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Phenology of two interdependent traits in migratory birds in response to climate change

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In migratory birds, arrival date and hatching date are two key phenological markers that have responded to global warming. A body of knowledge exists relating these traits to evolutionary pressures. In this study, we formalize this knowledge into general mathematical assumptions, and use them in an ecoevolutionary model. In contrast to previous models, this study novelty accounts for both traits—arrival date and hatching date—and the interdependence between them, revealing when one, the other or both will respond to climate. For all models sharing the assumptions, the following phenological responses will occur. First, if the nestling-prey peak is late enough, hatching is synchronous with, and arrival date evolves independently of, prey phenology. Second, when resource availability constrains the length of the pre-laying period, hatching is adaptively asynchronous with prey phenology. Predictions for both traits compare well with empirical observations. In response to advancing prey phenology, arrival date may advance, remain unchanged, or even become delayed; the latter occurring when egg-laying resources are only available relatively late in the season. The model shows that asynchronous hatching and unresponsive arrival date are not sufficient evidence that phenological adaptation is constrained. The work provides a framework for exploring microevolution of interdependent phenological traits.

1. Introduction

Climate change has caused an advance in phenology in many species [1]. In migratory birds, the effect of warming is thought to flow up the trophic levels: warmer temperatures lead to earlier plant phenology (e.g. budding) [2], which leads to earlier peaks in the abundance of insect larvae, for example, which are an important food source for raising nestlings [3]. This advance in prey phenology puts pressure upon birds to advance their own breeding phenology [4].

Migratory birds have responded to warmer weather by both arriving earlier [5,6] and laying earlier [7,8]; however, generalization is difficult. First, synchrony with the food peak is the result of two separate variables that are under (at least partial) behavioural control: the time of arrival to the breeding site after migration, and the delay between arrival and the start of breeding. It is possible for one to respond and not the other; for example, Dutch pied flycatchers (*Ficedula hypoleuca*) have advanced their laying date but not arrival date, and Finnish pied flycatchers have advanced arrival but not laying [9]. This raises the question: under what circumstances will birds respond by advancing one trait or the other, or both?

Second, some migratory bird populations have not kept pace with their prey's phenology, leading to asynchrony between hatching date and nestling food that has been implicated in population declines [4]. It is typically assumed that pressure to lay earlier will translate into pressure to arrive earlier, and so a 'mismatch' between hatching date and nestling food is ultimately attributed to inflexibility in the arrival date owing to factors constraining the rate of adaptation [10] (e.g. migratory cues [11], conditions en route [12], conditions in other parts of the year [13,14]). However, there is a growing literature showing that asynchrony

may be adaptive in certain circumstances [15–18], and so disentangling when asynchrony is to be expected from when it is not is the first step towards understanding phenological responses to climate.

In this paper, we go beyond previous work on a single phenological trait [16,17,19] to investigate the interdependent responses of both arrival date and hatching date. We ask, given the current state of knowledge about the relationships between phenology and fitness, when do we expect one or both of these traits to respond to an advancing food peak, and in what way? We use the adaptive dynamics framework [20]; however, our purely adaptationist approach is not to assert that phenological response is free of genetic constraint [21] or able to adapt fast enough, nor that idiosyncratic population-specific extrinsic forces might not constrain adaptation [10].

Furthermore, mechanisms such as individual plasticity [18] or carryover effects of changing natal conditions [22], to name only two, can produce patterns similar to microevolutionary mechanisms that compare well with observations. Rather, we are interested in taking generally applicable selective mechanisms to their logical conclusion, and asking, if we could focus upon the microevolutionary responses alone, what would we expect to see? The evolutionary endpoints we identify generate alternative hypotheses for the wide variety of historical scenarios and climate responses observed.

2. Model and methods

We both investigate a general model analytically (§2a) and investigate a fully specified model (§3b). We introduce the fully specified model, first, to provide a concrete example of the general model and its numerical implementation, and second, in order to demonstrate some of the more counterintuitive predictions made by the general model that may not be immediately apparent from the analytical treatment alone.

(a) General model

The breeding-season timeline of a migratory bird is described as follows. The bird arrives on the breeding grounds at date y'. It then spends a period of time on the breeding grounds before laying its eggs, which we call the pre-laying period z'. After a period of incubation, which we take as a fixed parameter z_n, the egg hatches on date x'. Nestlings are then fledged, and the birds depart for the winter migration. Because $x' = y' + z' + z_n$, the phenological strategy can be summarized by the hatching and arrival dates (x', y') for an individual, and (x, y) for the population's prevailing strategy, and both influence the fitness of the individual.

