Evolution of resident bird breeding phenology in a landscape with heterogeneous resource phenology and carryover effects

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Abstract

It is generally expected that, in environments with pronounced seasonal resource peaks, birds' reproductive success will be maximised when nestlings' peak food demand coincides with the timing of high food availability. However in certain birds that stay resident over winter, earlier breeding leads juveniles to join the winter flock earlier, which by the prior residence effect increases their success in breeding territory competition. This trade-off between reproduction and competition may explain why, in certain species, breeding phenology is earlier and asynchronous with the resource. This study extends a previous model of the evolution of breeding phenology in a single habitat type to a landscape with two habitat types: 'early' and 'late' resource phenology. The offspring's natal habitat type has a carryover effect upon their competitive ability regardless of which habitat type they settle in to potentially breed. We find that, when the difference in resource phenology between habitats is small (weak carryover effect), breeding phenology in the late habitat evolves to occur earlier and more asynchronously than in the early habitat, to compensate for the competitive disadvantage to juveniles raised there. However if the difference is large (strong carryover effect), then the reproductive cost of earlier breeding outweighs the benefit of the compensation, so instead breeding phenology in the late habitat evolves to become more synchronous with the resource. Recruitment is generally asymmetric, from early to late habitat type. However if the early habitat is less frequent in the landscape or produces fewer offspring, then the asymmetry is reduced, and if there is some natal habitat-type fidelity, then recruitment can have an insular pattern, i.e. most recruits to each habitat type come from that same habitat type. We detail the different scenarios in which the different recruitment patterns are predicted, and we propose that they have implications for local adaptation.

Keywords Adaptive dynamics · Dominance hierarchy · Parids · Phenological mismatch · Source-sink · Isolation by ecology

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Introduction

A fundamental aspect of life-history evolution is phenology, which is the timing of key recurring biological events. Synchrony in phenology between a species and its resource has been the focus of much research, for example the match/mismatch in the timing between nestlings' peak food demand and the peak in food abundance (Visser and Both 2005; Vátka et al. 2016). All else being equal, the importance of provisioning offspring with food suggests that breeding phenology should be synchronised with resource phenology (Johansson et al. 2015). However breeding phenology also influences and is influenced by selection on processes at other stages of the life cycle, notably the competitive processes leading up to the breeding stage (Jonzén et al. 2007; Johansson et al. 2012).

The effect of breeding phenology on juveniles' competitive success at later life stages (e.g. Arcese and Smith 1985; Desrochers et al. 1988) may explain why some winter-resident birds breed before synchrony with the resource peak. Breeding date influences the timing of natal dispersal, which in turn influences arrival date of juveniles to the winter flock, and in resident species such as parids, earlier arrival to the winter flock can give juveniles a competitive advantage in breeding-territory competition (Nilsson and Smith 1988; Nilsson 1990; Koivula et al. 1993). Therefore we expect synchrony between breeding and resource timing to be traded against juvenile competitive ability, resulting in asynchrony between breeding and resource (Johansson et al. 2014). This mechanism may be part of the explanation for why the breeding phenology in some populations of willow tits (*Poecile montanus*) (Vátka et al. 2011), coal tits (*Parus ater*) (Both et al. 2009), and marsh tits (*Poecile palustris*) (Wesołowski 1998) is early and asynchronous with the caterpillar peak.

A landscape is likely to consist of a mix of habitat types with different resource phenologies, which raises the possibility that landscape composition will influence inter-habitat recruitment dynamics and selection on breeding date. For example, deciduous forests have an earlier caterpillar phenology than evergreen forests (Veen et al. 2010), and this constrains the breeding phenology of birds that can successfully breed within them (Blondel et al. 1993; Lambrechts et al. 1997). Given that resource phenology influences breeding phenology which in turn influences competitive ability (e.g. Arcese and Smith 1985; Desrochers et al. 1988), we would therefore expect that juveniles raised in evergreen forest patches will be competitively disadvantaged in breeding-territory contests against juveniles raised in deciduous forest patches (Johansson et al. 2014). How the breeding phenology in the different habitat types evolves in response to these carryover effects (*sensu* O'Connor et al. 2014) is an open question.

Ecoevolutionary theory can guide empirical work by elucidating how the evolution of functional traits depends on multiple selection pressures and trait-dependent competitive interactions. In this theoretical study, we model the evolution of breeding phenology in a parid population residing in a heterogeneous landscape, with habitats that differ in their resource phenology. We model selection on breeding phenology as a trade-off between synchrony with resource phenology to maximise parents' reproduction, versus earlier breeding to increase offspring's chance of winning a breeding territory. We explore how breeding phenology responds to landscape composition, the degree of difference between habitat types (strength of carryover effect), and natal-habitat fidelity.

Materials and methods

Natural history and model scope

Four key stages in the life cycle of resident birds were modelled—reproduction, fledgling dispersal and establishment in a winter-flock hierarchy, over-winter survival, and competition for the breeding territory—occurring in a population on a landscape of two (or more) habitat types (Fig. 1). The life-cycle model and assumptions were taken from the single-habitat model of Johansson et al. (2014), and extended to consider multiple habitat types with different resource phenologies. This choice allowed us to model a concrete scenario that emphasises our mechanisms of interest, namely the trade-off between reproduction and competition, and extend it to a landscape scenario where habitat type influences competitive ability.

