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Timing of avian reproduction in unpredictable environments

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Abstract Organisms living in periodically varying environments adjust their life history events to the changes in food availability. When these changes are not entirely predictable animals face a trade-off between maintaining physiological preparedness (which can be costly) and being unprepared (which decreases the chances of successful reproduction). To investigate this problem, we developed an optimal annual routine model of gonad regulation in birds. Most birds regress their reproductive organs during non-breeding periods, but to start breeding again they need to have functional gonads. Maintaining the gonads in this state is costly, but because it takes time to achieve this state, if gonads are not functional the bird may miss a possible breeding opportunity. We explore the resolution of this trade-off in environments where favorable periods can occur at any time of the year and variability in the length of good and bad periods can be altered. Consistent with empirical studies of reproductive behavior in unpredictable environments, we find that birds maintain the gonads partially activated during unfavorable conditions in many cases. However, gonad regulation may differ strikingly depending on the consistency of the good and bad periods. Furthermore, seasonal changes in food availability lead to the entrainment of reproduction and the segregation of the breeding and non-breeding season, even if the magnitude of seasonality is small compared to the degree of environmental fluctuations. These results indicate that several aspects of the environment need to be taken into account to understand reproductive behavior in unpredictable environments. Given that the trade-off between the costs and benefits of maintaining physiological preparedness is not limited

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to birds, our results have implications for understanding behavioral flexibility in other organisms as well.

Keywords Phenotypic flexibility · Annual routine · Gonadal cycle · Breeding season · Opportunism

Introduction

In periodically changing environments animals organise their major life history events to match the regular changes in food availability. Proper timing is very important because the costs and benefits of performing a given action (e.g. migration, molt) vary over the year (Lack 1968; Perrins 1970; Houston and McNamara 1999; Barta et al. 2006, 2008; McNamara and Houston 2008; Wingfield 2008); in particular, reproductive success often depends on appropriate timing of breeding (e.g. Brinkhof et al. 1993; Visser and Verboven 1999). To cope with the changing environmental circumstances, animals have to adjust their state, resulting in reversible changes in body mass, internal morphology and physiology (Piersma and Drent 2003). If the environment is at least partly predictable, animals can use their internal biological rhythms to tune the timing of these changes to the environment. On the other hand, if information on the future is restricted (i.e. the environment is unpredictable) then animals need to be flexible and behave opportunistically (Bronson 1989; Zann et al. 1995; Hahn et al. 1997; Barea and Watson 2007; Robin et al. 2009).

Examples of temporal or spatial opportunism occur in a wide range of organisms: in anurans for instance, most species inhabiting arid or semiarid regions use ephemeral rain pools for reproduction (Wells 2007). These animals remain inactive for several months each year, but the entire population starts reproducing almost instantaneously after rainfall (Wells 2007). Opportunistic breeding is also frequent in birds, especially in the Australian avifauna, where food availability depends very strongly on rainfall and the birds can breed only during periods with high food availability (for an overview, see Robin et al. 2009). Similarly, small mammals inhabiting the tropics and commensal rodents associated with humans, such as house mice (*Mus musculus*) and Norway rats (*Rattus norvegicus*) generally have a very flexible reproductive system with the possibility of year-round reproduction, depending on actual food availability (Bronson 1989).

Opportunistic breeding implies that animals need to respond very quickly to changes in the environment. In some cases this is achieved relatively easily, as in the desert anurans (see above). In other cases, however, responding instantaneously to the changing environment is not as simple, because starting reproduction may require a suite of lengthy physiological preparations. For example, some female true seals (family Phocidae) do not feed during weaning but rely entirely on stored fat reserves to raise offspring (they are capital breeders; Stephens et al. 2009); accumulating these reserves takes time. Similarly, most birds regress their gonads outside the breeding period (Murton and Westwood 1978), presumably to reduce body mass and hence decrease the metabolic costs of flight (Dawson and Sharp 2007) or the risk of predation (cf. Lind et al. 1999). From this regressed state it may take several weeks or months before the reproductive organs are again fully functional (Murton and Westwood 1978). Because gonads have to be fully developed in order to reproduce, birds need to start regrowing their gonads well before the time of highest food availability to ensure that the energetically expensive egg-laying and chick-rearing periods fall within the time window of abundant food sources. Here we use birds as an example to investigate how lengthy physiological preparation influences the timing of important life history events in unpredictable environments. Our study can, however, provide insight for other organisms where such preparation is required.

In stable seasonal environments the reactivation of gonads in spring is triggered by long-term predictive information from the environment, mainly photoperiodic cues (e.g. Wingfield et al. 1992; Dawson and Sharp 2007). This enables birds to develop their reproductive organs in anticipation of the favorable season. In contrast, when the environment is stochastic and hence there is unpredictable variation in the onset of the favorable season, animals face a twofold problem, because they (1) cannot fully anticipate the expected start of the reproductive season (it is stochastic) and (2) cannot respond immediately to changes in the environment (because physiological development takes considerable time). Hence, in such environments there is a trade-off between (1) reactivating reproductive organs earlier, which incurs the cost of maintaining the gonads during unfavorable periods and (2) delaying reactivation, which increases the chance that periods with high food availability will be missed. The consequences of missing the peak of suitable food are especially serious in birds whose offspring require specialized, protein-rich food, because these species cannot easily buffer the effect of environmental variability e.g. by providing milk (Zann et al. 1995; Barea and Watson 2007).