The growth of a migratory bird population with n females may be modelled as

$$n_{t+1} = n_t s (a P_s P_e P_h P_r + P_s) \qquad (2.1)$$

where t is the year, a is the (female) clutch size, P_s is the probability of adult survival over the breeding period focusing upon processes at arrival and during the early breeding season, P_e is the probability of acquiring a nesting territory, P_h is the hatching success, P_r is the recruitment success, and s is the common portion of both adult and yearling survival for the rest of the year. Each of the fitness components P may take a value between 0 and 1, depending upon the values of the phenological traits. A migratory bird must therefore

time its arrival and laying as a compromise between the fitness components.

We use a female-only (or asexual) model, which is a common approach and simplifies the analysis (cf. [17,19]). It should be noted that this neglects any mechanisms particular to a sex or involving interactions between the sexes. For example, if pair-bonds persist over multiple years, then timing of arrival to coincide with mate arrival is more relevant than territory competition [23].

Through consideration of the biology of migratory birds like the *Ficedula* spp., and through review of the modelling literature, a set of minimal assumptions can be formulated to describe the consequences of the phenological trait values upon each of the fitness components (table 1).

Assumption 2.1. *The probability of early-season adult survival P_s increases with later arrival.* The main cost of early arrival is lowered survival owing to food scarcity and harsher weather conditions [25–27]. This is also supported by evidence that earlier arrivers have higher condition [25,28], the reasoning being that only individuals in good condition can survive the harsh early season.

Assumption 2.2. *The probability of early-season adult survival P_s is independent of the hatching date.* Hatching occurs after arrival and later in the season, so the hatching date necessarily has no effect upon early-season adult survival.

Assumption 2.3. *The probability of obtaining a nesting territory P_e decreases with later arrival.* The main benefit of early arrival, which is well established for many species, is that the earlier-arriving male has a higher probability of obtaining a quality territory and defending it, and of subsequently attracting a mate and producing a clutch [26,28,29]. Early arrival also benefits females in competition for males [30].

Assumption 2.4. *The probability of obtaining a nesting territory P_e decreases with increasing population size.* Migratory birds often (though not always) compete for a limited number of suitable nesting territories, such as cavity-nesting birds competing for nest holes [31]; therefore, territory acquisition is density-dependent and decreases with an increasing number of competitors for those sites.

Assumption 2.5. *The probability of obtaining a nesting territory P_e is independent of the hatching date.* Hatching occurs after the territory is acquired, so the hatching date necessarily has no effect upon territory acquisition.

Assumption 2.6. *The probability of obtaining a nesting territory P_e is a function of the focal individual's arrival time relative to its competitors and the number of such competitors.* Territory acquisition is a competitive process; therefore, early arrival is only beneficial relative to the arrival dates of one's competitors [17]. If all individuals have the same mean arrival date, then P_e is some function of how many nesting sites are available compared with how many individuals are competing for those sites. However, if an individual with a variant strategy (i.e. y') arrives earlier compared with the others (y) it will have the advantage in gaining a territory. Therefore, it is assumed that the probability of obtaining a nesting territory is a function of the difference between the variant arrival date and mean population arrival date, and the population

Table 1. Fitness components, common empirical generalizations about the relationship between components and bird breeding phenology (see text), and model assumptions reflecting those generalizations.

	empirical generalization	model assumption	examples from models
P_s	survival is lower with arrival earlier in season owing to harsh weather conditions	1. $\partial P_s/\partial y' \geq 0$	positive-sloped sigmoid [19]
	necessary consequence if no carryover effects	2. $\partial P_s/\partial x' = 0$	
P_e	an individual that arrives earlier than other birds has a greater probability of acquiring a territory	3. $\partial P_e/\partial y' \leq 0$	negative-sloped linear [17], negative-sloped sigmoid [19]
	birds compete for limited nesting territories	4. $\partial P_e/\partial n \leq 0$	[17,19]
	necessary consequence if no carryover effects	5. $\partial P_e/\partial x' = 0$	
	function of relative arrival time and number of competitors only, no seasonal effect	6. $P_e = f(y - y', n(x, y))$	[17,19]
P_h	a greater pre-laying period provides more time to acquire resources towards producing higher-quality eggs	7. $\partial P_h/\partial x' \geq 0$ and $\partial P_h/\partial y' \leq 0$	saturating function [24]
P_r	recruitment success is a simple hump-shaped curve in time with a single peak corresponding to e.g. the caterpillar peak	8. $\partial P_r/\partial x' = 0$ exists at $x' = x_c$ and $\partial^2 P_r/\partial x^2 < 0$ there	Gaussian [17], integral of Gaussian [19]
	recruitment success depends on match to food peak only	9. $\partial P_r/\partial y' = 0$	
s	rest-of-year survival probability independent of breeding phenology, no carryover effects	10. $\partial s/\partial y' = 0$ and $\partial s/\partial z' = 0$	[17,19]

size only. A corollary of this assumption is that there is no seasonal effect upon competition. Competition is determined by the relative timing of birds, not their absolute timing relative to calendar date. Therefore, the only effect of calendar date will be the indirect effect that early or late arrival might have on the population size.