Reproduction rate of a predator is generally expected to be maximised when there is a temporal match between its most energy-demanding life-stage and the highest availability of its prey, i.e. the ‘match/mismatch hypothesis’ (reviewed in Johansson et al. 2015). Birds are also expected to match breeding phenology to resource phenology to match the timing of peak energy-demand, typically of nestlings (Lack 1950, 1954), but alternatively of fledglings (e.g. Pakanen et al. 2016) or egg-producing females (e.g. Perrins 1970). Our model assumed that the number of fledglings produced was maximised when there was a match between breeding and resource phenology.

Fledglings disperse from the natal territory to join a winter flock, which in many parids contains the breeding pair and a number of adults and juveniles who live in a social dominance hierarchy centred around a breeding territory (Hogstad 1989; Matthysen 1990). Our model concerns birds in which early hatching results in higher fitness, because prior residency in flock or territory establishment affects dominance (e.g. the marsh tit population described in Wesolowski 1998). Competitive advantages from early establishment in

Fig. 1 An illustration of the key stages of the life cycle modelled: reproduction, fledgling dispersal and establishment in a winter-flock dominance hierarchy, over-winter survival, and competition for the breeding territory. Multiple territories exist (not shown) in two habitat types that differ by their resource phenology. Key model assumptions are: number of fledglings produced depends upon synchrony in timing between breeding (x_i^*) and resource peak; earlier breeding leads to earlier juvenile dispersal and higher rank in the winter flock (i.e. carryover effect); winter-flock dominance hierarchy is linear and stable; over-winter survival is independent of rank and age; and the winner of the breeding territory is the highest-ranking surviving flock member

flocks or territories has been demonstrated in multiple bird taxa (Brawn and Samson 1983; Ekman 1989; Cristol et al. 1990; Snell-Rood and Cristol 2005), suggesting that early hatching should give a competitive advantage in social interactions (Eden 1987; Nilsson and Smith 1988; Velando 2000). The prior residence effect may occur because prior residency is an otherwise irrelevant cue for settlement of ambiguous games with a mixed strategy ESS (Maynard Smith 1979; Yasukawa and Bick 1983), or because prior residence confers a direct advantage through site familiarity and accumulated knowledge of the area (Krebs 1982) or the accumulated experience of agonistic encounters (Arcese and Smith 1985; Koivula et al. 1993). Importantly, prior residence can be a strong effect, and has been demonstrated to override other factors of resource-holding potential, such as size and age (Nilsson and Smith 1988; Cristol et al. 1990; Sandell and Smith 1991; Koivula et al. 1993).

When an individual in the flock dies, the model assumed that their position in the hierarchy was filled by the flock-member immediately below in rank, and so on down the hierarchy. This describes species for whom the dominance hierarchy is linear and stable (Hogstad 1989; Hay 2003), and is not universal for parids (reviewed in Ekman 1989).

Given that the prior residence effect was assumed to operate through social rank directly, over-winter survival was given a simple treatment in our model: it was assumed that survival probabilities of all fledglings and adults are equal. In reality, individuals with higher status benefit from priority access to food (Baker 1978; Carrascal et al. 1998; Hay 2003) and lower predation risk foraging areas (Ekman and Askenmo 1984; Hogstad 1988), but may also suffer from higher metabolic rate and reduced immunocompetence (reviewed in Hay et al. 2004).

Competition for the breeding territory was also modelled in a very simple way: ownership goes to the highest-ranking surviving flock member. It was further assumed that all subordinate members are chased away from the territories before the breeding season and die (e.g. marsh tits Nilsson and Smith 1988), so juveniles only have one chance to be recruited to the breeding population.

The single habitat-type model above was extended to multiple habitat types in the following way. We assumed that the effect of hatching date on competitive ability operates regardless of which habitat type the juvenile disperses to, so that natal habitat type has an irreversible carryover effect upon competition *sensu* O'Connor et al. (2014). It was assumed that each individual has one hatching-date trait per habitat type, which was cued by breeding in that habitat type, so this represented perfect cue response and phenotypic plasticity. This removed all other constraints on breeders' ability to 'match' their breeding to resource phenology, which allowed us to focus upon the effects of competition and carryover effects alone. Finally, while it was assumed that winter-territory selection is random, the model includes a parameter that biases juveniles to join flocks in territories with the same habitat type as their natal territory. This may reflect either coarseness in the spatial distribution of habitat types, or behavioural effects such as natal habitat preference induction (Davis and Stamps 2004).

Ecoevolutionary model

The ecoevolutionary dynamics of breeding phenology was modelled using the adaptive dynamics framework (Geritz et al. 1999; Brännström et al. 2013). We considered individuals who have a hatching-date x_i for each habitat-type i , and so their breeding phenology was described as a vector $\mathbf{x}$ of length h . We focused mainly on $h = 2$ habitat types, i.e. with early and late resource phenology, but the model can be extended to more habitats (see Appendix

S1). Given that the single-habitat model predicts asynchrony between breeding and resource phenology (Johansson et al. 2014), we focus on *hatching-date asynchrony*, which we define as the difference between the evolved hatching date x_i^* and the date that that would maximise the number of fledglings $\hat{x}_i$:

$$\text{hatching date asynchrony} = x_i^* - \hat{x}_i \quad (1)$$

We assumed a monomorphic population, so all individuals have the same hatching-date strategy $\mathbf{x}$, and we assumed clonal reproduction (a typical adaptive dynamics assumption).

The adaptive dynamics framework assumes that the population dynamics are fast relative to evolutionary dynamics (i.e. separation of timescales), so the ecological dynamics can be assumed to be at steady-state when a mutant hatching-date strategy $\mathbf{y}$ appears. Therefore the model involved a two-step process detailed below: (1) the ecological dynamics for a monomorphic population, with population size as a function of breeding phenology, were resolved to their steady state; then (2) given the solution found for the ecological steady state, the steady-state of the evolutionary dynamics were found.