As a result of this trade-off, birds living in highly variable environments are thought to maintain their reproductive system in a partially regressed state (Immelmann 1973; Morton 2009), and observations of Australian opportunistic breeders provide some support for this prediction (e.g. Immelmann 1973; Astheimer and Buttemer 1999; Morton 2009; but see Perfito et al. 2007). However, even if the favorable period can start at any time of the year, the fitness benefit of staying prepared during periods with low food availability (and as a result the level of preparedness during these periods) may differ between environments. Thus, all else being equal, a longer period of continuous preparedness incurs a higher cost of maintaining gonads between two consecutive breeding periods. Similarly, the fitness benefit of staying prepared and starting reproduction quickly after the onset of the good period is higher when the good period is shorter, because in this case only individuals with high levels of preparedness can successfully complete a reproductive attempt. These relationships should also depend on the food availability during the unfavorable period: if food availability is low then staying prepared is more costly; accordingly, most temperate zone birds regress their gonads completely during winter, e.g. there is a 200-fold decrease in gonad size in starlings *Sturnus vulgaris* (Murton and Westwood 1978; Dawson and Sharp 2007), whereas gonads are maintained at a relatively high level in some tropical species (Bosque et al. 2004; but see Wikelski et al. 2003 for contrasting patterns of gonad regulation in tropical birds).

Past theoretical studies of evolution in stochastic environments mainly focussed on life history adaptations such as reproductive investment (e.g. Schaffer 1974; Schultz 1991), and the evolution of risk-spreading (bet-hedging) strategies (e.g. Cohen 1966; Philippi 1993; McNamara 1995). Studies of bet-hedging provided comprehensive analyses of several timing problems, such as the timing of germination in desert plants (e.g. Philippi 1993), the use of diapause in insects (e.g. McNamara 1994), or timing of maturation (e.g. Tuljapurkar and Wiener 2000). However, much less is known about the importance of unpredictability for the optimal timing of life history events when sequential decisions are made in complex environments.

Our aim in this paper is to develop an optimal annual routine model to investigate the timing of reproduction in unpredictable environments when breeding requires lengthy physiological preparation. Using this approach, we extend the framework of annual routine models developed to analyse optimal behavior in seasonal environments (Houston and McNamara 1999; McNamara et al. 2004; Barta et al. 2006, 2008) by including year-to-year variation. We assume that the animal knows the current level of food availability but has incomplete knowledge about future conditions. First, we explore the regulation of reproductive organs and timing of reproduction in environments differing in the length and predictability of bad and good periods, assuming that these periods can occur at any time of the year and food availability is aseasonal. Second, by acknowledging that unpredictable environments may have a seasonal pattern of food availability (e.g. because of seasonal variation in temperature), we also explore cases where mean food availability changes during the course of the year and there are fluctuations around the mean. Because a large proportion of tropical and near-tropical ecosystems show considerable variation in environmental conditions (Wingfield et al. 1992; Hau 2001; Shine and Brown 2008), this approach is necessary to understand the reproductive behavior of animals inhabiting environments with lower seasonality.

The model

The behavior of the modelled organisms is followed over an annual cycle divided into $T = 52$ decision epochs (i.e. $t = 0, 1, 2, \ldots, T$ weeks). Time 0 is the first week of the year, time T is exactly 1 year later and is also time 0 of the next year. An animal is characterized by four state variables: development status of reproductive organs o ($0 \leq o \leq o_{\max}$), brood age a ($0 \leq a \leq a_{\max}$), experience e ($0 \leq e \leq e_{\max}$) and food level f. At the start of each week, the bird simultaneously modulates the size of reproductive organs (*increase, decrease* or *maintain* gonad size) and chooses a breeding option: *subsist* (do not start a brood, or desert brood if there is one), *start* a brood or *care* for the young. The bird has to balance its energy expenditure with its energetic gain over a week (McNamara et al. 2008, also see below).

The environment

All aspects of the environment except food are constant over time. Food availability varies over the course of the year, its variation being determined by two sources. First, the mean amount of food, $g(t)$, changes seasonally over the year according to the equation:

$$g(t) = A + \epsilon\left[1 + \sin\left(\pi\frac{t-13}{26}\right)\right]. \tag{1}$$

Here A controls the overall amount of food in the environment and ϵ sets the degree of seasonality; larger values of ϵ determine higher seasonality, that is, the difference between winter and summer food availability is higher.

Second, the actual amount of food, $g_F(t)$, fluctuates around the mean, $g(t)$. We consider two possibilities: food availability can be either high ($F = G$) during good periods or low ($F = B$) during bad periods. If food availability is high then the actual amount of food available for an individual is $g_G(t) = g(t) + \delta, 0 \leq \delta < A - \epsilon$. If food availability is low, the amount available is $g_B(t) = g(t) - \delta$. Hence δ gives the amplitude of fluctuations in the environment. The parameter A is adjusted until the population growth rate is 1, thus we assume that the per capita amount of food available is density dependent (for details see McNamara et al. 2008).

Transitions from bad to good food and vice versa can happen all year round with the following restriction. After a transition (e.g. from bad to good) the food must stay at its current level (e.g. at good) for a given amount of time (the minimum duration of the period, D_F, $F = B$, G) before it can switch back (e.g. to bad). After the minimum length of time has elapsed the transition occurs with a given probability per week which causes uncertainty about when the period of a given food condition actually ends. By changing the probability of the transition the average length and variability of the duration of a given food condition can be controlled; low probability results in long mean duration with high variance, while high transition probability means short average length with low variance in the duration of a given condition (for details see Appendix A in Electronic Supplementary Material).

The minimum duration of the period, D_F, captures the consistency of a given environmental condition. Low D_F corresponds to a situation with low consistency, like in the Arctic where a sudden snowstorm can instantaneously terminate a favourable period which has just started. Apart from these extremes climatic conditions often show a higher degree of consistency; for example rainfall may cause vegetation growth and this can predictably provide good living conditions for a considerable period of time after the rain. This can be modelled by long D_F.