Assumption 2.7. *The hatching success P_h increases with increasing pre-laying period*. Once the bird has arrived, it must gather resources, such as calcium, proteins, lipids and carotenoids (see [32] for review), in order to produce eggs. This is most true of income breeders; however, it is known that, for example, capital breeders cannot carry sufficient calcium in their bones for egg formation and so must gather some on-site [33]. Therefore, hatching success increases with the time available for these resource-gathering activities. A longer pre-laying period may also improve female body condition and increase clutch size [34].

Assumption 2.8. *The hatchling recruitment success P_r has a hump-shaped relationship with hatching date*. Hatching date has evolved to synchronize offspring requirements to food availability [35]. Nestling food availability (e.g. insect larvae) is typically a hump-shaped curve in time [36,37]. Recruitment success depends upon food availability during the nestling period, and so depends upon the synchrony between the hatching date and the integral of this food availability curve over the feeding period [37]. If we allow this integral to be a simple single-hump-shaped curve with a peak at the optimal hatching date x_c, then this implies that hatchling recruitment success is also a hump-shaped curve.

This also implies that the shape and magnitude of P_r is fixed in time, making the common assumption [17,19] that predator–prey dynamics between the birds and their food source can be neglected (cf. [36]).

Assumption 2.9. *The hatchling recruitment success P_r is independent of the adult arrival date*. Nestling food availability is obviously unaffected by adult arrival date; however, this assumption also neglects the potential effect of arrival date on the parents' ability to forage for and feed the nestlings (e.g. mediated by condition or energetic effects).

Assumption 2.10. *The common portion of adult and yearling survival for the rest of the years is a constant*. This is a simplifying assumption, though any lowered survival rate of the offspring owing to poor condition is also incorporated into the recruitment success (P_r) component. We constrain our focus to the breeding period only, and so over-winter survival is assumed to be constant.

Most of these assumptions are well grounded in the literature and represent the bare minimum necessary to give the model biological meaning (e.g. assumption (2.1)). Some simplify biological reality in their minimalism; for example, resource availability is generally hump-shaped (assumption (2.8)), though it may have more than one local peak [38]. Other assumptions, however, have been chosen to reflect the major, often implicit assumptions made in the literature. We stress that we do not believe that these assumptions are applicable in every circumstance nor cover all of the important factors needed to understand a particular population.

Rather, by specifying them rigorously, and by following them mathematically to their logical conclusions, we aim to elucidate a line of reasoning from proposed mechanisms to expected observations. We highlight two major assumptions here.

The first major assumption is the phenological synchrony hypothesis underlying assumptions (2.8) and (2.9), that the only phenologically dependent influence on recruitment is how well the nestlings were fed. It does not permit, for example, some second temporally varying resource on the breeding grounds upon which newly fledged juveniles may depend. It also excludes multi-species interactions, such as predation, which may have their own phenology [39]. Further, the emphasis on caterpillar phenology in particular (e.g. as applied to the *Ficedula* spp. [12]) does not take into account the possibility of food preference shifting and needs further support [40]. Nevertheless, assumption (2.8) allows a curve with any shape or width (e.g. the wide and flat curve expected if food composition shifts throughout the season); therefore, this formulation applies to any situation where a temporal window for nesting exists within which the recruitment is maximized.

A second major assumption, implicit in assumption (2.2) and (2.5), is that carryover effects [14,41,42] can be neglected. For example, assumption (2.5) will be violated if early hatching leads to higher-quality winter territory and subsequent earlier arrival the following year [22], or if the timing of breeding influences time available for other energy-intensive stages such as moult [43,44]. Assumption (2.10) similarly neglects carryover effects, such as if the timing of reproduction influences subsequent female over-winter survival and future reproduction [45,46].

Figure 1a illustrates how each of the phenological traits relates to the fitness components, and gives a qualitative example of the shape of the fitness components given the assumptions made about them above. It is convenient to split the analysis into the three cases shown in figure 1b–d, which can be understood in terms of climate and how far advanced the nestling food peak is compared with the arrival date. In case 1 (figure 1b), the food peak is late enough that the pre-laying period is long and hatching success is maximal ($P_h = 1$), and the arrival date is late enough that birds do not suffer mortality risk from early-season weather, and survival is maximal ($P_s = 1$). In case 2 (figure 1c), the food peak is late enough that hatching success is maximal ($P_h = 1$), but the arrival date is early enough that survival is not maximal ($P_s < 1$). In case 3 (figure 1d), the food peak is early enough to constrain the pre-laying period such that neither hatching success nor survival are maximal ($P_s < 1$, $P_h < 1$).