Ecological dynamics

Reproduction

The number of fledglings produced by each individual in habitat i is modelled as a Gaussian function of the difference between its hatching-date trait x_i and the resource-synchronous hatching date $\hat{x}_i$ in that habitat

$$E_i(x_i) = E_{0,i} \exp \left(-\frac{(x_i - \hat{x}_i)^2}{2\sigma_{E,i}^2} \right), \quad (2)$$

where $E_i(x_i)$ is the number of fledglings produced, $E_{0,i}$ is the maximum number of fledglings that can be produced in habitat i , and $\sigma_{E,i}$ is a parameter describing the width of the temporal distribution resource in habitat i . Therefore individuals maximise their reproduction by synchronising their hatching date in each habitat type to the resource-synchronous hatching date in that habitat type.

Dispersal and habitat-type fidelity

Winter territory selection is modelled as random, without regard to the number of other juveniles in the flock, however a parameter is included to account for natal habitat-type fidelity. It is assumed that a fraction r of juveniles will choose a territory at random, so that the habitat type is selected in proportion to its frequency in the landscape, while the remaining $1 - r$ will only select from territories with the same habitat type as their natal territory. Then the proportion $p_{i,j}$ of juveniles dispersing from habitat-type i to habitat-type j is (c.f. Ives and Andow 2002)

$$p_{i,j} = \begin{cases} \frac{K_j}{\sum_{l=1}^h K_l} r, & \text{if } i \neq j \\ (1 - r) + \frac{K_j}{\sum_{l=1}^h K_l} r, & \text{if } i = j \end{cases} \quad (3)$$

where h is the number of different habitat types, and K_i the number of territories with habitat-type i in the landscape.

Prior residence effect and recruitment

In order to describe the relationship between hatching date and a juvenile's probability of obtaining first rank in the winter-flock dominance hierarchy, three intermediate steps are modelled: (1) the translation of hatching date in a particular habitat type to a probability distribution of arrival times to the winter flock (Eq. 4); (2) the arrival rates of juveniles from all habitat types to a given territory (Eq. 5); and (3) the probability that a given juvenile will, at the end of winter, rank first in the dominance hierarchy given 1 and 2 (Eq. 7). A juvenile is recruited into the adult breeding population if it has first rank in the dominance hierarchy and the territory has no adult owner at the end of winter (Eq. 9).

Rank is determined by an individual's time of arrival to the winter flock relative to its competitors. If we assume that the time from hatching to family break-up is a constant, then arrival time is only influenced by differences in hatching date between habitats. Therefore we describe the probability distribution of relative arrival times t of a juvenile to any winter flock as lognormal relative to their hatching date x_i

$$g(t, x_i; \mu_g, \sigma_g) = \frac{1}{(t - x_i)\sigma_g \sqrt{2\pi}} \exp\left(-\frac{(\ln(t - x_i) - \mu_g)^2}{2\sigma_g^2}\right), \quad (4)$$

where μ_g and σ_g are the scale and shape parameters, respectively. For a fixed σ_g , the arrival distribution may also be described by the mean arrival time $m_g = e^{\mu_g + \sigma_g^2/2}$. Mean arrival time m_g can also be interpreted as the mean number of days after family group break-up that juveniles arrive at winter flocks, and is used to parameterise the models below.

Because we now have a description of the probability distribution of arrival times of a fledgling from each habitat type, it can be combined with the number of fledglings produced in each habitat type to give the arrival rates of juveniles from all habitat types to a territory with habitat type j who will survive the coming winter (proportion s_j)

$$\lambda_j(t, \mathbf{x}, \mathbf{n}) = \frac{s_j}{K_j} \sum_{i=1}^h n_i E_i(x_i) g(t, x_i) p_{ij}, \quad (5)$$

where $\mathbf{x}$ is the vector of hatching dates x_i and $\mathbf{n}$ is the vector of population sizes n_i in each habitat type, and the sum is taken over each of the habitat types including j itself. Equation 5 can be understood as follows: for a given habitat-type i from which juveniles are dispersing, $n_i E_i(x_i)$ is the number of fledglings produced in that habitat type, $g(t, x_i)$ is their arrival distribution given that they hatched at date x_i , and p_{ij} is the probability of them travelling to habitat-type j , so the rate of arrival to habitat-type j is the sum over all i divided by the number territories of type j .

To obtain the probability of being first in the dominance hierarchy, it is assumed that arrival is a Poisson process, so the probability that a juvenile with a particular relative arrival time τ takes the first position in a flock in habitat j is

$$f_j(\tau, \mathbf{x}, \mathbf{n}) = \exp\left(-\int_{\min(\mathbf{x})}^{\tau} \lambda_j(t, \mathbf{x}, \mathbf{n}) dt\right). \quad (6)$$

Juveniles from habitat i have relative arrival times distributed according to Eq. 4 with $x_i \leq t < \infty$. Therefore the probability of any juvenile from habitat i obtaining the first position when joining a flock in habitat-type j is the integral of f_j over their arrival time distribution

$$F_{ij}(\mathbf{x}, \mathbf{n}) = \int_{x_i}^{\infty} g(t, x_i; \mu_g, \sigma_g) f_j(t, \mathbf{x}, \mathbf{n}) dt. \quad (7)$$

