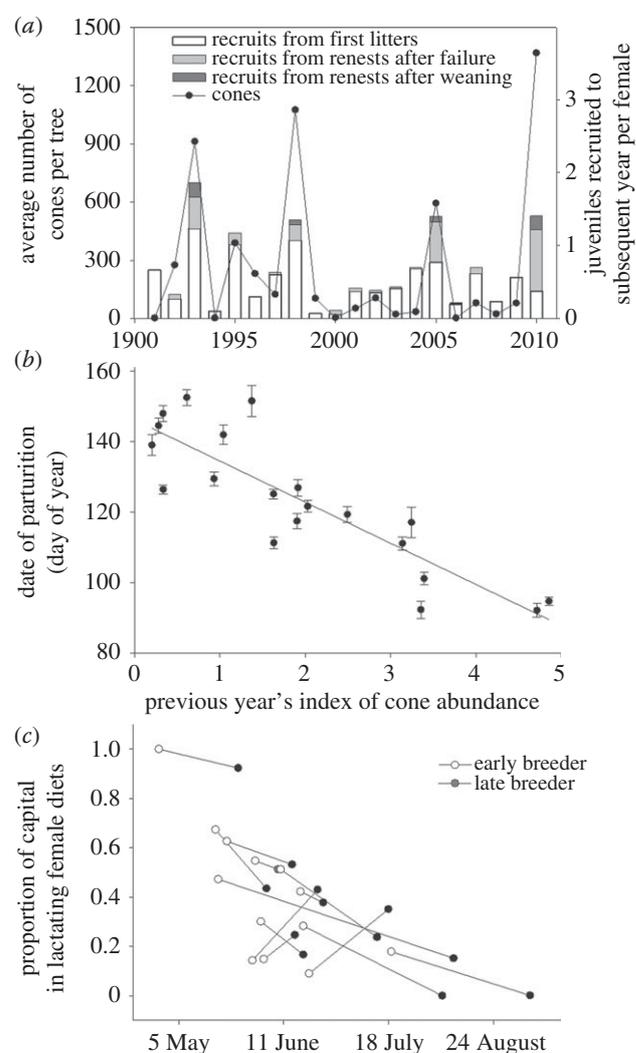


Figure 4. Recruitment success of red squirrels has varied substantially over the past 20 years due to high annual variation in the production of cones by white spruce (a). Timing of reproduction in food-hoarding red squirrels is dictated by the size of the previous year's spruce cone crop (b), which determines the amount of capital available for reproduction. Females that breed earlier are more reliant on capital, both within and across years (c). In panel (c), each pair of points connected by a solid line represents one study year; early- and late-breeding squirrels reached mid-lactation (35 days postpartum) prior to, or after, the yearly median mid-lactation date, respectively. Panels (a) and (b) from [82], panel (c) from [23].

precocial and start to take up solid food in their second week of life, 80% of their energy intake prior to weaning is obtained via milk [114].

Both female and male hares deposit substantial body fat stores during autumn and winter, which peak just prior to reproduction onset in January, and are entirely depleted over the breeding season [115]. Valencak *et al.* [116] used an experimental approach, pairing hares in spring, summer and autumn, to assess the investment of these body fat reserves into reproduction. To differentiate between capital and income resources, a saturated fatty acid, undecanoic acid (C11:0), which does not naturally occur in the diet of hares, was added to the food provided to females. Mothers were fed this marker each time they were gestating, but not during lactation. These feeding trials showed that females transferred previously stored fatty acids to milk early in the season, but not at all during lactation of the last litters. Interestingly, although females had equal opportunities to allocate nutrient lipids to

body fat stores, they apparently did so only in spring, which points to a seasonally 'programmed' rhythm of energy storage. Accordingly, milk fat content continuously decreased over the breeding season. As an apparent compensation for the depletion of body fat stores, lactating females significantly increased their energy intake in autumn. Overall, the European hare can still be placed close to the income end of the C–I continuum, as even in spring the contribution of body fat reserves was only approximately 25% of the total milk energy transfer to young. However, the study by Valencak *et al.* [116] clearly indicates that in the course of the breeding season, females gradually switched from a capital-aided to a pure income-breeding strategy of resource allocation.

Interestingly, clear evidence for seasonal shifts from capital to income-breeding in other mammals currently seems absent. This could be partly because pursuing this question requires differentiating between the origin of resources by the use of added markers [116] or stable isotopes [108], which can be laborious. Moreover, shifts in strategy as seen in brown hares require that animals are capable of depositing substantial body energy stores and have several reproductive bouts per year. The first criterion probably limits candidate species for such changes in breeding strategies to mammals with a body mass above approximately 1 kg, because smaller mammals typically reduce, rather than increase, body mass and fat stores prior to the next reproductive season [117]. The second criterion, multiple litters per year, is rarely met by large mammals, as gestation time increases and the yearly number of litters decreases with increasing body mass [118]. Thus it seems possible that regular seasonal shifts of individual breeding strategies along the C–I

continuum are restricted to species of an intermediate body size, such as the European brown hare.

8. Conclusion

To date, much of the research on capital and income breeding has focused on the diversification among species in tactics of resource use. However, plasticity in the allocation of capital towards reproduction is common in many species, and we speculate this plasticity provides resilience to environmental change and is linked to the endocrine and neuroendocrine systems that control the reproductive axis. As such, better delineating these endocrine and neuroendocrine circuits may help in identifying target genes for monitoring adaptive genetic responses to environmental change. Additionally, reproductive phenology, fecundity and energy allocation strategies are all interconnected and, to be fully understood, these life-history traits should be examined within a single framework rather than in isolation [100]. Although climate change can disrupt trophodynamics resulting in mismatched timing among linked trophic levels, more attention needs to be placed on the temporal scale at which birds and mammals match energy supply and demand and on how the allocation of capital towards reproduction influences this relationship.

Data accessibility. This article has no additional data.

Authors' contributions. All authors provided text for the manuscript and edits on the entire manuscript.

Competing interests. We have no competing interests.

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