(b) The fully specified model

The fully specified model is defined in table 2, and details of its derivation may be found in the electronic supplementary material, §S4. This model represents one example of a group of possible models that may be used to describe arrival date and hatching time response to the environment while conforming to the assumptions in table 1. The P_s, P_e and P_r components are adapted from previous models [17,19]; however, the P_h component is novel, and so we focus upon that here.

P_h creates an interdependence between arrival date and hatching date via hatching success. It describes the acquisition, on the breeding grounds, of some resource necessary to egg production. It is known that resource availability can be variable throughout the pre-laying period and is likely to be lower earlier in the season [47]. Therefore, the availability of the resource R is described by a sigmoid curve in time. Resource acquisition is described by a saturating function such that the longer the pre-laying period is the greater the hatching success, thus satisfying assumption (2.7). A key parameter in P_h is u_q, which determines the midpoint of the sigmoid curve describing egg production resource availability. The higher its value, the later in the season it is before resources for egg production can be acquired. Therefore, it possible for the rate of P_h gain to constrain the laying date [48].

A concrete example of what P_h might describe is the egg-laying resource calcium, which is necessary to create eggshell. Birds may rely upon calcium sources like snail shells [49]; however, snails have their own phenology, with activity increasing over the season [50]. Therefore, P_h describes both the change in availability over the season, as well as the time required to gather the resource at those times and how they contribute towards hatching success.

(c) Ecoevolutionary analysis

The assumptions in table 1 and the population dynamics in equation (2.1) allow us to derive the fitness (*sensu* [20]) of the variant strategy (x', y') as

$$F(x', y', x, y, n)) = s(aP_s(y')P_e(y', y, n)P_h(x', y')P_r(x') + P_s(y')). \qquad (2.2)$$

Equilibrium density n^* solves

$$F(x, y, x, y, n^*(x, y)) = 1 \qquad (2.3)$$

and so the invasion fitness of a variant strategy is

$$\begin{aligned} W(x', y', x, y) &= F(x', y', x, y, n^*(x, y)) \\ &= s(aP_s(y')P_e(y', y, n^*(x, y))P_h(x', y')P_r(x') + P_s(y')). \end{aligned} \qquad (2.4)$$

Equation (2.4) can be used to predict how the phenological traits will adapt to changes both in the environment and within the population. We identify the evolutionarily singular strategy (x^*, y^*), which is where the fitness gradient is zero. Where possible, we determine whether the singular strategy is at an optimum in the fitness landscape ('ESS-stable') and if it is an evolutionary attractor ('convergent stable'; electronic supplementary material, §S2). In the fully specified model, the singular strategy and its properties can be fully determined using the same framework as the general model, and can be evaluated numerically using code available at doi:10.5281/zenodo.10005. Readers unfamiliar with the approach may refer to electronic supplementary material, §S1 for an illustrative example.