A territory will have no adult owner at the end of winter either because it was unoccupied in previous breeding season, or because it did have an owner but they died. Therefore the probability that a territory in habitat j has no adult owner at the end of the winter is

$$A_j(n_j) = \frac{K_j - s_j n_j}{K_j}. \quad (8)$$

In order for a juvenile to be recruited into the adult population, it must: (1) come first of the surviving juveniles in the territory, F_{ij} ; (2) survive the winter itself, s_j ; and (3) choose a territory that will have no adult owner at the end of the winter, A_j . Therefore the per-capita recruitment rate from habitat-type i to habitat-type j is

$$w_{ij}(\mathbf{x}, \mathbf{n}) = p_{ij} E_i(x_i) s_j F_{ij}(\mathbf{x}, \mathbf{n}) A_j(n_j). \quad (9)$$

Steady-state population size and recruit flow between habitats

The number of adults in habitat-type i at year $t + 1$ is modelled as a system of difference equations

$$n_{i,t+1}(\mathbf{x}) = s_i n_{i,t}(\mathbf{x}) + \sum_{j=1}^h w_{ji}(\mathbf{x}, \mathbf{n}_t) n_{j,t}(\mathbf{x}). \quad (10)$$

It is convenient for understanding to express this in matrix form. For two habitat types for example, the system of equations obtained from Eq. 10 is written

$$\begin{pmatrix} n_1 \\ n_2 \end{pmatrix}_{t+1} = \begin{pmatrix} s_1 + w_{1,1}(\mathbf{x}, \mathbf{n}_t) & w_{2,1}(\mathbf{x}, \mathbf{n}_t) \\ w_{1,2}(\mathbf{x}, \mathbf{n}_t) & s_2 + w_{2,2}(\mathbf{x}, \mathbf{n}_t) \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix}_t \quad (11)$$

Define a matrix $W(\mathbf{x}, \mathbf{n}_t)$ with elements $w_{ij}(\mathbf{x}, \mathbf{n}_t)$, and a matrix $\text{diag}(\mathbf{s})$ with elements s_i along the diagonal, then the matrices can be combined to define the 2×2 matrix that appears on the right-hand side of Eq. 11

$$U(\mathbf{x}, \mathbf{n}_t) = (W(\mathbf{x}, \mathbf{n}_t) + \text{diag}(\mathbf{s}))^T \quad (12)$$

Therefore the system of difference equations in Eq. 10 can also be written

$$\mathbf{n}_{t+1}(\mathbf{x}) = U(\mathbf{x}, \mathbf{n}_t) \mathbf{n}_t(\mathbf{x}) \quad (13)$$

which can be solved numerically to find the steady-state population size $\mathbf{n}_{t+1}(\mathbf{x}) = \mathbf{n}_t(\mathbf{x}) = \mathbf{n}^*(\mathbf{x})$, and the stability of the steady-state can be verified numerically (Appendix S3).

Equation 13 says that the population growth or decline rate results from the product of the sequence of matrices $U(\mathbf{x}, \mathbf{n}_t)$. At the ecological steady state, the population size neither increases nor decreases, therefore its growth rate is 1. This growth rate is the result of the

repeated products of $U(\mathbf{x}, \mathbf{n}^*)$, therefore the growth rate can also be calculated as the dominant eigenvalue of the matrix

$$\max(\text{Re}(\text{eig}(U(\mathbf{x}, \mathbf{n}^*)))) = 1. \quad (14)$$

Recruit flow between habitats at the population steady-state is quantified by finding the proportion of recruits to habitat j that were from habitat i

$$\phi_{ij}(\mathbf{x}) = \frac{w_{ij}(\mathbf{x}, \mathbf{n}^*) n_i^*}{\sum_{k=1}^h w_{kj}(\mathbf{x}, \mathbf{n}^*) n_k^*}. \quad (15)$$

We call recruitment *insular* when most new recruits to all habitats originated in that same habitat, i.e. if all $\phi_{ii} \geq 0.5$. This can be contrasted with *asymmetric recruitment*, where one habitat (typically the late habitat) receives more new recruits from the other habitat (typically the early habitat), i.e. if at least one of the $\phi_{ii} < 0.5$.

Ecoevolutionary dynamics

To analyse the ecoevolutionary dynamics we consider the scenario of a rare mutant hatching-date strategy $\mathbf{y}$ invading a steady-state population where the prevailing hatching-date strategy is $\mathbf{x}$ (Appendix A, Kisdi 2002). Because it is assumed that the mutant is rare and that the $\mathbf{x}$ -strategist population is at steady state, then we know that the $\mathbf{x}$ -strategists have a growth rate of 1 (Eq. 14). Therefore in order for the rare mutant strategy to invade, it will need a growth rate during invasion that is greater than 1.

The growth rate of the rare mutant strategy is obtained as follows. The probability of a mutant obtaining the first position when travelling from habitat-type i to habitat-type j is

$$F_{ij}(y_i, \mathbf{x}, \mathbf{n}^*) = \int_{y_i}^{\infty} g(t, y_i; \mu_g, \sigma_g) f_j(t, \mathbf{x}, \mathbf{n}^*) dt \quad (16)$$

and its per-capita recruitment rate between habitats is

$$w_{ij}(y_i, \mathbf{x}, \mathbf{n}^*) = p_{ij} s_j E_i(y_i) F_{ij}(y_i, \mathbf{x}, \mathbf{n}^*) A_j(n_j^*) \quad (17)$$

where $\mathbf{n}^*$ again refers to the steady-state population sizes of the prevailing $\mathbf{x}$ -strategists. Similar to Eq. 12, the growth rate of the rare mutant with strategy $\mathbf{y}$ is determined by the repeated product of the matrix

$$U(\mathbf{y}, \mathbf{x}, \mathbf{n}^*) = (W(\mathbf{y}, \mathbf{x}, \mathbf{n}^*) + \text{diag}(\mathbf{s}))^T. \quad (18)$$