To increase tractability we consider only a low ($D_F = 1$ week) and a high ($D_F = 11$ weeks) consistency situation in most cases investigated. In both situations the probability governing the transition at the end of the minimum period is set in such a way that the average duration of a given food condition is the same ($\sim$20 weeks) in both situations. If $D_F = 11$, i.e. the consistency is high, the individuals have enough time to perform at least one breeding attempt (see below). Given these two situations we consider four environments: (1) both good and bad periods are characterized by low consistency ($D_B = 1$, $D_G = 1$), (2) both good and bad periods are characterized by high consistency ($D_B = 11$, $D_G = 11$), (3) low consistency bad periods alternate with high consistency good periods ($D_B = 1$, $D_G = 11$), and vice versa (4) high consistency bad periods alternate with low consistency good periods ($D_B = 11$, $D_G = 1$).

Behavior and state dynamics

Gonad size

The state variable o ($0 \leq o \leq o_{\max}$), gives the developmental status of the reproductive organs. The animal can only start a brood if $o = o_{\max}$ but reproductive organs can be regressed after that (i.e. care of brood is possible with $o < o_{\max}$). Let the animal's reproductive organ be in status o_t at the beginning of week t. The animal can either *increase* the size of its gonads, $o_{t+1} = o_t + 1$, if $o_t < o_{\max}$, *decrease* it, $o_{t+1} = o_t - 1$, if $o_t > 0$, or *maintain* it in the same status, $o_{t+1} = o_t$. Having the organ in status o costs $\Delta(o) = c_o o$ amount of energy (maintenance cost) per week, where c_o is a parameter of the model (Table 1).

Reproduction

If an animal does not have a brood at the beginning of week t ($a_t = 0$) and it has fully developed gonads ($o_t = o_{\max}$) it can start breeding, $a_{t+1} = 1$, or subsist ($a_{t+1} = 0$). If the animal has a brood at the beginning of week t ($1 \leq a_t < a_{\max}$), it can either continue to care for the brood, $a_{t+1} = a_t + 1$ or desert it ($a_{t+1} = 0$). If the parent dies between t and $t + 1$, the brood also dies. If the brood reaches the maximum age, $a_t = a_{\max}$, the parent abandons the young at the beginning of week t, and the brood becomes independent ($a_{t+1} = 0$). We assume that the newly fledged young have zero experience (see below), the status of their reproductive organs is zero, and they experience the same environmental conditions as their parents at the time of abandonment.

For simplicity, we assume that brood size is fixed, which is a reasonable assumption for several avian taxa with invariant clutch sizes, such as shorebirds (Charadroidea and Scolopacoidea; del Hoyo et al. 1996–1997) or the pigeons and doves (Columbidae; del Hoyo et al. 1996–1997).

Experience

Foraging efficiency increases with experience (e); newly fledged animals have $e = 0$. Experience tends to increase with age towards its maximum value ($e_{\max}$); if a bird has experience e at the start of week t, it is still e at $t + 1$ with probability $1 - p_e$, and is

$$e' = \min(e_{\max}, e + 1) \tag{2}$$

at $t + 1$ with probability p_e.

The actual energetic intake rate of the bird will depend on its experience, thus:

$$\gamma_F(e, t) = g_F(t)\theta^{e_{\max} - e}. \tag{3}$$

The parameter determining the foraging efficiency of the young, θ, has a value between 0 and 1, thus we assume that juveniles with less experience ($e < e_{\max}$) are less efficient foragers than adults, and that energy intake increases with experience.

Energy balance

For simplicity, we assume that the bird's weekly intake must cover its weekly energy expenditure (for details, see McNamara et al. 2008). If the proportion of time spent foraging during that week is u, then u must satisfy the balance equation

$$\gamma_F(e, t)u = C + c_f u. \tag{4}$$

Here, the left hand side denotes the energy intake of a bird during a whole week and the right-hand side denotes energy expenditure. The parameter c_f determines how energy expenditure of foraging scales with the proportion of time spent foraging. C is the metabolic cost associated with gonad size and breeding; for a subsisting individual, this is just

$$C = c_b + c_o o, \tag{5}$$

where c_b is the basal metabolic expenditure, while c_o gives how energetic expenditure scales with reproductive organ size.

Starting a brood or caring for young has an additional metabolic cost of c_{start} and γ_b, respectively, therefore C is incremented by c_{start} or γ_b for birds deciding to start a brood or continue to care for an existing brood.

Sources of mortality

The bird can die because of predation or starvation. Predation hazard depends on the proportion of time spent foraging; the more time a bird spends foraging, the more exposed it is and the less time it has to watch out for predators. Moreover, if there are times of the day when foraging is more risky (in terms of predation hazard), a bird that forages for only a small part of the day can avoid the more risky periods, whereas a bird that forages for the whole day cannot. To capture this accelerating effect of foraging activity on predation hazard, the probability of mortality per week which is unrelated to starvation is determined as a quadratic function of u:

$$M(u) = p_b + p_m u^2. \tag{6}$$

Here, p_b is the background mortality, which is unaffected by the state of the animal or its behavior, and p_m is the mortality parameter associated with the time spent foraging.

Starvation occurs if the bird cannot balance its weekly energy expenditure; i.e. it needs to forage for more time than is available. We assume that u is the proportion of an average week that is required for foraging. However, because of variation in environmental conditions the bird sometimes has less and sometime has more time available than average. To represent this, the probability of starvation is taken to be

$$S(u) = 1 - 1/(1 + u^L). \tag{7}$$

Here, L is a large value (200 in the present model), so that the probability of starvation increases sharply from 0 to 1 around $u = 1$ (cf. McNamara et al. 2008).