3. Results

(a) General model

In case 1 (figure 1b), the arrival date is very late such that birds do not suffer mortality risk from early-season weather (late y so that $P_s = 1$), and the food peak is very late such that the pre-laying period is long (long z implies $P_h = 1$). It can be shown (details in the electronic supplementary
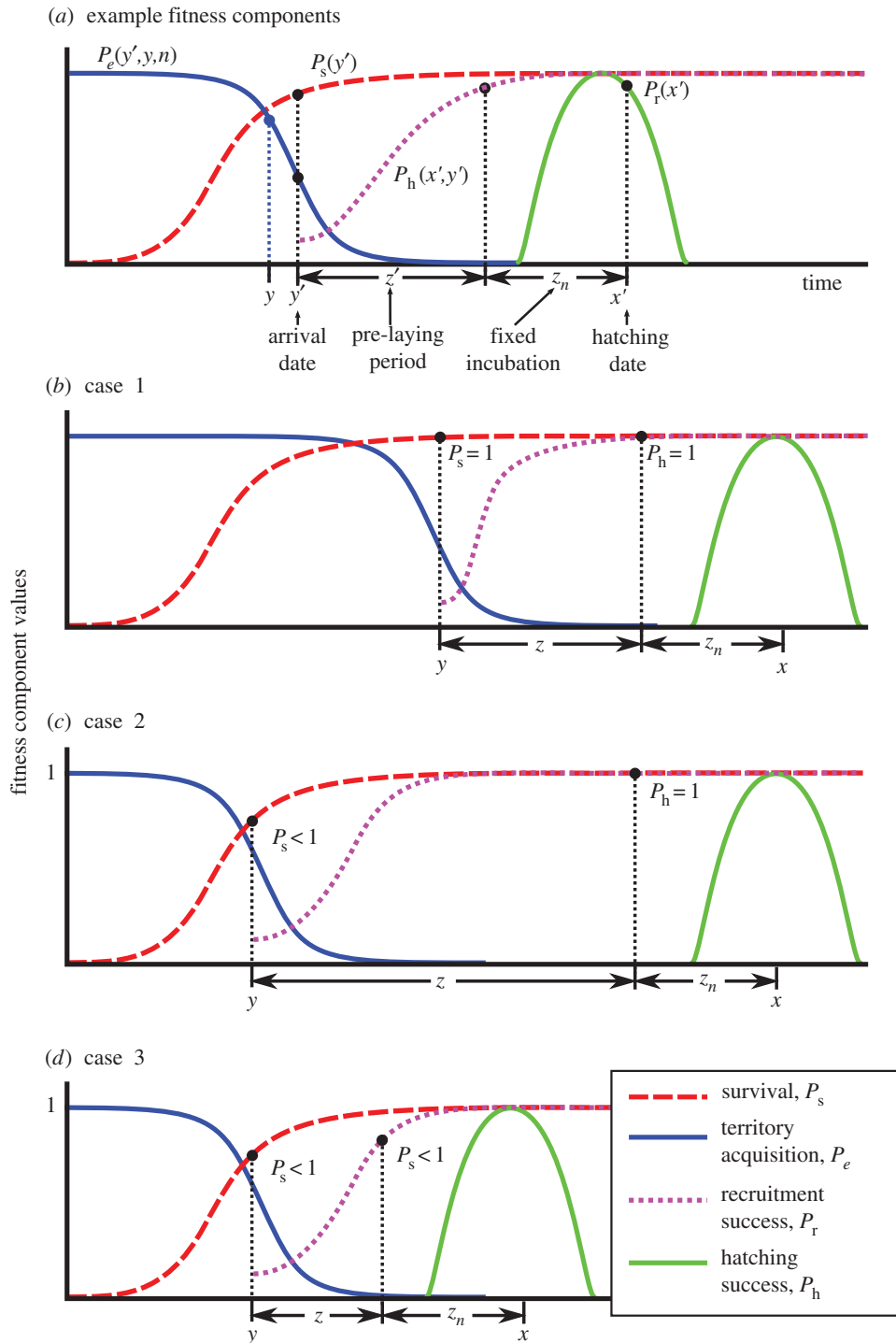
Figure 1. An illustrative example of (*a*) how each of the fitness component functions may relate to the phenological traits given the assumptions made, and (*b*–*d*) the three cases into which the analysis is split. (*b*) Case 1 has no early-season mortality and a late food peak. (*c*) Case 2 has early-season mortality and a late food peak. (*d*) Case 3 has early-season mortality and an early food peak. (Online version in colour.)

material, §S3.1) that under these conditions, the assumptions in table 1 imply that

$$x^* = x_c \tag{3.1a}$$

and

$$\frac{\partial W}{\partial y'}\Big|_{(x',y')=(x,y)} < 0. \tag{3.1b}$$

Equations (3.1) describe a system in which competition drives the arrival date ever earlier, whereas the pre-laying period adjusts itself, so that the hatching date remains at the optimum x_c.

The arrival date will continue to advance until the birds are arriving early enough that they suffer a mortality risk. This is case 2, where an earlier y occurs with $P_s < 1$, and $P_h = 1$ as before (figure 1*c*). In case 2, it can be shown (electronic supplementary material, §S3.2) that the assumptions in table 1 imply that the evolutionarily singular strategy occurs when

$$x^* = x_c \tag{3.2a}$$

and

$$0 = \frac{\partial}{\partial y'}((aP_eP_s + P_s))\Big|_{y'=y}. \tag{3.2b}$$

Table 2. A fully specified model (derivation details in the electronic supplementary material, §S4).

fitness component	parameters	
$P_s = \exp\left(\dfrac{\lambda_s}{b_s}(e^{-b_s(y'+z'+z_f+z_n)} - e^{-b_s y'})\right)$	λ_s	maximum instantaneous mortality rate
	b_s	exponential decline rate of mortality rate over the season
	z_n	incubation time
	z_f	time from hatching to fledging
$P_e = \dfrac{e^{b_e \hat{t}(n)}}{e^{b_e \hat{t}(n)} + e^{b_e y'}}$,	K	twice number of nesting territories available
	b_e	competition strength
where $\hat{t}(n) = y + (1/b_e)\ln((K/n)/(1-(K/n)))$	$\hat{t}$	variant arrival time difference at which $P_e = 0.5$
which also implies $P_e(y'=y) = K/n$		
$P_h = \dfrac{C \exp(R(y'+z'))}{1 + C \exp(R(y'+z'))}$,	b_q	slope of sigmoid egg-laying resource availability curve
	u_q	time at which sigmoid egg-laying resource availability curve at half maximum value
where $C = \dfrac{Q_0}{\exp(R(y))(1-Q_0)}$	Q_0	initial P_h at arrival
and $R(t) = t - u_q + \dfrac{\ln(\exp(b_q(u_q - t)) + 1)}{b_q}$		
$P_r = \exp\left(\dfrac{-(x'-x_c)^2}{2\sigma^2}\right)$	x_c	optimal hatching date that maximizes P_r
	σ	spread of hatchling recruitment success curve