Then the growth rate of the rare mutant strategy, which is also called the invasion fitness, is the real part of the dominant eigenvalue of $U(\mathbf{y}, \mathbf{x}, \mathbf{n}^*)$

$$\Lambda(\mathbf{y}, \mathbf{x}) = \max(\text{Re}(\text{eig}(U(\mathbf{y}, \mathbf{x}, \mathbf{n}^*)))) \quad (19)$$

$\Lambda(\mathbf{y}, \mathbf{x})$ is called the invasion fitness because it indicates whether or not the invading mutant's population size will increase or decrease. For example, if the mutant strategy was the same as the resident strategy $\mathbf{y} = \mathbf{x}$, then $U(\mathbf{y}, \mathbf{x}, \mathbf{n}^*) = U(\mathbf{x}, \mathbf{n}^*)$ and $\Lambda(\mathbf{y}, \mathbf{x}) = 1$. If $\Lambda(\mathbf{y}, \mathbf{x}) > 1$ then the mutant's population size will increase and it can invade the population, whereas and if $\Lambda(\mathbf{y}, \mathbf{x}) < 1$ then it will decrease until it is removed.

The evolutionarily singular strategy $\mathbf{x}^*$ is found when the fitness gradients are zero

$$g_i(\mathbf{x}) = \left. \frac{\partial \Lambda(\mathbf{y}, \mathbf{x})}{\partial y_i} \right|_{\mathbf{y}=\mathbf{x}} = 0, \quad (20)$$

so the evolutionarily singular strategy $\mathbf{x}^*$ satisfies $\mathbf{g}(\mathbf{x}^*) = 0$. If the evolutionarily singular strategy is at a peak in the fitness landscape, then it is evolutionarily stable, which means that a population with that strategy cannot be invaded by a rare mutant strategy. The evolutionary stability of the singular strategy can be established by investigating the Hessian and Jacobian matrices (Leimar 2009) (see Appendix S4). If an evolutionarily singular strategy is both a fitness maximum and an evolutionary attractor then it is known as the continuously stable strategy (CSS) (Geritz et al. 1999), which represents the expected endpoint of gradual, evolutionary change, barring genetic correlations and other constraints (Dieckmann and Law 1996; Teplitsky et al. 2014) or trade-offs with other fitness components not considered in the model.

The selection of the default parameter values can be found in Table 1, and details found in Appendix S2.

Results

Hatching date evolves to occur earlier than resource synchrony

In both the early and late habitats, the hatching dates evolve to a single continuously stable strategy (Fig. S3, Fig. S5) and this hatching-date strategy is always earlier than the resource-synchronous hatching date that would maximise the number of fledglings produced (Fig. 2a). Therefore we present the remainder of results in terms of the magnitude of *asynchrony* between bird and resource phenology (c.f. Fig. 2a, b), which is calculated according to Eq. 1.

Degree of asynchrony depends on difference in resource phenology between habitats

In both habitats, the magnitude of asynchrony is smallest when the difference in resource phenology between habitats, and therefore the strength of the carryover effect, is greatest. This is true for the default parameter values (Fig. 2b) and across the parameter space (examples in Fig. 2, all parameters in Fig. S2).

The relationship between asynchrony and difference in resource phenology differs qualitatively between habitat types. In the early habitat, the relationship is monotonic, so that asynchrony always increases as the difference in resource phenology between habitats decreases to zero (red curves in Fig. 2). In the late habitat however, the relationship is hump-shaped, so that the magnitude of asynchrony is largest when the difference in resource phenology between habitats is some small value (blue curves in Fig. 2).

As a consequence of the qualitative differences above, testable predictions of the relationship between breeding phenology and habitat types depend upon the parameter values and the strength of the carryover effect (Fig. 3). For example, if one were comparing the breeding phenologies of two species who differed in mean arrival time, then the early-arriving species will be more asynchronous than the late species. However each species may be more or less asynchronous in the early compared to late habitat, depending upon how different the resource phenologies are and the mean arrival times themselves (Fig. 3a–c). The existence of different patterns depends upon the other parameters. For example, the asynchrony curves in each habitat may cross each other 0, 1, or 2 times, depending upon the width of the resource peak in the late habitat (compare Fig. 2d, f; full

Table 1 Key parameters and default values

Symbol	Default	Meaning	Justification
s_i	0.6	Survival probability	Based on willow tit (Lahti et al. 1996)
m_g	15 days	Mean arrival time after earliest possible time	A compromise between marsh tits [$\approx 50\%$ by 5 days (Nilsson and Smith 1988)] and great tits [≈ 22 days (Saitou 1979; Nilsson and Smith 1988)]
$\mu_g; \sigma_g$	2.4; 0.79	Scale and shape parameters for arrival distribution	Fitted marsh tit arrival distribution from Nilsson and Smith (1988), then variance held fixed and recalculated values assuming default $m_g = 15$
E_0	4.5	Max. no. fledglings per adult	A high estimate based on blue tits (<i>Cyanistes caeruleus ogliastreae</i>) (Lambrechts et al. 1997)
σ_E	10 days	Food peak width	Chosen so that a marsh tit would have ~ 10 day asynchrony (Vatka et al. 2011)
K_i	$K_i = K_j \forall i, j$	No. of territories with habitat-type i	Default value set to 50 territories of each type in 2-habitat type scenario. Was varied to explore parameter effect
r	0.8	Fraction of juveniles who choose territory at random	Was varied to explore parameter effect. Natal habitat fidelity may be quantified by its opposite: $1 - r$