Determination of the optimal strategy and the expected behavior

The optimal strategy is a rule that specifies the dependence of the actions taken on the state variables and time of year. This strategy maximises asymptotic growth rate of numbers of descendants and is calculated by dynamic programming, working backwards from the future and iterating to convergence (McNamara 1991; Houston and McNamara 1999). Details of this procedure are described in Appendix B in ESM.

To obtain the realized behavior of birds we first calculated the steady state distribution of a large population of individuals following the optimal strategy. To do so, we follow the population forwards in time, at each time t calculating the distribution over states at time $t + 1$ in terms of the distribution at time t. The process is continued for several years until the state distribution settles down (Houston and McNamara 1999).

After the state distribution has been calculated, we use Monte Carlo simulations to study the realized behavior of the modelled birds. The initial state distribution of the birds in the simulation is the steady state distribution derived from the forward runs at week 0. When the birds reproduce, the offspring are entered into the population as new individuals, whereas birds that have died are removed. However, only data from adult birds (i.e. birds with $e = e_{\max}$) were used to quantify reproductive readiness.

Results

Aseasonal environments

To explore the effect of year-round unpredictability on the reproductive behavior of birds we performed a series of runs in environments where variation in environmental conditions is determined solely by fluctuations in food availability (i.e. there are no regular seasonal changes in food availability; $\epsilon = 0$). In these aseasonal environments there is no distinct breeding season; reproduction occurs continuously throughout the year (for $\delta = 0$) or breeding follows the fluctuations in food availability (for $\delta > 0$), independent of the time of year. We first investigated how the size of reproductive organs changes with the environmental conditions by plotting mean gonad size over favorable periods of a fixed length of 20 weeks followed by an unfavorable period of the same length (which is the average length of both periods). A summary of the key predictions of the model is given in Table 2.

The investigation of the actual trajectories of gonad size over time reveals the following patterns (Fig. 1). When the length of the good period is highly consistent birds have enough time to complete a breeding attempt during each good period ($a_{\max} < D_G$). To be able to exploit this possibility, however, they have to be prepared at the beginning of the good period. Therefore, reproductive readiness is high during the bad period (Fig. 1a, b) except when there is no chance that the good period starts next week (i.e. during the first part of a highly consistent bad period; Fig. 1a). The level of environmental fluctuations, δ, influences the birds' behavior during the good periods. When the level of fluctuations is low ($\delta \leq 0.25$) birds breed only once per good period and then keep their reproductive organs deactivated. In contrast, when the level of fluctuations is high, birds keep breeding, and hence maintain large gonads, over all of the good period. This is a consequence of density dependence, which leads to lower survival rate in juveniles when environmental

Table 1 The model's parameters and their baseline values

Parameter	Symbol	Value
Probability of changing experience class	p_e	0.025
Parameter determining the foraging efficiency of inexperienced birds	θ	0.7
Basal metabolic expenditure	c_b	0.15
Metabolic cost of foraging	c_f	0.3
The metabolic cost associated with the reproductive organs	c_o	0.01
The metabolic cost of starting a brood	c_{start}	0.9
Gross intake needed to provide nestling	γ_b	0.9
Background mortality	p_b	0.0005
Mortality parameter associated with time spent foraging	p_m	0.005
Maximum organ size	$o_{\max}$	5
Maximum experience	$e_{\max}$	2
Maximum brood age	$a_{\max}$	7
Brood size	n_{brood}	1
Minimum length of the good period	D_G	
Minimum length of the bad period	D_B	

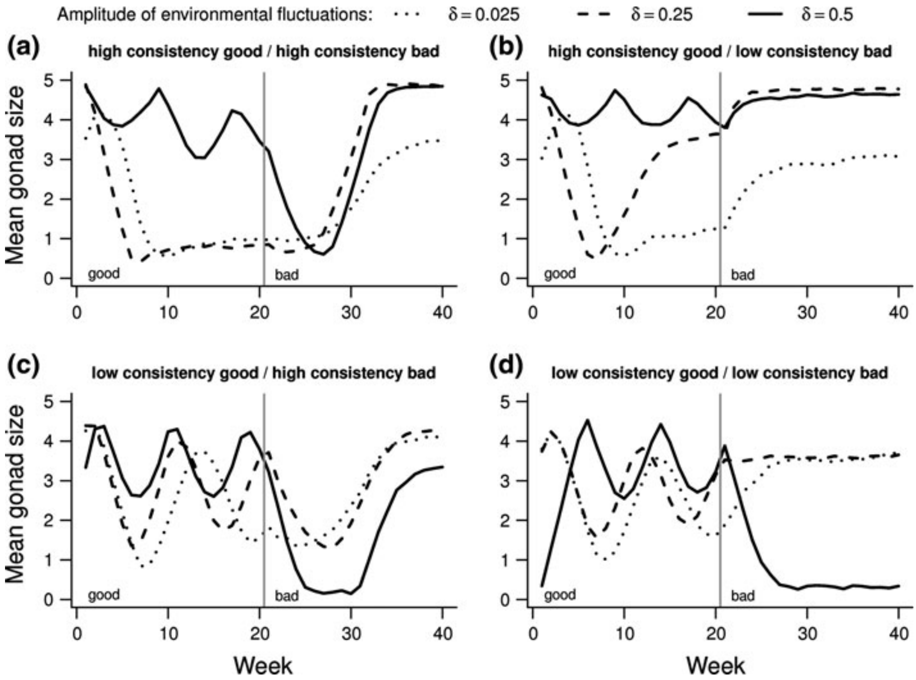


Fig. 1 Changes in mean gonad size in aseasonal environments ($\epsilon = 0$) during a simulated period consisting of a 20-week good period followed by a 20-week bad period in the four environments differing in the consistency of the bad and good periods, at increasing amplitudes of environmental fluctuations (δ). The *vertical grey line* demarcates the transition from high to low food availability. All other parameters are set to their baseline values (see Table 1)

fluctuations are large. This, in turn, selects for increased reproductive investment in the adults (see Appendix C in ESM).