Equations (3.2) describe a system in which the hatching date is phenologically 'matched' to the caterpillar peak, and the arrival date is at the optimal compromise (see below) between the survival cost and territory acquisition benefit of arriving early. The arrival date evolves independently of optimal hatching date in this scenario; therefore, the system will respond to advances in the food peak by adjusting the hatching date only. This singular strategy is also at an optimum in the fitness landscape when

$$\frac{\partial^2}{\partial y'^2}(s(aP_e P_s + P_s))\Big|_{\substack{(x',y')=(x,y)\\(x,y)=(x^*,y^*)}} < 0, \tag{3.3}$$

which is likely for biologically realistic functions of survival and territory acquisition (see electronic supplementary material, §S3.2.5).

The final case 3 occurs if the pre-laying period is constrained; short z occurs with $P_h < 1$ and an early y occurs with $P_s < 1$ (figure 1d). This can occur if the food peak advances, for example, owing to late-season warming under a climate change scenario. It may also represent a species in which the arrival date is late in the season, such as is typical for longer-distance migrants. In this case, it can be shown (electronic supplementary material, §S3.3) that the assumptions in table 1 imply that the evolutionarily singular strategy occurs when

$$x^* > x_c \tag{3.4a}$$

and

$$\frac{\partial}{\partial y'}(aP_r P_h P_e P_s + P_s)|_{(x',y')=(x,y)} > 0. \tag{3.4b}$$

Equations (3.4) describe a situation in which the bird is now forced to compromise between reproduction and survival in order to maximize fitness overall. Equation (3.4a) implies that the bird is phenologically asynchronous, such that hatching date is too late to optimize recruitment. Similarly, equation (3.4b) implies that the arrival date will be earlier than the date that would have otherwise provided the optimal compromise between survival and territory competition. Note, however, that density dependence implies that the timing of this optimal compromise can shift temporally as well, and therefore a simple description of how arrival date responds to advancing food peak (i.e. by advancing, delaying or staying the same) cannot be obtained analytically (electronic supplementary material, §S3.3.4).

(b) Fully specified model

Figure 2 shows the behaviour of the fully specified model from table 2. Consistent with the analytically derived results for cases 1 and 2, when the food peak is late and x_c is late ($x_c \gtrsim 60$), then the arrival date is constant ($y^* = 130.3$), and an advance in x_c results in an advance in the hatching date x^* only, which is achieved via a shortening of the pre-laying period z^* (figure 2a–c). Also consistent with the analytical results for case 3, when x_c is sufficiently advanced that the pre-laying period z^* becomes constrained, asynchrony forms between the hatching date and optimal date x_c such that the hatching date is too late to maximize recruitment. This asynchrony also causes a decrease in the population size (individuals per territory available n^*/K decreases with earlier optimal hatching date x_c).