Fig. 2 The effect of the difference in resource phenology between habitat types upon the relative hatching date (**a**), and upon the hatching date asynchrony (**b–f**), at the continuously stable strategy (i.e. evolutionary end-point). The carryover effect is absent when the difference in resource phenology between habitats is zero. In the early habitat (red lines), the magnitude of asynchrony decreases monotonically with increasing difference in resource phenology, whereas in the late habitat (blue lines) asynchrony is largest at some small value of resource phenology difference. The results shown are for the default parameter values (**a**, **b**), for high and low values of the mean arrival time after earliest possible arrival m_g (**c**, **e**), and for high and low values of the width of the resource peak in the late habitat $\sigma_{E,2}$ (**d**, **f**). (Color figure online)

Fig. 3 Model predictions for hypothetical cross-species (a–c) and cross-landscapes (d–f) comparisons of breeding phenologies. Breeding phenology may be more or less asynchronous in the early compared to late habitat, depending upon the difference in resource phenology between habitat types

results in Fig. S2) and these cross-overs separate regions where asynchrony is greater in the early or late habitat.

Recruitment is typically asymmetric, from early to late habitat, but may be reversed early-habitat disadvantages

The carryover effect promotes asymmetric recruitment, with most recruits to both the early and late habitats coming from the early habitat (Fig. 4; see Fig. S4 for all parameter values). However this asymmetry can be reversed if the early habitat is disadvantageous in certain ways, for example if the early habitat is less frequent in the landscape, or produces fewer offspring per territory. A disadvantage in the early habitat shifts the balance of recruitment to more recruits coming from the late habitat (to the left of the vertical dotted lines in Fig. 4b, c, e, f, respectively). Natal habitat-type fidelity creates a region in the parameter space where most new recruits to each habitat type will have originated from that same habitat type, i.e. insular recruitment (Fig. 4a, d; Fig. S7). Therefore if the carryover effect is combined with natal habitat-type fidelity, a disadvantage in the early habitat can lead to insular recruitment (Fig. 4c, f).

Discussion

Our model assumed that breeding phenology involved a trade-off between reproduction and competition, and further assumed that natal habitat type had a carryover effect upon competitive ability. We have explored how this scenario will determine the evolution of breeding phenology and the rates of recruitment between habitat types.

Fig. 4 The proportion of recruits to each habitat type that originated from that same habitat (ϕ_{ii}), for combinations of presence/absence of natal habitat-type fidelity ($1 - r = 0.2$) and presence/absence of carryover effect ($\hat{x}_1 - \hat{x}_2 = 15$ days). The default parameter values, where both habitats are otherwise equal, is shown by a dotted line. The effect of natal habitat-type fidelity (a, d) is to create a region in parameter space where recruitment is insular (i.e. proportion in both habitat types $\phi_{i,i} > 0.5$). The effect of the carryover effect (b, e) is to cause asymmetric recruitment from the early to late habitat. When natal habitat-type fidelity and carryover effect are combined as in the default model (c, f), recruitment is asymmetric, however the asymmetry can be reversed or become insular if a lower percentage of the landscape is early habitat or early habitat has lower productivity

Model predictions

Similar to the single-habitat model from which our model is derived (Johansson et al. 2014), our model predicts that hatching date will be asynchronous and earlier than resource phenology. This prediction follows as a logical consequence of the assumption that breeding phenology involves a trade-off between reproduction and competition. This trade-off relationship is also key to interpreting the basic results of our model. For example, a wider resource peak (high $\sigma_{E,2}$) lowers the reproductive cost of asynchrony, and an earlier mean arrival time (low m_g) strengthens competition, therefore both increase the magnitude of asynchrony (Fig. 2d, e).

The model assumes that offspring who hatch earlier are competitively advantaged, and this carryover effect on competition is key to understanding the model's other predictions about recruit flow and asynchrony. Juveniles raised in the early habitat typically hatch and fledge earlier than juveniles raised in the late habitat (Fig. 2a), which gives them the advantage in breeding territory competition. This difference in competitive

ability is a carryover effect *sensu* O'Connor et al. (2014): the effect is initiated at an early life stage (i.e. at hatching) but its fitness consequences manifest at a later life stage (i.e. breeding territory competition), and the effect is carried with each juvenile regardless of which habitat it disperses to. This carryover effect influences recruit flow because, all else being equal, juveniles from the early habitat have a higher probability of being recruited into the adult population in both habitat types. This carryover effect also influences the selective trade-off between competition and reproduction in each habitat. For example, when there are many weak-competitor juveniles from the late habitat in the population, then the competition component of selection on hatching date in the early habitat is less important.

Whether the hatching date in the late habitat evolves to become more synchronous or less synchronous than in the early habitat (Fig. 3) depends upon whether compensating for the late habitat's competitive disadvantage is worth the reproductive cost. The larger the difference is between the resource phenologies in each habitat, the stronger the carryover effects are, and the larger the competitive disadvantage is of being raised in the late habitat. Then juveniles from the early habitat are faced with fewer strong competitors, which decreases the importance of the competition component of the selective trade-off, shifting the selective balance towards greater reproduction and increased synchrony. Meanwhile, juveniles in the late habitat must somehow compensate for their competitive disadvantage. One way is to improve competitive ability by evolving to have an even earlier and more asynchronous breeding phenology. However asynchrony comes at a reproductive cost, which is only worthwhile when the difference in resource phenology between habitats is small. When the difference in resource phenology between habitats is large, then it is not possible for juveniles in the late habitat to hatch early enough to compete with those from the early habitat without also greatly reducing the number of fledglings their parents produce. In that case, the only possible way to compensate is to increase synchrony with the resource phenology, to produce a larger number of fledglings albeit with low competitive ability each.