When the consistency of the good periods is low, birds cannot successfully breed in each good period. To compensate for this loss of breeding opportunity, they have to use all the available time suitable for breeding, i.e. they have to keep their gonads ready for breeding during the whole good period, independently of δ (Fig. 1c, d). During the bad periods the birds behave similarly to the cases where the consistency of good periods is high, i.e. they are prepared for breeding when there is a chance that the good period will start next week. There is, however, one exception; birds keep their gonads regressed over the bad period when both the good and bad periods are characterized by low consistency and the level of environmental fluctuations is high (Fig. 1d). Under this condition the advantage of being prepared during the bad period is lowered because of the high uncertainty in the length of the good period. Furthermore, the cost of keeping gonads activated is also high because of the relatively low level of food during bad periods caused by density dependence and the large difference between bad and good periods (cf. McNamara et al. 2008). This cost is lower for the case when the bad period is highly consistent (Fig. 1c) because the period during which birds should be prepared (i.e. when good period can start) is shorter on average in this case.

To see the effect of environmental consistency in more detail, the minimum length of both the good and the bad period was gradually increased from 1 to 11 weeks, while holding the minimum length of the other period constant, thereby creating environments

Table 2 The effect of changing key parameters on the optimal behavior-main predictions of the model

Parameter	Predictions
Aseasonal environments	
Consistency of good periods (D_G)	Reproductive readiness during bad periods is high when D_G is long enough to finish a brood
	Brood desertion is frequent when D_G is small
Consistency of bad periods (D_B)	If D_B is large, gonads can be regressed between successive good periods
Amplitude of environmental fluctuations (δ)	If δ is large, the number of brood attempts per good period increases; gonads size is large throughout good periods
	Reproductive readiness during bad periods decreases with increasing δ
Metabolic cost of gonads (c_o)	Reproductive readiness during bad periods decreases with increasing c_o
Maximum gonad size ($o_{\max}$)	Gonad recrudescence starts earlier and reproductive readiness is higher on average during bad periods when $o_{\max}$ is larger
Background mortality (p_b)	Higher levels of reproductive readiness when p_b is high
Seasonal environments	
Amplitude of environmental fluctuations (δ)	Gonads are activated for a longer period when δ is high
Background mortality (p_b)	Length of breeding season increases with p_b

with intermediate levels of consistency (Fig. 2). The pattern of reproductive readiness in these environments is consistent with the previous conclusions: gonads are fully developed during periods of low food availability when good periods last long enough for birds to complete a brood with high probability (Fig. 2). The largest effect of changing the consistency of either the good or the bad period on the optimal level of reproductive readiness is observed when the minimal length of the other period is small (Fig. 2).

Seasonal environments

To investigate the effect of environmental fluctuations when food availability also has a seasonal trend, we computed the optimal behavior in environments with seasonality ranging from $\epsilon = 0.05$ to $\epsilon = 0.5$ and fluctuations in food availability with a magnitude ranging from $\delta = 0.025$ to $\delta = 0.25$ (i.e. for each value of ϵ, δ was increased from 0.025 to 0.25). We chose this range of parameters so that the difference between the highest food availability in summer and the lowest amount in winter is not very large, because a large difference would result in very high winter mortality rates and an average life span of less than 1 year. With the chosen parameters, the largest difference between summer maximum and winter minimum is $2\epsilon + 2\delta = 1.5$, which is of a magnitude similar to previous annual routine models (Barta et al. 2006, 2008; McNamara et al. 2008).

In contrast to the aseasonal environments where reproduction can occur at any time of the year, the breeding and nonbreeding seasons in seasonal environments are segregated. This entrainment occurs at all values of ϵ, i.e. even at very low seasonality ($\epsilon = 0.05$). The breeding season is short and gonad regulation shows a seasonal pattern where reproductive organs are increased during the middle of the year but regressed at other times (Fig. 3a). Broods are initiated only during good periods that start around the middle of the year; however, if environmental conditions remain unfavorable during this period the birds skip breeding. As a result, the average number of brood fledged per year in these environments is low (Appendix C in ESM).