It is not possible to provide a simple answer to the question of how arrival date responds to an advance in
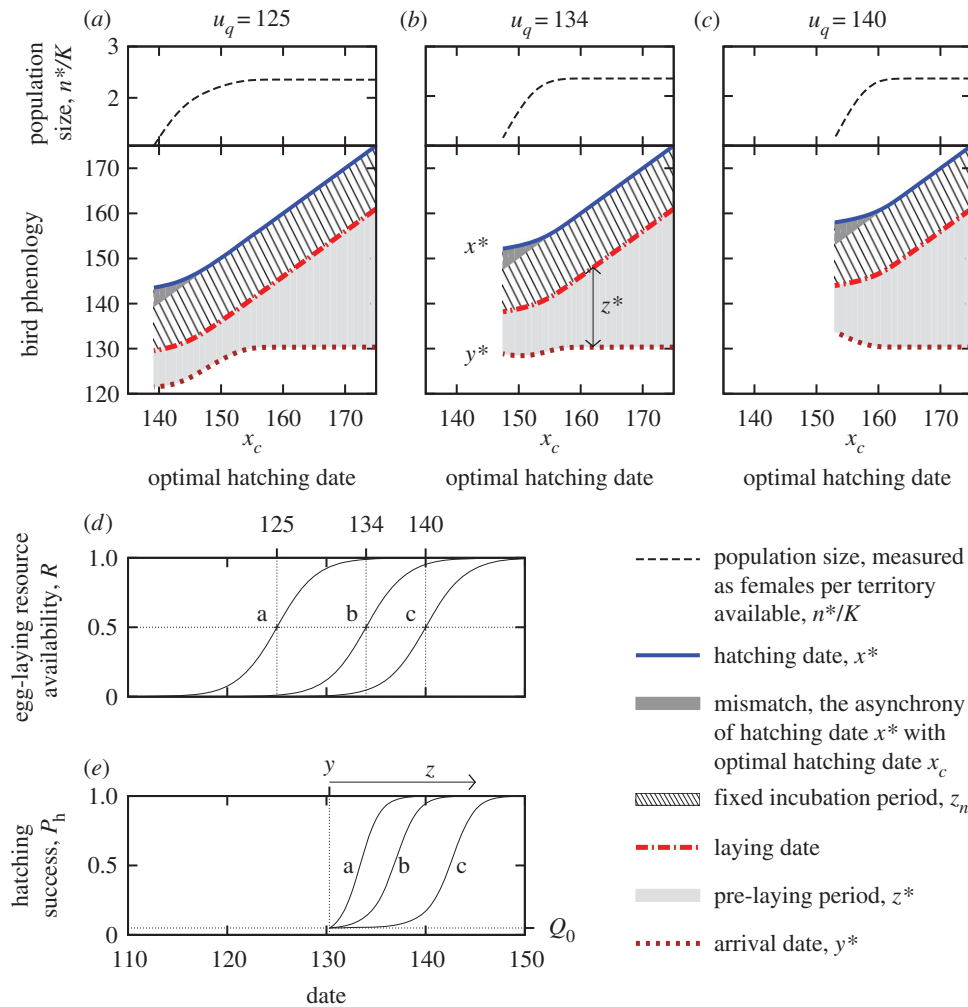
Figure 2. The response of the migratory bird population's evolutionarily singular strategy to changes in the timing of the nestling food peak measured via its effect on the optimal hatching date x_c. The response of population size and the evolutionarily singular phenological attributes are shown for three different parameter-value scenarios: (a) $u_q = 125$, (b) $u_q = 134$, (c) $u_q = 140$. The parameter u_q influences the underlying (d) timing of the egg-laying resource availability curve, which subsequently influences (e) the hatching success given arrival y and pre-laying period z. Other parameter values are: $K = 100$, $b_e = 0.03$, $a = 3$, $\sigma = 5$, $Q_0 = 0.05$, $b_q = 0.5$, $L_m = 170$, $b_s = 0.075$, $s = 0.5$, $z_f = 40$, $z_n = 14$. Model and code available at doi:10.5281/zenodo.10005. (Online version in colour.)

the food peak in case 3 (electronic supplementary material, §S3.3.4), and comparing across figure 2a–c shows why. When x_c advances far enough, the arrival date can advance (figure 2a), show little response (figure 2b), or even become delayed (figure 2c). Its response depends upon the parameter u_q, which determines the timing of the availability of the egg-laying resource (figure 2d) and, consequently, the rate of increase of hatching success during the pre-laying period (figure 2).

An advancing food peak constrains the pre-laying period z^* and reduces hatching success P_h. When egg-laying resources are available early in the season (e.g. the early u_q scenario; figure 2a), adaptation can respond by advancing the arrival date, which recovers the lost hatching success by increasing the pre-laying period earlier in the season. However, if egg-laying resource availability R is low at arrival date (e.g. the late u_q scenario; figure 2c), then arriving earlier, though extending the length of the pre-laying period, will not allow more egg-laying resources to be gathered, and thus it will not be selected for. Meanwhile, as x_c advances, the declining recruitment and hatching success decreases population density, weakening competition for nest sites. Given that arrival date is primarily a compromise between early-season survival and nesting-site competition, this weakened competition causes the arrival date to become delayed.

4. Discussion

We have gathered together the common essential mechanisms underlying migratory bird phenology, formalized them into a mathematical model and analysed their logical consequences. Three key predictions are made by the general model, which find support in the literature.

First, the general model predicts that, provided that the food peak is late enough that adequate time exists between arrival and laying (case 1), competition for territories will drive the arrival date ever earlier until counteracted by the early-season survival cost (equation (3.1b)). This implies that if early-spring temperatures increase without a corresponding shift in later-spring temperatures, then arrival date will advance and pre-laying period increase while hatching date remains the same. This has been observed in a Finnish flycatcher population, which has responded to early-spring warming by speeding up migration and advancing arrival date, but which now wait longer to begin breeding [9,51].