When the carryover effects are strong enough (i.e. large difference in resource phenology between habitats), recruit flow between habitats is typically asymmetric, therefore a source-sink like relationship is created between habitats by a carryover effect. Hatching date in the late habitat can only evolve to compensate for its competitive disadvantage when the difference in resource phenology between habitats is small enough that it is worth the reproductive cost. When compensation does not occur, juveniles from the early habitat are competitively advantaged, and therefore most recruits to both the early and late habitat were raised in the early habitat (Fig. 4 and Fig. S1). This asymmetric recruitment creates a source-sink like relationship between habitats; however, in contrast to traditional source-sink dynamics, which are caused by a difference in habitat quality such that the sink cannot sustain a population in the absence of the source (e.g. Pulliam 1988), in our model the population in the late habitat can be sustained in isolation.

The asymmetric recruitment from early to late habitat can be reversed if the early habitat is less frequent in the landscape or produces fewer offspring. In cases where that is combined with natal-habitat fidelity, then the asymmetric recruit flow between habitats (above) can be replaced with a more insular pattern (Fig. 4). Natal-habitat fidelity may occur due to behavioural effects, such as natal-habitat preference induction (Grunberger and Leisler 1990; Davis and Stamps 2004) or a condition-dependent habitat choice (cf. Verhulst et al. 1997). Natal-habitat fidelity may also occur due to a coarse-grained landscape such that territories of similar habitat type are more likely to occur in closer spatial proximity to one another.

Empirical relevance

Our hypothesised mechanism, of a competition-reproduction trade-off, could explain why some populations of willow tits (Vatka et al. 2011), coal tits (Both et al. 2009) and marsh tits (Wesołowski 1998) have historically bred before the peak in nestling food resources. Asynchronous breeding phenology is not universal (e.g. Both et al. 2009), however in cases where it does occur, a trade-off with competition is often discussed as a likely cause (e.g. Wesołowski 1998; Vatka et al. 2011; Pakanen et al. 2016; Källander et al. 2017). For example, when discussing how marsh tits breed much earlier than other species in the area, Wesołowski (1998) emphasised the strong negative correlation in this species between relative fledging time and the juvenile's probability of successfully establishing.

We also propose that our broader hypothesis, that breeding phenology is influenced by competition at other life stages, is supported by its apparent ability to explain synchrony/asynchrony differences between migratory and non-migratory birds. For example, Both et al. (2009) contrasts a population of pied flycatchers (*Ficedula hypoleuca*), whose maximal nestling food-demand occurs after the resource peak, and therefore whose synchrony has decreased with climate-induced food-peak advance, to a population of coal tits whose maximal demand occurs before the peak and whose synchrony has increased. The pied flycatcher is a migratory species and competition for territories is also subject to the prior residence effect (Alatalo et al. 1986; Kokko 1999); however if the food peak is early enough then breeding synchrony with the food peak is traded against adult survival during migration and in the early season, resulting in a breeding date that is later than the peak (Johansson and Jonzén 2012; Kristensen et al. 2015). In contrast, the coal tit is a winter-resident species, for which no such trade-off with migration and survival exists. Instead, we propose that the prior residence effect gives the juveniles of early-breeding parents a competitive advantage in territory competition via earlier natal dispersal. Therefore synchrony is traded against juvenile competitive ability resulting in a breeding date that is earlier than the peak (Johansson et al. 2014).

Empirical evidence for the heterogeneous landscape effects that we predict has not been reported in the resident-bird literature, and so our model serves only to predict what we expect to occur in the scenario envisaged. We believe that marsh tits, willow tits, and coal tits are good candidates for testing our model. We also note that phenological heterogeneity of the type we envisage is common, such as landscapes with a mix of deciduous (early phenology) and evergreen (late phenology) habitat (e.g. Dias et al. 1996; Vatka et al. 2011).

Other taxonomic groups also face situations where the natal habitat type influences competitive ability and there is a pressure to trade-off with other traits relevant to fitness. For example (Kavanagh et al. 2010), young grayling fish (*Thymallus thymallus*) developing in cold tributaries hatch late and so have restricted time to reach sufficient size to survive the first winter. The pressure to grow faster and in a colder environment induces a trade-off between muscle and skeletal development. In addition, after developing in separate tributaries for the first few months of their lives, juveniles from cold tributaries move to lakes where they must compete for food resources with larger and more competitive juveniles from warmer tributaries. Therefore we expect that graylings from cold tributaries, similar to our model birds from late habitat, are under a double burden of trade-off pressure: first to obtain sufficient size to meet survival requirements and to compete with each other, and second to compete with individuals from other natal habitats who are competitively advantaged due to carryover effects.