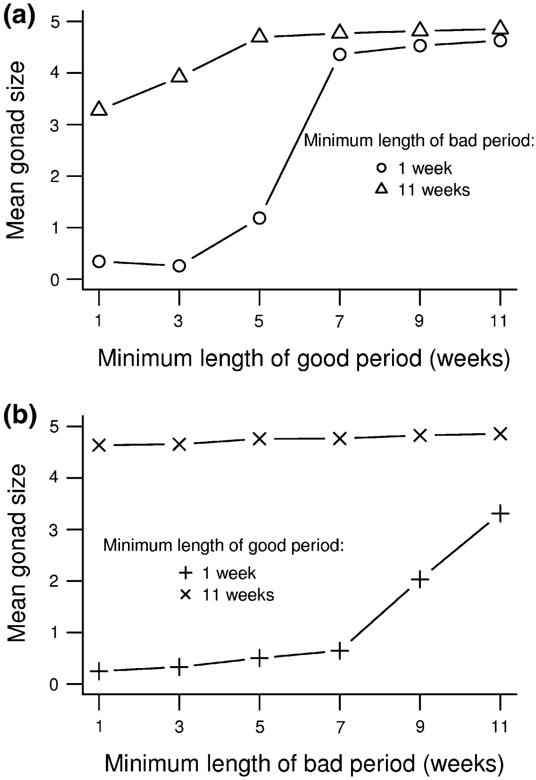


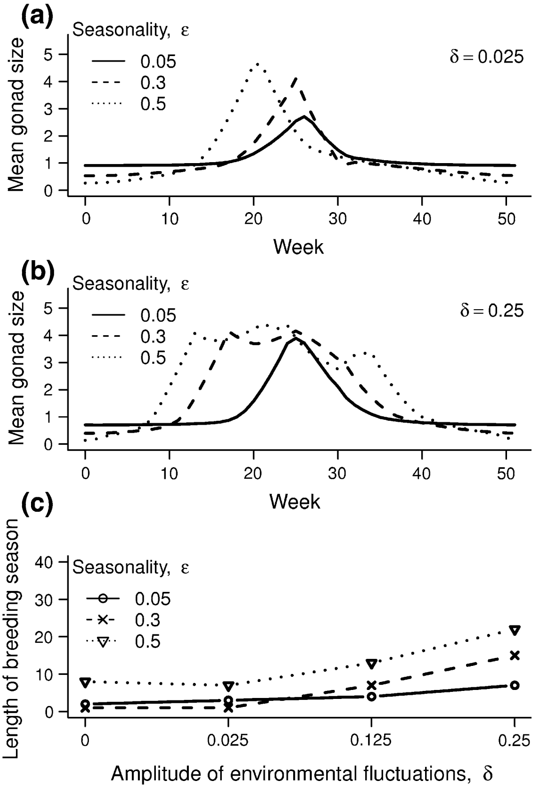
Fig. 2 The effect of transforming either the good (**a**) or the bad period (**b**) from low to high consistency at high levels of environmental fluctuations ($\delta = 0.5$) on reproductive readiness. In the first case (**a**), the minimum length of the bad period was held fixed (either at 1 or 11 weeks) while increasing the length of the good period from 1 to 11 weeks. In the second case (**b**) the same was done with the role of the bad and good periods reversed. The effect of the different environmental conditions on the reproductive readiness of birds was evaluated by calculating the mean gonad size at the end of a 20 week bad period

In seasonal environments where the amplitude of environmental fluctuations (δ) is larger, gonads are kept activated for a longer time (Fig. 3b) and the breeding season lasts longer (Fig. 3c). This is explained by the fact that when the fluctuations are high, winter mortality also increases causing less intense competition for food during the summer. The consistency of environmental conditions has only a minor effect on the modulation of reproductive organs (results not shown), because the birds initiate reproduction after unpredictable surges in food availability that occur during the middle of the year even if the length of these favorable periods is highly unpredictable.

The effects of background mortality

In the results presented above the annual survival rate is relatively high (around 0.9 when $\delta > 0$; Appendix C in ESM). To investigate gonad regulation in short-lived birds, we increased the background mortality from $p_b = 0.0001$ to $p_b = 0.01$. For $p_b = 0.01$ annual survival rate is around 0.55; because survival is uncertain, the reproductive value of current breeding attempts increases and the optimal behavior differs in several aspects from the baseline case. In aseasonal environments short-lived birds in general show higher levels of reproductive readiness. This difference is most pronounced when the consistency of both the good and bad periods is low; here long-lived birds maintain low or intermediate levels of preparedness, but for $p_b > 0.0001$ birds maintain their gonads close to the maximal size (Fig. 4). In seasonal environments the main effect of the increased background mortality is that the breeding season becomes longer because the birds try to breed even when food

Fig. 3 Gonad regulation during the annual cycle and length of the breeding season in seasonal environments with different levels of environmental fluctuations in high consistency good / high consistency bad environments. In these seasonal environments, breeding occurs only in the middle of the year and gonads are upregulated only during this period (**a**). Gonads are maintained in a high development state for longer when there are environmental fluctuations (**b**, $\delta = 0.25$ in this case). The length of the breeding season (defined as the number of weeks in which at least 0.1% of the population initiates a brood) increases with the amplitude of the fluctuations (**c**). The behavior of the birds is similar in the other three environments (i.e. high consistency good / low consistency bad, low consistency good / high consistency bad and low consistency good / low consistency bad)



availability is lower. When seasonality is low ($\epsilon = 0.05$), background mortality is high ($p_b = 0.01$) and there are large fluctuations in food availaibility ($\delta = 0.25$), the birds breed almost year-round (Fig. 5c).

Sensitivity analyses

To see how the cost of maintaining reproductive readiness (c_o) or the time required to become fully prepared ($o_{\max}$) affects the patterns of gonad regulation, we made a series of runs where the values of these parameters were altered (Appendix D in ESM). The results from these analyses indicate that the effect of environmental variability is similar under a wide range of parameter values; however, mean reproductive readiness during bad periods decreases when the metabolic cost associated with the gonads is higher or the time required to become fully prepared is shorter (Appendix D in ESM).

Discussion

Life history models originally focussed on annual decisions, often taking the only state of an organism to be its age or its size. However, many life history trade-offs are mediated by physiological state variables that vary on a variety of timescales (McNamara and Houston 1996, 2008; Zera and Harshman 2001; Harshman and Zera 2007). These variables include