Second, the general model predicts that, for a late food peak, arrival date and hatching date evolve independently of one another (case 2, equations (3.2)). This implies that if two populations exist that differ only in the timing of the nestling food peak, they could nevertheless arrive at the same time. An approximation of this scenario may be found in

the pied and collared flycatcher (*Ficedula albicollis*) populations on Öland and Gotland. The collared flycatchers are more abundant in the deciduous forests, and there the larval peak occurs earlier than in the coniferous forests where the pied flycatcher is more abundant [37]. Yet the two species arrive at approximately the same time [37], and synchrony of hatching date with the food peak is obtained by their different laying dates [52].

Finally, the general model predicts that, if the food peak is early enough, then the hatching date will occur after the peak (case 3, equation (3.4*a*)). Significantly, this implies that a hatching date 'mismatch' can be adaptive and confer the highest fitness when taking into account all fitness components. Such asynchronies have been observed, for example, in a Dutch pied flycatcher population, and were attributed to external factors constraining adaptation [11]. The latter explanation may yet be true; however, our result reinforces the message that simply observing asynchrony between nestling food availability and breeding phenology is not sufficient evidence that populations are not responding adaptively [16].

The general model unifies many different observations made across populations into a single framework, and explains those differences in terms of the relative timing of early- versus late-season processes. The quite different responses of, for example, Dutch and Finnish flycatchers [9], above, were both explained by our one model. Likewise, species with quite different life histories can be described equally well within this framework. For example, shorter-distance, earlier-arriving species that wait longer to begin breeding (e.g. black-tailed godwits *Limosa l. limosa* in The Netherlands [53]) versus species that are time-constrained and breed as soon as possible after arrival (e.g. approx. 5 days in pied flycatchers in The Netherlands [9]) can both be modelled by changing the relative timing of the survival and hatchling recruitment success curves.

The core message of both models is that historical phenology and phenological response to change will depend upon the relative timing and change of early- and late-season processes. For example, a non-correlation between arrival date and egg-laying may occur when birds arrive early owing to nesting site competition with another factor constraining the onset of egg-laying (cf. [53]). As another example, one should expect that a population for which the pre-laying period is already constrained is more at risk of population decline in the face of advancing food peak, and that risk is greater if the arrival date does not respond. This intuitive understanding is explicated mechanistically by the analytical work.

In addition to making reasonable predictions, the model also provided a counterintuitive prediction that was illustrated using the fully specified model. It is generally expected that arrival date will respond to an advancing food peak by itself advancing, and a failure to do so, particularly when coupled with a 'mismatch' (phenological asynchrony), is typically attributed to some upstream constraint on arrival date [10,11]. This expectation reflects an implicit understanding that

pressure for earlier hatching date translates to earlier laying date, which translates to earlier egg production, and so on, ultimately leading to pressure for earlier arrival. However, this mental model does not take into account the density dependence of territory competition in its role in determining arrival date. We have shown that, when the mechanisms thought to determine arrival date and to link it to hatching date are made explicit, it can imply that arrival date might not respond or might even become delayed in the face of an advancing food peak. This occurs when egg-laying resources are only available late in the season relative to arrival dates. Further, we hypothesize that this effect will be less likely in capital breeders, compared with income breeders, who rely more strongly upon resources gathered at the breeding grounds.

There have been a few cases where migratory birds appear to have delayed arrival in recent times, and this result is more common in Asia [54]. The explanations currently favoured for unresponsive or delayed arrival date are that it is caused by a constraint upon adaptation [10] or it is a statistical artefact [54,55]. The model result provides another possible explanation that can be tested in these systems. The model result also shows that the mechanisms determining arrival date are in a feedback with population size, suggesting that caution should be taken when reasoning about the changes in arrival date of populations in decline.

5. Conclusion

The ecoevolutionary model presented here makes explicit the mechanistic relationship between two key phenological measures for migratory birds—arrival date and hatching date—bridging between theory focusing on reproduction or migration alone. Considering the two simultaneously permitted us to determine under what circumstances one, the other or both should be expected respond to environmental change. It also revealed that, even assuming perfect adaptability and very minimal assumptions, a wide variety of responses are possible, including responses that appear inadequate or are opposite to the expectation. We hope that by making explicit the assumptions underlying the mental models used to understand migratory bird phenology, and by following those assumptions to their mathematical conclusions, we can shed light on the general patterns observed across systems, and assist workers in identifying incorrect assumptions or missing mechanisms when their study systems deviate from the expectation. Apart from inspiring more specific tests, we hope that the analytical framework presented here serves as a platform for new ways to think about interlinked phenological traits.

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10

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