Our model predicts when carryover effects will lead to source-sink dynamics or insularity, and these different recruitment patterns may have implications for gene flow and local adaptation (Kristensen et al. 2018). Habitats that differ in phenology also differ in other characteristics, e.g. deciduous forests with early resource phenology have different physical structure and are often richer than evergreen forests with late resource phenology (Braillet et al. 2002). Therefore populations may have other characteristics that are under different selection pressures in the different habitat types, such as clutch size, body size, and other morphometric and behavioural traits (Blondel 2007; Charmanier et al. 2016). Source-sink dynamics often lead to maladaptation to the sink habitat, due to gene-swamping and because the sink contributes less to the future gene pool (Holt 1996). Therefore we may expect that asymmetric recruitment, with higher gene-flow from the early to late habitat type, will favour adaptation of birds' other traits to the early habitat's other characteristics (c.f. Dias and Blondel 1996). In contrast, the insular pattern of recruit flow will reduce gene flow between habitat types. If the population is under divergent selection, then reducing the gene flow between habitats may initiate a positive feedback leading to a pattern of isolation by ecology (Shafer and Wolf 2013).

Model caveats

Our model makes a number of simplifying assumptions, and is structured to emphasise the mechanisms of interest, therefore the strength of the patterns predicted by the model will depend upon how well a particular species and system matches these assumptions.

The model is premised on the match/mismatch hypothesis (reviewed in Johansson et al. 2015), and so it was assumed that the number of fledglings produced is directly determined by a match between breeding phenology and resource phenology. Synchrony with resource timing is expected to exert a major selection pressure on resident birds (Visser et al. 1998); for example, asynchrony has been suggested as a yardstick to measure how well natural populations have adapted to climate change (Visser and Both 2005). However to speak of 'synchrony' also implies a strongly temporally-peaked resource curve [e.g. peaks in the abundance of caterpillars (Sanz 2001; Veen et al. 2010)] with a strong penalty for missing the peak (for counter-example see Wesołowski and Rowiński 2014). This is commonly reported (e.g. Visser et al. 1998) and assumed in models (e.g. Kristensen et al. 2015), but not necessarily certain nor applicable in all systems (reviewed in Cholewa and Wesołowski 2011), and greatly simplifies the reality of multiple peaks of alternative food resources that vary year-to-year (Vatka et al. 2016).

We focused on discrete-flocking systems such as the marsh tit (Nilsson and Smith 1988) and willow tit (Hogstad 1987), and so the model assumed that the carryover effect influenced rank which in turn directly determined which flock member won the breeding territory. An alternative model would have been that rank improves over-winter survival, e.g. via priority access to food or lower predation-risk foraging areas, which determines recruitment probability indirectly.

The details of the winter social system in parids vary both between (Ekman 1989; Matthysen 1990) and within (Nilsson and Smith 1988; Broughton et al. 2015) species. For our hypothesis, it is irrelevant if the early hatching results in higher likelihood to obtain the breeding territory due to social dominance directly or due to higher survival probability, as long as the mechanism is prior residency, and available evidence suggest social advantages in winter flocks and territory establishment from early hatching (Nilsson and Smith 1988; Nilsson 1990, 1999).

The model makes a strong assumption about the durability of the carryover effect: when an individual in the flock dies, its position in the rank is filled by the flock-member immediately below in rank, and so on down the hierarchy. This is a reasonable assumption for species with stable dominance hierarchies (Hogstad 1989; Hay 2003), but that is not universal. For example, in black-capped chickadees (*Parus atricapillus*) recruitment can occur from the bottom of the rank (reviewed in Ekman 1989). Our assumption is also consistent with the ‘hopeful dominants’ scenario: that in saturated environments juveniles join flocks to await the death of the territory owners and individuals with higher status for their chance to breed (Lahti et al. 1996). Therefore our model also omitted other mechanisms for improving rank such as surveying nearby flocks (e.g. Hogstad 1999). Deviations from these assumptions will weaken the mechanisms in our model, though provided that natal habitat has some effect on competitive ability, then the predicted patterns will remain true.

The model assumes that non-breeders have zero survival. This is the simplest possible way to link prior residence to competition, however there are many species in which winter-flocks include non-breeders from the previous year (reviewed in Ekman 1989). Nevertheless it is not a biologically unreasonable assumption; for example, empirical data on marsh tits (Nilsson and Smith 1988) have indicated that non-breeders to large extent disappear from the system through mortality or have low reproductive success, as a consequence of being expelled to marginal habitats. An alternative would have been a more complicated, age-structured, model, which would also permit us to model difference in survival probability between age groups. We expect that variation in these survival rates would affect our predictions. For example, increasing non-breeder survival and assuming they engage in competition for territories would make it less likely that an early born offspring obtains a territory in its first year, and would reduce selection for early reproduction. However, even if we assume equal survival and equal competitive ability of breeders and non-breeders, we still expect the ESS to deviate somewhat from the reproductive maximum ($\hat{x}_i$). An early and a late born offspring would namely have the same prospects of reproducing from year two onward and thus prior-residency effects among one-year-olds would still convey some advantage for early reproduction. The scenario studied here, with zero non-breeder survival, is however of particular interest because therein all individuals that contribute to fitness are found in a single state, at a single time point in time and the model can be collapsed to non-structured model. That greatly facilitates the analytical study of its evolution, as shown here, and in this way our study serves as a reference point for investigations of more complex cases.

Conclusion

Our model explores a novel aspect of the evolution of phenological asynchrony between a species and its resource: the effect of landscape heterogeneity. The model was inspired by certain species of winter-resident parids, however we note that the prior residence effects central to the model have been observed in a wide range of taxa, from insects (Waage 1988) to mammals (Haley 1994), and that breeding phenology influences competitive ability in other species (e.g. salmon, Huntingford and Leaniz 1997). Depending upon the particular scenario, our model predicted that either an asymmetric or a more insular pattern of recruit flow between habitat types could occur, which will influence gene flow between habitat types. Therefore we suggest that the consequences of carryover effects on source-sink dynamics and local adaptation are areas for future work.

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