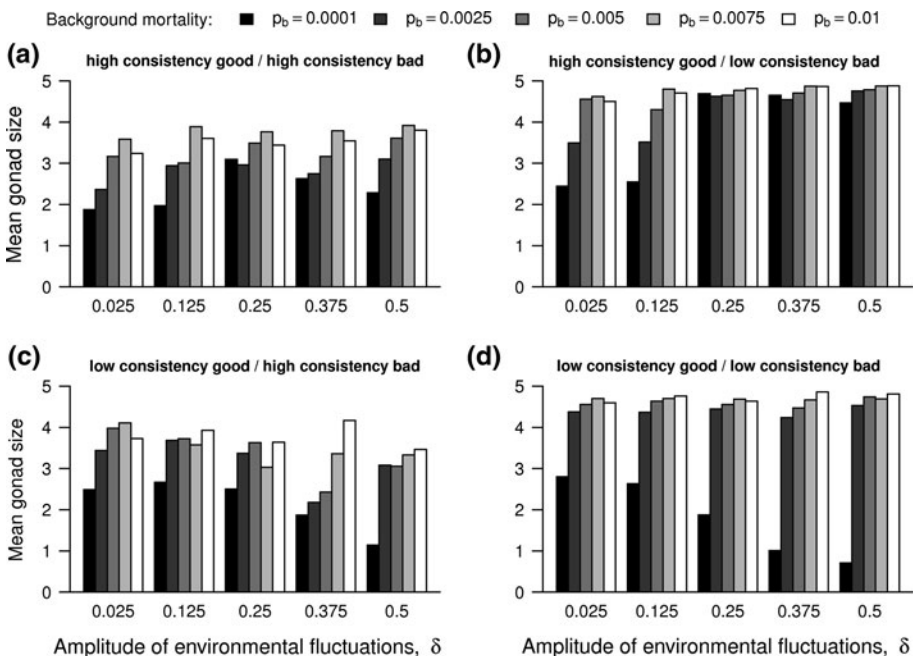


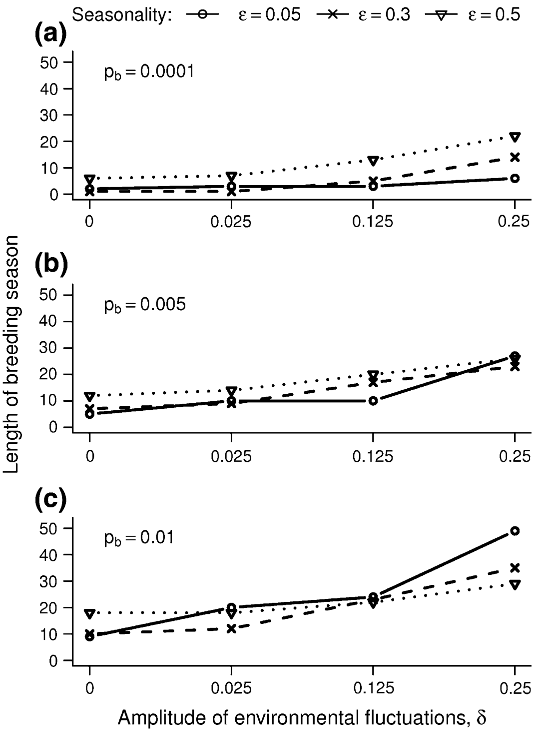
Fig. 4 The effect of background mortality rate on the optimal level of reproductive readiness (mean gonad size during bad periods) in aseasonal environments ($\epsilon = 0$). Mean gonad size was calculated for all adult birds, irrespective of the time elapsed since the end of the last good period, thus the presented values reflect the average level of preparedness of the population during bad periods

energy reserves, parasite load, hormone levels, feather condition and oxidative damage. Such variables are not easily taken into account in models based on annual decisions. To capture the appropriate physiology, models which consider a sequence of decisions over the course of a year are needed. Recent models (e.g. Houston and McNamara 1999; Barta et al. 2006, 2008; McNamara et al. 2008) have incorporated such detail. The models explicitly take seasonality into account, but assume that all years are the same. Here for the first time we have built a model that includes year-to-year variation as well as seasonality. Our model involves decisions about both reproductive behavior and the associated reproductive physiology. This combination of physiology and behavior in a complex environment is a crucial feature of realistic life history models.

An important aspect of our model is that it is not possible to change physiology (gonad size) instantaneously. As a result there is a tension between maintaining the gonads in readiness and saving energy by reducing gonad size after reproduction. Distinct life-history stages emerge from the optimal response to this tension. Thus in addition to unifying physiology, behavior and ecology, our framework provides a formal derivation of life-history stages as envisaged by Jacobs and Wingfield (2000) and Wingfield (2008).

In our model, all individuals are subject to the same year-to-year variation. The population is also structured. Thus the correct fitness measure is the dominant Lyapunov exponent of the appropriate projection matrix (Metz et al. 1992). Finding an optimal strategy in our setting is extremely complex (cf. McNamara 1997). Fortunately, when fluctuations primarily affect reproductive success and organisms are long lived, it is reasonable to approximate fitness by the mean growth in descendant numbers (Haccou and

Fig. 5 The length of the breeding season in seasonal environments with fluctuations in food availability under three different background mortality rates: low ($p_b = 0.0001$, **a** medium ($p_b = 0.005$, **b** and high ($p_b = 0.01$, **c** background mortality. The length of the breeding season was measured as the number of weeks in which at least 0.1% of the population initiates a brood



McNamara 1998). Optimal strategies then can be found using dynamic programming (McNamara and Houston 1996, 2008; Houston and McNamara 1999), as we have done here.

A key result emerging from this model is that, despite the uniform distribution of favorable and unfavorable periods during the course of the year, opportunistic breeding schedules and the regulation of reproductive organs in unpredictable environments may be strikingly different depending on several factors, such as: (1) the length of the favorable period—if the good period is long enough to finish a brood with high probability, birds will maintain their gonads in a more developed state even if this is costly; (2) the amplitude of environmental fluctuations—when fluctuations are small, there is relatively more food during bad periods and maintaining high readiness is less costly; (3) longevity—short-lived birds invest more into current reproductive attempts and generally show higher levels of reproductive readiness than long-lived birds; (4) the time required to reach fully developed gonads—the less time is required to reach full preparation, the lower the reproductive readiness is, because birds can respond more quickly to changes in the environment.

One strategy that opportunist breeders were thought to employ to cope with temporal variability in food resources was to maintain the reproductive system only partially regressed during the whole year, thereby minimizing the time required to fully activate the gonads (Immelmann 1973; Morton 2009). This conclusion is largely based on observation of Australian desert birds that may start reproductive activities (courtship and nest building) within hours after a heavy rainfall (Immelmann 1973; Hahn et al. 2008; Morton 2009), suggesting that the reproductive system of these birds could be activated within very short time. Although reports of such extremely flexible breeding may not be representative

(Zann et al. 1995; Hahn et al. 2008), inspection of the gonads of birds known to breed year-round showed that a partially activated reproductive system does occur in some species (Astheimer and Buttemer 1999; Perfito et al. 2007). However, not all opportunistic breeders maintain the reproductive system activated year-round: red crossbills (*Loxia curvirostra*) and white-winged crossbills (*L. leucoptera*), which also have a very flexible breeding schedule regress their gonads and have low levels of circulating reproductive hormones during parts of the year when molting occurs (Hahn 1998; Deviche and Sharp 2001). Small ground-finches (*Geospiza fuliginosa*) that breed after unpredictable rainfalls in the Galápagos archipelago also regress their gonads entirely between two favorable periods (Hau et al. 2004). Thus, while breeding in temporally unpredictable environments has only been investigated in detail in a few cases, even these show interspecific differences in the regulation of the reproductive system.

Our results suggest that maintaining the gonads in a partially developed state during periods with high food availability is indeed an optimal strategy under some conditions, but not in others. Thus, we found that gonads are maintained at an intermediate level when the amplitude of environmental fluctuations is not large. By contrast, optimal reproductive readiness in environments with high levels of environmental fluctuations is much more variable, with both completely regressed and fully developed gonads observed in environments differing in the consistency of the bad and good periods. Higher levels of environmental fluctuations result in more food being available during favorable periods, resulting in high reproductive success. Because food is density dependent, competition for food increases if the number of young produced or their survival rate is higher. All else being equal, this will result in a decrease in food availability, ultimately leading to lower levels of reproductive readiness during bad periods. Such effects of the amplitude of environmental fluctuations may explain why some species can maintain relatively large gonads during unfavorable periods, whereas others regress their gonads completely.

The optimal gonad size during bad periods also depends on the reproductive advantage of staying prepared and starting a brood as soon as possible after the onset of a good period. Thus, when favorable periods are expected to last long enough to complete a breeding attempt with high probability, high levels of preparedness may be optimal even during periods of low food availability. In contrast, when breeding attempts may be terminated by unpredictable reversals to bad food conditions, the birds use a different strategy, namely, they only start increasing their gonads when a favorable period has begun, and breeding attempts are finished only if the favorable conditions last long enough. Such high uncertainty in the outcome of breeding attempts has been observed for example in king penguins (*Aptenodytes patagonicus*) that try to breed a second time after a successful breeding attempt, despite the fact that fledging rate of chicks born later is extremely low (Brodin et al. 1998). Unpredictable surges in food availability during chick provisioning, coupled with a relatively low cost of reproduction could explain why penguins frequently start broods despite such high failure rates (Brodin et al. 1998). Taken together, variation in the length of the favorable period could have a strong impact on optimal breeding schedules in unpredictable environments and quantifying breeding failures could be helpful in understanding reproductive decisions of birds inhabiting these environments.

In some environments, unpredictable variation in food supply may not be uniform during the course of the year. For example, even if food availability depends largely on rainfall, a winter rain may not yield as much food as a summer rain, if there is seasonality in temperature. In the zebra finch breeding may occur at virtually any time of the year in the arid interior of Australia (Zann et al. 1995; Perfito et al. 2007), where rainfall is unpredictable and seasonality in temperature is relatively small. However, breeding is more synchronized, and is much less likely to occur during the winter at a site in southern Australia, where temperature seasonality is higher (Perfito et al. 2007). While precipitation is also more predictable at this second site, the difference in the predictability of breeding was much larger than differences in rainfall patterns (Perfito et al. 2007). Our model predicts that, when food conditions are unpredictable but actual food availability depends on time of year, birds start reproducing during unpredictable surges in food only if these occur at a specific time of year (during the period with the highest long-term average food). This effect may occur even if annual variation in food availability is small compared to the degree of fluctuations, especially in long-lived birds as it is particularly important for such birds to avoid breeding at suboptimal times (McNamara et al. 2004). As a result, seasonal patterns in reproductive behavior may be observed even in highly variable environments with continuous, marked fluctuations in food availability, provided there are small but consistent differences in food availability between different parts of the year. This entrainment of breeding irrespective of the degree of environmental fluctuations may explain why so many tropical and subtropical species show seasonality in reproduction, even though the amplitude of seasonal changes is believed to be small and their year-to-year predictability is low (Moreau 1950; Murton and Westwood 1978; Hau 2001; Wikelski et al. 2003). Our model also predicts that birds do not initiate reproduction when environmental conditions during the long-term seasonal maximum are unfavorable. Thus, reproductive behavior in seasonal environments with unpredictable variation in food availability differs from seasonal environments with no variability in that there is a relatively high frequency of reproductive year-skipping.

In conclusion, the optimal pattern of breeding and gonad state in unpredictable environments appear to depend on several aspects of the environment, such as the amplitude of environmental fluctuations, the consistency of environmental conditions and whether there are any differences in food availability at different times of the year. Moreover, there are considerable differences in the reproductive behavior of long-lived and short-lived birds, which is reflected in the patterns of gonad regulation and reproductive readiness. Taking these factors into account may be necessary to obtain a fuller understanding of the breeding behavior of birds living in variable environments. Lastly, although our model was developed with birds in mind, where gonad regulation is a prolonged process, the effect of various environmental factors proved to be important even when maximum gonad size was lower and consequently the time required for preparation was shorter. Thus, our conclusions should apply to other organisms living in unpredictable environments if their reproduction requires physiological preparation, even if the transitions in reproductive condition occur more rapidly.

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